

SYSTEMATICS, ANATOMY AND BORING MECHANISMS OF THE ROCK-BORING MYTILID BIVALVE *BOTULA*

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ABSTRACT: The mytilid *Botula* is shown to contain a single species, *B. fusca* Gmelin, which is widespread in tropical and sub-tropical waters of the Indian, Pacific and western Atlantic Oceans. Shell morphology and anatomy of this species are described. It is siphonate and bores in calcareous rocks and dead corals by means of non-acid secretions from large boring glands in the mantle folds anteriorly and posterodorsally. Its nearest living relatives are the species of *Lithophaga* s.s. and the genus is placed in the Lithophaginae along with *Adula*, *Lithophaga*, *Leiosolenus* and *Fungiacava*.

Recent classifications place the mytilid *Botula* Mörch 1853 in the Modiolinae (e.g. Soot-Ryen 1969, Keen 1971). Other genera placed in that group are non-siphonate byssally attached 'nestlers' while *Botula* is a siphonate, rock-borer. Lamy (1937) and other authors place *Botula* in the Lithophaginae. This paper reports results of an anatomical study of *Botula fusca*, undertaken to determine the affinity of the genus, to review its species taxonomy, and to determine the nature of the boring mechanism.

METHODS

Living specimens of *Botula fusca* were collected and studied at the Heron Island Marine Research Station, in the Great Barrier Reef Marine Park, Capricorn Zone. Supplementary preserved specimens were examined from several other Queensland and Western Australian localities. For comparative purposes sections were made of the pallial boring glands of *Leiosolenus lessepsianus*, also collected at Heron Island.

Isotonic MgCl₂ was used as an anaesthetic prior to dissection. Anatomical drawings were done from the anaesthetised specimens, free-hand or using a camera-lucida. Specimens for histological work were fixed in Bouin's solution, stored in 70% ethanol, routinely processed into paraffin blocks and sectioned at 5 μ . Sections were taken in a plane perpendicular to the mantle edge (transversely across the boring gland) and stained with Mayer's haematoxylin and eosin, Mallory's triple stain or Wiegert's iron haematoxylin. The periodic acid-Schiff reaction (P.A.S.) in conjunction with Alcian Blue (pH 2.35) was used as a test for acid or neutral mucopolysaccharides (Mowry 1956).

Shells of the specimens on which the anatomical study is based are deposited in the Museum of Victoria Melbourne, the Australian Museum Sydney, and the Western Australian Museum Perth. Abbreviations for repository institutions are as follows: AM—Australian Museum, Sydney. ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia. BM(NH)—British Museum (Natural History), London. CAS—California Academy of Sciences, San Francisco. LACM—Los Angeles County Museum, Los Angeles. MCZ—Museum of Comparative Zoology, Harvard University, Boston. MNHN—National Museum of

Natural History, Paris. NMV—Museum of Victoria, Melbourne. SAM—South Australian Museum, Adelaide. SDNHM—San Diego Natural History Museum, San Diego. WAM—Western Australian Museum, Perth.

SYSTEMATICS

Class BIVALVIA
Family MYTILIDAE
Genus *Botula* Mörch 1853

1853 *Botula* Mörch, p. 55.

1939 *Botulopa* Iredale, p. 414. (Type species: *Botulopa silicula* *infra* Iredale, 1939 (= *M. fusca* herein))

TYPE SPECIES: *Mytilus fuscus* Gmelin 1791 by subsequent designation of Dall 1898.

DIAGNOSIS: Shell cylindrical, inflated, arcuate, smooth or finely concentrically striate, rather thin, white with a uniform thin, smooth, glistening brown periostracum. Umbos terminal, prosogyrate conspicuously incurved; hinge-line and ligament short, ligament opisthodontic, parivincular; margins smooth except for fine vertical striae beneath and immediately posterior to the ligament.

Incurrent and excurrent siphons long but usually divided; with a muscular septum within the tubular excurrent siphon and a prominent digitate ventral siphonal branchial membrane. Ctenidia filibranchiate and heterorhabdic, eleutherorhabdic. Boring glands present in the inner mantle folds anteriorly and posterodorsally. Posterior siphonal retractor muscles and scars present; anterior pedal retractors attach close to the margin of the hinge just below the umbos; posterior pedal-byssal retractors small.

Mussels which bore in dead corals, coral-rock or other calcareous rocks.

REMARKS: Mörch assigned to *Botula* only the species *arenaria* Meusch. (with *vagina* Lamarck, and *castaneus* 'Rumphius' Gray (*non* Say) listed as synonyms) and *fusca* Gmelin (with *Mytilus brunneus* Solander, *Modiola cinnamomea* Lamarck and *M. favanii* Potiez and Michaud listed as synonyms). Subsequently Dall (1898) selected *fusca* Gmelin as type. In these authors' opinion *arenaria*, a large, thin-shelled, siphonate mytilid which

burrows in soft substrates of the central Indo-Pacific region, is not congeneric with *fusca*, although its correct generic affinity is yet to be determined.

Botula most resembles *Lithophaga* s.s. in that the shell has a strong periostracum but no secondary calcareous accretions, there are prominent plicate membranes in the roof of the mantle cavity, and boring is aided by chemical secretions from anterior and dorsal boring glands. It is easily distinguished from that genus by the short, arcuate shell form, the large, strongly incurved umbos, and the divided posterior siphons.

***Botula fusca* (Gmelin 1791)**

Figs 1 A-P, 2 B-F, 3-7

- 1785 *Mytilus cinnamominus* Chemnitz, pl. 82, fig. 731. (Refers to Lister, 1687, fig. 197.) (Type locality: Jamaica.) (Non-binomial publication.)
- 1791 *Mytilus fuscus* Gmelin, p. 3359. (Refers to Lister, 1687, fig. 197.) (Type locality: Jamaica.)
- 1793 *Mytilus cinnamomeus* Schreibers, p. 293. (Refers to Chemnitz, 1785, pl. 82, fig. 731.)
- 1807 *Modiolus cinnamomeus* Link, p. 147. (Refers to Chemnitz, 1785, pl. 82, fig. 731.)
- 1819 *Modiola cinnamomea* Lamarck, p. 114. (Type locality: l'Isle de France (Mauritius, Indian Ocean), leg. M. Desetangs.)
- 1819 *Modiola silicula* Lamarck, p. 114. (Type locality: 'Nouvelle Hollande' probably collected by Peron during the Baudin Expedition at Shark Bay, Western Australia.)
- 1844 *Modiole favanni* Potiez & Michaud, p. 130, pl. 54, fig. 9. (Type locality: 'Exotique'.)
- 1892 *Lithodomus projectans* Tate, p. 130, pl. 1, fig. 1. (Type locality: 'Port Darwin'.)
- 1938 *Botula hawaiiensis* Dall, Bartsch & Rehder, 1938, p. 59, pl. 12, figs. 1-4. (Type locality: 'dredged by the U.S. Bureau of Fisheries Steamer "Albatross" at Station 3845 off the south coast of Molokai (Hawaii) in 60-64-0 fathoms on sand, pebble and shell bottom; bottom temperature 71°F'.)
- 1938 *Botula laysana* Dall, Bartsch & Rehder, 1938, p. 60, pl. 12, fig. 5. (Type locality: 'dredged by the U.S. Bureau of Fisheries Steamer "Albatross" at Station 3936, near Laysan Island (Hawaiian Islands) in 79-130-0 fathoms on small broken shell and coralline bottom; bottom temperature 68°F'.)
- 1939 *Botulopa silicula infra* Iredale, p. 415, pl. 6, fig. 26. (Type locality: Low Isles, Queensland.)
- 1959 *Botula cylista* Berry, p. 108. (Type locality: Punta Cameron, Mazatlan, Sinaloa, Mexico.)

See Table 1 for details of type specimens.

DISTRIBUTION: Widespread in the tropical and subtropical seas of the Indian, Pacific and western Atlantic Oceans. Apparently absent from the tropical eastern Atlantic. Figure 7 is based on verified museum specimen records and selected literature records.

HABITAT: *Botula fusca* is a boring mytilid inhabiting dead corals, coral rocks and other calcareous rocks. It is common in the intertidal zone and has been collected from suitable substrates to depths as great as 291-190 fathoms (off Hawaii, see Dall, Bartsch & Rehder 1938). It is often extraordinarily abundant in coral rocks and the coral-rock platform of the reef-crest zone, sometimes most commonly with the burrows opening on the underside of the rocks. The species may also be abundant burrowing in sloping beach-rock relatively high in the intertidal zone, e.g. along the southern shore of Heron Island (Queensland) below the research station. It is also known to burrow in the shells of other molluscs such as *Strombus gigas* (Chemnitz 1785) and oysters (Berry 1959). In northern Australia it is common boring in massed shells of rock-oysters (*Saccostrea*) high in the intertidal zone.

Gohar and Soliman (1963) have described and figured burrows of this species (identified as *Modiolus cinnamomeus* Bruguière) from the Red Sea. The burrow lacks a calcareous lining and is differentiated into two parts. The outer or siphonal part is roughly dumb-bell shaped in cross-section and it widens distally. The inner part, which is occupied by the shell, is kidney-shaped like the shell.

DESCRIPTION: Shell. White to pale brown, covered by a uniform tan to dark-brown or almost black glossy smooth periostracum. Cylindrical-arcuate, anterior and posterior ends broadly rounded; prosogyrate umbos large and terminal, sometimes conspicuously projecting and incurved. Ligament opisthodontic, parivincular, short and thick, resilium entire, sub-ligamental ridge lacking; hinge edentulous, margins smooth except for very fine, oblique striae on the dorsal margin beneath and immediately behind the ligament. Exterior smooth except for weak concentric growth striae and, in some cases, series of concentric ridges presumably representing successive growth phases (Fig. 1D, G; cf. *Lithophaga teres* and *L. antillarum*, Wilson 1979, p. 440, 448). Scars of anterior and posterior retractors weak but usually discernible, scar of siphonal retractor very weak but discernible.

Anatomy (see also Pelseneer 1911, Soot-Ryen 1955,

Fig. 1—A, B *Modiola cinnamomea* Lamarck; syntype (left valve of the whole specimen), MNHN (Paris); from 'l'Isle de France', leg. M. Desetangs. C, *Modiola silicula* Lamarck; type MNHN (Paris); from 'Nouvelle Hollande'. D, E, *Botula hawaiiensis* Dall, Bartsch & Rehder; holotype, USNM484180; off Molokai, Hawaii. F, *Botula laysana* Dall, Bartsch & Rehder; holotype, USNM335614. G, H, *Botula fusca* USNM257854; (34°05'N, 77°18'W). I, J, *Botula fusca* NMVF51471; Heron I., Queensland. K, *Botula fusca* USNM150313; St. George Cay, Belize. L, M, *Botula cylista* Berry; paratype; SDNHM428303; Punta Cameron, Mazatlan, Mexico. N, *Botula fusca* USNM173161; off Green Cay, Bahamas. O, P, *Botula silicula infra* Iredale; holotype, AMC60400; Low Isles, Queensland.

MYTILID BIVALVE *BOTULA*

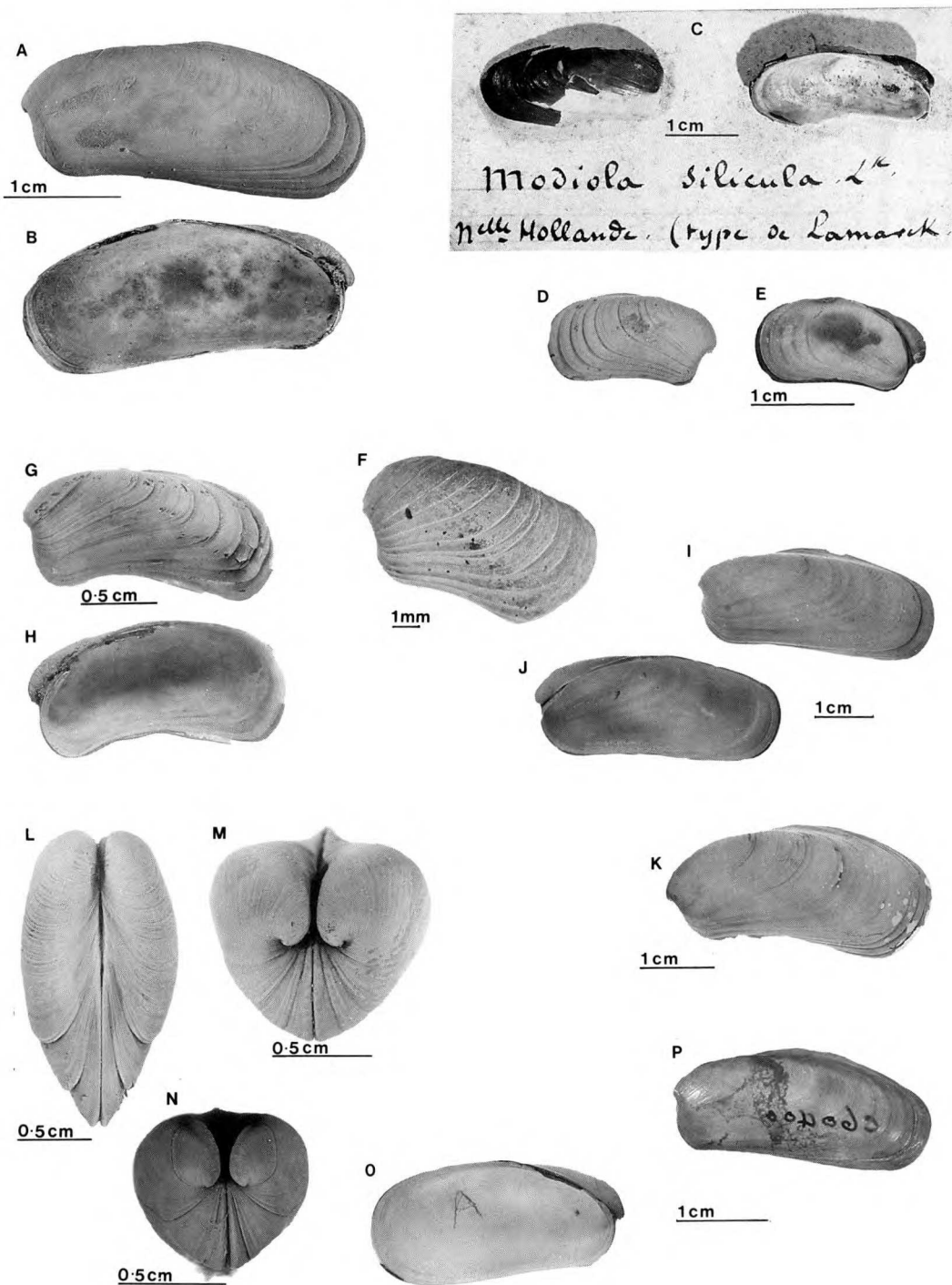


TABLE 1
LOCATION AND DIMENSIONS OF TYPES

		Length cm	Height cm	Width cm	Lig. Length cm
<i>Modiolus cinnamomea</i> Lamarck	2 syntypes: 1 whole shell and 1 left valve, Lamarck Collection, MNHN (Paris)	2.69 2.94	1.48 1.60	1.23 0.63(½)	1.26 1.54
<i>Modiolus silicula</i> Lamarck	Whole specimen, Lamarck Collection, MNHN (Paris)	2.47	1.12	1.06	1.37
<i>Modiolo Favanni</i> Potiez & Michaud	Type not located	—	—	—	—
<i>Lithodomus projectans</i> Tate	Whole specimen, SAMD14615	—	—	—	—
<i>Botula hawaiiensis</i> Dall, Bartsch & Rehder	Whole specimen, USNM484180	1.50	0.99	0.93	0.78
<i>Botula laysana</i> Dall, Bartsch & Rehder	Whole specimen, USNM335614	0.94	0.62	0.71	—
<i>Botulopa silicula infra</i> Iredale	Whole specimen, AMC60400	2.73	1.71	1.17	1.08
<i>Botula cylista</i> Berry	Holotype not located Paratype, whole specimen SDNHM42803	1.93	1.21	1.07	—

Gohar & Soliman 1963). Anterior adductor elongate-ovate and lies close to the antero-ventral margin. Posterior adductor ovate, rather small, conspicuously divided into 'quick' and 'catch' parts, and located quite far posteriorly. Anterior retractors moderately strong and insert close to the hinge margins below the umbones. Posterior retractors small (compared with byssal-attached mytilids such as *Modiolus*) insert above the antero-dorsal side of the posterior adductor; although separate pedal (anterior) and byssal (posterior) retractor strands arise contiguously (but distinguishable at the place of origin in the foot-byssus complex) they merge dorsally and insert as a single muscle block. A wide band of scattered siphonal retractor strands, originating from the mantle in the region of the siphon, inserts on the side of each valve antero-ventral to the posterior adductor.

The edges of the mantle from the umbo ventrally around to the postero-dorsal corner possess inner, middle and outer folds, as in other mytilids, the outer and middle folds adhering closely to the shell margins. The inner folds meet and fuse antero-ventrally from the umbo to a point a short distance behind the anterior adductor, and also along the postero-dorsal side; ventrally they are separate but appositioned in life to enclose the mantle cavity; posteriorly they are thickened, muscular and form extensible muscular siphons as in *Lithophaga*, *Leiosolenus* and *Adula* (see Pelseneer 1911, Yonge 1955, Soot-Ryen 1955, Fankboner 1971, Wilson 1979).

In most specimens the siphons are separate for most of their length (Figs 3, 6) but in odd individuals they are joined as in *Lithophaga* and *Leiosolenus*. They are fused by a horizontal branchial septum anteriorly, beneath which the gill axes attach.

The dorsal excurrent siphon is complete and tubular. Internally across its inner (anterior) end there is a thin but muscular suprabranchial valve or diaphragm with a

horizontal aperture and backward folded rim (Fig. 3). It forms a 'tube within a tube', presumably functioning as a velocity control device for the excurrent water flow. A similar structure occurs in *Lithophaga* and *Leiosolenus* (Wilson 1979).

The ventral incurrent siphon is flanked by muscular flaps which form a functional siphonal tube by apposition of the ventral edges. The branchial septum bears a ventral digitated 'valvular siphonal membrane' (Yonge 1955) like that of *Mytilus* (Kellogg 1915), *Lithophaga* (Yonge 1955, Wilson 1979), *Adula* (Fankboner 1971) and *Xenostrobus* (Wilson 1967). Soot-Ryen (1955, fig. 72) illustrates this structure. The membrane is usually asymmetrically digitated, with 10 or more digits on the large central flap, a smaller flap with 2 or more digits on each side, and a single digit in each lateral corner. Yonge (1955) suggested that this organ 'serves to shield the (outgoing) waste materials from the broad incoming stream of water'.

The ctenidia are filibranchiate, eleutherorhabdic and heterorhabdic. There are no inter-lamellar junctions as in *Mytilus*, but every 5th or 6th filament is a 'principal filament' (see Type B(1b) of Atkins 1937, text-fig. 4) with a connecting septum rising to about half way up the gill. The inner and outer demibranchs are about equal in height; ascending lamellae are a little shorter than the descending ones. The free edges of the ascending lamellae meet (but do not fuse with) the mantle or visceral mass. Conspicuous food grooves run along the bottom edge of each demibranch. The labial palps are broad and strongly plicate on their inner surfaces. The hind-gut is normally looped, has no special style-sac, and the rectum passes through the ventricle. The auricles are heavily pigmented reddish-brown. Pericardial glands are not evident on the walls of the pericardium. There is a dorsal cul-de-sac of the mantle cavity running forward

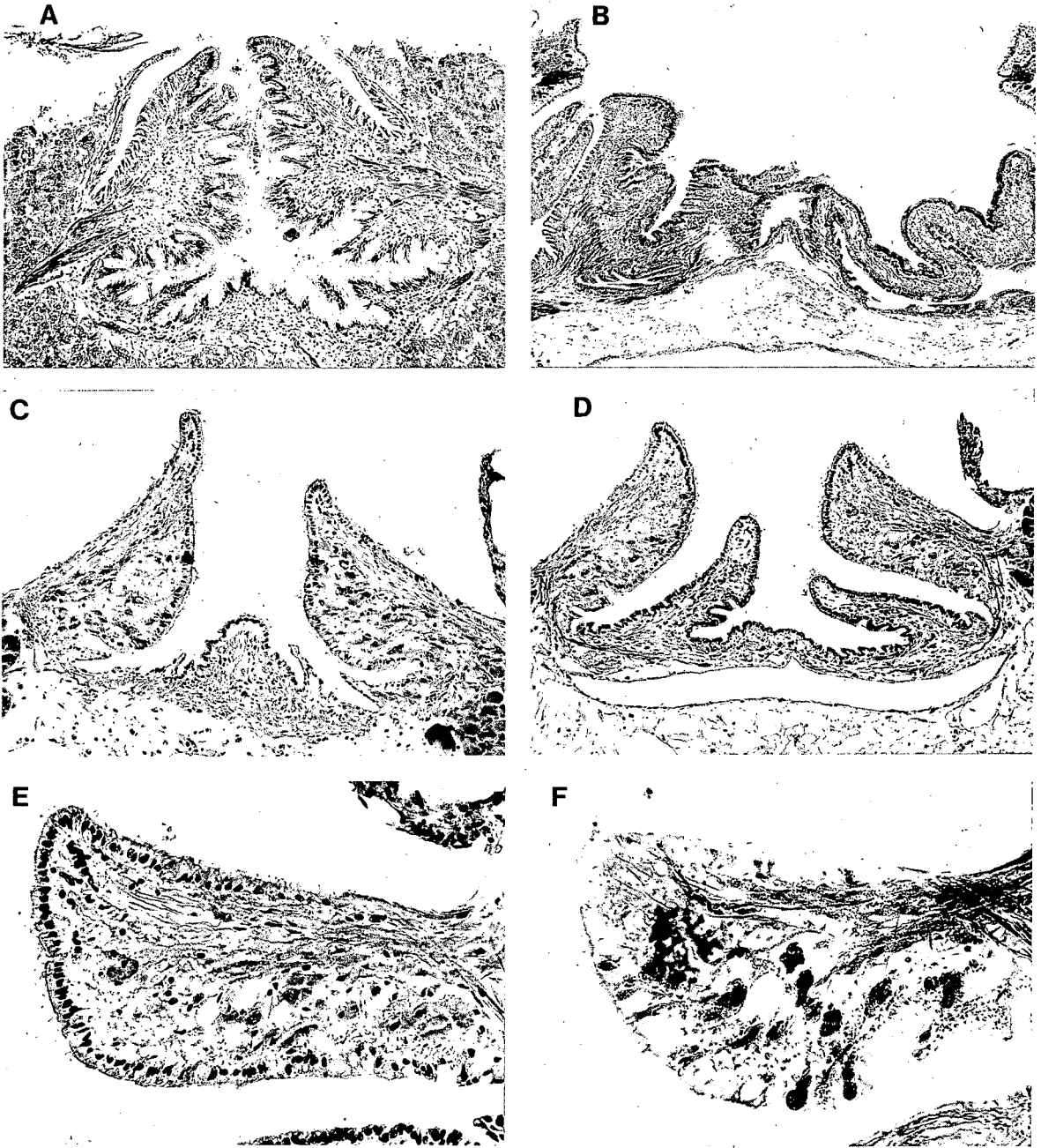


Fig. 2—Histology of the pallial boring glands in *Botula fusca* and *Leiosolenus lessepsianus* (the latter from a living *Acropora* colony) from Heron Reef, Queensland. A, *Leiosolenus lessepsianus* NMVF31815; horizontal section through the anterior gland showing a diverticulate lumen. Stained with H & E. $\times 160$. B, *Botula fusca* (NMVF31814); horizontal section through the anterior gland showing glandular middle and inner folds. Stained with H & E. $\times 87$. C, *Botula fusca* (NMVF31817); transverse section through the dorsal gland in an anterior position over the pericardium showing fusion of the inner folds down a mid-line ridge with small secondary lateral flaps, thick and glandular middle folds, and thin outer folds (visible on the right side only). Stained with H & E. $\times 260$. D, *Botula fusca* (NMVF31817); as for Figure C but sectioned further posteriorly, behind the pericardium and over the dorsal cul de sac of the mantle cavity; note the enlarged secondary flaps of the fused inner folds. Stained with H & E. $\times 220$. E, *Botula fusca* (NMVF31817); enlargement of the dorsal gland middle fold. Stained with H & E. $\times 530$. F, *Botula fusca* (NMVF31817); as for figure E, but stained with Mallory's Triple Stain. Note dark bodies stained red with Acid Fuchsin. $\times 530$.

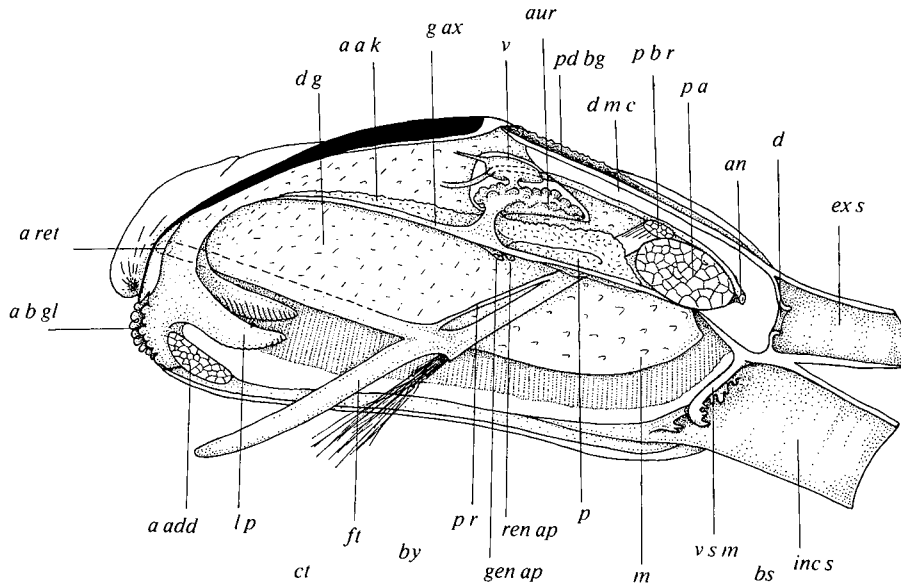


Fig. 3—Generalized diagram of the anatomy of *Botula fusca* from Heron Island, Queensland (NMVF51471). Left valve, mantle lobe and ctenidium removed; posterior siphons shown in sagittal section. Mid and fore-gut not shown. Abbreviations: *a b gl*—anterior boring gland. *a a k*—anterior arm of kidney. *a add*—anterior adductor muscle. *an*—anus. *a ret*—anterior retractor muscle. *aur*—auricle. *bs*—branchial septum. *by*—byssus. *ct*—ctenidium. *d*—diaphragm within excurrent siphon. *dg*—digestive gland. *d m c*—dorsal mantle cavity cul de sac. *ex s*—excurrent siphon. *ft*—foot. *g ax*—gill axis (left side, gill detached). *gen ap*—genital aperture. *int*—intestine. *inc s*—incurrent siphon. *l p*—labial palps (left). *m*—mesosoma *m & o m f*—middle and outer mantle folds. *pa*—posterior adductor muscle. *pd bg*—postero-dorsal boring gland. *p br*—posterior byssal retractor muscle. *pl m*—plicate membranes. *p r*—posterior pedal retractor muscle. *rec*—rectum. *ren ap*—renal aperture. *s r m*—siphonal retractor muscles. *v*—ventricle. *vs m*—valvular siphonal membrane.

above the posterior adductor and rectum to the posterior wall of the pericardium as in *Mytilus*, *Lithophaga* and *Modiolus*. Left and right kidneys comprise a relatively thick-walled tubular organ, lined with heavily pigmented (reddish-brown) tissue, with renopericardial openings in the anterolateral corners of the pericardium. An arm of the kidney tube runs forward for a short distance above the ctenidial axis; the broader part of the kidney runs backwards to the anterior and ventral edges of the posterior adductor and then recurves ventrally, lying above the gill axis, terminating at the renal aperture in the roof of the mantle cavity in a position approximately below the centre of the pericardium. There are large, conspicuous plicate membranes on both sides and the full length of the gill axes (Fig. 4).

Gonad tubules lie superficially over the digestive gland dorsally, fill much of the space between the diverging posterior retractors, invest the mantle lobes, and fill a large mesosoma. The genital aperture is located on a papillum adjacent to but not contiguous with the renal aperture (Fig. 4).

Boring glands are located in the middle and inner folds of the mantle lobes anteriorly and in the middle folds posterodorsally. The anterior boring gland is a conspicuous, convoluted organ located between the anterior adductor and the umbos, just below the junction of the outer mantle folds (Fig. 3). Middle and inner mantle folds (Fig. 2B) are covered with ciliated columnar epithelium composed of cells 9–24 μ in height. The middle fold has a longitudinal furrow on its median surface, also lined with ciliated cells. A shallow layer of heavily vacuolated subepithelial cells overlies a dense bundle of collagen fibres which runs longitudinally along the edge of the fold. This bundle occupies the bulk of the middle mantle fold so that secretory activity is restricted to the peripheral area. The inner mantle folds are convoluted and covered with a minutely folded epithelium of secretory and ciliated cells 16–22 μ in height. The subepithelial region is a loose matrix of collagenous fibres with a large number of spaces. The glands are drained by a large number of short, branched ducts, all lined with ciliated columnar epithelium. In the

epithelium, and some vacuoles in the subepithelium, bodies 7-15 μ in diameter can be seen. Presumably, these are secretory droplets; they show a positive P.A.S. reaction, but do not stain with Alcian Blue.

In the posterodorsal region behind the ligament the inner mantle lobes appear to have little secretory activity. The epithelial cells are cuboidal with round nuclei and have no visible inclusions. However, the middle mantle folds in this region are glandular (Fig. 2 C-F) with many eosinophilic inclusions staining red with Acid Fuchsin (Fig. 2F), and a secretory, ciliated epithelium of columnar cells 10-12 μ in height. The subepithelium is a loose matrix with a large number of intra and extra-cellular droplets which can be seen to pass to the exterior through minute and otherwise invisible ducts. These secretory droplets stain strongly P.A.S. positive using an Alcian Blue, P.A.S. technique.

Ventrally, the middle folds of the mantle lobes do contain secretory cells, but there is no enlarged gland. Nor was any glandular structure observed in the posterior siphons.

DISCUSSION

MORPHOLOGICAL VARIATION AND TAXONOMY OF THE SPECIES

Intra-population variation in shell morphology of these mussels is extreme, apparently relating to the nature of substrates in which they bore. No geographic patterns of variation could be discerned, even between the Western Atlantic and Indo-West Pacific populations. The few specimens we have seen from the eastern Pacific fall well within the range of variation of the entire series. We can find no morphological grounds for giving that population separate taxonomic status and we confidently place *Botula cylista* Berry in the synonymy of *B. fusca*.

One feature of interest is the colour of the periostracum. In some specimens it is light chestnut brown; in others, it is dark brown or black. Both colour forms are found throughout the species' range, and in some places (e.g. Heron Island) they may be found burrowing in the same rocks. The significance of this dimorphism is unknown to us.

Anatomically, this mussel is quite uniform. The only character showing variation is the digitation on the valvular siphonal membrane on the ventral side of the branchial septum (see anatomical description and Fig. 5A, B). However, there is no evidence of geographic pattern in this variation.

We have pondered at length the widespread nature of this mussel and whether more than one species might be involved. The logical *modus operandi* must be to assume a single species unless, or until, there is evidence of reproductive isolation or morphological or other evidence which implies genetic divergence. In this case (with the worrying exception of periostracum colour) evidence of discrete morphs is lacking. Therefore we conclude that there is but a single living species of *Botula*, widely distributed in coastal tropical waters with the apparent exception of the eastern Atlantic.

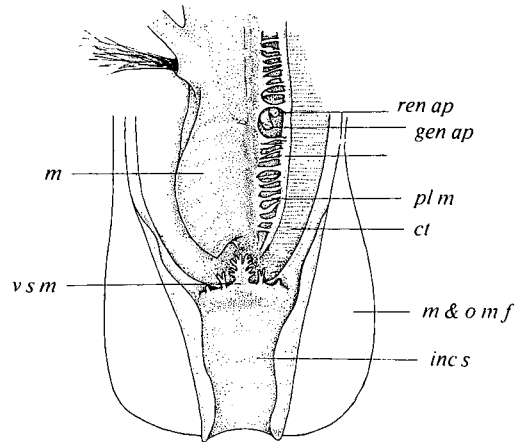


Fig. 4—Diagram of posteroventral area; mesosoma displaced to the right exposing the plicate organs, genital aperture and renal aperture of the left side between the visceral mass and the gill axis. (Specimen from Heron I., Queensland; NMVF51471).

FOSSIL RECORD

Botula fusca appears to have a long fossil history as well as a wide distribution. Dall (1898) reported a fossil under this name from the Oligocene of Florida. *Botula cordata* (Lamarck 1807) from the Eocene of France, Senegal, Libya and Egypt (see Freneix & Gorodiski 1963) and *Lithophaga mcknighti* Hanna 1927 from the Eocene of California (see Moore 1983, pl. 19, figs 9, 10) may also be this species. A plastotype of the latter fossil in the collections of the CAS is indistinguishable from living *B. fusca* shells.

SPECIES NOMENCLATURE

The first published reference to this species is a poor but recognizable illustration by Lister (1687). No locality is given specifically for this figure but it is framed with a figure of a *Modiolus* which bears the word 'Jamaic'.

Chemnitz (1785) published a reasonably good figure, referred to duplicate material in the Spengler collection from the Nicobar Islands, and stated that the species bores in the shells of other molluscs and corals and that his own material was found in a West Indian specimen of *Strombus gigas*. With this illustration, Chemnitz introduced the name '*Mytilus cinnamominus*'. It is clear that the Lister and Chemnitz figures illustrate the same species.

In the *Portland Catalogue*, Lightfoot (1786, p. 104, number 2275) listed *Mytilus Brunneus* but gave no reference or description. Although some authors (e.g. Lamy, 1937, p. 179) place this name in the synonymy of *cinnamomea* (= *fusca*) it should be regarded as a *nomen nudum*.

In 1791 Gmelin referred to the figure by Lister and provided for it the name '*Mytilus fusca*' but gave no locality data. Subsequently, Schreibers (1793) and Link

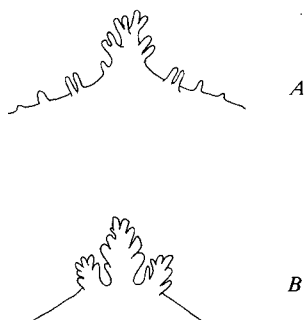


Fig. 5—Valvular siphonal membrane of *Botula fusca* (compare also with Fig. 2): A, ex Brittomart Reef, Queensland (NMVF51472). B, ex Isla Tortuga, Venezuela (redrawn from Soot-Ryen 1955, text-fig. 72).

(1807) used the name '*cinnamomeus*' citing the Chemnitz illustration.

In 1819 Lamarck used '*Modiola cinnamomea*' citing both the Chemnitz and the Lister figures (referring to the latter as 'var. (b)') but also referring to specimens in his own collection from 'l'Isle de France'. Types exist in the MNHN (Paris) Lamarck Collection (Fig. 1A, B). There are two samples. One sample consists of a whole specimen and a single left valve, labelled as the l'Isle de France material collected by M. Desetangs; the specimens have a chestnut brown periostracum. The other sample consists of four whole specimens and two valves without locality and the type status of this material is uncertain.

In the same publication Lamarck described another mussel, under the name *Modiola silicula*, from New Holland (Western Australia). The type (Fig. 1C) is a whole specimen in the MNHN (Paris) Lamarck Collection. It is clearly conspecific with the types of *M. cinnamomea* Lamarck, although it possesses a dark brown periostracum.

The publication of Chemnitz is not an accepted source of available names and so *M. fusca* Gmelin 1791 becomes the first available name which is based on the Lister figure and we may assume that the type locality is Jamaica in the Atlantic.

The names *M. cinnamomea* Lamarck and *M. silicula* must be associated with the Indo-West Pacific population because of the clearly designated Indian Ocean localities with the type material. Some authors (e.g. Iredale 1939) have assumed that the Atlantic and Indo-West Pacific populations are different species. In that case *M. fusca* Gmelin would be the available name for the Atlantic form, but *M. cinnamomea* Lamarck could not be used for the Indo-West Pacific form because the name was already validly used by Schreibers and Link for the Chemnitz figure (i.e. it is a subjective synonym of *M. fusca* Gmelin). It was for this reason that Iredale used the second available name of Lamarck, i.e. *silicula*, for the Indo-West Pacific population when he unnecessarily provided the subspecific name *infra* for the Queensland form (Fig. 10, P). However, this problem

becomes unimportant once it is accepted that there is but a single species widely distributed in the Indian, Pacific and Atlantic Oceans. The oldest available name, *M. fusca* Gmelin, must be used for all. It is unfortunate that this name is based on a poor illustration, with dubious provenance, in a rare publication, and that there is no type.

BORING MECHANISM

Boring in calcareous substrates is achieved by certain mytilids by mechanical abrasion (rubbing of the shell valves against the burrow wall), by chemical means, or by a combination of the two. Boring glands in the mantle folds have been described in species of *Lithophaga* (Pelseneer 1911, Turner & Boss 1962, Wilson 1979, Morton & Scott 1980) *Leiosolenus* (Yonge 1955, Wilson 1979, Kleeman 1980, Morton & Scott 1980) and *Fungiacava* (Goreau, Goreau, Soot-Ryen & Yonge 1969, Goreau, Goreau & Yonge 1972).

Morton and Scott (1980) have described the histology and morphology of anterior and posterodorsal boring glands in the middle mantle folds of a number of *Lithophaga* and *Leiosolenus* species. They established that there is a 'progressive degree of complexity from simple epithelial to ducted sub-epithelial structures coinciding with increasing specialization of habitat from natural limestone to species specific live coral dwellers.' They also described a siphonal gland in the more specialized species (of *Leiosolenus*).

Lithophaga lithophaga (Linnaeus) and *L. teres* (Philippi) which bore in limestones and dead corals, are examples of species with large but histologically simple anterior and posterodorsal boring glands and no siphonal glands. *Leiosolenus simplex* (Iredale) (= *lessep-siana*, see Wilson 1979) and *Leiosolenus mucronata* (Philippi) are the extreme examples of the specialized live-coral dwellers.

In *Fungiacava eilatensis*, which bores in living *Fungia*, boring is exclusively chemical. The shell never comes in contact with the walls of the burrow and there are large boring glands in the middle mantle folds, including in the siphonal regions (Goreau *et al.* 1972).

Yonge (1955) compared the boring mechanisms of '*Botula*' and '*Lithophaga*', concluding that they are essentially mechanical in the former and chemical in the latter. Although the results of that study are not disputed here, they apply not to *Botula* and *Lithophaga* but to *Adula* and *Leiosolenus*. The species studied were *Adula falcata* (identified as *Botula (Adula) falcata*) and *Leiosolenus plumula* (identified as *Lithophaga plumula*).

Gohar & Soliman (1963) discussed the boring mechanism of *Botula fusca* (misidentified as *Modiolus cinnamomeus*) from the Red Sea, but failed to observe boring glands. They described the boring mechanism in this species as 'by mechanical abrasion, in a rocking movement'.

In this study it is shown that *Botula fusca* has large but histologically simple anterior and posterodorsal boring glands and lacks siphonal glands, thus matching the

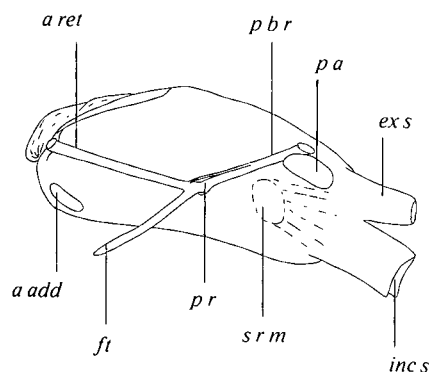


Fig. 6—Musculature of *Botula fusca*. (Specimen ex Heron I., Queensland; NMVF51471).

condition of *Lithophaga* s.s. and the least specialized *Leiosolenus* species which bore in calcareous rocks and dead corals.

Morton & Scott (1980) postulate a 'progressive reduction in shell length relative to width and height' and 'a progressive reduction in size of the adductor and byssal retractor muscles' in the *Lithophaga-Leiosolenus* series correlating with habitat specialization. *Botula fusca* is short, cylindrical, blunt ended and has very small posterior byssal retractor muscles, and it does not fit this postulated morphological trend.

Many authors (Carazzi 1903, Pelseener 1911, Yonge 1955, Franc 1960, Turner & Boss 1962) have supposed that the chemical agent secreted by the boring glands of lithophagines is a free acid and the organs are referred to in the older literature as the 'acid glands'. More recent authors accept a contrary view that the boring agent is a calcium-binding neutral mucoprotein, following the results of histo-chemical studies on *L. lithophaga* by Jaccarini *et al.* (1968). In that species secretory cells from the boring glands are strongly P.A.S. positive and do not stain with Alcian Blue, thereby excluding the possibility of an acid mucopolysaccharide secretion. The results of our histo-chemical tests confirm that this is the case in *Botula fusca* also.

FAMILY PLACEMENT OF *BOTULA*

Although Lamy (1937) placed *Botula* with *Lithophaga*, Dall (1898) Iredale (1939) Keen (1937, 1971) Soot-Ryen (1955, 1969) and others have considered that *Botula* is a relative of *Modiolus* in view of similarity of shell form though noting the peculiar musculature of *Botula*. In fact, the cylindrical, slightly arcuate shell of *Botula* with its large, terminal and incurved umbos and wide, blunt anterior end, is quite atypical of *Modiolus*. Nor does *Botula* possess a hirsute periostracum which is an important feature of *Modiolus*; the periostracum is thin and glossy smooth.

Anatomically there are many differences besides musculature. Most significantly, *Botula fusca* has large extensible siphons with an internal diaphragm within the excurrent siphon, boring glands in the mantle folds and a large, digitate valvular siphonal membrane on the ventral side of the branchial septum and the posterior retractor muscles are small. These major anatomical characters exclude any possibility of a close affinity with *Modiolus*. On the contrary, these features and the burrowing lifestyle are consistent with a lithophagine affinity.

Wilson (1979) commented on significant anatomical differences between *Lithophaga* s.s. (as represented by *L. lithophaga* Linnaeus, *L. niger* d'Orbigny, *L. teres* Philippi, and *L. antillarum* d'Orbigny) and the series of species which possess secondary calcareous accretions on the posterodorsal parts of the valves. Further evidence for generic separation of these two groups of boring mussels has been provided by Morton and Scott (1980) who showed differences in the structure and location of the boring glands.

Waller (1983) has shown that the periostracum of the *Lithophaga* s.s. series has a mineralized outer layer containing calcium hydroxyl-apatite, with an X-ray diffraction pattern like that of dahllite, apparently a device for hardening the periostracum helping to protect the shell from abrasion during burrowing. This substance is lacking in the periostracum of the species with secondary calcareous accretions which appear to be an alternative

TABLE 2
DIAGNOSTIC CHARACTERS OF THE GENERA OF LITHOPHAGINAE

ADULA	LITHOPHAGA	BOTULA	LEIOSOLENUS	FUNGIACAVA
Shell elongate—cylindrical	Shell elongate—cylindrical	Shell short—cylindrical	Shell elongate—cylindrical	Shell high, ovate
Umbones subterminal	Umbones subterminal	Umbones terminal, strongly incurved	Umbones subterminal	Umbones subterminal, strongly incurved
Boring glands lacking	Anterior and posterodorsal boring glands present, simple; siphonal boring glands lacking.	Anterior and posterodorsal boring glands present, simple; siphonal boring glands lacking.	Anterior and posterodorsal glands present, simple or complex; siphonal boring glands present.	Boring glands present.
?	Plicate membranes present.	Plicate membranes present.	Plicate membranes lacking.	?
Siphons undivided	Siphons undivided	Siphons divided	Siphons undivided	Siphons undivided

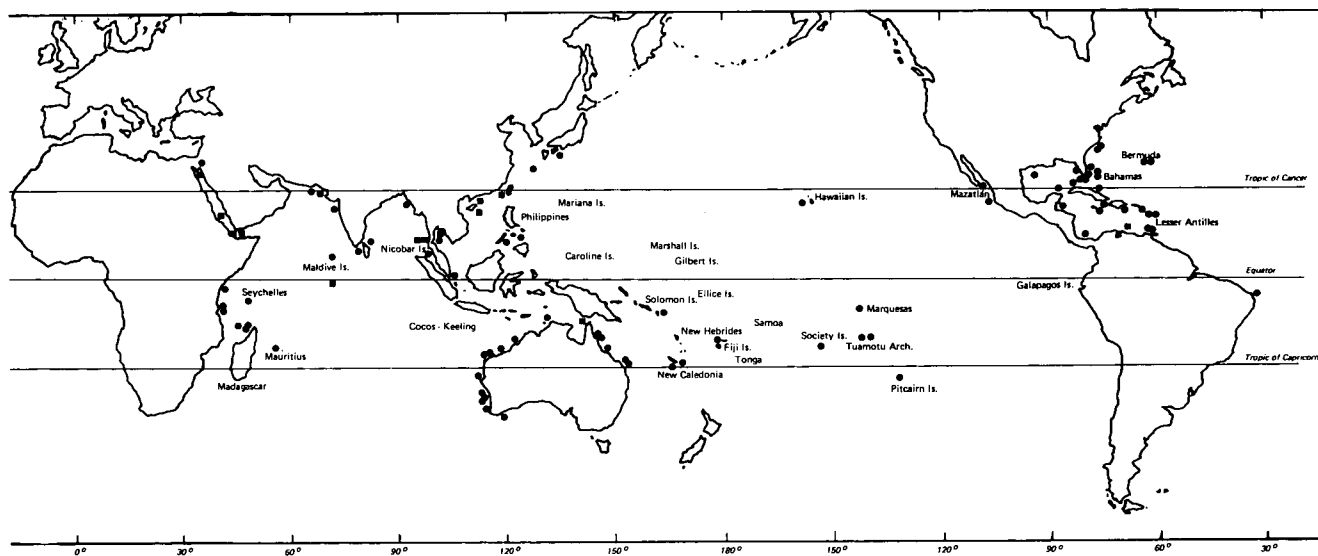


Fig. 7—Distribution of *Botula fusca* based on specimens in museum collections examined by the authors (●), and selected literature records (■).

device serving, in part, the same function. For these reasons *Leiosolenus* is here restored to generic rank to include the species which possess secondary calcareous accretions on the shell valves but lack a mineralized outer layer in the periostracum, and possess pocket-like supra-branchial chambers between the gill axes and the visceral mass but lack plicate membranes.

Goreau *et al.* (1970) argued that *Fungiacava* is most closely related to *Solamen* and *Crenella* (subfamily Crenellinae) but Morton & Scott (1980) favour a lithophagine affinity for this unusual genus. The latter view is accepted here.

It is proposed here that the subfamily Lithophaginae be redefined to include five genera of siphonate, rock-boring mytilids (Table 2): *Adula* which bores by mechanical means and *Lithophaga*, *Leiosolenus*, *Fungiacava* and *Botula* which bore by means of chemical secretions from boring glands located in the mantle folds. *Botula* appears to be most closely related to *Lithophaga*.

LOCALITY RECORDS

The following list is based on verified museum specimen records and selected literature records where these add significant information. Abbreviations and spelling are as given on the original record.

ATLANTIC

North Carolina: In coral rock, 14 fms, 34°05'N, 77°18'W (USNM); 14 fms, 25 miles SE of Cape Fear (USNM); 18 fms, 27 miles SE of Cape Fear (USNM).

South Carolina: Sullivan I. (MCZ).

Florida: Miami (ANSP, MCZ, USNM, BMNH); 3-30 fms off Miami (USNM); 25-60 fms, off Fowey Light (USNM); 30 ft, 8-10 m. W of Mullet Key, Fort Dade (ANSP); 10-14 fms, off Palm Beach (ANSP); Middle Grounds, NW of Johns Pass, off St. Petersburg (MCZ); Tampa Bay (MCZ); 65 fms off Western Dry Docks (USNM); Key West (MCZ, ANSP, USNM); 65 fms off Ragged Key (USNM); 1 m off Soldier Key (MCZ); Bonefish Key (ANSP); in soft rock, No Name Key, near Big Pine Key (USNM); 15-16 fms, Tortugas (USNM); Garden Key (CAS).

Texas: 103 and 107 mi. SE of Galveston (MCZ).

Bahamas: Off Green Cay (USNM); Grand Bahamas (USNM); N end Elbow (Little Guana) Cay, Great Abaco (ANSP); Bimini Lagoon (ANSP); 3 fms, Caicos Bank off Ambergris Cay (MCZ); Andros (MCZ).

Bermuda: (BMNH); 80-100 fms, ¾ mi. S of Castle Road (MCZ); 4-5 fms, Castle Roads, Castle Harbour (MCZ).

Cuba: 25 fms Cabanas Harbour (USNM); Cape Cajon (USNM); 1-12 fms Bahia Honda (USNM); Cao Cruz del Padre, Santa Clara (USNM).

Dominican Republic: Santa Barbara da Samang, Santo Domingo (MCZ).

Haiti: (BMNH).

Puerto Rica: Punta Arenas, Vieques (USNM); Mayaguez Harbour (USNM).

Virgin Islands: St. Thomas (ANSP, MCZ, USNM).

Barbados: 10-20 ft, off Pelican I. (USNM).

Belize: Coral reef near St. George Cay (USNM).

Trinidad: Chaguaramas Bay (USNM).

Tobago: E of Pigeon Point (USNM).

West Grenada: 6 ft, Morne Rouge Bay (ANSP); 30 ft, ½ m W of Fort George, St. George (ANSP).

St. Lucia: Boat Harbour, Castries (MCZ); Marigot Harbour (MCZ).

Jamaica: (Type locality): Lister (1687); (MCZ).

Mexico: 25 fms, off Cape Catoche, Yucatan (USNM).

Curacao: 30 ft, Oranjestad Lagoon, Aruba I. (ANSP).

Panama: 10 fms Limon Bay (CAS). 10 fms, 2 m. off Colon (MCZ).

British Honduras: Punta Gorda (ANSP); 12 ft, reef E of Cangreja Cay (ANSP).

Venezuela: Isla Tortuga (Soot-Ryen 1955).

Brazil: 20 fms, off Cuba Sao Roque 6°59'S, 34°47'W (USNM).

EASTERN PACIFIC

Mexico: Boring in *Ostrea iridescens*, Punta Camaron, Mazatlán (SDNHM). Mazatlán (CAS); 5-10 fms, Maria Madre Is., Tres Marias Group (CAS).

INDO-WEST PACIFIC

Madagascar: 0-5 ft, E of Nosy Ambariole, SE of Nossi Bé (ANSP); 16 fms, 2-3 mi S of Nosy Iranja, 32 mi. SW of Nossi Bé (ANSP); 0.6 ft, E Bay between Nosy Ambariole & Nosy Ambariotelo, SE of Nossi Bé (ANSP); 0.8 ft, Pointe Lokobe, SE Nossi Bé (ANSP); 0.6 ft, Iles Radama, 52 mi S of Nossi Bé (ANSP).

Kenya: Shimoni (BMNH).

Mauritius: MNHN (Paris); (BMNH); 0.8 ft, Pointe Fayette (ANSP); Blue Bay (ANSP).

Aldabra: (BMNH).

Seychelles: (BMNH); 30-36 ft, Cerf I., NE Mahé (ANSP); 18 ft, St. Anne I., NE Mahé (ANSP).

Zanzibar: (BMNH); 11-12 fms, Pwakuu I. (ANSP); 11 fms, 1 mi W. Nyange I. (ANSP); 5-8 fms, 3 mi. SE Bawi I. (ANSP); 0-6 ft, Chumbe I. (ANSP).

Red Sea: Eilat (WAM); Djibouti and Aden (Lamy, 1937); Ghardaga (Gohar & Soliman 1963).

Aden: (BMNH).

Iran: Gadani, E of Samniani, Baluchistan (BMNH).

Pakistan: Ibrahim Maidari, near Karachi (BMNH); Karachi (CAS).

India: Hare I., 6 mi SW Mandapam, Gulf of Mannar (ANSP); Bombay (MCZ, BMNH).

Sri Lanka: Pearl Banks, Gulf of Mannar (BMNH).

Burma: Arakan and Mergui (BMNH).

Thailand: Kata, near Khao Lan, Phuket I. (ANSP); Mutapone I., Chumpon (MCZ); 1-30 fathoms in old coral blocks, Cape Liant to Koh Chang (Lyngé 1909).

Nicobar Islands: (Lyngé 1909).

Mergui Archipelago: (Lyngé 1909).

Maldivé Archipelago: Addu Atoll (BMNH); Suvadiva Atoll (Lyngé, 1909).

Malaysia: Palau Bidang, N of Penang (BMNH).

Singapore: Boring in coral rocks, Palau Salu (WAM).

Philippines: Boring in dead coral, Apat Bay, Calauage Bay, S. Quezon (WAM); 15 fms, N of Laminusa Is., Siasi, Sulu (WAM); 1 fm, dead coral, Laguio Pt., Lopez Bay, S. Quezon (WAM).

Taiwan: (Wen-Lung Wu, 1980).

Okinawa: Ryuku Is. (ANSP).

Japan: Shigeo Hashimoto, Kii (ANSP).

People's Republic of China: Coast of Guangdong to Hainan I. (Tsi & Ma, 1980).

Solomon Islands: 180 ft. boring in dead coral boulders, W side of Malapaina I., SE San Cristobal (WAM).

New Caledonia: 0-10 ft, Baie de l'Orphelinat, Noumea (ANSP); Recaudy Reef, Noumea (ANSP); 50 ft, 3 mi NE Dunebea Pass (ANSP); 0-18 ft, Santa Marie (Isle Ngea), Magenta (ANSP).

Fiji: (ANSP, MCZ, CAS).

Society Islands: Fauni Pt., Bora Bora (USNM).

Tuomotu Archipelago: 10 fms, coral rocks, Rangiroa Lagoon (WAM); Ngarumaoa Is., Raroia (USNM); Tatau I. (USNM).

Marquesas: 37-40 fms, W of Fatu Hiva (USNM).

Pitcairn I.: 40-58 fms (USNM).

Australia: Northern Territory: Darwin (Tate 1892). *Queensland*: Torres Strait (Melville & Standen, 1899); 3 m, in dead *Porites*, Watson Bay, Lizard I. (WAM); in dead coral, Rocky Point, Lizard I. (WAM); reef flat, Low Isles (WAM, AM); Britomart Reef (NMV); South Keppel I. (WAM); in dead coral, outer reef rim and reef crest, Heron I. (WAM); 4 m, reef-front slope, in dead coral, Heron I. (WAM); boring in beach-rock, south side of Heron I. (NMV). *Western Australia* (All WAM): Upper intertidal zone, boring in oyster shells, Derby; 22 fms, 40 mi. W of Cape Jaubert; oyster shells, upper intertidal zone, Kendrew I., Dampier Arch; dead coral rocks, reef ridge, Kendrew I., Dampier Arch; 3 m, Rosemary I., Dampier Arch; 10 mi, S of Exmouth, Exmouth Gulf; 18 m, shell, coral rubble & lithothamnion nodules, 5 km ESE of Cape Heirisson, Shark Bay; reef flat, Long I. Passage, Abrolhos; 15 m, 24 km N of Dongara; 82.3 m, 35 km W of Jurien Bay; Mosman Beach & Hall Bank, Fremantle; 11-17 m, off Fremantle; 10 fms, 1½ m W of south end of Garden I.; 54 ft, Dunsborough, Geographe Bay; 46 m, in dead coral, Cheyne Beach.

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