

Sanitation with sponge and plunger: western Atlantic slit-wormsnails (Mollusca: Caenogastropoda: Siliquariidae)

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Siliquariid *Tenagodus* (synonym: *Siliquaria*) snails are obligatory sponge commensals, with uncoiling and laterally slitted shells embedded inside Demospongiae hosts, and shell apertures facing the outside allowing for respiratory and gill-filter-feeding activities. Live-collected animals observed *in situ* within hosts provide the first detailed functional morphological study of the group, and form the basis for systematic revision of the western Atlantic members of type genus *Tenagodus* (Siliquariidae, synonym: Tenagodidae). Three species are recognized. Overall anatomical features of wide-ranging Atlantic *T. modestus* (Dall, 1881) and *T. squamatus* (de Blainville, 1827) [= *T. anguillae* Mörch, 1861] are similar to those previously described for New Zealand *Pyxipoma*. A third species, ***Tenagodus barbadensis* sp. nov.**, is described from Barbados, based on shell characters. The three species live embedded in a few species of halichondriid and thrombid sponges at depths ranging from *c.* 20 to several hundred metres and show several characters not previously documented for the family. These include a short compressed-S-shaped osphradium, an anal opening positioned in the posterior mantle cavity, and cuspidate inner marginal radular teeth. Presence of shell septa sealing earlier parts of the shell, first described in the early 1800s but subsequently disputed, was verified. Observations on living *T. squamatus* demonstrated the use of the large tight-fitting operculum in plunger-like fashion, flushing the mantle cavity and discharging waste material (including faeces from the posteriorly located anus) through the shell slit into the host sponge's aquiferous canal system. Uncoiling shells, shell and mantle slits, and specialized opercular, gill and gut morphology are interpreted as adaptive traits of the sessile mode of life embedded in sponge tissue. Actively maintained linkage between snail and sponge water-flow systems provides mutual benefits; these include the allowance for rapid defensive withdrawal and return-to-feeding position of the snail (by using the sponge canal system as a vent or reservoir for displaced water), sanitation of the mantle cavity (waste material can leave the snail through the shell slit at the posterior end of the mantle cavity, avoiding fouling of the gill-feeding system), and by providing increased water flow and, potentially, extra nutritional particles for the sponge (food and waste particles stemming from the snail's activity). The lectotypes selected herein are *Serpula anguina* Linnaeus, 1758, *Tenagodus anguillae* Mörch, 1861, and *Siliquaria modesta* Dall, 1881. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 307–333.

ADDITIONAL KEYWORDS: anatomy – Cerithioidea – commensalism – Gastropoda – morphology – mutualism – Porifera – sessility – systematics – taxonomy.

INTRODUCTION

More than 2300 years ago, in his *Historia animalium*, Aristotle noted that a 'sponge provides a home for animals inside itself, worms and other creatures'. Today, it is well known that sponges interact with a remarkable variety of organisms. Symbioses with bacteria and microalgae are particularly widespread and occur

in the large majority of marine and freshwater Demospongiae as well as in Calcarea and Hyalospongiae (Sarà *et al.*, 1998). Sponges also provide substratum and food sources for, and interact with, an extensive suite of metazoans. Marine sponge–animal interactions have long been known and can include numerous species in a single sponge. Duarte & Nalesso (1996), for example, listed 92 species over 1 mm in size from numerous phyla endobiotic in one sponge species, *Zygomycale parishii* (Bowerbank, 1875), from Brazil. Pansini (1970) and Koukouras *et al.* (1996) conducted

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similar studies. The interactions of these organisms often reach the level of commensalism and/or parasitism (e.g. Connes, Paris & Sube, 1971; Hendler, 1984). Among filter-feeding molluscs, these include sponge–scallop associations (Bloom, 1975) such as the unspecialized (and probably facultative) commensal-protective mutualism between an enveloping epizoitic sponge *Halichondria panicea* (Pallas, 1766) and the scallop *Chlamys varia* (Linnaeus, 1758) on the Atlantic coast of Ireland (Forester, 1979). A similar relationship has been reported between the oyster *Cryptostrea permollis* (Sowerby, 1871) and the host sponge *Stelletta grubii* Schmidt, 1862, in the Gulf of Mexico of Florida (Forbes, 1966). Koukouras *et al.* (1996) listed several gastropod–sponge relationships.

A much more specialized case of mollusc–sponge association involves the siliquariid ‘worm-snails’, a marine group of worldwide distribution that includes vermiform gastropods with uncoiling shells, adapted to obligatory sessile life within a sponge host. Early molluscan workers knew and described siliquariid gastropods mostly from their empty shells, but hinted at a sessile life inside sponges. Sowerby & Sowerby (1826: 1–q) for instance found ‘reason to believe, that in their natural situation they are attached to and embedded in a species of sponge’. In the following century, their occurrence within masses of sponges was occasionally reported as a phenomenon: Annandale (1912), for example, introduced a newly discovered variety of sponge under the name ‘*siliquariae*’ in a description of associated–associated sponges from the Bay of Bengal, and a photograph published by the Hirase Conchological Museum (1915) showed a cluster of siliquariid ‘worm snails’ embedded in a sponge. Over time, a close association became recognized, and Hoshino (1981) introduced an aptly named sponge genus *Siliquariaspongia*. In a recent systematic survey, Pansini *et al.* (1999) reported 35 sponge species hosting siliquariid gastropods from the Mediterranean, the eastern Atlantic, and the Indo-Pacific, living at depths of between 10 and 440 m.

Morphologically, members of the small gastropod family Siliquariidae (synonym: Tenagodidae) belong to the caenogastropod ‘wormsnails’, a grouping also including the uncoiling members (genus *Vermicularia*) of family Turritellidae, and the true wormsnails, Vermetidae (Vermetoidea). The polyphyletic nature of this assemblage has long been recognized by molluscan anatomists (Morton, 1951, 1953), but ecological and poriferan literature still mistakenly treat these taxa as ‘vermetids’ (e.g. Soest & Stentoft, 1988).

Most siliquariids appear to be obligatory sponge-dwellers. Because of their hidden, literally ‘in-faunal’ mode of life and their occurrence below comfortable scuba depth, they are rarely observed and collected. Their shells are readily recognized, being fairly large,

uncoiled, ‘piled-up’ or ‘corkscrew-like’; in most taxa they possess a conspicuous longitudinal slit or series of holes for most of the teleoconch (postlarval shell) length. Siliquariids display many unique features among gastropods, among them the ability to break and modify the shape of their own shells to adjust their shell growth (Savazzi, 1996). The shell slit alone intrigued generations of malacologists and palaeontologists, and its presumed function became the subject of much speculation (e.g. Lamarck, 1818: 337; Gould, 1966: 10). Depending on the underlying assumption of anatomical organization within the snail’s shell, the resulting hypotheses explaining the slit were often contradictory.

Despite the general interest in these peculiar snails and their sponge hosts, few studies have actually explored the biology and anatomy of the gastropods involved. Their unusual, setose and frequently dome-shaped opercula (the horny ‘lids’ attached to the snails’ feet that can close the shell apertures) were noticed and occasionally described (e.g. Mörch, 1865; Sato, 1989), but little is known about the anatomical features and phylogenetic relationships of siliquariids. Lack of published data as well as of accessible anatomical material caused the omission of the family in comprehensive studies such as those by Houbriek (1988) and Simone (2001) on cerithioidean gastropod phylogeny. Recent hypotheses of relationship and introduction of higher taxonomic units such as subfamily levels have remained based on characters of empty shells (Bandel & Kowalke, 1997; Faber & Moolenbeek, 1999) or features of the operculum (Schiaparelli, 2002). A few studies provided detailed anatomical information on this family. Morton (1951, 1953) and Morton & Keen (1960) examined species of the nominal genera *Stephopoma* and *Pyxipoma* in New Zealand and western Africa. Bieler (1997) described the anatomy of a *Stephopoma* species from Western Australia. Hughes (1985) also provided some data on the gross morphology of a *Stephopoma* species from Panama, but the reported occurrence of a cephalic penis (a feature that would be highly unusual in the other aphyllid superfamily Cerithioidea where Siliquariidae is placed) needs corroboration. Healy & Wells (1998: 718), who treated *Tenagodus*, *Pyxipoma* and *Stephopoma* as members of a single genus, summarized much of the published data on this group and concluded that pallial tentacles are usually absent, that the operculum has long branching bristles, and that the marginal teeth of the radula do not bear cusps. It is noteworthy that today’s concept of siliquariid anatomy is thus largely based on *Stephopoma*, a group whose members do not live inside sponges and lack shell perforations. Except for some subsequently overlooked anatomical notes in the European literature of the early 19th century (Audouin, 1829a,b; Philippi,

1836), Morton's (1955: 5) outline sketch of a siliquariid head-foot 'based on *S[iliquaria] maoria*', and a brief preview of the current study (Bieler, 1990), the anatomy of the type genus has remained undocumented.

In two very interesting papers based on preserved siliquariids in their host sponges, Savazzi (1996) and Pansini, Cattaneo-Vitti & Schiaparelli (1999) recently described morphological *in-situ* relations between siliquariids and their Demospongiae hosts and hypothesized water flow patterns and mutual benefits of the participating organisms. The present study is the first to actually observe living specimens and their interactions with the host sponge. Several previous hypotheses concerning this mutualism are now superseded and an explanation is given for the development of the peculiar, oversized operculum characteristic of this group.

In the past, collections of siliquariid species from western Atlantic waters were the product of rare chance encounters while dredging in deep water or came from occasional specimens washed ashore. Most of the existing knowledge thus stems from empty shell records obtained by United States Fish Commission dredgings in the late 1800s. As part of a general review of western Atlantic 'wormsnails', four previously described siliquariid species in three nominal genera are here recognized in the extant fauna of the western Atlantic: *Stephopoma myrakeenae* Olsson & McGinty, 1958; *Hummelinkiella borinquensis* Faber & Moolenbeek, 1999, and two species of the type genus *Tenagodus* (= *Siliquaria*), *T. modestus* (Dall, 1881) and *T. squamatus* (de Blainville, 1827). In addition, a new species is described from off Barbados.

Material of the two previously known and one undescribed western Atlantic *Tenagodus* species have recently become available with sponges collected by manned submersibles during biochemical prospecting off Florida, the Bahamas, Barbados and St. Vincent, and from commercial trawling off the Venezuelan coast. This new material, together with a critical review of existing museum holdings and published record, provides the opportunity to:

- (1) Describe and delineate the western Atlantic *Tenagodus* species (including one new species) emphasizing anatomical characters.
- (2) Compare this first detailed study of the type genus *Tenagodus* to the available data on previously studied members of the family and discuss the available anatomical data for Siliquariidae, addressing various incorrect assumptions made for this group.
- (3) Based on this new understanding of *Tenagodus* anatomy, contribute to the discussion of sponge-siliquariid interaction and decide between the conflicting hypotheses based on the first observations of living organisms.

MATERIAL AND METHODS

For *T. modestus*, alcohol-preserved material was available for anatomical study. Sponge tissue and gastropods had been preserved together, and the poor degree of preservation of the majority of the material allowed only for gross dissection of major structures. In addition to alcohol-preserved specimens, living animals of *T. squamatus* were available for study (provided in November 1990 by Dr Shirley Pomponi). A fist-size piece of a sponge colony, containing several *T. squamatus* animals, was maintained in a 15°C incubator at the Smithsonian Marine Station in Ft. Pierce, Florida, then transferred to the Shedd Aquarium in Chicago where the animals were studied by the author for a period of 10 days (until the sponge died). During that time, individual snails were removed and transferred to the Field Museum for anatomical study. Live observations of water flow patterns were aided by use of carmine particles and fluorescent dye. If not already separated, animals were removed from sponge and shell by manually removing the sponge tissue and breaking the shell using a strong forceps. Soft parts were measured and their gross anatomy studied using a dissecting microscope. For histological studies, specimens were embedded in paraffin, sectioned at 7–8 µm and stained with Periodic-Acid-Schiff (PAS)–Alcian Blue at pH 2.5 and Harris' Hematoxylin counterstained by Eosin Y. Radulae were extracted by dissolving the surrounding tissue with 5% household bleach. The 3-D reconstruction software SURFDriver 3.5 was used to investigate the anterior alimentary tract and surrounding nervous system based on 150 histological serial sections of *T. modestus*. Head-feet, mantle-cavity organs, wet opercula (cut in half by razorblade), and samples of stomach and gut contents were passed through an ethanol series ending in acetone, and then critical point dried. These samples, together with air-dried shells, radulae, and opercula were coated with gold/palladium, and observed and photographed using a Zeiss Novascan 30 scanning electron microscope. Only shell material, partly embedded in dried sponge tissue, was available for the third, previously undescribed species. Type material was studied from various institutions, especially that of Mörch (Copenhagen, London, Berlin; see Bieler, 1996) and Dall (MCZ, USNM). Selected listings of examined material are placed with each species description.

INSTITUTIONAL AND ORGANIZATIONAL ABBREVIATIONS

- AMNH American Museum of Natural History, New York, USA
 ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
 BMNH The Natural History Museum, London, UK.

CAS	California Academy of Sciences, San Francisco, USA
DMNH	Delaware Museum of Natural History, Wilmington, Delaware, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
FSBC	Florida Marine Research Institute, Florida Department of Natural Resources, St. Petersburg, Florida, USA (formerly Florida State Board of Conservation)
HBOM	Harbor Branch Oceanographic Museum, Ft. Pierce, Florida, USA
MCZ	Museum of Comparative Zoology, Harvard University, Massachusetts, USA
NMFS	National Marine Fisheries Service, USA
USFC	United States Fish Commission
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMK	Zoologisk Museum, København (Copenhagen), Denmark

DESCRIPTION OF WESTERN ATLANTIC *TENAGODUS* SPECIES

ORDER CAENOCASTROPODA COX, 1960
 SUPERFAMILY: CERITHIOIDEA FLEMING, 1822
 FAMILY SILIQUARIIDAE ANTON, 1838
 (SYNONYM TENAGODIDAE GILL, 1871)
 GENUS *TENAGODUS* GUETTARD, 1770

Type species by subsequent designation (Adams & Adams, 1853-4: 360–361): *Serpula anguina* Linnaeus, 1758 (Indo-Pacific). Linnaeus' (1758: 787) *Serpula anguina* was based on more than one species, and the Linnaean collection contains several taxa under this name, without indication of type specimen (Hanley, 1855: 448). Linnaeus had adopted the species name from the nonbinominal '*Solen anguinus*' of Rumphius (1705: 125) and referred to illustrations in that work. The specimen illustrated by Rumphius (1705: pl. 41, fig. H) from Ambon, Moluccas, Indonesia, as cited by Linnaeus, is here selected as lectotype. *Siliquaria* Bruguière, 1789, is an objective synonym of *Tenagodus*, with *Serpula anguina* Linnaeus, 1758, as type species by subsequent monotypy (Lamarck, 1799: 79). The complex synonymies at the generic and familial levels were discussed by Bieler (1992).

TENAGODUS MODESTUS (DALL, 1881)
 (FIGS 1, 2, 7–9, 26–28, 31–33, 36, 37, 41–43)

Siliquaria modesta Dall, 1881: 39. Tryon, 1886: 191. Paetel, 1888: 499. Agassiz, 1888: 71, fig. 296. Dall, 1889a: 260, pl. 26, fig. 4. Dall, 1889b: 144, pl. 26, fig. 4. Dall, 1896: 25 [‘The first reported since the original types’]. Maury, 1922: 104. Abbott, 1974: 96, fig. 926

(from Dall, 1889a,b). Rios, 1985: 47, pl. 18, fig. 210. Rios, 1994: 66, pl. 22, fig. 253. Díaz & Puyana, 1994: 140, pl. 44, fig. 481. Pointier & Lamy, 1998: 48. Hartman & Hubbard, 1999: 1 ff.

Siliquaria?modesta: Mikkelsen, 1981: 47.

Tenagodus modestus: Bieler, 1990: 21. Leal, 1991: 69. Pansini *et al.*, 1999: 429.

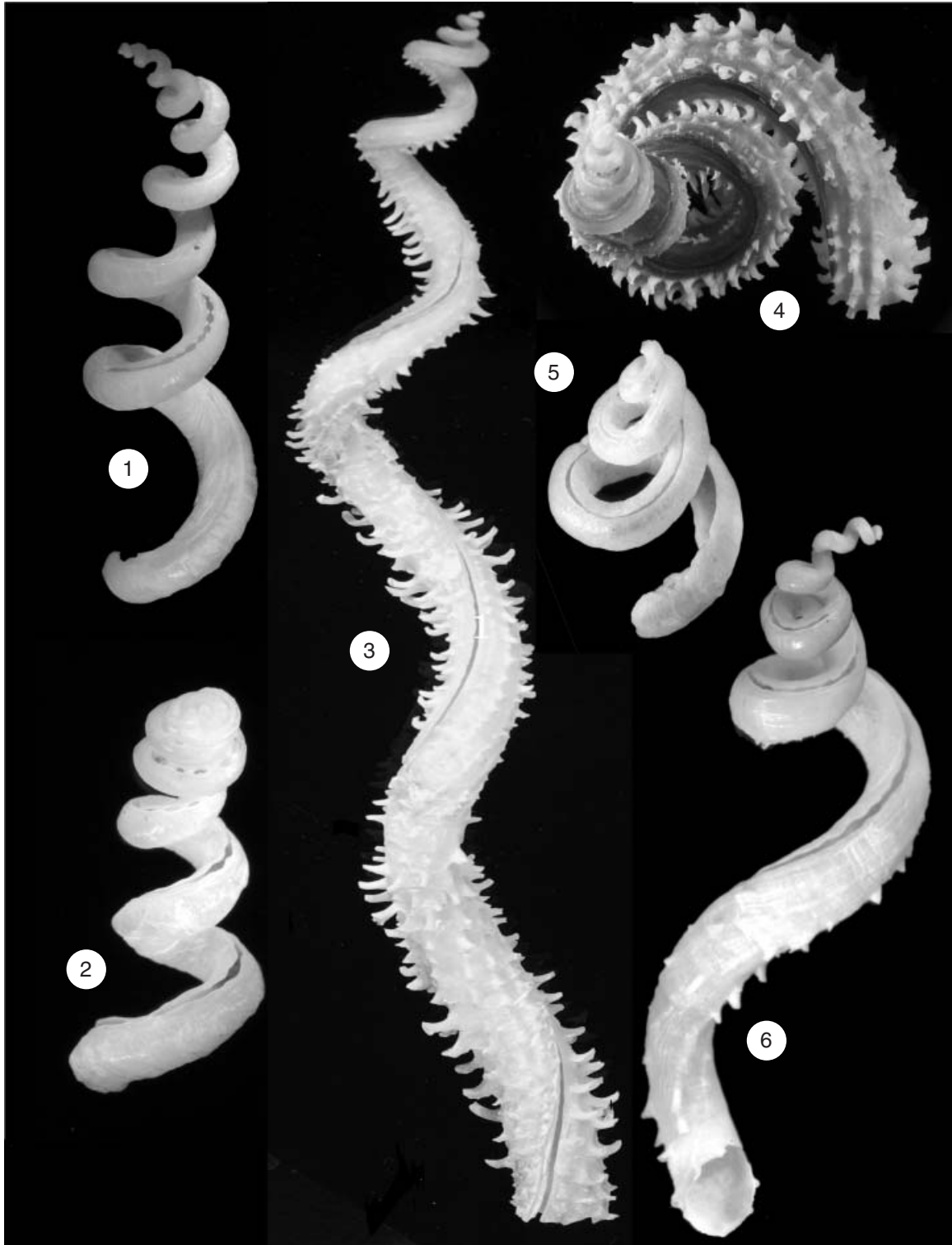
Type material: Dall (1881: 39) described this species based on R/V Blake material ‘found in all depths from 80 to 800 fathoms.’ He did not formally select a type specimen but added, ‘The specimen from which the description was taken lived in 220 fathoms (Station 20)’, a locality off Bahia Honda, Cuba. Eight years later, Dall (1889a: 260, pl. 26, fig. 4) listed individual stations, including number 20, and illustrated a specimen without indicating its provenance. Agassiz (1888: 71, fig. 296) illustrated another specimen from an unspecified Blake station. A comparison of the original material in the USNM and MCZ collections showed Dall's (1889a) figure to be based on a specimen from the originally cited Blake station 20. The 22.8 mm specimen (MCZ 341075; Fig. 2) is here selected as lectotype, with three paralectotypes remaining as MCZ 7419. The type locality is here thus restricted to US Coast Survey Steamer *Blake* station 20, off Bahia Honda, Cuba, Blake Expedition 1877–78, 220 fathoms (402 m), 23°02'30"N, 83°11'00"W.

Specimens examined: See Appendix 1.

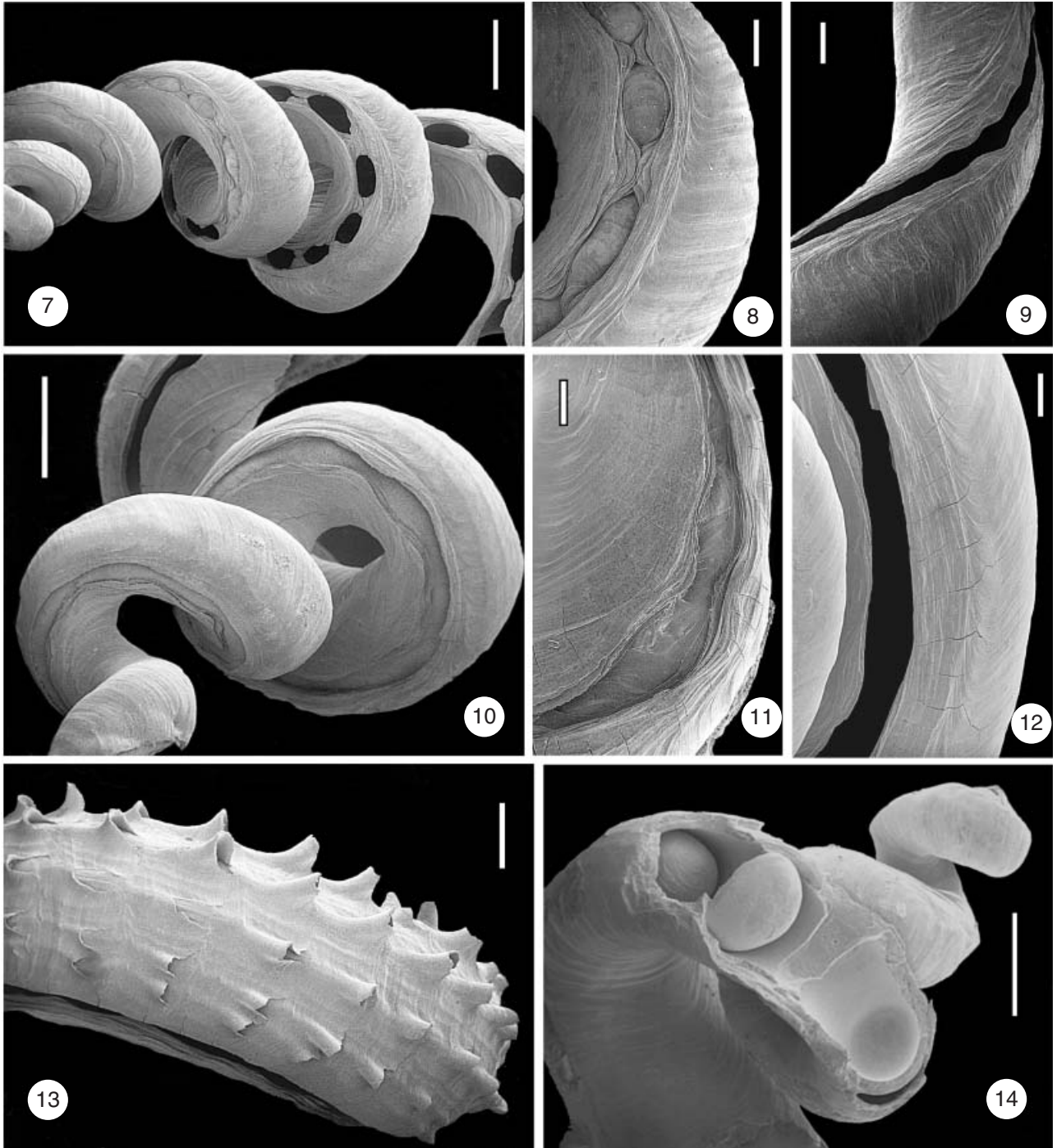
Description

Shell (teleoconch) (Figs 1, 2, 7–9, 42, 43). Relatively large, very loosely coiled; specimens usually less than 8 cm in total length, with inner apertural diameter of 4–6 mm, but occasionally reaching a length of 15 cm (USNM 86776, Trinidad). Sculpture consisting entirely of incremental growth marks, without spiral ribs or striae. Earliest whorls often internally closed off by concave calcareous septa (as shown in Fig. 14 for a different species). Early part of open shell slit (corresponding to region of posterior mantle cavity) narrowed by lateral ingrowths to a – usually very regular – series of holes (Fig. 7); the most recent (body whorl) slit left open with slightly undulating margins (Fig. 9). Slit of earlier whorls (now in the region of digestive gland and gonad) filled-in with shell material that often protrudes outward through the holes (Figs 7, 8). Fresh specimens have somewhat glossy shell surface, particularly on early whorls; later whorls often chalky externally. Colour off-white, sometimes with light tan mottling.

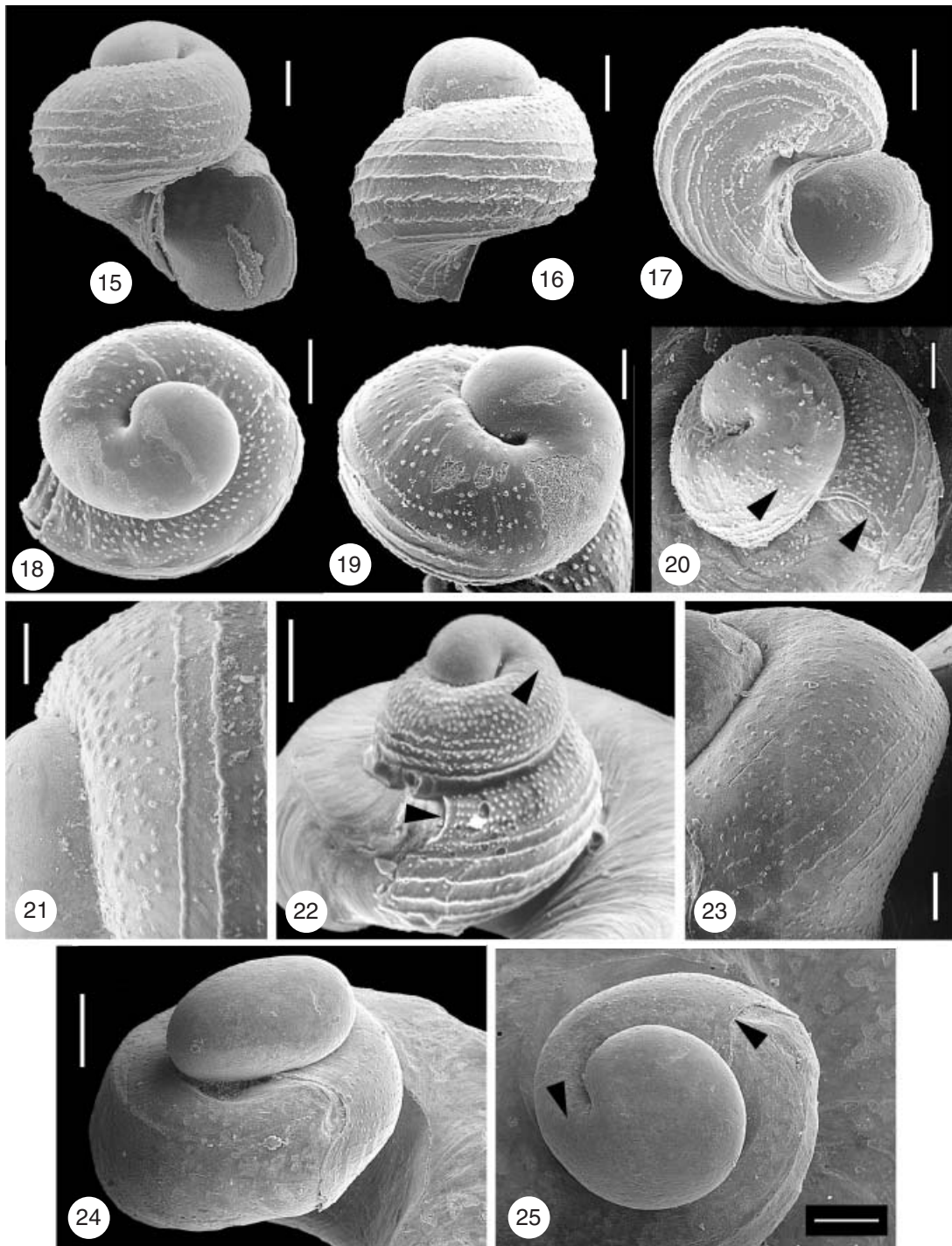
Protoconch (Figs 15–21). Fragile, easily decollated and rarely retained in museum specimens [in fact, Dall's (1889a: 260) original description of live



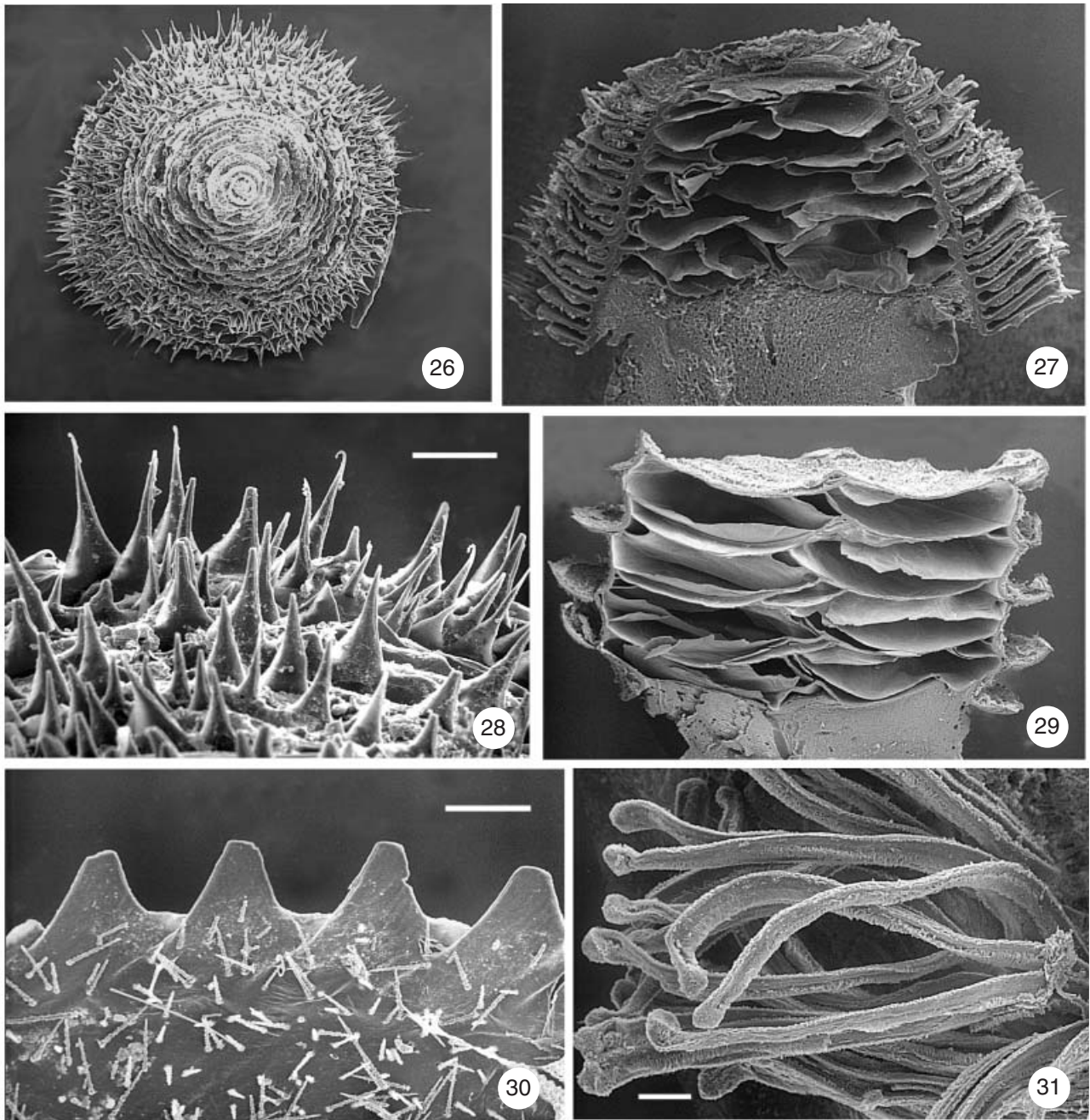
Figures 1–6. Figs 1, 2, *Tenagodus modestus*, shell. 1: Florida Keys, 56 m, FMNH 296716; greatest length = 48 mm. 2: lectotype of *Siliquaria modesta* Dall, 1889, Cuba, MCZ 341075; greatest length = 22.8 mm. Figures 3–5, *Tenagodus squamatus*, shell. 3: Venezuela, Golfo Triste, 46–55 m, FMNH 296706; greatest length = 165 mm. 4: Bermuda, 110 m, FMNH 296697; greatest dimension (diameter of spiral) = 46.6 mm. 5: lectotype of *Tenagodus anguillae* Mörch 1861, Anguilla; ZMK; greatest length = 11.6 mm. Fig. 6, *Tenagodus barbadensis* sp. nov., shell; Barbados, 69 m, FMNH 301239; greatest length = 35.8 mm.



Figures 7–14. Figs 7–9, *Tenagodus modestus*, teleoconch detail (Florida Keys, FMNH 296716). 7: transition from shell covering posterior organs (shell slit filled) to posterior mantle cavity region (shell slit narrowed to series of holes). 8: detail of Fig. 7; note regular, layered restrictions. 9: late shell; slit unrestricted. Figs 10–13, *Tenagodus squamatus*, teleoconch detail (Bahamas, FMNH 296709). 10: transition from shell covering posterior organs (shell slit filled) to posterior mantle cavity region (shell slit open). 11, 12: detail of Fig. 10; note incomplete restrictions when compared to Fig. 8. Fig. 13: adult sculpture; note fluted hollow spines. Fig. 14, *Tenagodus barbadosis* sp. nov., teleoconch detail (FMNH 301290); early whorls opened to display internal septation by calcareous plugs. All SEM. Scale bars = 300 μ m (Figs 8, 11, 12) and 1 mm (all others).



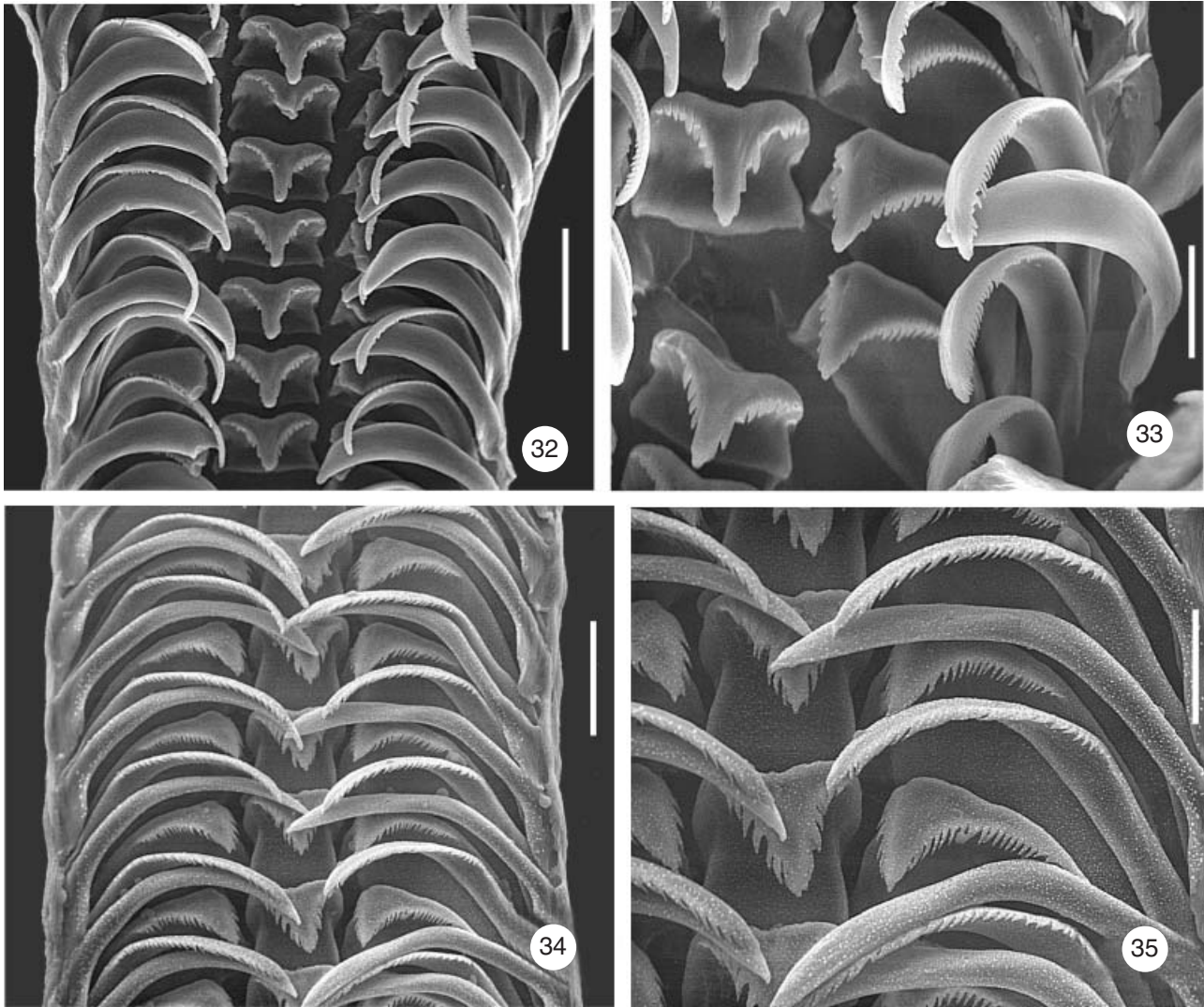
Figures 15–25. Figs 15–21, *Tenagodus modestus*, protoconch (Florida Keys, FMNH 296716). 15, 16: side aspects. 17: basal aspect with larval shell umbilicus. 18: apical aspect, showing smooth embryonic shell and sculptured larval shell. 19, 20: oblique aspects of protoconch. 21: detail of sculpture, pustules and striae (embryonic shell on the left). Fig. 22, *Tenagodus squamatus*, protoconch (courtesy J. Leal). Figs 23–25, *Tenagodus barbadosis* sp. nov., protoconch (FMNH 301290). 23: detail of sculpture, pustules and striae (embryonic shell on the left). 24: side aspect showing large embryonic shell. 25: apical aspect, showing smooth embryonic shell and comparatively small larval shell. All SEM. Arrows marking simple apertural margin of embryonic shell (PC-I) and sinuous apertural margin of larval shell (PC-II). Scale bars = 20 μm (Fig. 20), 80 μm (Figs 22, 24, 25), and 40 μm (all others).



Figures 26–31. Figs 26–28, *Tenagodus modestus*, operculum (Florida Keys, FMNH 296716). 26: outside (heads-on) aspect, diameter = 2.5 mm. 27: razorblade section of whole mount attached to foot, showing internal compartments; diameter = 2.5 mm. 28: detail of Fig. 26, spines on lamellar margin. Figs 29, 30, *Tenagodus squamatus*, operculum (Bahamas, FMNH 296703). 29: razorblade section of whole mount attached to foot, showing internal compartments; diameter = 5.6 mm. 30: details of Fig. 29, spines on lamellar margin (note attached sponge spicules). Fig. 31, *Tenagodus modestus*, highly flexible ctenidial filaments (FMNH 296716). All SEM, critical-point dried. Scale bars = 100 μ m.

material maintained that it 'shows no sign of a regularly formed spiral nucleus', approximately 212–240 μ m high and 200–216 μ m wide, with 2 whorls. First whorl represents smooth, bulging embryonic

shell (protoconch I, hereafter PC-I), about 129–133 μ m in diameter, with circular aperture; second whorl formed by helically coiled, broadly rounded, sculptured larval shell (protoconch II, hereafter



Figures 32–35. Figs 32, 33, *Tenagodus modestus*, radula (Florida Keys, FMNH 296716). 32: part of whole mount showing entire rows. 33: half row, rachidian teeth on left (partly dislocated to show base), smooth outer marginal on right. Figs 34, 35, *Tenagodus squamatus*, radula (Bahamas, FMNH 296701). 34: part of whole mount showing entire rows. 35: half row, rachidian tooth in centre left, smooth outer marginal on right (surface pattern resulting from preservation artefact). All SEM. Scale bars = 40 μm (Figs 32, 34) and 20 μm (Figs 33, 35).

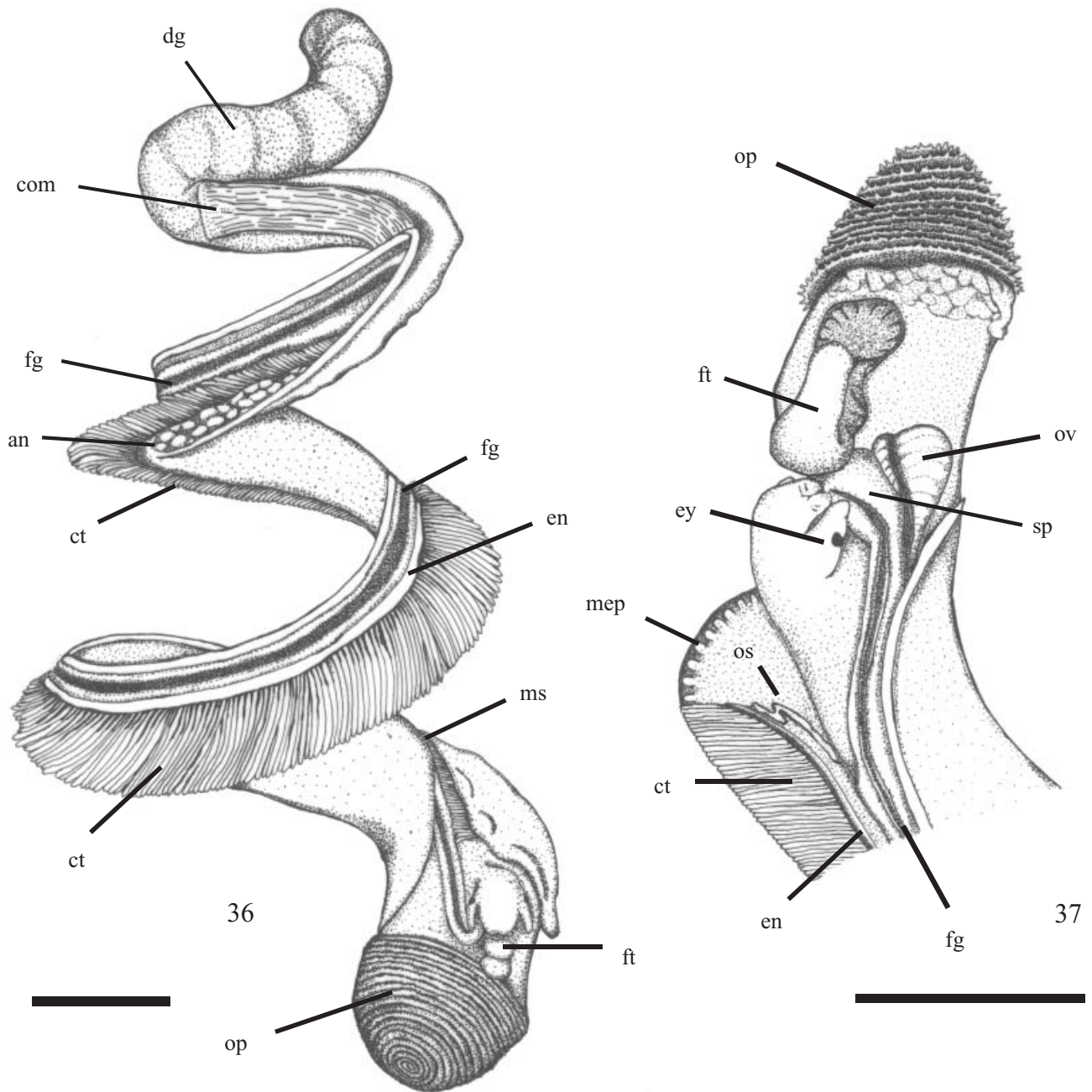
PC-II). Sculpture consisting of about 5 very irregular rows of distinctly demarcated pustules on upper part of whorl, followed below by about 7 finely granulated spiral striae (which appear as rows of fused pustules). Areas between striae and region around open larval umbilicus with more or less distinct irregular rows of finer pustules. Aperture strongly sinuous, deeply embayed on upper whorl surface at point of contact with teleoconch slit area. Translucent white, lower half of PC-II brown.

Operculum (Figs 26–28, 36, 37). Large (2.5–2.8 mm in diameter) in relation to body width, dome-shaped,

multispiral, tightly fitting inside shell tube, composed of 20–30 spiral layers of corneous lamella. Edge of each layer beset with rounded, thorn-like spines. Lamella not continuous internally: core filled with triangular compartments, about 6 per whorl, spirally arranged around a central axis.

Anatomy (Figs 31–33, 36, 37; for measurements, $n = 12$).

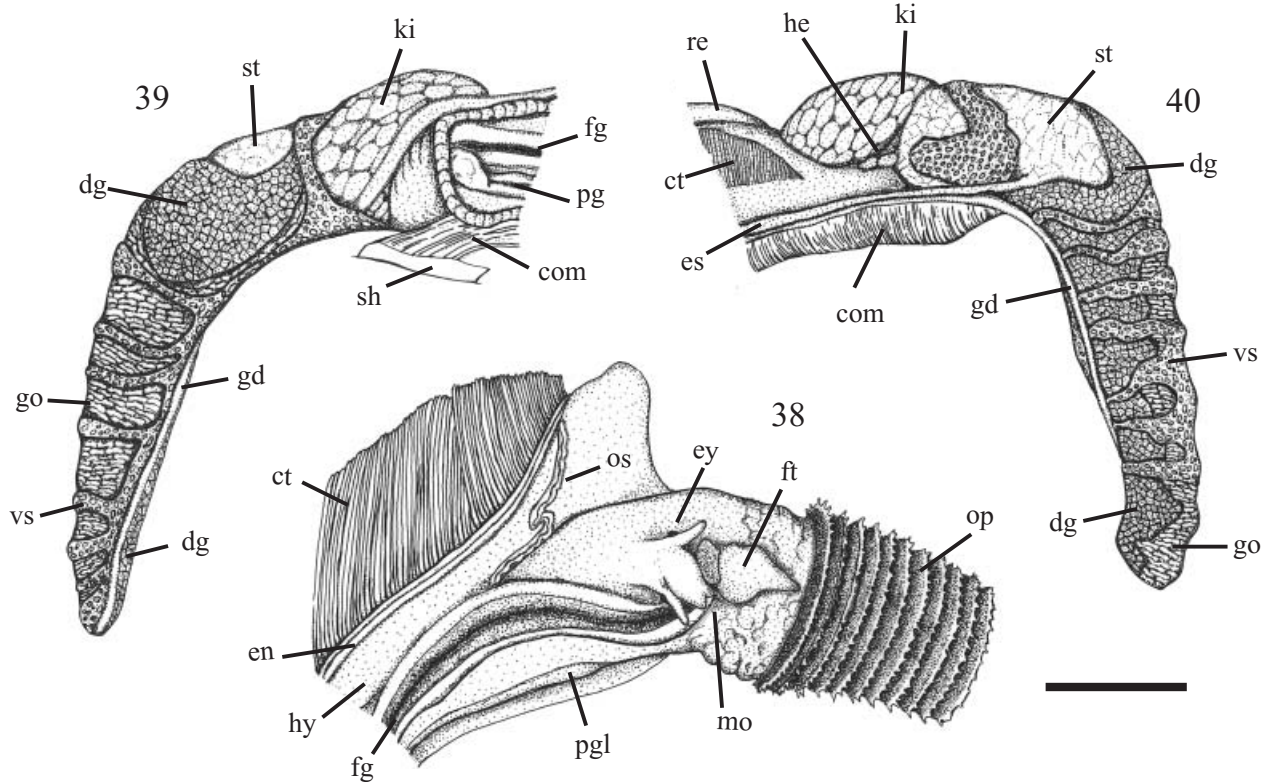
Head-foot: Body long and slender, spirally coiled, forming approximately 3 whorls, 2 of which occupied by mantle cavity; overall body length of preserved animal (excluding operculum) 35–42 mm. Mantle cavity



Figures 36–37. *Tenagodus modestus*, external softbody anatomy, from preserved specimen (Florida Keys, FMNH 296715). 36: overall morphology; ctenidial filaments reflected out of naturally slitted mantle cavity to expose food groove; note greatly reduced cephalic and pedal region compared to rest of body. 37: oblique lateral aspect of head-foot region, mantle reflected along naturally occurring slit; note short looped osphradium, glandular pad, absence of rectum, and weak mantle papillae on inner mantle margin. Scale bars = 2 mm. *Abbreviations:* an, anus; com, columellar muscle; ct, ctenidium; dg, digestive gland; en, endostyle; ey, eye on outer base of tentacle; fg, food groove; ft, foot; mep, mantle edge papillae; ms, mantle slit; op, operculum; os, osphradium; ov, ovipositor.

up to 30 mm long; body width in mid-mantle region approximately 1.3 mm. Foot forming a round column bearing the large operculum; small (0.6 × 1.0 mm), glandular, transversely furrowed area of foot (the

'sole') in front of the mouth. Head small in comparison to width of body; snout short, bluntly rounded, with mouth a vertical slit at its tip. Two cephalic tentacles about as long as snout, with black eyes at their outer



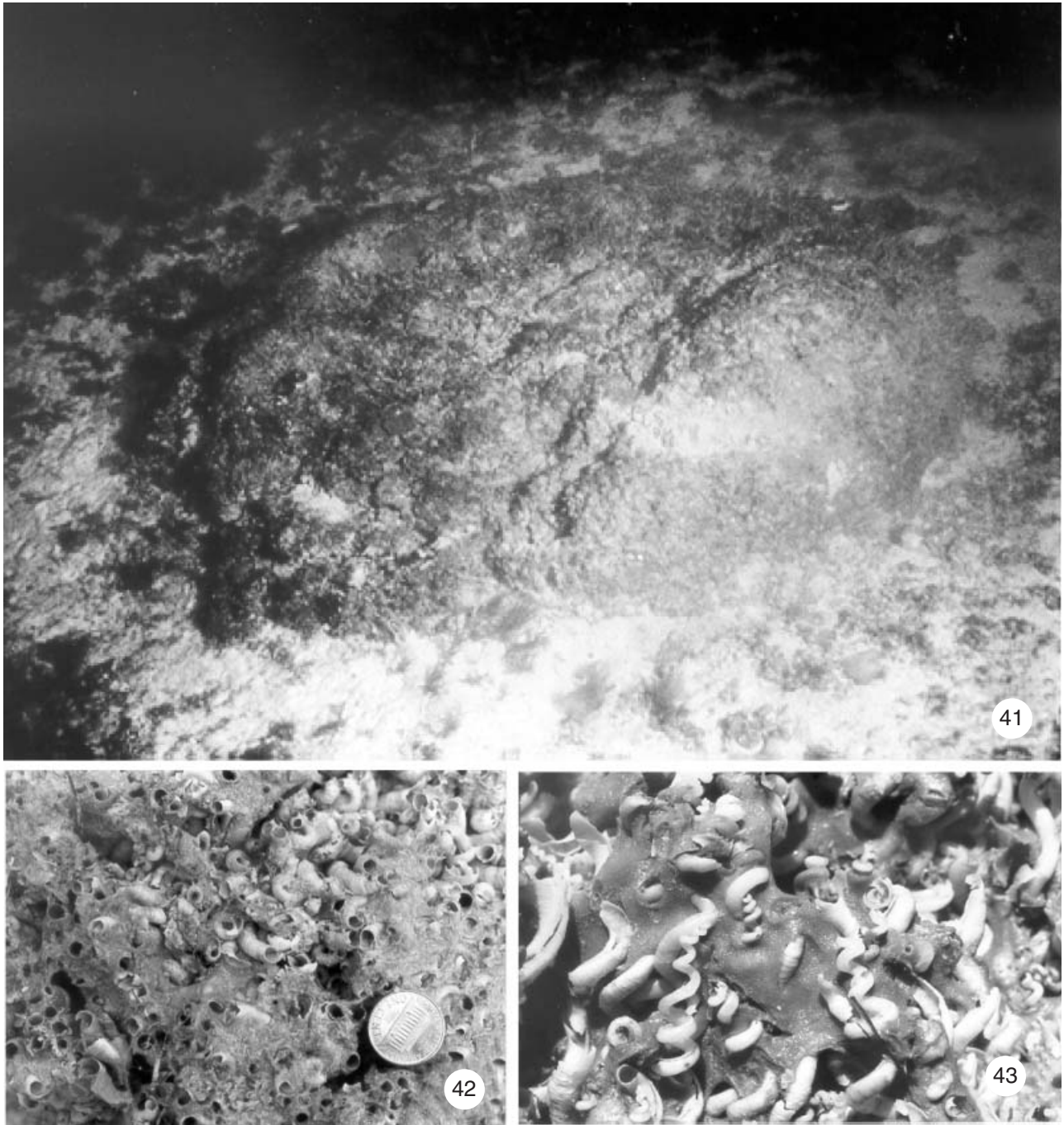
Figures 38–40. *Tenagodus squamatus*, from living and preserved specimens (Bahamas). 38: oblique dorsal aspect of head-foot region, mantle reflected along naturally occurring slit; note small head and massive operculum, short looped osphradium, absence of rectum, and simple mantle margin (FMNH 296703, from preserved animal). 39: posterior animal, right side (FMNH 296700, from living specimen). 40: posterior animal, left side (as before, different animal). Scale bar = 5 mm. *Abbreviations:* com, columellar muscle; ct, ctenidium; dg, digestive gland; en, endostyle; es, oesophagus; ey, eye; fg, food groove; ft, foot; gd, gonoduct; go, gonad; he, heart; hy, hypobranchial gland; ki, kidney; mo, mouth opening; op, operculum; os, osphradium; pg, pallial gonoduct; pgl, lamella attached to right side of pallial gonoduct; sh, shell; st, stomach; vs, vascular system with embedded crystals.

bases. Mantle margin simple but with small weak papillae on inner side. Head-foot and area between mantle papillae with brownish pigment (black before preservation?). No pedal tentacles or pedal mucous gland.

Pallial cavity: Corresponding to shell fissure, dorsal right side of mantle with slit, longitudinally opening mantle between rectum and pallial gonoduct. Ctenidium extending as far as mantle slit, its filament lengths gradually decreasing posteriorly; curved, rod-shaped gill filaments long (to 1.8 mm), narrow (about $30 \times 80 \mu\text{m}$ in cross section), and very flexible (Fig. 31). In addition to rows of relatively short frontal and abfrontal cilia, a row of very long (up to $40 \mu\text{m}$) lateral cilia on either side; thickened, club-shaped tip ciliated (details not observed due to poor preservation). Row of filaments extends across mantle cavity top right side of animal. Osphradium restricted to anterior part of

mantle cavity, beginning next to and shortly behind anteriormost gill filaments; about 2.4 mm in total length, compressed-S-shaped, with posterior leg the longest; its sensory zone with weak meanders. Endostyle forming a narrow glandular tract between gill axis and osphradium, along entire length of gill. Sharply demarcated food groove on dorsum of animal, with thick, tall ridges; groove extending straight in about mid-line from posterior end of mantle cavity to neck region and then looping around right side of head, ending with spoon-like process at mouth opening (Fig. 37, sp.).

Alimentary system: Mouth opening flanked by pair of slender jaws made up of platelets in palisade-like fashion. Simple oesophagus (without dorso-ventral division or crops) with two salivary glands, the latter somewhat increasing in bulk posteriorly and ending well in front of concentrated nerve ring, passing



Figures 41–43. *Tenagodus modestus* in sponge *Thrombus* sp. (Florida Keys, HBOM 065 : 00767, 065 : 02026). 41: sponge colony in 56 m depth off Key Largo; approximately 3 m in length (underwater photograph by submersible). 42: detail of Fig. 41, sponge surface with apertural openings of gastropods (alcohol-preserved). 43: side view of dissected, alcohol-preserved sponge, showing density *in situ*. Coin diameter = 19 mm.

straight to stomach as a simple tube. Digestive gland a single lobe. Simple intestine loops forward and continues as short rectum (about 2.4 mm within mantle cavity), with anal opening in posterior part of mantle cavity; weak ciliated groove leading from anus forward

to mantle cavity. Stomach with style sac and gastric shield. Radula small (Figs 32, 33; length 0.94–1.00, width 0.10–0.12 mm), taenioglossate, with 52–54 rows, transparent; rachidian with strong, finger-like projecting main cusp and 8–12 short flanking cusps on

either side, smooth basal platform, no lateral or basal projections. Lateral tooth with slender, triangular main cusp and 8–12 short inner flanking cusps and about 20 outer flanking cusps. Marginal teeth hook-like, bluntly tipped; cutting edge of inner marginal tooth finely cuspidate on either side, of outer marginal tooth smooth.

Reproductive system: All sexable animals (5) female. Ovipositor (Fig. 37, ov) with central groove anterior and to the right of head.

Habits and habitat

According to Dall (1881: 39, original description): 'Found at all depths from 80 to 800 fathoms [146–1463 m], but not in less than 80 fathoms. The specimen from which the description was taken lived in 220 fathoms'. Hartman & Hubbard (1999) described a large aggregation in a sponge (*Thrombus*) at a depth of 21.5 m (Trinidad). Live material in the present study came from between 56 and 73 m, while shells were recorded from between 18 and 1472 m. *Tenagodus modestus* was originally described from live material (Dall, 1881: 39), but no reference was made to its anatomy or even to the fact that it was collected in or with a sponge. Specimens in the present study were found completely embedded in a colony of an unidentified species of *Thrombus* (Porifera: Demospongiae: Choristida: Thrombidae; S. Pomponi, pers. comm.) at c. 56 m. *In situ*, only the apertural openings were visible from the outside. The density of individuals inside the sponge was very high, with about 54 shell apertures emerging from a surface area of 5 × 5 cm. This translated into 5400 snails per surface square metre of the sponge colony (see also Figs 42, 43). There was relatively little sponge tissue between the gastropods, explaining the intertwined and contorted condition of shells as a result of competition for space.

Geographical distribution

Widely distributed in deeper waters of the western Atlantic, ranging from Bermuda, Florida, Bahamas to Brazil (Bahia to Espírito Santo, all seamounts; Rios, 1994), the Gulf of Mexico and the Caribbean Sea.

Taxonomic remarks

Tenagodus modestus was once considered to be 'the young' of *T. squamatus* (Abbott, 1954: 145). Many collection specimens labelled '*modestus*' were found to be juvenile or strongly eroded (and thus smooth-shelled) *T. squamatus*. The latter species has fluted spines on its shell, does not have its shell slit narrowed to form a regular series of holes, and its protoconch is very different (see below).

TENAGODUS SQUAMATUS (DE BLAINVILLE, 1827)

(FIGS 3–5, 10–13, 22, 29, 30, 35, 38–40)

Siliquaria squamata de Blainville, 1827: 213. Chenu, 1842–43: 3, pl. 2, fig. 12. Mörch, 1861: 414. Paetel, 1869: 56. Dall, 1889a: 260. Dall, 1889b: 144. Nutting, 1920: pl. 40, fig. 2. Maury, 1922: 103–104. Peile, 1926: 78. Merrill & Petit, 1965: 60. Gould, 1966: 1–11, figs 1–3, 6 (photographs of protoconchs reversed). Abbott, 1968: 84, fig. 4. Rios 1970: 40, pl. 8, fig. Abbott, 1974: 96, fig. 925. Rios, 1975: 46, pl. 13, fig. 171. Emerson & Jacobson, 1976: 74, pl. 6, colour fig. 1. Abbott & Dance, 1982: 61, fig. Rios, 1985: 46, pl. 18, fig. 209. De Jong & Coomans, 1988: 40. Leal, 1989: 8, fig. 9 (SEM photomicrograph of protoconch and juvenile teleoconch). Harasewych, 1989: 48, pl. 32. Lipe & Abbott, 1991: 52, fig. on 53. Rosenberg, 1992: 52–53, fig.? Rios, 1994: 66, pl. 22, fig. 252. Díaz & Puyana, 1994: 140, pl. 44, fig. 482.

Siliquaria squammata [*sic*], Chenu, 1842–43: figure caption, pl. 2, fig. 12 (erroneously giving '*nobis*', i.e. Chenu, as authority). Chenu, 1859: 322, 309 (from Chenu, 1842–43).

Tenagoda [*sic*] *squamata*, Adams & Adams, 1853–54: 361.

Tenagodus squamata, Mörch, 1861: 414.

Tenagodus squamatus, Mörch, 1865: 99. Mörch, 1877: 110. Abbott, 1954: 145, pl. 21, fig. G. Parker & Curray, 1956: 2434. Bieler, 1990: 21. Leal, 1991: 68, pl. 6, figs I, J. Bandel & Kowalke, 1997: 263. Turgeon *et al.*, 1998: 69, 213. Pansini *et al.*, 1999: 429. Redfern, 2001: 23, pl. 12, fig. 95A, B.

Tenagodus (Pyxipoma) anguillae Mörch, 1861: 410, 412. Mörch, 1877: 110.

Tenagodus (Agathirses) squamata, Mörch, 1861: 411.

Siliquaria (Tenagodus) aquillae [*sic*] Mörch, Sowerby in Reeve, 1876: last page ('species not known').

Tenagodus ruber (Schumacher), Mörch, 1877: 109 [Bermuda and St. Thomas] [non *Anguinaria rubra* Schumacher, 1817].

Siliquaria (Agathirses) anguina (Linnaeus), Tryon, 1886 [in part]: 190, pl. 58, fig. 25 (after Chenu, 1842–43) [non *Serpula anguina* Linnaeus (1758)].

Siliquaria anguina Vr. *squamata*, Paetel, 1888: 499.

Siliquaria anguillae, Paetel, 1888: 499. Menzies *et al.*, 1966: 408 [as *S. angullae*], 414, 428. Morris, 1973: 145, pl. 41, fig. 9. Wolfe & Wolfe, 1970: 14. Porter, 1974: 15. Lipka, 1974: 148, 168, fig. 13. Warmke & Abbott, 1975: 67, pl. 12 fig. g.

Siliquaria (Tenagodus) ruber Schumacher, Heilprin, 1889: 172 [Bermuda, following Mörch].

Siliquaria ruber Schumacher, Dall, 1889a: 259.

'*Tenagodus*, or *Siliquaria ruber*' Verrill, 1905: 139 [Bermuda].

Siliquaria rubra, Peile, 1926: 78 [Bermuda, following Verrill].

Tenagodus (Agathirsus) squamatus, Haas, 1941: 171. *Siliquaria angullae* [sic] Mörch, Abbott, 1974: 96 (in synonymy). Rios, 1985: 46 (in synonymy). Rios, 1994: 66 (in synonymy).

Type material: De Blainville's original material of *Siliquaria squamata* has not been located. A lectotype for *Tenagodus anguillae* Mörch, 1861, is here designated (Anguilla, Leeward Islands; before 1848; ex coll. Hornbeck; ZMK; Fig. 5), from a lot that also contains 1 paralectotype and 1 loose operculum.

Specimens examined: See Appendix 2.

Description

Shell (teleoconch) (Figs 3–5, 10–13). Large and very loosely coiled; some specimens exceed a total length of 17 cm and inner apertural diameter of 10 mm. Juvenile shell with little sculpture except growth marks; shell later develops faint longitudinal lines becoming rows of spines. Smaller specimens with seven, larger lines with 9–12 longitudinal rows of spines (occasionally more numerous, sometimes with finer ridges interspersed, especially near shell slit); spines strongest on underside of coils, and nearly absent in what would be the umbilicus in a regularly coiled shell. Spines curved and fluted tube-like, with open side facing aperture. Later part of shell has healed breakages throughout. Earliest whorls often internally closed off by concave calcareous septa (as shown in Fig. 14 for a different species). Early part of open shell slit (corresponding to region of posterior mantle cavity) narrowed by lateral ingrowths, but not normally forming complete holes (Fig. 11); the most recent (body whorl) slit barely restricted, with near-even margins (Fig. 12). Slit of earlier whorls (now in the region of digestive gland and gonad) filled-in with shell material (Figs 10, 11). Fresh specimens with glossy shell surface; strongly eroded specimens often without spines, but with longitudinal sculpture still discernible. Shell light tan to reddish brown, darker near shell slit (older specimens usually faded to yellowish-white).

Protoconch (Fig. 22). Extremely fragile and easily decollated, rarely retained in museum specimens [in fact, Dall's (1889a: 260) original description maintained 'The most perfect spires I have seen showed no sign of a regularly spiral nucleus'. Data presented here obtained from descriptions and images in Gould (1966; note that all protoconch images in that work are reversed), and Leal (1991; pers. comm.)]. Approximately 0.26–0.29 mm high and 0.26–0.27 mm wide (based on 10 specimens studied by Gould, 1966: 6), of two and a quarter whorls. The first part represents smooth, bulging, almost planispiral embryonic shell

with circular aperture; the following whorl formed by helically coiled, broadly rounded, sculptured larval shell. Sculpture consisting of 5–8 rows of small pustules on upper part of whorl, followed below by finely granulated spiral striae (which appear as rows of fused pustules); contact between the two types of ornament at the whorl periphery relatively sharp. Aperture strongly sinuous, deeply embayed on upper whorl surface at point of contact with teleoconch slit area. Embryonic shell whitish brown, larval shell light golden brown.

Operculum (Figs 29, 30, 38). Very large (5.0–6.6 mm in diameter) in relation to body width, cylindrical, multispiral, tightly fitting inside shell tube; composed of numerous spiral layers of corneous lamellae, the earlier ones usually decollate and only 8–12 remaining attached to the animal (height of operculum then 6.8–12 mm). Edge of each layer with flat spine-like projections (Fig. 30); lamella not continuous internally: core filled with triangular compartments, about 6 per whorl, spirally arranged around a central axis (Fig. 29).

Anatomy (Figs 34, 35, 38–40; for measurements, $n = 3$).

Head-foot: Body long and slender, spirally coiled, approximately 3 whorls, 2 of which occupied by mantle cavity; overall body length (excluding operculum) 55–67 mm. Mantle cavity to 52 mm long; body width in mid-mantle region approximately 1.3 mm. Foot forming a round column bearing the very large operculum; small (3.5 × 1.5 mm), glandular, transversely furrowed area of foot (the 'sole') in front of the mouth, with tip of the sole always pointed. Head very small in comparison to width of body; snout short, bluntly rounded, with mouth a vertical slit at its tip. Two cephalic tentacles about as long as snout (1.0–1.3 mm), with black eyes on their outer bases. Mantle margin smooth, but with fine papillae in gill region (when animal retracted). Head and anterior foot region salmon-coloured to rust-red; uppermost skin layer with fine brown-black pigment (fading to light-brown when ethanol preserved), especially on snout, tentacle and metapodium. Numerous white granules embedded in head-foot tissue. No pedal tentacles or pedal mucous gland.

Pallial cavity: Corresponding to shell fissure, dorsal right side of mantle with slit, longitudinally opening mantle between rectum and pallial gonoduct; slit usually lined on outside with yellow to tan. Ctenidium extending as far as mantle slit, its filament lengths gradually decreasing posteriorly; 25–31 filaments per mm. Curved, rod-shaped gill filaments very long (6.8–7.5 mm), narrow and very flexible (details of ciliation not observed due to poor preservation); row of filaments extends across mantle cavity top right side of

animal. Osphradium restricted to anterior part of mantle cavity, beginning next to and shortly behind anteriormost gill filaments; short, 5.3–7.8 mm in total length, compressed S-shaped, with anterior leg somewhat longer, its sensory zone with weak meanders. Endostyle forming a narrow glandular tract along entire length of gill.

Alimentary system: As in *T. modestus*, anal opening of short rectum (7.9–9.6 mm in mantle cavity) likewise in posterior part of mantle cavity; weak ciliated groove leading from anus forward to mantle cavity. Radula small (Figs 34, 35), length about 1.36 mm, width 0.18 mm), taenioglossate, with 48–52 rows, transparent brown; rachidian with strong, slender triangular main cusp and 8–12 short flanking cusps on either side, smooth basal platform, no lateral or basal projections. Lateral tooth with slender, triangular main cusp and 7–12 short inner flanking cusps and about 25 outer flanking cusps. Marginal teeth hook-like, bluntly tipped; cutting edge of inner marginal tooth finely cuspidate on either side (up to 30 cusps on outer side), of outer marginal tooth smooth.

Reproductive system: Sexable animals (2) female, with developing eggs in gonad.

Habits and habitat

Tenagodus squamatus is usually found associated with the sponges *Spongosorites ruetzleri* (Soest & Stentoft, 1988) and *S. siliquaria* Soest & Stentoft (1988). In the original descriptions of *S. ruetzleri* (as ?*Halichondria*) and *S. siliquaria*, Soest & Stentoft, 1988: 92–93) noted the association of ‘vermetids’ with the former and members of the genus *Siliquaria* [= *Tenagodus*] with the latter. Shells in the present study came from depths ranging between 13 and 366 m, with live records from between 51 and 213 m. Abbott (1974: 96) and Rios (1994: 66) reported maximum depths of more than 700 m for the siliquariid.

Geographical distribution

Widely distributed in the deeper waters of the western Atlantic, from Bermuda, the Carolinas (e.g. Merrill & Petit, 1965), Florida, Bahamas, to Brazil (Amapá to Espírito Santo, all Seamounts; Rios, 1994), the Gulf of Mexico and the Caribbean Sea.

Taxonomic remarks

In teleoconch characters, *Tenagodus squamatus* is very similar to the type species of *Tenagodus*, *T. anguinus* (Linnaeus, 1758; originally described as *Serpula*) of the Indian Ocean. Tryon (1886: 190) even synonymized the two. The anatomy of the type species remains unstudied. *T. barbadensis* sp. nov. is also very

similar in teleoconch characters, but differs greatly in its larval shell morphology (see below).

Tenagodus squamatus specimens from Bermuda are frequently dark reddish brown in colour and have been called ‘*Tenagodus ruber* (Schumacher, 1817)’. Verrill (1905) thought that it was this form that gives the reddish tint to the ‘pink beaches’ of Bermuda, which in fact is caused by the abundant shells of the foraminiferan *Homotrema rubrum* (Lamarck, 1816). Schumacher (1817) gave a short description for his *Anguinaria rubra* and therein referred to ‘*Serpula anguina*’ sensu Martini (1769: 50, pl. 2, figs 13, 14), non Linnaeus, 1758. Martini’s original figures show several different forms. Mörch (1861: 403) excluded Martini’s references and restricted Schumacher’s *Tenagodus ruber* to a purple-shelled form with the type locality ‘Moluccas’, but later (Mörch 1877: 110) used the name again for material from Bermuda and St. Thomas. Mörch’s earlier (1861) decision is followed here, applying Schumacher’s *A. rubra* to an Indo-Pacific species.

The type material of *Tenagodus anguillae* Mörch, 1861, consists of two incomplete, eroded juvenile shells without protoconch (11.6 and 10.7 mm), and one damaged, incomplete operculum. The somewhat larger shell is here selected as lectotype (ZMK; Fig. 5). The specimens agree in their morphology with beach-worn juvenile *T. squamatus* and the nominal species is thus placed in its synonymy. *Siliquaria ‘anguillae’* and *S. ‘anguillae’* of authors are subsequent misspellings without nomenclatural status. North Carolina records of ‘*Siliquaria anguillae*’ are here interpreted as having been based on eroded (and thus smooth) shells of *Tenagodus squamatus*, although it is possible that *T. modestus* specimens might have been commingled.

TENAGODUS BARBADENSIS SP. NOV.

Type material: Holotype (Fig. 6): 35.8 mm overall shell length, 3.6 mm inner apertural diameter, about 7 teleoconch whorls, FMNH 301239. Paratypes (ranging in overall length 13.8–48.9 mm): 15 shells, 15 fragments (incl. SEM specimens, Figs 14, 23–25), FMNH 301290; 10 shells, HBOM 065 : 00000; 10 shells, AMNH 308079. Type locality: off Speightstown, Barbados (13°14.82’N, 59°39.82’W), 101 m; collected by suction device, submersible Johnson-Sea-Link II, dive 1732, with R/V Seward Johnson; previously embedded in unidentified sponge (not *Spongosorites*).

Description

Shell (teleoconch) (Figs 6, 14). Very loosely coiled, with most known specimens between 20 and 45 mm in total length and with inner apertural diameter of 3–

4 mm (4.6 mm in largest fragment collected). Juvenile shells with little sculpture except growth marks, but developing numerous fine spiral striae of increasing strength on subsequent whorls; after 5–6 whorls only some of these striae developing into 4–6 rows of spines, the others continuing as finer riblets interspersed between them. Spines strongest on underside of coils, and nearly absent in what would be the umbilicus in a regularly coiled shell. Spines curved and fluted tube-like, with open side facing aperture. Earliest whorls often internally closed off by concave calcareous septa (Fig. 14). Early part of open shell slit (corresponding to region of posterior mantle cavity in the living animal) narrowed by lateral ingrowths, but not forming series of regular, complete holes (Fig. 6); the most recent (body whorl) slit barely restricted, with undulating to near-even margins (Fig. 6). Slit of earlier whorls (corresponding to region of digestive gland and gonad) filled-in with shell material. Fresh specimens with glossy shell surface. Shell light tan, often blotchily darker on earlier whorls.

Protoconch (Figs 23–25; $n = 2$ for measurements). Fragile and readily decollating (only 2 retrieved), 303–337 μm high and 298–320 μm wide, most of its bulk represented by a large embryonic shell (PC-I) 228–235 μm in diameter; larval shell (PC-II) of only 1/3 whorl. Sculpture consisting of very small pustules on upper part of whorl, followed below by finely granulated spiral striae (which appear as rows of fused pustules); aperture strongly sinuous, deeply embayed on upper whorl surface at point of contact with teleoconch slit area. Embryonic shell whitish brown, larval shell light tan.

Operculum and anatomy: unknown.

Habits and habitat

Only known from single locality, as empty shells embedded *in situ* in unidentified sponge (not *Spongosorites*), from 101 m depth.

Geographical distribution

Only known from off Barbados.

Comparison

The teleoconch morphology is very similar to that of *T. squamatus*, with rows of fluted shell spines. From the limited material at hand it appears that *T. barbadensis* has more and better-defined spiral striae between the spine-bearing ribs than *T. squamatus*. Its shell slit does not show the regular pattern of restriction to well-defined holes as present in comparatively smooth-shelled *T. modestus*. It

remains to be seen whether the collected specimens of *T. barbadensis* are fully grown or whether this species also reaches much larger shell sizes. The key characters that set this new species apart are in the protoconch. Its sculpture is much finer, with less distinction of the area of pustules and the rows of striae than seen in the two other western Atlantic species (compare Figs 19, 22, 24). As in the latter, the protoconch is roughly as wide as it is tall, but it shows different allometry. The embryonic shell is much larger (in fact, it is larger than the entire protoconch of *T. modestus*), and there is a much shorter section of the larval shell (PC-II): *T. modestus* grows an entire whorl following the embryonic shell, *T. squamatus* about one-and-a-quarter, but *T. barbadensis* develops only a third of a whorl (compare Figs 20, 22, 25). Note that eroded teleoconch fragments of this species are hardly distinguishable from those of *T. squamatus* and collections might contain shells of both under the latter name.

DISCUSSION

COMPARISON OF THE TYPE GENUS *TENAGODUS* TO AVAILABLE DATA ON SILIQUARIIDAE

The molluscan nature of *Tenagodus* has been known since the first anatomical observations by Audouin (1829a,b), who mentioned the similarity with the wormsnailed genus *Vermetus* (Vermetidae). An earlier anatomical account by Montfort (1808–10) appears to have been based on an erroneous composite of an annelid worm and a fragment of a pelagic *Janthina* gastropod shell (Mörch, 1861: 401). A drawing of the gross morphology of Audouin's siliquariid was published by Chenu (1842–43, pl. 1, fig. 2). Its overall morphology with a long mantle slit, food groove, small head-foot and large operculum matches closely the one described here for *Tenagodus squamatus*. Osphradial shape or position of rectum were not described or illustrated. [Neither Audouin nor Chenu mentioned the origin of the material, but Rang (1829: 188) asserted that Dr Busseuil of the frigate *Thétys* brought the specimen from the East Indies. Mörch (1861: 402) suggested it to be *Tenagodus gigas* Lesson, 1830.]

Philippi (1836: 172) described the gross anatomy of a Mediterranean siliquariid identified as '*Siliquaria anguina* Lamarck'. However, his illustrations (1836: pl. 9, figs 24, 24c) show the relatively smooth-shelled siliquariid originally described as *Anguinaria obtusa* Schumacher, 1817. Philippi claimed the animal to be hermaphroditic, and rectum and gonoduct were said to run in parallel on the right side. Philippi's illustrations (later reprinted by Adams & Adams, 1853–54: pl. 39, figs 5–5c) show gills, food groove,

head and operculum, but offer no further anatomical detail.

It took more than 100 years for additional anatomical data to appear in print. Morton (1951) studied the anatomy of New Zealand representatives of two other nominal genera, *Stephopoma* Mörch, 1860, and *Pyxipoma* Mörch, 1861. *Stephopoma*, with imperforated shells and flat opercula beset with elaborately branching bristles, differs considerably in its anatomical features from the known slit-bearing forms. Detailed anatomical data are available on *Stephopoma roseum* (Quoy & Gaimard, 1834) (see Morton, 1951), *S. mamillatum* Morton & Keen, 1960, and *Stephopoma abrolhosense* Bieler, 1997. Except for the peculiar pustulate protoconchs and complexly bristled opercula, *Stephopoma* species are rather similar in anatomical organization to *Vermicularia* (Turrillidae) as described by Morton (1953) and Bieler & Hadfield (1990). *Pyxipoma*, based on observations on *Pyxipoma weldii* Tenison-Woods, 1875, has a shell slit with corresponding mantle slit and a dome-shaped horny operculum with a core of triangular cells that bears short spines at the edges of the spiral lamella (Morton, 1951).

In both *Stephopoma* and *Pyxipoma*, the rectum was described as ending in typical cerithioidean snail fashion, i.e. on the right side of the head, near the shell aperture. The osphradium in these groups is a simple ridge extending along the base of the gill. The recently introduced genus *Petalopoma* Schiaparelli, 2002, is based on the simultaneously named Mediterranean siliquariid *P. elisabettae*, a form with irregular shell slits and flattened opercula beset with stalked petal-like bristles. Sketchy anatomical information (from rehydrated material) indicates a relatively short mantle slit and the anus positioned near the shell opening (Schiaparelli, 2002: 250, 252).

The gross morphology of the western Atlantic *Tenagodus* species described herein is similar to Morton's (1951) description of *Pyxipoma weldii*. However, several characters separate the two groups. The cutting edges of the inner marginal radular teeth in the studied *Tenagodus* species are cuspidate (not so described for *Pyxipoma*). The osphradium of *Pyxipoma* does not have the peculiar S-shaped looping seen in *T. squamatus* and *T. modestus*. The protoconch of the *Tenagodus* species is small (roughly 200–300 µm), helicoid in shape, and readily decollating, as compared to a large (450 µm, given for embryos in the brood pouch; Morton, 1951: 36), nautiloid, and firmly attaching protoconch in *Pyxipoma*. In *P. weldii* (as well as *Stephopoma* and, apparently, *Petalopoma*), the anus is situated at the mantle edge, to the right of the neck region, not in the posterior mantle cavity as in *T. squamatus* and *T. modestus*.

Thus, in contrast to earlier published statements about Siliquariidae, members of *Tenagodus* have:

- (1) Shell septa closing off earlier whorls (see also discussion below).
- (2) Osphradium arranged in S-shaped configuration and restricted to the anterior part of the mantle cavity.
- (3) Anal opening in the posterior part of the mantle cavity.
- (4) Cuspidate inner marginal radular teeth.

Sponge–SILIQUARIID INTERACTIONS: OBSERVATIONS ON LIVING ORGANISMS

Adaptations to sessile life and sponge–snail interaction

Early observations often interpreted siliquariids as free-living organisms. The fragile nature of the isolated shell then found alternative explanations: Dall (1881: 39) believed the animal 'evidently suited only to a soft and quiet bottom'. Most published illustrations show isolated specimens (as are the shells in collections). When they were encountered inside sponges, boring behaviour analogous to shipworms in wood was assumed: A publication issued by the Hirase Conchological Museum (1915) shows a photograph of more than hundred siliquariid individuals embedded in a large piece of sponge, described as 'a swarm of *Siliquaria cumingii* which have bored into a sponge'. The – at least for the snails – obligatory relationship was only recently understood.

In their description of new species, Soest & Stentoft (1988: 92–94) introduced ?*Halichondria* (now *Spongosorites*) *ruetzleri* as 'riddled with vermetid tubes' and the aptly named *Spongosorites siliquaria* as 'riddled with vermetid gastropod tubes of the genus *Siliquaria*'. For the latter, they mentioned that the 'name reflects its symbiosis with the vermetid genus *Siliquaria*', and about its ecology stated 'apparently with an obligatory relationship with the vermetid'. Diaz, Pomponi & van Soest (1993) described the sponge masses of these two western Atlantic halichondrid species and showed photographs of the sponge holotypes, with large assemblages of siliquariids. More recently, the astrophorid species *Thrombus sphaeroidocladus* Hartman & Hubbard, 1999, was described as containing *Siliquaria* [= *Tenagodus*] *modesta*. A close species-specific association was not found by Pansini *et al.* (1999) in a review of sponge–siliquariid interactions, but it appears that only a small number of sponge families serve as host to siliquariids.

This snail–sponge commensal relationship is apparently of substantial benefit for the organisms involved. Among these are mechanical and biochemical protection for the snails, and increased water flow and food

particles from the snails' breathing and feeding activities for the sponge. Siliquariid-associated sponges of the order Lithistida are recognized for their bioactive components (e.g. Sata *et al.*, 1999; for *Siliquariaspongia*). However, the biochemical interplay between the parties remains unexplored and might provide a fruitful field of study. Sponge tissue of a snail-bearing colony can show dramatically different biochemical reactions than those without: *Spongosorites ruetzleri* is a bright yellow sponge when alive, but turns black when stored in ethanol. However, this reaction only occurs when siliquariids are embedded in the tissue, not when each is preserved alone. It is assumed that the colour change is a biochemical reaction of the sponge to the presence of these snails, and that the occurrence or patterns of distribution of secondary metabolites in the sponge might be result of, or influenced by, the association (Pomponi *et al.*, 1991: 156, Diaz *et al.*, 1993: 302; pers. observ.).

Strategies of shell growth and modification

After postlarval settlement on the host sponge, the snails not only need to be covered by the growing sponge, but also must adjust their own growth pattern to the speed and direction of the sponge growth. Space competition within the sponge, and the need to keep the shell apertures near the exposed outside of the sponge colony for breathing and feeding, will control the degree of translation of the shell aperture about the coiling axis and the occasional change of direction – resulting in irregularly uncoiled, at time intertwining, shells (see also Savazzi, 1996: 166).

In addition to varying the coiling pattern, siliquariids have evolved two other remarkable techniques of coping with sudden needs for growth modification. Sowerby & Sowerby (1826: p. 1-q) first noticed the peculiar 'cracked' appearance of the siliquariid shell: 'The *S. anguina* [a misidentified *Tenagodus obtusus*] is remarkable for numerous deep transverse furrows, which have the appearance of being caused by the contraction of the shell in drying, and which singularly resembles the contraction of the muscles of a fish being scored: we can only account for such an appearance, by supposing the parts of the shell that present it to have been deposited in a soft or gelatinous state, and afterwards to have hardened and contracted'. Instead, it turned out that siliquariids are able to *modify the hardened shell* by breaking and re-gluing – they have a unique capacity to modify adult shell shape. As shown by Savazzi (1996: 157, as *Siliquaria*), *Tenagodus* is 'unique among gastropods in that it periodically increases the width of the shell and/or the cross sectional area of the whorl by cracking the whorl periphery into wedges, pushing them outward, and subsequently reattaching them together'. This fea-

ture, particularly pronounced in the thicker-shelled, non-spiny species, allows circumferential growth of the snail's softbody, without concomitant lengthening of the shell spiral that normally would occur.

Another mechanism allows achieving the opposite – lengthening of the shell spiral without actual growth of the body inside. This is accomplished with calcareous septa that close off earlier portions of the shell. Morton (1951: 37, 1955: 11) stated that the siliquariid shell, in contrast to the vermetid shell, is never internally septate. This is not the case: *Tenagodus* species often show well-developed septa. As already stated in the subsequently overlooked text by Sowerby & Sowerby (1826; p. 1-q: 'Transverse septa are sometimes observable in the tube; of course these are always posterior to the animal, and shew that as it increases in size, it does not fill the whole length of the tube.' Septa were also described for an Eocene siliquariid, by Faujas-St.-Fond (1803: pl. 3), later named *Agarthirses furcellus* Montfort, 1808. Such transverse shell septa, closing off earlier parts of the shell, are known from disparate groups throughout the Gastropoda. They are particularly common in Recent sessile snails (Siliquariidae, Vermetidae, pers. observ.), but also occur in unrelated vagile species (e.g. Campanilidae, Houbriek, 1981: 269; Architectonicidae, Bieler, 1993: fig. 3). Their function in sessile wormsnails is readily explained: it allows rapid shell growth (to keep up with the host's growth, to overcome high sedimentation rates, or to allow for major repositioning of the shell aperture) by adding shell material to the apertural tube end, without concomitant growth of the overall softbody. It also allows abandoning early shell whorls that might be exposed to corrosion and/or other damage. The observed white crystalline lining of much of the posterior vascular system in the western Atlantic species (Figs 39, 40) might serve as a calcium carbonate reservoir allowing rapid shell deposition during such growth spurts.

Shell sculpture

The ridges and (in particular) hollow curved spines on the shells of many siliquariid species apparently serve as holdfasts for the sponge rather than offer mechanical protection as they would in most vagile gastropods. Savazzi (1996: 169) suggested a secondary function for these spines: 'as shock absorbers, by breaking under the impact of objects tossed by waves'. However, this function seems unlikely for the sponge-embedded deepwater forms of *Tenagodus*. Pansini *et al.* (1999) discovered an interesting pattern: all spiny siliquariid species studied occur in halichondriid sponge hosts, i.e. sponges that have unordered skeletal growth. Smooth-shelled siliquariids, on the other hand, occur in sponge groups with radial skeletal

growth (e.g. families Geodiidae, Coppatiidae, Ancorinidae). It thus seems clear that siliquariid shells spines are adaptive to the host's morphology.

Water flow and waste removal – opercular plunger, shell perforations, and anal position

Operculum. Philippi (1836: 172) marvelled at the 'valde mirabile' operculum of Mediterranean '*Siliquaria anguina*' (referring to the species described as *Anguinaria obtusa* Schumacher, 1817). Morton (1955: 10), based on his observations on a species identified as '*Siliquaria maoria*', was at loss to explain its function and considered 'a nonadaptive specialization – one of those extravagances of evolution which seem so often to recur among gastropods at the level of family and generic systematic characters'. The *Tenagodus* operculum is indeed a peculiar structure, a large dome-shaped plug made up of a horny spiral lamella with lateral bristles, with an internal hollow space subdivided into chambers (Figs 26–30). Its outsized proportions dwarf the comparatively small headfoot of the animal (Figs 36–38), with the operculum filling the entire diameter of the shell's aperture. Its relatively tight fit allows for a plunger-like action, pushing or 'sucking' the water column in the shell tube when it is moved.

Similar opercular shapes are known from gastropod families that are not closely related, such as Vermetidae (*Dendropoma*), Hydrobiidae (*Gocea*), and Architectonicidae (*Heliacus*, *Pseudotorinia*, *Spirolaxis*). These have different functions and different morphologies, but it is noteworthy that these groups also convergently share the feature of a partly uncoiling shell in some or all members; the cone-shaped operculum may be linked to that trait (Bieler, 1993: 18).

Shell perforation and gill

Earlier authors, including Lamarck (1818: 337), Sowerby & Sowerby (1826), and Chenu (1859: 322) suggested that the shell slit functioned in respiration as a path of water influx and/or gill protrusion. Mörch (1861: 400) called it a 'branchial slit' and indeed it follows the active length of the ctenidium. Morton (1951: 33–34) believed that the slit in siliquariids 'may reasonably be supposed to have arisen as an adaptation for the rapid expulsion of waste in a ciliary feeder dependent upon a pallial water current ... The same adaptation may also serve as a means for the rapid expulsion of water when the head and trunk are sharply retracted into the pallial cavity'. He later (Morton, 1955: 11–12) modified this hypothesis somewhat, by assuming that such functional advantage of a slit was only important to '*Agathirses* and those

siliquariids which do not deeply embed themselves in the substratum'. He concluded that any 'advantage once derived from an accessory exit from the pallial cavity would seem here to have been entirely sacrificed, especially as the slit in the shell becomes very narrow, at times almost obsolete, and is always occluded by the overgrowth of sponge tissue and spicules across it'. Gould (1966: 10), in another review of this issue, compared the siliquariid slit to that of 'archaeogastropods, including pleurotomarians, bellephontids, murchisonids, and emarginellids' where it presumably functioned as a mechanism to prevent fouling of water at the aperture. In these groups the anus is at the apical terminus of the slit and Gould concluded, based on anatomical data inferred from Morton's study on *Stephopoma* and *Pyxipoma*, that 'similar reasoning cannot be invoked to explain its adaptive significance' in siliquariids, since 'the siliquariid anus is situated, as in most gastropods, near the shell aperture'.

Thus, Morton assumed that the slit in sponge-dwelling siliquariids was a largely dysfunctional relic, and Gould came to the conclusion that solid waste deposition through the slit was not involved. Both hypotheses can be falsified. Siliquariid slits and holes are in communication with the sponge's canal system. Some sponges have been documented to show tissue reactions to the presence of polychaete, amphipod, or barnacle commensals and parasites. These include massive proliferation of microscleres, and increase of fibrogenesis, strengthening of canals, and surrounding 'invaded' oscula with spongin fibres as a response to the 'tenant' (Connes *et al.*, 1971). In the sponge-siliquariid association the morphological adaptation to the intruder is carried one step further. Both parties provide, adapt, and modify this communication through openings as the organisms grow. This is of relevance to our taxonomic interpretation of shell characters: If indeed one siliquariid species can live in different host sponges with different morphologies, this should be reflected in the shell morphology, particularly its slit development.

A series of three recent publications, based on siliquariid shells preserved *in situ* within the sponge tissue, renewed the discussion. Savazzi (1996) speculated on siliquariid-sponge interactions, based on Recent and fossil shell material, particularly specimens collected from unidentified sponges in shallow water off Cebu Island, Philippines, and identified as *Siliquaria anguina* (Linnaeus, 1758). Like Morton before him, he discussed several hypothetical scenarios of water flow direction in, and waste removal from, the mantle cavity. Like Gould (1966), he dismissed Morton's (1951) waste removal idea, and also deemed passage of solid matter from the sponge to the gastropod unlikely. Because the sponge would have already

strained the water, a hypothetical current from the sponge through the snail is seen as of little benefit to the gastropod.

Savazzi preferred the alternative explanation, that of water flowing from the mantle cavity of the gastropod into the canal system of the sponge. Here, two scenarios were envisaged: (1) the excurrent of the snail mixes with the excurrent of the sponge (the adaptive value of the slit would be in reducing or avoiding the need for the mollusc to maintain an exhalant current following the extremely long and narrow path back to the shell opening), and (2) the sponge tissues facing the shell slit contain ostia or inhalant canals (in which case the pumping action of the sponge would suck water into the mantle cavity and through the ctenidia of the snail). Savazzi concluded that scenario 2 would amount to parasitism, as the siliquariid would take advantage of the feeding activity of the host sponge and partly impair it (by feeding the host with strained water), with no corresponding advantage for the host.

Hartman & Hubbard (1999: 2–3) investigated the spatial relationships of *Tenagodus modestus* specimens embedded in sponge fragments, described as *Thrombus sphaeroidocladus* Hartman & Hubbard, 1999. As in Savazzi's (1996) study, the preserved material did not permit distinction between incurrent/excurrent flow directions.

Pansini *et al.* (1999) took the study of preserved *in situ* material to the next level, by employing X-ray photography and resin casts to explore the spatial snail–sponge relationships and to infer in- and out-currents. The authors (p. 427) come to the conclusion that 'As soon as the mollusk begins development it opens a slit along its entire length, hence commencing close interactions with the sponge. The mollusk is able to modify the shape of the longitudinal slit, adapting it to the sponge aquiferous system by transforming the slit into a series of contiguous holes that communicate with the sponge's excurrent [sic] canals. Based on the trend that there is a successively decreasing diameter of these canals, it seems evident that the siliquariid conveys self-drained water into the sponge incurrent canal system'.

The present study, as the first to actually observe behaviour and flow patterns in *Tenagodus*, can add missing pieces to the puzzle and decide between the conflicting hypotheses:

- (1) During normal breathing/gill-filtering mode, the snail keeps its operculum-bearing head-foot in an extended position that allows water to enter the shell aperture. Ciliary action creates a noticeable incurrent, which passes through the mantle cavity, over the gills, and out through the shell slit into the excurrent canal system of the sponge (pers. observ., using soluble tracer).
- (2) Rapid withdrawal of the snail (particularly when mechanically disturbed) results in a massive surge of water through the sponge. The tightly fitting operculum is pulled back in a plunger-like fashion, while the aquiferous system of the sponge acts as a vent for the retreating snail.
- (3) While the regular ciliary-induced water flow into the sponge will be rather nutrient-depleted after having passed through the snail's gills, any rapid withdrawal flushes food particles from the snail's mantle cavity into the sponge, thus potentially (if the expelled nutrients reach the sponge's choanoderm) providing benefits to the host.
- (4) Returning from deep withdrawal, the operculum plunger is slowly pushed forward, using the sponge's aquiferous system as a reservoir.
- (5) Plunger action can dislodge the snail's faecal pellets from the anus at the *posterior* end of the mantle cavity and push them through the shell slit into the larger connected openings of the sponge's canal system, providing potential extra nutrition to the sponge (in case the expelled materials eventually reach the host's choanoderm) while avoiding fouling of the anterior parts of the snail's mantle cavity.

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APPENDIX 1

TENAGODUS MODESTUS (DALL, 1881): SELECTED SPECIMENS EXAMINED

BERMUDA: 1 shell, Argus Bank 55 m, FMNH 13675; 2 shells, Challenger Bank, MCZ 228069. USA: FLORIDA (Atlantic Ocean): fragments of alcohol-preserved sponge colony with embedded and isolated specimens (Figs 41, 42; Demospongiae: Choristida: Thrombidae: *Thrombus* sp.); off Key Largo, Elbow Reef (25°07.79'N, 80°14.32'W), 56 m, 06-VI-1979, by R/V Johnson/submersible Johnson-Sea-Link-I dive 688, HBOM 065 : 00767 (sponge), HBOM 065 : 02026 (with isolated specimens, intact protoconch), HBOM 065:T0021, T0022 (photographic documentation), DMNH A00625, DMNH 181857, FMNH 296715, 296716 (with SEM samples), 296717 (histological slides); 1 shell, 0.5 miles off Lauderdale-by-the-Sea, 50–100 ft [15–30 m], DMNH 40578. FLORIDA (Gulf of Mexico): alcohol-preserved sample of thrombid (?) sponge with embedded siliquariids, about 48 nm NW of Dry Tortugas, Gulf of Mexico, Florida Shelf (25°06.91'N, 83°37.05'W), 43 m, bottom with gravel, sand, *Halimeda* algae, 16-VII-1992; R/V Johnson, 15 ft trawl, HBOM 65-002-93, FMNH 296711; 2 alcohol-preserved samples in sponge, 92 miles W of Sanibel Island Light, Lee County (26°24'N, 83°43'W), 73 m, R/V Herman Cortez Sta. M 1965, FSBC I 957, FSBC I 1196; 1 shell, due W of Tampa, 91 m, DMNH 38096; 1 shell, off Tarpon Springs, 30 m, DMNH 84284; 1 shell,

W Gulf, 60 m, DMNH 175374; 2 shells, W of Egmont Pass, 55–110 m, DMNH 105493; 3 shells from large 'sponge mass' collected with 'some fifty or sixty other specimens', 75 miles SW of Egmont Key, DMNH 105931; 2 shells, off Pensacola, 64 m, ANSP 193119. TEXAS: 8 shells, 107 miles SE of Galveston (27°54.5'N, 93°35.2'W), 18 m, MCZ 199223. BAHAMAS: 5 shells, Lucaya, Grand Bahama Island (26°29'45"N, 78°37'15"W) ANSP 372431, 373596, 411178; 2 shells, Tamarind, Grand Bahama Island (26°30'45"N, 78°36'00"W), ANSP 374748, 374585. 2 shells, off Black Rock, W side of Abaco Island, submersible Johnson-Sea-Link I, dive 1906, R/V Seward Johnson, 182 m, FMNH 296694. CUBA: several shells, off Havana, USFC R/V Albatross 1884–1885 stations 2164, 2332, 2333, 2348, 285–386 m, USNM 94177, 193557, 193563, 225007; 7 shells, off Havana, USFC R/V Blake 1877–78, 415 m, MCZ 7420; 1 shell, off Havana, USFC R/V Blake 1877–78, 823 m, MCZ 7422; 3 shells, off Bahia Honda, USFC R/V Blake 1877–78, 402 m, MCZ 7419 (paralectotypes as above); 10 shells, 4 miles from Havana, USFC R/V Blake 1877–78, 1472 m, MCZ 7417, 7418 (the latter illustrated by Agassiz, 1888; see above). PUERTO RICO: 1 shell, Ramey Air Force Base (beach), DMNH 110235. Many shells, Johnson-Smithsonian Deep Sea Expedition, station 16, 69 m (18°29'40"–31°00"N, 66°08'30"–10°15"W), USNM 430166. LEEWARD ISLANDS: VIRGIN ISLANDS: Saint Croix: 1 shell, USFC R/V Blake 1879, 929 m, MCZ 7425; 3 shells, USFC R/V Blake 1879, 210 m, MCZ 7426. ANTIGUA: many shells, Smithsonian University of Iowa Expedition 1918, station 115, 219 m, USNM 500079. 4 shells, NMFS R/V Oregon, station 5070, 91–110 m (17°06'30"N, 62°39'W), USNM 811132. WINDWARD ISLANDS: DOMINICA: many large shells, NMFS R/V Oregon station 5920, 30 miles NE of Roseau, 69 m (15°37'N, 61°22'W), USNM 811136; 2 shells, USFC R/V Blake station 177, 65 m, USNM 87243; 3 shells, USFC R/V Blake 1879, 216 m, MCZ 7427. MARTINIQUE: 3 shells, NMFS R/V Oregon station 5000, 73 m (14°53'N, 61°06'W), USNM 811130; 4 shells, USFC R/V Blake 1877–78, 311 m, MCZ 7428. ST. VINCENT: 7 shells, USFC R/V Blake 1879 station 231, 105 m, USNM 87241. THE GRENADINES: USFC R/V Blake 1879, 298 m, MCZ 7429. Grenada: 1 shell, USFC R/V Blake 1879, 402 m, MCZ 7430. BARBADOS: many shells, Smithsonian-University of Iowa Expedition 1918 various stations (e.g. 24, 44, 67, 78, 85), 64–183 m, USNM 500049, 500052, 500056, 500067, 500071, and others; several specimens in sponge, off Barbados, USFC R/V Blake 1879, 172 m, MCZ 7423; 1 shell, USFC R/V Blake 1879, 183 m, MCZ 7424; several specimens in sponge, off Barbados, R/V Blake 1879 station 278, 126 m, MCZ 259091; 1 shell, St. James, Holetown, 13°10'52"N, 59°38'30"W, ANSP 353540; 19 shells, off Speightstown, 101 m

(13°14.82'N, 59°39.82'W; 17-IV-89), submersible Johnson-Sea-Link II, dive 1732, R/V Seward Johnson, FMNH 296712, HBOM 065 : 0000; 2 shells, off Speightstown, 74 m (13°14.80'N, 59°39.50'W), submersible Johnson-Sea-Link II dive 1736, R/V Seward Johnson, (FMNH 296710. TRINIDAD: 12 shells, off Monos Island, 21 m, collected in *Thrombus* sponge, USNM 86776. VENEZUELA: 4 shells, trawled off Morrocoy, Golfo Triste, 46–55 m (10°40'–53'N, 68°00'–10'W), FMNH 296714. COLOMBIA: 7 shells, NMFS R/V Oregon station 4904, 50 miles SW of Cartagena, 146–183 m (10°00'N, 76°05'W), USNM 811129. PANAMA: 1 shell, NMFS R/V Oregon station 5737, 15 miles E of Punta San Blas (9°37'N, 79°03'W), 66 m, USNM 811135. BRAZIL: 19 shells and fragments, Martin Vaz Islands, off SE Brazil, R/V 'Marion-Dufresne' (Bouchet, Leal & Metivier 05/1987) MD55 station DC55 (20°32'S, 28°52'W), 780–795 m, ex J. Leal, DMNH 184929, FMNH 29713.

APPENDIX 2

TENAGODUS SQUAMATUS (DE BLAINVILLE, 1827):
SELECTED SPECIMENS EXAMINED

Some teleoconch fragments in collections might belong to the very similar *Tenagodus barbadensis* sp. nov.

BERMUDA: 2 shells and fragment, 2.5 miles off Castle Roads, St. David's Island, 110 m, taken alive from sponge, FMNH 296697 (Fig. 4). USA: FLORIDA (Atlantic Ocean: 6 shells, NMFS R/V Silver Bay station 3252, 50 miles SE of Melbourne, 37 m (27°50'30"N, 80°07'W), USNM 811144; 1 shell, off Palm Beach, 30–40 fms [55–73 m], ANSP 188796; 9 fragments, R/V Eolis station 76, off Fowey Light, 73 m, USNM 435006, 435007; 1 shell, NMFS R/V Silver Bay station 2445, Florida Straits, 100 miles S of Miami, 252 m (24°08'N, 80°08'W), USNM 811141; SE of Dry Tortugas, 91–213 m, FMNH 194581. FLORIDA (Gulf of Mexico: 1 cluster embedded in (?thrombid) sponge, loose shell fragments, c. 48 nautical miles NW of Dry Tortugas, 73 m (25°06.91'N, 83°37.05'W), HBOM 065 : 0000; 5 shells, same station, FMNH 301289; 2 clusters embedded in sponge, R/V Hernan Cortes Sta. M1965, 92 miles W of Sanibel Island Light, Lee County, 73 m (26°24'N, 83°43'W), FSBC I957, I1196; 1 shell, 70 miles SW of Egmont Key, 51–58 m, from sponge mass, USNM 606956; 11 shells (with black sponge remains), 95 miles W of Egmont Key, 27°34'N, 84°15'W, 73 m, ANSP 396091; 1 shell (with operculum), Egmont Key, Tampa Bay, MCZ 207246; 1 shell, W of Sanibel Island/Naples area, Bureau of Land Management no. 210, 77 m (26°16.1'N, 83°46.3'W, FMNH 296698. LOUISIANA: 1 shell, NMFS R/V Silver Bay station 331, 125 miles SE New Orleans, 91 m (29°15'N, 88°19'W), USNM

801714 [alc.]; 3 shells, NMFS R/V Oregon station 4597, 175 miles SW of New Orleans, 13 m (29°28'N, 093°30'W), USNM 801713 [alc.]; 2 shells, approx. 140 miles SSE of Calcasieu Lake, 137 m, MCZ 260307. MEXICO: 1 shell, 1 fragment, Tuxpam, Veracruz, MCZ 194995. BAHAMAS: 8 specimens in fist-sized part of yellow sponge colony (*Spongosorites* sp.), Goulding Cay, off New Province Island (24°59.74'N, 77°33.17'W, 6-XI-90, S. Pomponi & P. Santos), 182 m, rock slope, 13.2°C bottom temperature, submersible Johnson-Sea-Link-I, dive 2840, R/V Seward Johnson, FMNH 296700 (observed and sketched alive; Figs 39, 40), HBOM 065 : 0000, with histological sections and radulae, FMNH 296701, and isolated shells, FMNH 296702; 7 alcohol-preserved specimens (5 of which incomplete) previously embedded in colony of halichondriid sponge *Spongosorites ruetzleri* (Soest & Stentoft, 1988), 3 km off Sweetings Cay, Grand Bahama Island (26°34.15'N, 77°54.17'W; 14-XI-87), 165 m, 30 degree slope, sand and rubble substrate, 18°C bottom temperature, submersible Johnson-Sea-Link-II dive 1530, R/V Seaward Johnson (see also Pomponi *et al.*, 1991: 151), FMNH 296703, with histological sections FMNH 296704; shell and animal fragments, from colony of halichondriid sponge *Spongosorites ruetzleri*, off Sweetings Cay, Grand Bahama Island (26°33.70'N, 77°53.91'W; 13-XI-87 157 m, slope, sand and rubble substrate, 18°C bottom temperature, submersible Johnson-Sea-Link-II, dive 1528, R/V Seaward Johnson, FMNH 296705 (sponge sample HBOM 003 : 00115, see also Pomponi *et al.*, 1991: 151); fragments (used for SEM), off Nassau Harbour (25°06.47'N, 77°20.67'W), 461 m, 15-III-1987, R/V Johnson/submersible Johnson-Sea-Link-I dive 1960, collected with halichondriid sponge *Spongosorites ruetzleri* (Soest & Stentoft, 1988), FMNH 296709 [sponge sample, HBOM 003 : 00112; see also Pomponi *et al.*, 1991: 151]; shell and animal fragments (used for SEM), off Freeport Harbour, Freeport, Grand Bahama Island (26°30.78'N, 78°48.22'W), 218 m, 22-III-1987, R/V Johnson/submersible Johnson-Sea-Link-I dive 1975, collected with halichondriid sponge *Spongosorites ruetzleri* (van Soest & Stentoft, 1988), FMNH 296708 [sponge sample, HBOM 003 : 00114; see also Pomponi *et al.*, 1991: 151]; 1 shell, off St. James, ZMK; 1 shell, NMFS R/V Silver Bay station 3494, S of Long Island, 183–366 m (23°36'N, 75°25'W), USNM 811147; 2 shells, Conception Island (23°52'N, 75°09'W), ANSP 392187. 60+ shells, Lucaya, Grand Bahama Island (26°29'45'N, 78°37'15'W), ANSP 367834, 367835, 411176, 411177; 11 shells, Indian Key, Grand Bahama Island (26°42'45'N, 78°39'15'W), ANSP 367026; 40+ shells, Grand Bahama Island (26°31'00'N, 78°46'30.5'W), ANSP 373886; 5 juvenile shells and fragments, Salt Cay, 6 mi NE of Nassau, New Providence Island, FMNH 280710. CUBA: several shells, USFC R/V Albatross 1885 stations 2321, 2323, 2326, 2332, off Havana, 210–355 m, USNM 94052, 181258, 193558, 193562; also MCZ 7416, 7421; 2 shell clusters in sponge, Harvard-Havana Expedition 'Atlantis' 1939 sta. 3303 (23°05'N, 82°33'W), MCZ 302516. JAMAICA: 1 shell, NMFS R/V Oregon station 3559, 250 miles SW of Kingston, 16°37'N, 80°15'W), USNM 811120. DOMINICAN REPUBLIC: 4 shells, NMFS R/V Silver Bay station 5147, 51–55 m (19°57'N, 71°52'30'W), USNM 811148. PUERTO RICO: 14 fragments, partly with sponge, near Mayaguez, CAS 47265; 2 fragments, Rincon, CAS 42398; 1 shell, ZMK. LEEWARD ISLANDS: VIRGIN ISLANDS: Saint Vincent: 3 incomplete alcohol-preserved specimens from sponge *Spongosorites* sp., York Bay, St. Vincent (13°09.65'N, 61°16.52'W; 31-III-89), 89 m, sand slope, Johnson-Sea-Link-II dive 1702, R/V Seward Johnson, FMNH 296692 and shell fragments FMNH 296699, HBOM 065 : 0000. SAINT CROIX: 1 shell, USFC R/V Blake 1879, 69 m, MCZ 7413; 1 shell, NMFS R/V Oregon station 6715, 100 miles E of SAINT THOMAS, 201–238 m (18°36'N, 63°27'W), USNM 811139. Tortola: 1 shell, ZMK. SAINT BARTHÉLEMY: 4 shells, ZMK. ANGUILLA: type material of *T. anguillae*, as above. WINDWARD ISLANDS: MARTINIQUE: USFC R/V Blake 1879, 176 m, MCZ 7414. ST. LUCIA: R/V Oregon II station 24273, 69–80 m (14°04.4'N, 61°02.3'W), HBOM 65: 1761; NMFS R/V Oregon station 5059, 24–29 m (14°02'30'N, 61°01'W), USNM 811131. BARBADOS: 1 shell, off Speightstown, 74 m (13°14.80'N, 59°39.50'W), submersible Johnson-Sea-Link-II, dive 1736, R/V Seward Johnson (FMNH 296690); many shells, Smithsonian – University of Iowa Expedition 1918 various stations (e.g. 3, 51, 79), 46–146 m, USNM 500017, 500018, 500021, and many others; 5 shells, USFC R/V Blake 1879 station 278, 126 m, MCZ 259090; 1 shell, Hassler Expedition 183 m, MCZ 258952; 1 shells, off St. James, ZMK. TRINIDAD: 1 shell, Chaguaramas Bay, USNM 518474. NICARAGUA: 1 shell, NMFS R/V Oregon station 4832, 150 miles E of coast, 219–238 m, USNM ex 811126; many shells, NMFS R/V Oregon, 219–238 m (14°15'30'N, 80°27'06'W), USNM 811127. HONDURAS: 1 shell, Swan Islands, MCZ 302513. VENEZUELA: Preserved specimens in sponge and 2 shells, Golfo Triste, off Morrocoy (10°40–53'N, 68°00–10'W), 46–55 m, FMNH 296706; specimens in 3 sponge fragments (2 alcohol preserved), Golfo Triste as above, about 60 m, 1992, FMNH 296691; 4 sponge fragments with embedded snails, Golfo Triste, off Morrocoy, about 60 m, 1992 (10°40–53'N, 68°00–10'W), FMNH 296691 (dry), FMNH 296693 (alcohol preserved). BRAZIL: 2 shells, NMFS R/V Oregon station 4227, 100 miles N of Sao Luis, 73 m (1°24'S, 43°11'W), USNM 811125; R/V Marion-Dufresne

(Bouchet, Leal & Metivier 05/1987; dredge DC81), off Espírito Santo State (19°00'S, 37°48'W), 120–135 m depth [J. Leal, photographs seen only; one photograph published by Leal (1989: 8, fig. 9)]; 6 shells and

fragments, R/V 'Marion-Dufresne' (Bouchet, Leal & Metivier 05/1987) MD55 station DC82, 85–105 m (18°56'S, 37°52'W), ex J. Leal, FMNH 296707, DMNH 228024.