Two New Tropical Western Atlantic Species of *Epitonium*, with Notes on Similar Global Species and Natural History

Robert Robertson
Department of Malacology
The Academy of Natural Sciences
1900 Benjamin Franklin Parkway
Philadelphia, PA 19103-1195, U.S.A.

ABSTRACT

Two large (up to 16.9 and 25.3 mm long), many-ribbed, shallow water species of *Epitonium* are newly described: *E. phymanthi* from southeast Florida, the Bahamas, and the West Indies, and *E. worsfoldi* from the Bahamas and the West Indies. Where possible, rib counts were made on each shell whorl to allow for ontogenetic changes. *Epitonium phymanthi* lives with and feeds on the sea anemone *Phymanthus crucifer* in Florida (where *E. lamellosum* and another epitoniid *Opalia crenata* also live with this anemone). Likewise, *E. worsfoldi* lives with and feeds on a sand-dwelling anemone that is either *Actinoporus elegans* or *Homostichanthus duerdeni* in the Bahamas. There it is more commonly parasitic on another anemone, *Stichodactyla helianthus*. Aquarium observations on *E. phymanthi* with *E. lamellosum* revealed some major biological differences between these co-occurring species, e.g. fully everted proboscis lengths and speed of movement. *Epitonium phymanthi* was found with *E. worsfoldi* at only one locality, as shells in the Virgin Islands.

Key words: Epitoniidae, new species, Western Atlantic.

INTRODUCTION

The family Epitoniidae contains a large number of described fossil and living species, and as with most groups of mollusks there is as yet no world monograph. In the interim, it could be argued that there should be a moratorium on describing any new epitoniids. The literature is very scattered and unsynthesized. There is not even a published list of names. Nevertheless, it is here believed that minimum requirements are met for describing two new species, albeit without anatomy.

This paper is a by-product of work on a book on the marine prosobranchs of the Bahamas being prepared by myself, Jack N. Worsfold, and Colin Redfern. New species are not being described therein.

The conchological systematics of Recent Epitoniidae (wentletraps) in the western Atlantic and eastern Pacific (where cognate forms, subspecies or species can be expected) are relatively well known thanks to Clench and Turner (1950b, 1951, 1952, 1953) and DuShane (1974, 1979). Little systematic work has since been done on the western Atlantic species. Even so, it was surprising to conclude that two large, many-ribbed, shallow-water *Epitonium* species had remained undescribed until now. One ranges from southeastern Florida and the Bahamas to the Lesser Antilles (Grenada). The other ranges from the Bahamas to Cuba, Puerto Rico and the Virgin Islands. Both may well have more extended ranges. As recently as 1967, one of the species was first collected alive; it was in less than 1 m of water within sight of a major marine laboratory!

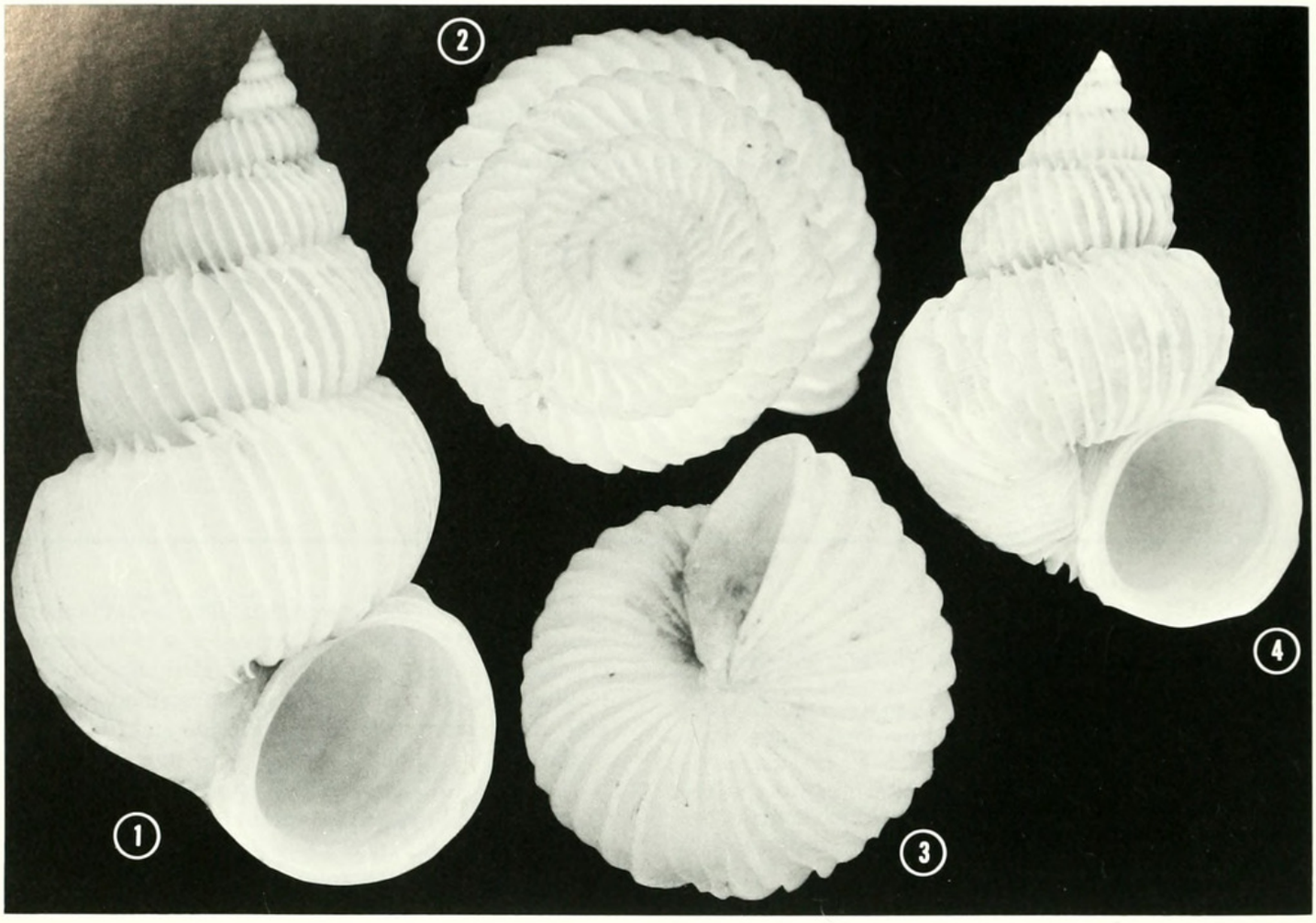
Clench and Turner had neither of these species available in the collections they studied [although a small, badly broken shell of one of them was mixed in a vial with one *E. albidum* (Orbigny, 1842) (MCZ 107820).

Some epitoniid species seem possibly or probably to be circumglobal (Robertson and Habe, 1965; Kilburn, 1972, 1985; DuShane, 1983; Paschall, 1987). Therefore, an attempt has been made to consider the two new species in a global context. Based on epitoniid collections at MCZ, AMNH, ANSP and USNM and literature, shells of 23 species from around the world (Appendix) were assessed to be most similar to the shells described here.

I have tried to survey all the descriptions and illustrations of Miocene to Recent species of *Epitonium*, *sensu lato*, known from the Americas, and of most Recent species from here and the rest of the world, especially Europe and the Mediterranean. These are the fossils and living animals most likely to be similar or identical to the shells discussed here. European fossil epitoniids were not surveyed because the literature is so extensive. Among the most important references consulted on *Epitonium*, *sensu lato* are:

1) world Recent species: Kiener (1838–1839); Sowerby (1844); Nyst (1871); Sowerby *in* Reeve (1873–1874); Tryon (1887); Clessin (1896–1897); de Boury (1912–1913); Kaicher (1980, 1981, 1983, the only really global contribution in this century, albeit incomplete).

2) American Recent species: Mörch (1875a, 1875b, 1876); Dall (1889); Clench and Turner (1950a–1953); Nowell-



Figures 1–4. *Epitonium phymanthi* Robertson, new species. **1.** Apertural, **2.** apical, and **3.** basal views of holotype. Shell 16.9 mm long, and 9.3 mm wide. Miami, Florida. ANSP 391939. **4.** Unusually low-spired shell (not a paratype), 12.0 mm long, and 8.6 mm wide.

Usticke (1959); Keen (1971); Abbott (1974); DuShane (1974, 1979, and references therein); Gundaker (1975); de Jong and Coomans (1988); Espinosa and Fernandez Garcés (1990).

3) American late Cenozoic fossil species: Olsson (1916); Maury (1910, 1917); Gardner and Aldrich (1919); Pilsbry (1922); Woodring (1928, 1959); Mansfield (1930, 1935); Pilsbry and Olsson (1941); Gardner (1947, 1948); Olsson and Harbison (1953); Weisbord (1962); Jung (1969).

4) European Recent species: Parenzan (1970); Franchini (1975–1976); Nordsieck (1982); Bouchet and Warén (1986); Poppe and Goto (1971).

5) Indo-Pacific, Japanese, Australasian and South African Recent species: Adams (1861); Melvill and Standen (1903); Jousseaume (1911); Iredale (1936); Kerslake (1958); Azuma (1962); Macpherson and Gabriel (1962); Kuroda, Habe and Oyama (1971); Masahito and Habe (1973–1976); Powell (1979); Kilburn (1985); DuShane (1988, 1990); Nakayama (1991).

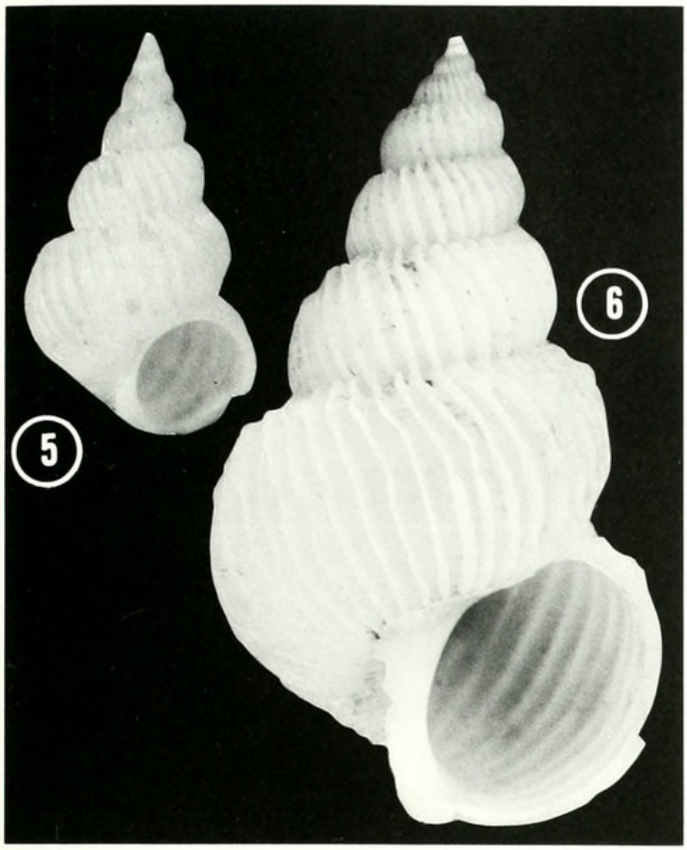
An attempt was made to count the ribs on each whorl of each shell. The need for doing so was explained in a previous paper (Robertson, 1983a). Counts on juveniles can be different from those on adults. Indeed, a rib count per whorl in species of *Epitonium* may increase, stay the same, decrease, or decrease and then increase as the shell grows in a species-specific manner. These taxonomic characters have hardly been used before.

The major study by Clench and Turner (1950b–1953) was published before epitoniids were found to live with or to forage for and feed on benthic coelenterates, either as parasites or predators (Thorson, 1957; Robertson, 1963, 1981, 1983b; DuShane, 1988; Yamashiro, 1990; Nakayama, 1991, etc.). Both species treated here have actinian (sea anemone) hosts.

MATERIALS AND METHODS

The specimens studied were assembled during almost two and a half decades. The two shallow-water species are curiously uncommon, and I personally saw neither of them alive. Only empty shells are available of *E. phymanthi*, but there are a few *E. worsfoldi* in alcohol (see ANSP "A" numbers in locality records).

Shells were studied with the aid of a Wild dissecting



Figures 5–6. *Epitonium phymanthi*. Incompletely grown paratype shells. **5.** Only shell known from Bahamas, juvenile, 5.6 mm long, 3.1 mm wide. **6.** Subadult topotype, 10.8 mm long, 6.3 mm wide.

microscope and camera lucida. First-whorl diameters were measured and whorls counted as advocated by Robertson (1985). The camera lucida and a protractor were used to measure spire angles to the nearest 5°. Specimen numbers in the Specimens Examined sections relate to Tables 1 and 2.

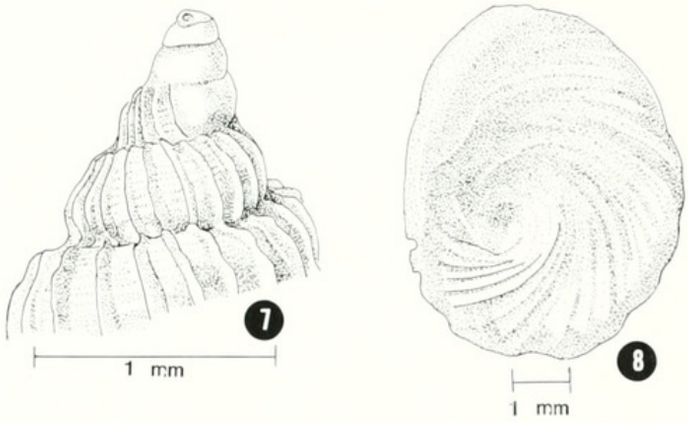
Rib counts were made on decollated shells by measuring the mean width of each whorl on intact shells and then extrapolating. As landmarks, some ribs were lightly marked with a pencil.

Repositories of examined specimens are indicated by the following acronyms:

AMNH—American Museum of Natural History, New York City
ANSP—The Academy of Natural Sciences of Philadelphia
MCZ—Museum of Comparative Zoology, Harvard University
USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS AND NATURAL HISTORY

Superfamily Epitonioidea
Family Epitoniidae
Genus *Epitonium* Röding, 1798



Figures 7–8. *Epitonium phymanthi*. **7.** Shell apex, showing a slightly decollated protoconch apex, the almost smooth protoconch, the protoconch varix (shown as a line), some of the early teleoconch axial ribs, and fine intervening spiral threads. Topotype. **8.** Operculum (exterior). Topotype.

Epitonium phymanthi Robertson, new species
(figures 1–11, 13)

?*Epitonium* spec.: de Jong & Coomans, 1988:54, fig. 276.Curaçao.

Shell morphology: Protoconch 0.42–0.50 mm long (excluding immersed base), 0.39–0.42 mm wide, with 3.2–3.4 whorls; first whorl diameter 0.09–0.13 mm; whorls slightly inflated, appearing smooth, shiny, microsculpture probably present; terminated with varix; cream-white, tinged with amber at suture, terminal varix, and columella (seen in transparency); some protoconchs slightly tilted on teleoconchs. Entire shell reaching 16.9

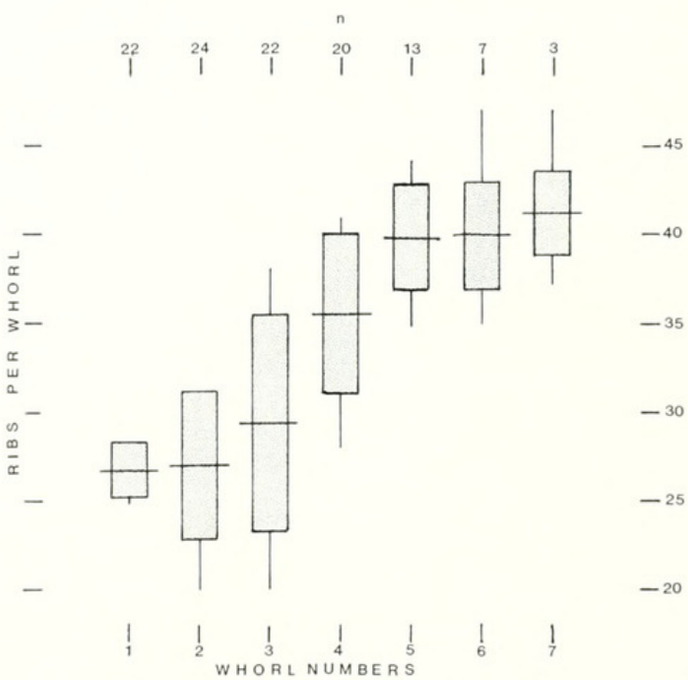


Figure 9. *Epitonium phymanthi*. Rib frequencies per whorl on each whorl. The horizontal lines show means, the vertical stippled boxes show ± one standard deviation, and the vertical lines show ranges; n = sample sizes.

Table 1. *Epitonium phymanthi* new species. Mensural and meristic shell characters. "+" indicates that a shell would have been larger had it not been slightly broken, or "++" badly broken. Specimen 21 is the holotype. All remaining specimens are paratypes except specimen 28, which was not included in figure 9 because of the high rib counts.

Specimen no.	Length (mm)	Width (mm)	Spire angle	Teleoconch whorls	Axial ribs per whorl						
					1	2	3	4	5	6	7
1	2.2+	1.5+	60°	2.5+	25	29	—	—	—	—	—
2	3.1+	2.0+	55°	3.4+	23	24	—	—	—	—	—
3	3.0+	1.6+	45°	3.2+	21	23	22	—	—	—	—
4	2.3	1.5+	55°	2.8	27	26	—	—	—	—	—
5	3.5	2.2	50°	3.8	23	24	28	—	—	—	—
6	4.2+	2.7+	50°	4.3+	25	24	23	25	—	—	—
7	4.8	3.1	55°	4.4	28	29	29	29	—	—	—
8	5.5+	3.7+	60°	4.7	27	30	29	33	—	—	—
9	5.3+	3.3	55°	4.8	25	28	30	35	—	—	—
10	7.8	4.7	50°	5.6	27	29	28	36	45	—	—
11	7.8	4.6	50°	5.7	24	25	27	28	39	—	—
12	6.7	4.0+	50°	5.3	24	30	27	31	38	—	—
13	5.0+	2.3+	55°	3.7+	24	27	26	—	—	—	—
14	8.7+	4.4+	55°	5.3+	24	—	28	37	44	—	—
15	12.2+	3.9+	50°	5.2+	—	26	25	29	—	—	—
16	8.6+	5.2+	50°	5.8+	—	23	26	36	42	—	—
17	9.5+	5.2+	50°	6.3+	24	24	21	26	32	42	—
18	11.2+	6.7+	50°	6.4+	27	28	29	30	35	45	—
19	10.3+	5.8+	45°	6.2	22	24	24	26	31	39	—
20	11.4	8.1	60°	6.2	23	21	23	26	33	34	—
21	16.9	9.3	55°	7.2	21	22	21	24	33	35	38
22	16.6	9.6	65°	7.7	23	24	22	23	26	34	40
23	15.3+	8.8	55°	6.2	—	21	25	26	40	36	—
24	5.6	3.1	45°	5.1	22	25	24	24	27	—	—
25	9.1+	5.6	50°	5.7+	—	21	25	28	—	—	—
26	16.9	9.5	50°	7.8	18	18	27	30	39	37	37
27	6.0++	4.5	—	2.6++	—	—	—	34	—	—	—
28	8.6++	4.6++	—	2.8++	—	—	39	45	—	—	—
29	5.9++	4.1++	—	1.6++	—	—	—	—	—	—	—

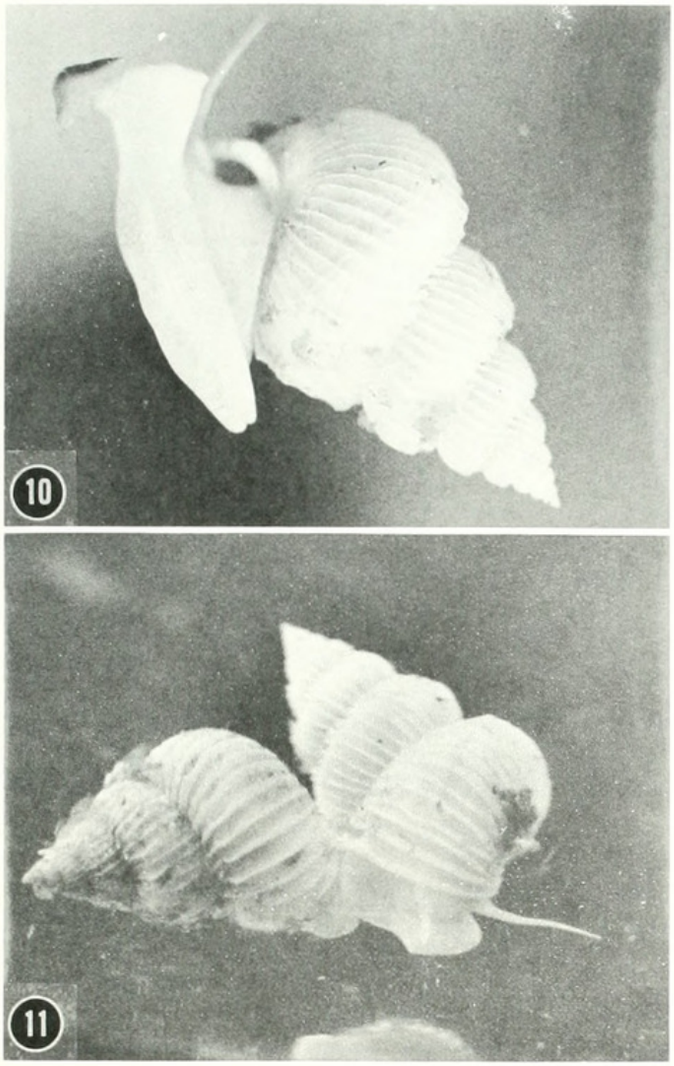
mm (Table 1). Teleoconch to 9.6 mm wide (including ribs), with 7.8 whorls, initially thick, becoming relatively thin, fragile with increasing shell size. Spire height variable, usually low, spire angle 45°–65° (mean 53°; Table 1). Spire profile at first straight, convex on later whorls of large shells. Whorls moderately to strongly inflated. Axial ribs 18–45 per whorl, number increasing with shell size (figure 9; table 1); ribs thick, low, with edges rounded on upper whorls, thinner, higher, wavy or crested at shoulder on later whorls. Apical whorls fully attached to preceding whorls, lower whorls slightly detached. Axial ribs aligned, attached erectly from one whorl to the next on upper whorls, rib alignment and attachment decreasing with increasing shell size; ribs on later whorls rarely in closely spaced pairs or bifurcating; ribs commonly curled away from aperture. Fine, regularly spaced spiral threads between ribs on early whorls (about 12 above suture), later whorls with irregular threads, smooth or with fine incised spiral lines. Basal spiral cord lacking. Umbilicus narrow, or reduced to chink. Aperture obliquely to roundly oval. Teleoconch color cream-white or pure white. Operculum not available.

Comparative remarks: This new species differs from *E. worsfoldi* Robertson (see below) in that the latter species has a thicker more highly spired shell, with coarser, uncrested, less numerous ribs (especially on the last whorl of large shells). *Epitonium phymanthi* most closely resembles species assigned to de Boury's (1912) "subgenus" *Foliaceiscala* (Appendix). The most closely similar species seem to be *E. irregulare* (Sowerby, 1844) from the Philippines and Japan, and *E. virgo* (Masahito and Habe, 1976) from Japan (Appendix).

Etymology: Of *Phymanthus*, the genus of sea anemone host.

Geographic range: SE Florida, the Bahamas, Virgin Islands and Grenada (Lesser Antilles). Not known from Bermuda or the Greater Antilles.

Material examined: (Table 1): SE Florida: Bear Cut, Miami (25°43′N, 80°09′ W), 1 m, N. and E. Leeman leg., 1965, Holotype—ANSP 391939, ANSP 391940 & ANSP 391941, specimens 19–23, Leeman collection 1 specimen. Bahamas: Dead Man's Reef beach, western Grand Bahama (26°34′45″N, 78°51′45″W), S. Bowers leg., Feb. 1981, via J.N. Worsfold, ANSP 374362, specimen 24. Virgin Islands: Lindbergh Bay, St. Thomas (18°20′N, 64°58′W), 2 m, M.R. Hyett leg., Oct. 30, 1968, ANSP,



Figures 10–11. *Epitonium phymanthi* living in aquarium. Topotypes.

specimen 26. Hams Bay, St. Croix (17°47′N, 64°53′W), G. Nowell-Usticke leg., Feb.-March 1957, AMNH 194365 (Specimens 1–18, 27–29)[co-occurred with 1 *E. worsfoldi*]. Lesser Antilles: Saint George's Lagoon, Grenada (12°03′N, 61°45′W), G. Nowell-Usticke Colln., AMNH 194429, Specimen 25. Specimen 21 is the holotype. All remaining specimens except unnumbered specimen in the Leeman collection and specimen 28 are paratypes.

A total of 29 specimens of *E. phymanthi* was available for this study. As with *E. worsfoldi*, many of the shells are broken.

Natural history: In 1965, Neal and Eleanor Leeman collected six living animals of *E. phymanthi* slightly below low tide line at a rocky area in Bear Cut, between Virginia Key and Key Biscayne, Miami, Florida, U.S.A. All were associated with the actiniarian sea anemone *Phymanthus crucifer* (Lesueur, 1817). The anemones were clinging to rock substrata, commonly in crevices, and turtle grass (*Thalassia testudinum* Banks and Solander ex König) rhizomes, most of which were buried in sand. The epitoniums were buried next to the *Phymanthus*

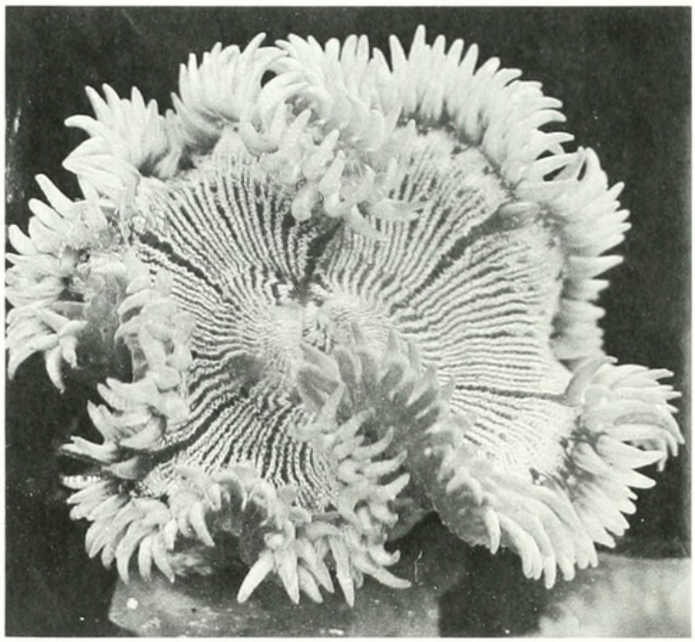
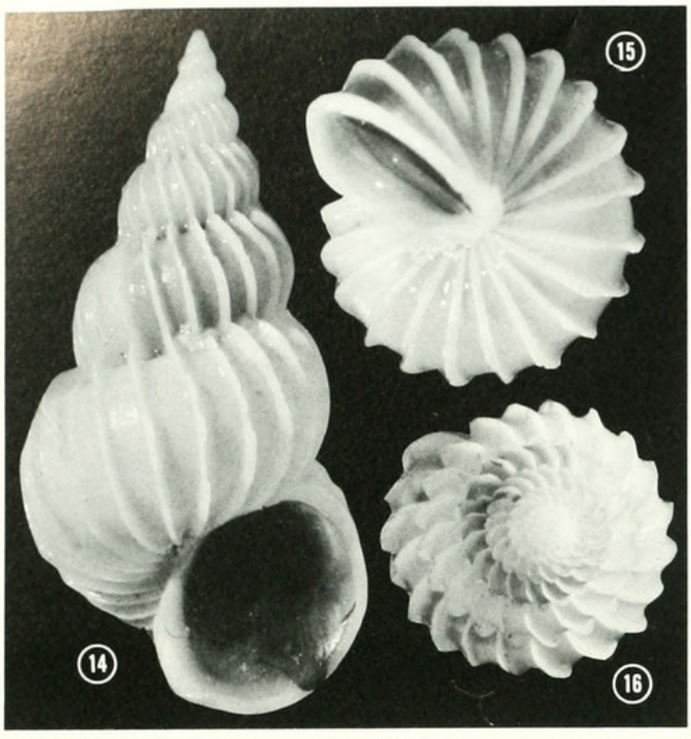


Figure 12. *Phymanthus crucifer*, the sea anemone host of *Epitonium phymanthi* at Miami, Florida. Size not recorded, but somewhat less than life size. The anemone colors and patterns vary considerably. Photo Neal Leeman.

columns under their radially extended oral discs. Only anemones buried in sand had *E. phymanthi* with them. A few clusters of sand-agglutinated *Epitonium* egg capsules were observed but not studied.

On April 17, 1965, a pair of *E. phymanthi* was found with one *Phymanthus*. On May 12, May 30, June 6, and August 8 of the same year, single *E. phymanthi* were found with *Phymanthus*. Unlike a predatory *Epitonium*, which swallows its coelenterate prey whole, *E. phymanthi* is a parasite, feeding on its large host polyp without killing it. When fully extended, a large specimen of *Phy-*

Figure 13. *Epitonium phymanthi* feeding on the upper column of its slightly contracted sea anemone host *Phymanthus crucifer*. Note the extraordinarily long everted acrembolic proboscis. Miami, Florida. Epitoniums, unlike pyramidellids, take tissues for food rather than fluids. Drawing based on photographs by Neal Leeman.



Figures 14–16. *Epitonium worsfoldi* Robertson, new species. **14.** Apertural, **15.** basal, and **16.** apical (at lower magnification) views of the holotype, 18.7 mm long, 9.1 mm wide. Smith's Point, Grand Bahama Island. ANSP A17192.

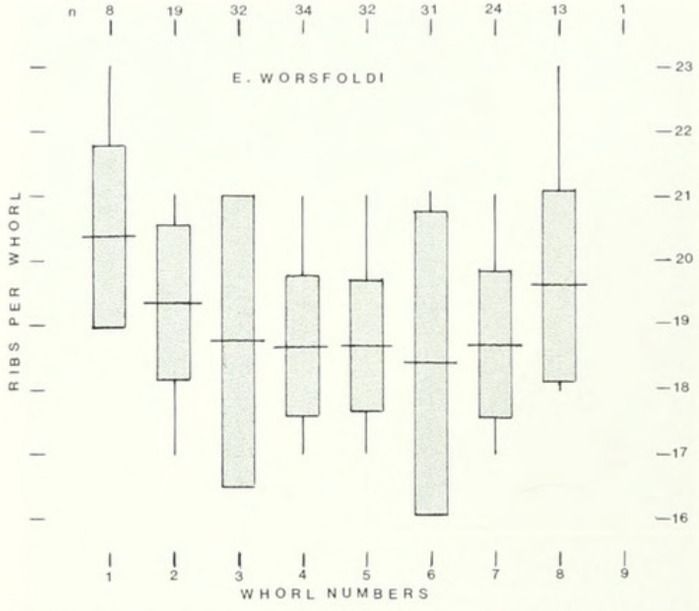


Figure 17. *Epitonium worsfoldi*, new species. Rib frequencies per whorl on each whorl. The horizontal lines show means, the vertical stippled boxes show ± one standard deviation and the vertical lines show ranges; n = sample sizes.

manthus crucifer is about 13 cm high and about 13 cm wide, much larger than the wentletrap.

Epitoniums can vary their host preferences from place to place. During the same year and months, at the same locality, and associated with the same species of sea anemone, the Leemans collected six living *Epitonium lamellosum* (Lamarck, 1822)(ANSP 391948, A16850) and one living *Opalia crenata* (Linnaeus, 1758)(ANSP A16851). Thus *Phymanthus crucifer* supports three parasitic epitoniid species at one locality. *E. phymanthi* may or may not be specific to *Phymanthus* elsewhere.

Colors and color patterns of *P. crucifer* vary considerably. Usually, these anemones are variegated with shades of green or brown. The white shell and body of *E. phymanthi*, and the white and reddish brown shell and nearly white body of *E. lamellosum*, make neither species cryptically colored with its host. At least during the day, both species are buried in sand next to the anemone.

The Leemans maintained *E. phymanthi* and *E. lamellosum* with *Phymanthus crucifer* in home aquaria from mid-April to mid-October, 1965 (two *E. lamellosum* for as long as three months). Their observations are abstracted below.

The external body coloration of *E. phymanthi* was white, that of *E. lamellosum* was white except for light yellowish tentacles that faded to white in aquaria. The fully everted proboscis of *E. phymanthi* was at least four times the shell length, while the fully extended proboscis of *E. lamellosum* was only slightly longer than the shell. Both species behaved as if they locate their host by chemotropism, using their tentacles and slightly everted proboscises as do two Californian species (Smith, 1977; Salo, 1977).

Both *E. phymanthi* and *E. lamellosum* were seen to feed on *Phymanthus* columns near the base and under the oral disc, ingesting column tissues (with fluid? mucus?). Anemone tentacles were not observed to be attacked by either species. Duration of feeding in *E. phymanthi* was 2–10 minutes (animals not starved; mean of 5 observations ca. 4 min.). *Epitonium lamellosum* (a larger species, up to 45 mm shell length) starved for 3–5 days fed for 45–97 minutes (mean of 4 observations: 64 min.). No purple secretion was seen to be released from the pigmented mantle organ by either species during feeding. One *Phymanthus* survived repeated attacks by the two species for upwards of one month. The anemone writhed near where it was attacked, and the column also swelled. The anemone reacted least to *E. phymanthi*, the smaller, slower species.

An *E. phymanthi* with a shell 7 mm long on August 11 grew to 11 mm by September 22, a mean rate of 0.11 mm/day. Growth initially was faster (between August 11 and 21: 0.2 mm/day), but there was no growth between September 22 and October 5. Another *E. phymanthi* fed and survived from August 11 to September 2 without growing (22 days). Growth of *E. lamellosum* was rather faster and also erratic, but growth appeared to be indeterminate (Leeman and Robertson unpublished).

Epitonium phymanthi was observed to move very slowly and remain motionless for long periods of time. *Epitonium lamellosum* was more active. On several occasions, *E. phymanthi* was observed following *E. lamellosum* mucous trails, and partially everting and inverting its proboscis, each time ending by touching an

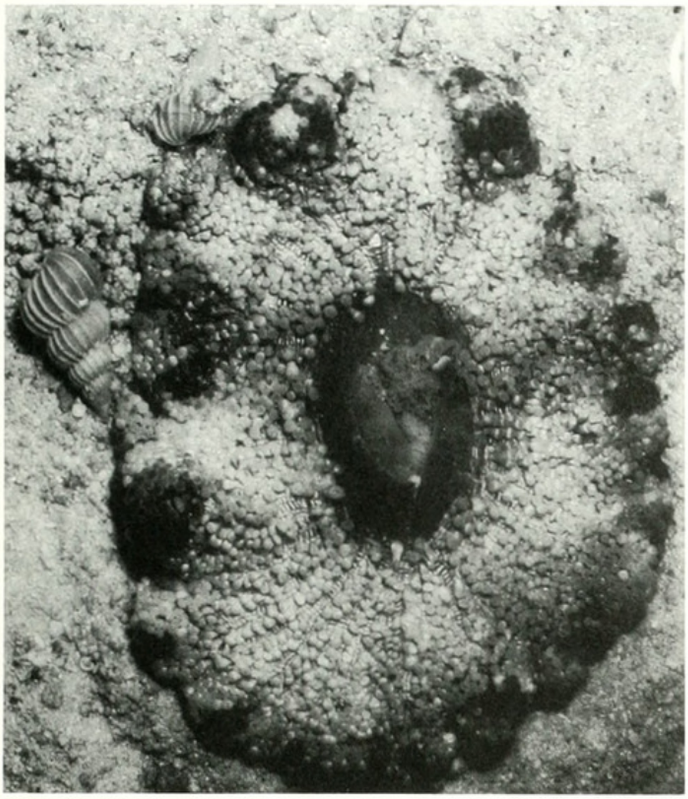


Figure 18. Oral view of either *Actinoporus elegans* or *Homostichanthus duerdeni*, a sand-dwelling sea anemone, showing beside it the holotype and egg capsules of *Epitonium worsfoldi* found with it. A paratype shell also shows. The anemone is 7.5 cm in greatest diameter. Smith's Point, Grand Bahama, Bahamas. Photo Jack N. Worsfold.

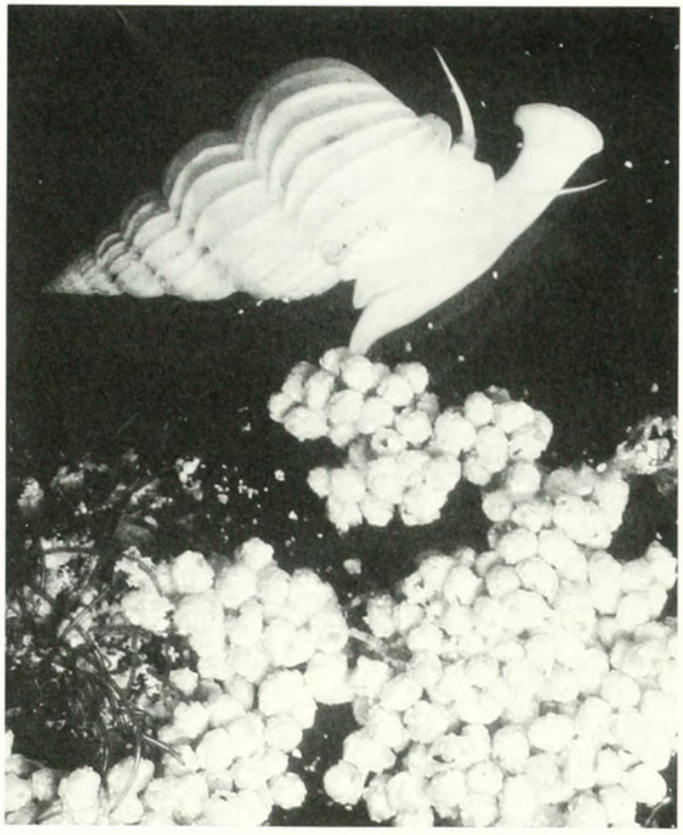


Figure 19. Living *Epitonium worsfoldi* near some of its sand-agglutinated egg capsules. Some of the shell ribs are abnormally bent. ANSP A17194. Shell 18.8 mm long, 9.8 mm wide. Grand Bahama. Photo Jack N. Worsfold.

E. lamellosum. On one occasion, an *E. lamellosum* approached an *E. phymanthi* in the same way. Once, individuals of the two species remained aperture to aperture for about one hour, with the four tentacles curled around each other.

Groups of egg capsules with *E. phymanthi* were found in early May, early June, and early October. After 36 days in isolation, one *E. phymanthi* had two groups of fresh egg capsules attached to it, indicating a capacity for sperm storage.

A small crab killed an *E. phymanthi* with a shell 10 mm long. Three other, larger animals died from unknown causes.

Epitonium worsfoldi Robertson, new species
(figures 14–19)

?*Turbo principalis* Pallas, 1774: 33, pl. 3, figs. 5–6. No locality. *Nomen dubium*. This species might not be large if the figures are enlarged. The spire angle (if accurately drawn)is 30°–35°.

?"*Scala principalis* (Pallas)": Mörch, 1875a, 1875b, 1876.Tortola, British Virgin Islands. Probably not of Pallas.

Unidentified. Huber, 1982: 202, 2 figs. S of Balmoral Island, Nassau, Bahamas. Reported to be 1 5/8″ long (= 41 mm).

"*Epitonium principalis* (Pallas, 1774)": Paschall, 1986:66, figs. 1a and b. Next to a sea anemone, Green Turtle "Key" [Cay], Abaco, Bahamas. Not of Pallas. Reported to be 1.75 inches long (= 44 mm).

?*E. principale* "Röding, 1798": de Jong & Coomans, 1988:54, fig. 275. "Rather common in Curaçao and Aruba." Too few axial ribs.

?"*E. frielei* (Dall): Espinosa and Fernandez Garcés (1990:6), probably not of Dall; three small shells from Bah!a Cienfuegos, Cuba, the longest 3.8 mm.

Shell morphology: Protoconch 0.52-0.54 mm long (excluding immersed base), 0.40–0.43 mm wide, with 4.1–4.2 whorls; first whorl diameter 0.12 mm; whorls slightly inflated; microsculpture as in *E. albidum* (Robertson, 1983b); white, with pale brown at suture, terminal varix. Entire shell attaining 25.3 mm (Table 2). Teleoconch to 11.5 mm wide (including ribs), with ca. 8.8 thin, fragile whorls. Spire high, spire angle 35°–50° (mean 44°); spire profile convex, rarely straight or initially concave; whorls moderately inflated. Axial ribs thick, low on upper whorls, thinner, higher, upright or recurved without subsutural or shoulder cresting (except remnants from breakage) on later whorls; numbering 16–21 on all but first and last whorls large shells (23 ribs on last whorl of 8.8+ whorl shell), with ribs/ whorl initially decreasing then increasing with shell size (figure 17); axial ribs on successive whorls usually attached, attachments erect, rarely offset away from aperture on lower whorls; rarely, all ribs bent medially after an injury (figure 19). Suture present in

Table 2. *Epitonium worsfoldi* new species. Mensural and meristic shell characters. "+" indicates that a shell would have been larger had it not been slightly broken, or "++" badly broken. Specimen 37 is the holotype.

Specimen no.	Length (mm)	Width (mm)	Spire angle	Teleoconch whorls	Axial ribs per whorl							
					1	2	3	4	5	6	7	8
1	17.9+	8.9+	45°	7.3+	—	—	21	18	18	18	18	—
2	18.8	9.8	45°	8.0	20	20	19	18	18	19	19	20
3	9.4	5.3	40°	6.5	20	20	20	19	19	20	—	—
4	8.8	5.4	45°	6.6	22	21	20	20	21	21	—	—
5	—	4.7	—	—	19	19	19	18	19	20	—	—
6	—	—	—	3.3	23	21	21	20	—	—	—	—
7	—	—	—	—	20	18	17	18	17	18	—	—
8	—	11.3+	—	ca. 8.8	—	—	—	—	—	—	—	20
9	22.1	10.3	40°	8.3	20	20	19	19	18	18	18	18
10	15.6+	7.7	35°	7.2	—	19	19	20	19	17	17	—
11	12.5	5.9+	40°	6.8+	19	19	19	18	19	20	—	—
12	17.2	8.0	40°	7.6+	—	—	21	20	19	19	19	—
13	14.3	7.2	40°	7.1	—	—	20	19	19	19	19	—
14	19.7+	9.9	40°	8.2	—	—	19	19	19	19	19	20
15	19.6+	9.7	40°	8.0	—	21	20	20	20	20	21	19
16	19.7	9.6	40°	7.8	—	20	18	17	18	18	18	—
17	14.9	8.1	40°	7.3	—	20	19	18	18	18	19	—
18	18.3	9.5	45°	7.9	—	17	18	18	17	18	18	—
19	19.2	9.2	40°	8.1+	—	—	21	19	19	19	19	23
20	4.4	2.4	40°	—	—	—	—	—	—	—	—	—
21	6.9	3.8	40°	5.4	—	20	18	19	19	—	—	—
22	25.3	11.5	45°	8.1	—	19	19	19	19	20	20	21
23	15.6	8.2	45°	8.0	—	—	—	—	—	—	—	—
24	21.5+	9.0+	40°	7.9	—	—	19	17	17	17	17	—
25	18.9+	9.2+	40°	7.8	—	—	—	19	19	19	—	—
26	17.7+	9.3+	45°	7.8	—	—	20	21	20	20	21	—
27	13.9+	6.4+	40°	6.9+	—	—	18	18	18	—	—	—
28	19.4	9.6	45°	7.7	—	—	20	20	20	20	20	—
29	15.0+	7.5+	45°	7.1	—	20	18	18	17	17	17	—
30	18.6+	10.0	40°	7.2	—	—	—	18	18	18	19	19
31	20.2	10.7	45°	8.2	—	18	18	18	18	18	18	19
32	18.8+	10.0	45°	8.0	—	—	18	18	18	18	18	19
33	22.4+	—	45°	8.3	—	—	20	20	20	20	19	21
34	17.1	8.4	45°	7.7+	—	—	18	17	18	18	18	19
35	12.9	7.2	45°	7.1	—	17	17	18	—	18	18	18
36	10.2+	4.7+	50°	5.5+	—	—	17	17	19	18	—	—
37	18.7	9.1	45°	7.8	—	19	19	20	20	19	20	—
38	6.0++	2.9++	45°	5.6++	—	—	—	—	—	—	—	—

inter-rib areas of uppermost whorls; middle, lower whorls slightly detached. Areas between axial ribs with faint, irregularly-spaced, incised spiral lines; axial growth lines present. Body whorl without basal spiral cord. Umbilical chink narrow (rarely almost closed). Columellar callus thin or thick, thinnest medially, not conforming to underlying ribs. Columellar chinks present. Aperture roundly oval. Teleoconch color pale tan, cream-white, pure white (when bleached?). Operculum paucispiral, growth wrinkles present, pale amber.

Comparative remarks: *Epitonium worsfoldi* most closely resembles species in the de Boury "subgenera" *Hyaloscala* [1889], *Limiscala* [1909], and *Papyriscala* [1909] (see Appendix) as discussed in Kilburn (1985). The shell of *E. worsfoldi* most closely resembles *E. kraussi* (Nyst, 1871) of South Africa and *E. melior* (Melvill and Standen, 1903) of the northern Arabian Sea (see Appendix).

Etymology: Named for Jack Nigel Worsfold, indefatigable naturalist and friend.

Geographic range: Bahamas, northern Cuba, and Puerto Rico. Not known from Bermuda, Florida, or the Lesser Antilles.

Material examined: (Table 2): Bahamas: Fleming Road beach, Mosquito Point, 8 km SE of West End, Grand Bahama (26°37′30″N, 78°54′00″W), J.N. Worsfold leg., ca. 1976, ANSP 370051, specimen 33.- Smith's Point, Grand Bahama (26°31′N, 78°37′W), 1 m, 1 living under *Stichodactyla* ["*Stoichactis*"] *helianthus*, 1 large, with egg capsules, living under either an *Actinoporus elegans*

or *Homostichanthus duerdeni* (Figure 18), J.N. Worsfold leg., August 1985, ANSP A17192, Holotype, ANSP A17193, specimens 35, 37.—SW of Sharp Rocks Point, near Peterson's Cay, S coast central Grand Bahama (26°33′45″N, 78°33′30″W), 1 m, 2 juveniles living with egg capsules under *Stichodactyla*, J.N. Worsfold leg., June 1984, ANSP A17194.—Gold Rock, S. coast central Grand Bahama (26°36′15″N, 78°22′15″W), 1 m, 2 juveniles living under *Stichodactyla*, J.N. Worsfold, leg., June 1984, ANSP A17195.—Treasure Cay and vicinity, Abaco, 12 shells, C. Redfern leg., Redfern collection, specimens 7, 23–32.—W coast N end Elbow (Little Guana) Cay, off NE Abaco (26°33′00″N, 76°56′45″W) K. A. Robertson leg. ca. 1954, ANSP 359100, specimen 16.—Wood Cay, Schooner Cays, W of S Eleuthera, M. McNeilus leg., Dec. 1980, McNeilus collection, specimen 1.—North East Point, Arthurstown, Cat Island (24°38′N, 75°38′W), 1 broken shell with an *E. albidum*, W.J. Clench and H.D. Russell leg., 1936, MCZ 107820, specimen 36.—Bahamas unlocalized, ANSP uncatalogued, specimen 34. Cuba: NW coast, Oasis Beach, Via Blanca Highway km 28, Matanzas (23°11′N, 82°04′W), C.J. Finlay leg. Feb. 1959, Finlay collection, specimen 15.—Same, km 27 (23°11′N, 82°05′W), C.J. Finlay, leg., 1951–1956, Finlay collection, specimens 5,9,10,11, ANSP 359101, specimens 13,14. Puerto Rico: Punta Ostiones, 7 km S of Punta Guanajibo, W coast, 1 shell, April 22, 1949, 3 shells, May 22, 1949, G.L. Warmke, leg., ANSP, specimens 3–4, 17–18.—Ramey Air Force Base, NW coast, A. Phares, leg., ANSP, specimen 19.—Piñones Beach, 8–10 km E of San Juan, NE coast (18°26.8′N, 65°55.7′W), Mrs. D. Humphrey leg., 1970, Finlay collection, specimen 8. Virgin Islands: Hams Bay, St. Croix (17°47′N, 64°53′W), with 21 *E. phymanthi* shells, Feb.–March, 1957, G. Nowell-Usticke leg. AMNH 194365, specimen 38. Specimen 37 is the holotype. All remaining specimens except specimen 34 are paratypes.

A total of 38 specimens of *E. worsfoldi* was available for study. Of these, 6 were collected alive: 2 large specimens (the smaller the holotype), 2 juveniles, 1 with the dried body deep in the shell, and 1 with the operculum but no body. The last 2 and most of the remaining shells were collected from beach drift.

Many of the beach shells are in poor condition. The fairly fragile shell, predators (crabs? fish?), and wave action presumably are responsible. Out of the 38 shells, only 1 has an intact protoconch.

Natural history: At Grand Bahama, this species was found alive three times with *Stichodactyla helianthus* (Ellis and Solander, 1786), the preferred host also of *Epitonium albidum* (Orbigny, 1842)(Robertson, 1983b) and an occasional host of *Epitonium lamellosum*. Like *E. albidum*, *E. worsfoldi* was under the broad oral disc, next to the column, in sand. The holotype of *E. worsfoldi* was collected with an anemone that was either *Actinoporus elegans* Duchassaing, 1850 or *Homostichanthus duerdeni* Carlgren, 1900, a sand-dweller (Figure 18). Feeding (parasitism) on the anemones was not observed but must occur. The sand-agglutinated egg capsules are like those of *E. albidum* (Figure 19). The bathymetric range is 0–2 m.

CONCLUSIONS

The data in this paper are believed to warrant description of the two new Recent western Atlantic species. Their fossil ancestors seem not to be known in the Americas. As documented in the Appendix, the most similar Recent shells appear to occur in Japan and South Africa.

It will be noted in the Appendix that the 23 species have been assigned to a variety of genera and "subgenera" (many of the latter named by de Boury). *Epitonium worsfoldi* has characteristics of three of these "subgenera" combined. Epitoniid genera and subgenera need to be much more broadly based.

It is surprising that two such large, shallow water species in a well-collected area should have remained undescribed until now. They show the continuing role that amateurs play in collecting, observing, photographing, and providing material for systematic and biological studies in museums and marine stations. Amateurs not only find undescribed species on rare occasions but, perhaps more usefully, they can also make aquarium observations such as those of the Leemans reported here.

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APPENDIX.

Conchological comparisons or notes on 23 species similar to, or confused with *Epitonium phymanthi* and *E. worsfoldi*, regardless of provenance.

Scala amathusia Melvill & Standen, 1903:341, pl. 7, fig. 1. Kaicher, 1980: card 2300 [*Epitonium*]. Gulf of Oman. Smaller than *E. worsfoldi* (6.5 mm), with more whorls (8–9) for size.

Scalaria costulata Kiener, 1838–1839:5–6, pl. 2, figs. 4. Tryon, 1887:pl. 12, fig. 59. Robertson, 1963:57–58, pl. 5, fig. 4. Robertson, 1970:45 [identification confirmed]. DuShane, 1988:30–32, fig. 1 (ribs curiously opisthocline). ANSP 230639. Red Sea to Philippines. Thought to be a synonym of *S. principalis* (Pallas) by Sowerby (1844:88 bis), which he recorded from "Xipixappi, West Columbia." Larger (35.3 mm); spire high (spire angle 30°); suture slightly disjunct; up to 28 ribs on last whorl; umbilicus narrow, deep.

Scalaria crassa Sowerby, 1844:91 bis, pl. 33, fig. 55. Kaicher, 1981: cards 3066, 3081 [*Epitonium*]. Philippines. Unlike *E. worsfoldi*, ribs unequal, slightly fewer (18) at largest size; may be spirally brown-banded.

Epitonium (*Limiscala*) *crypticocorona* Kilburn, 1985: 309–310, figs. 79, 126. South Africa. Smaller (7 mm); weak "coronation" inside suture; 12–19 ribs; low spiral lirae.

Scalaria dubia Sowerby, 1844:90 bis, pl. 33, fig. 41. Not *Epitonium dubium* Röding, 1798:92. Sowerby in Reeve, 1873: species 45, 45b wrongly as 75b. Tryon, 1887: 60, pl. 12, figs. 67–68. De Boury, 1912:95–97, pl. 7, fig. 4. Kilburn, 1985:327. Type species of *Foliaceiscala* de Boury, 1912. ANSP 19573 (broken); USNM G.177. Australia, Samoa, etc. Larger (37 mm); spire angle 45°; like *E. phymanthi* but lacks crests; ribs very low, thin, slightly recurved, rarely enlarged, up to 42 on last whorl; suture impressed but not disjunct; spiral threads crowded, variable; last whorl inflated; umbilicus very narrow.

Scala emiliae Melvill & Standen, 1903:343–344, pl. 7, fig. 6. Kaicher, 1980: card 2313 [*Epitonium*]. Kilburn, 1985:307, figs. 120–121. Pakistan to South Africa. Smaller than *E. phymanthi* (12 mm); spire slightly higher (spire angle 40°); 21–36 low, thread-like ribs; pale brown (if not faded).

Scalaria friabilis Sowerby, 1844:95 bis, pl. 33, fig. 74. Kaicher, 1980: card 2329 [*Epitonium*]. Southern Australia. Higher spire than *E. phymanthi* (spire angle 30°–35°); spire profile evenly convex; no umbilicus.

Scala frielei Dall, 1889:313. Not illustrated. USNM 83727 (syntypes); AMNH 194388. North Carolina; Virgin Islands. Clench & Turner (1952:300–301) and Warmke & Abbott (1962:81, pl. 14a) misidentified this species. Smaller (6.4 mm); 24–31 ribs on last whorl; no shouldering; strong spiral threads; umbilicus narrow; spire fairly high (spire angle 45°). *Epitonium phymanthi* has been misidentified as this species.

Epitonium (*Nitidiscala*) *hancocki* DuShane, 1970:332, pl. 51, fig. 1. DuShane, 1974:32–33, fig. 73. Kaicher, 1983: card 3612. Galápagos. Smaller (13 mm); spire higher (spire angle 30°); fewer ribs (21); rib crests wavy.

Scalaria imperialis Sowerby, 1844:91–92 bis, pl. 33, figs. 56–57. Wilson & Gillett, 1972, pl. 13, figs. 5, 5a [color]. [*Epitonium imperiale*]. Kaicher, 1980: card 2304. AMNH 136625, 157310; ANSP 181726, 195661, 253841, 253842, uncat.; MCZ 294909, 294914; USNM 694170. East Africa, Western Australia, Philippines and Queensland. Larger (40 mm); pale tan to dark reddish or purplish brown, commonly in spiral bands (ribs white); more ribs, increasing to 48 on last whorl; umbilicus wide and deep; operculum grey-black.

Scalaria irregularis Sowerby, 1844:90 bis, pl. 33, figs. 40, 60. Philippines; Japan. USNM 343440. Up to 18 mm long; spire angle 65°; ribs crowded, 37 on last whorl, irregular in thickness but generally thin, with slight cresting; strong spiral threads; slightly umbilicate; 1 pale brown subsutural band present or absent on white. Resembles *E. phymanthi*.

Scalaria kraussi Nyst, 1871:116. Kilburn, 1985:293–295, figs. 97–100 [*Epitonium* (*Hyaloscala*)]. +*Epitonium shepstonense* E.A. Smith, 1910:204, pl. 7, fig. 15. Kaicher, 1981: card 3113. South Africa. Smaller (10–16 mm); spire averages higher (spire angle 25°–40°); 17–37 fine, low, erect or slightly reflexed ribs on later whorls; umbilicus closed. Species believed to be most similar to *E. worsfoldi*.

Perlucidiscala lacrymula Jousseaume, 1911:198, pl. 5, figs. 37–42. Kaicher, 1981: 3063 [*Epitonium "lachrymula"*]. Gulf of Aden. Smaller (5 mm); spiral threads towards apex.

Scalaria latifasciata Sowerby *in* Reeve, 1874: species 117. Type species of *Papyriscala* de Boury. Taki, 1956 [anatomy]. ANSP 70738, 219307, 234733, 243255; MCZ 294908 and 5 uncat. lots. Mozambique; Mauritius; Japan. Up to 18 mm long; spire low (spire angle 55°); trace of whorl disjunction; thin, low ribs mostly not connected from whorl to whorl; 32 ribs on last whorl, some irregularly spaced or thickened; weak to strong spiral threads; no crests; 2 or 3 brown spiral bands; slightly umbilicate.

Scalaria lineolata "Kiener" Sowerby, 1844:91 bis, pl. 33, figs. 45, 46, 48. Confused with *S. lineata* Kiener not Say. Nyst, 1871:118, pl. 2, fig. 5, pl. 6, fig. 20. Kaicher, 1981: card 3125 [*Epitonium*]. ANSP 70742, 86246, 243289; MCZ 294911 and 2 uncat. lots; USNM 198709. Gulf of Aqaba; Mauritius; Philippines; Japan. Up to 19 mm long; spire angle 40°; ribs more numerous (16–33) and more irregularly spaced and thickened ribs; no spiral sculpture; umbilicate; 1–3 brown spiral band(s) per whorl; operculum dark brown.

Scalaria lyra Sowerby, 1844:89 bis, pl. 32, figs. 38–39, pl. 34, figs. 81–82; Sowerby *in* Reeve, 1873: species 23.

Kaicher, 1980: card 2341 [*Epitonium*]. Kilburn, 1985: 308–309, figs. 122]. ANSP 19566, 19567, 119638; MCZ 187720; USNM 431817, 306339; 820891. Type species of *Limiscala* de Boury. Fiji to Japan and the Red Sea to Mozambique. Slightly smaller (20+ mm); spire lower (spire angle 60°); 27–45 erect ribs; spiral threads fine and dense; 0, 2 or 3 brown spiral bands.

Scala melior Melvill & Standen, 1903:345, pl. 7, fig. 9. Kaicher, 1980: card 2333 [*Epitonium*]. ANSP 164808 (syntype); USNM 424868. Pakistan; Gulf of Oman. Smaller (6.5 mm+); 8 (teleoconch?) whorls; spire angle 30°; up to 23 ribs per whorl; spiral threads present or absent. Resembles a small *E. worsfoldi*.

Scala micromphala Mörch, 1875a:258 ("Vieques," Puerto Rico, one specimen collected by A.H. Riise). Not illustrated. Photograph of holotype in Clench and Turner (1951:258–260, pl. 112, fig. 3), wrongly synonymized by them with *E. occidentale* Nyst, 1871, which according to them has "12 to 15 costae on the body whorl." According to Mörch there were 18 ribs on the 5 mm.-long shell. An *E. phymanthi* that long would have had more than 20 ribs. In addition, *E. micromphala* has subsuturally crested ribs; in *E. phymanthi* the crests are on the shoulders of the ribs. Mörch wrongly likened *S. micromphala* to *S. imperialis* (see under that species).

Scala (*Viciniscala*?) *minuticosta* de Boury, 1912:87–90, pl. 7, fig. 1. Compared with *Scala costulata* and *S. principalis*. "West Columbia." DuShane (1974:20–22, figs. 20–26). Larger than *E. worsfoldi* (35 mm); spire high (spire angle 35°); 21 mainly thin, low ribs on last whorl; whorls all narrowly disjunct, but ribs attached; traces of spiral striae; umbilicus narrow, deep; ribs slightly reflexed; crowded spiral threads.

Turbo principalis Pallas, 1774. Nomen dubium. *Epitonium principale* (Pallas) Röding, 1798:91. De Boury, 1912:89–90, 97. See above in synonymy of *E. worsfoldi*.

Scalaria robillardi Sowerby, 1894:42–43, pl. 4, fig. 5. Kaicher, 1981: card 3037. Kilburn, 1985:305–307, figs. 118–119 [*Epitonium* (*Papyriscala*)]. Red Sea and India to South Africa. Smaller (15 mm); more ribs (20–24 on last whorl); umbilicate; pale tan with 2–3 brown spiral bands (rarely absent).

Epitonium shepstonense. See above under *E. kraussi*.

"*Foraceiscala*" [=*Foliaceiscala*] *virgo* Masahito & Habe, 1976:172, figs. 2–3. Compared with "*Foraceiscala*" *dubia* (Sowerby, 1844). Japan. Paratype most resembles *E. phymanthi*; spire angle 40°; 50–60 weakly lamellate growth riblets; suture slightly disjunct, whorls connected by ribs; aperture constricted (holotype); oblique spiral threads.

Epitonium (*Nitidiscala*) *willetti* Strong & Hertlein, 1937:171, pl. 35, fig. 5. DuShane, 1974:38–39, fig. 72. Tropical eastern Pacific. Much smaller (3.2 mm); 18–22+ ribs.