Studies on Bathyal and Abyssal Buccinidae (Gastropoda: Neogastropoda): 1. *Metula fusiformis* Clench and Aguayo, 1941

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ABSTRACT

Based on the morphology of the radula and shell, *Metula fusiformis* Clench & Aguayo, 1941 is transferred to the predominantly Indo-western Pacific genus *Manaria*. This species occurs in upper continental slope communities (183–578 m) of the Caribbean Sea and the northern coast of South America. The holotype was collected dead in 2,633 m, well below the depth inhabited by this species. The large well-developed gland of Leiblein, a separate sperm ingesting gland between the capsule gland and albumin gland, and three-cusped rachidian teeth are features that *Manaria* shares with other fusiform buccinids (*e.g., Penion, Serratifusus*) as well as with primitive members of other families within Muricacea. These features are interpreted as being symplesiomorphic, and suggest that the fusiform buccinids are among the more primitive members of the Buccinidae.

Key words: Buccinidae; Caribbean; bathyal; *Manaria; Metula.*

INTRODUCTION

The family Buccinidae comprises one of the most diverse and dominant groups of predatory prosobranch gastropods at high latitudes and at bathyal, abyssal and hadal depths. It is represented in the fossil record of the Lower Cretaceous (Albian), and ranks among the oldest of the neogastropod families (Taylor *et al.*, 1980). Like most predatory prosobranch families, it is believed to have evolved in temperate climatic zones at higher latitudes (Sohl, 1987). Although the majority of these families became predominantly tropical during the Cenozoic, most Buccinidae remained in temperate and polar regions, were the family diversified since the late Miocene (Taylor *et al.*, 1980). The success of Buccinidae at high latitudes and in the deep sea has been attributed to their broad habitats and diets, which are considered to be adaptations to unpredictable resources (Taylor, 1978).

Despite the high diversity and abundance of Buccinidae, the systematics of this group is poorly understood at all taxonomic levels. This is due, in large part, to the fact that the vast majority of taxa are based exclusively on features of the shell and operculum, supplemented occasionally by observations on radular morphology. Shells of Buccinidae tend to be simple, and offer few readily discernible morphological characters. These are subject to convergence, especially in polar regions and the deep sea, where effects of habitat on shell form are most pronounced (Graus, 1974).

Detailed anatomical data are available for comparatively few, mainly shallow-water taxa (*e.g.*, Dakin, 1912; Golikov, 1963, 1980; Kosuge, 1967; Ponder, 1973; Lus, 1981; Kantor, 1990). The lack of well-defined, synapomorphic anatomical features (other than radular morphology), even between the families Buccinidae, Nassariidae, Fasciolariidae, and Melongenidae have led Ponder (1973a) to suggest these groups might all be considered subfamilies of Buccinidae. This arrangement was subsequently adopted by Ponder and Warén (1988).

Bouchet and Warén (1985) revised the deep-water Buccinidae (*sensu* Wenz, 1943) of the northeastern Atlantic Ocean, and later (Bouchet & Warén, 1986) reviewed many of the tropical deep-water species. Despite these significant contributions, most of the nearly 200 supraspecific taxa within Buccinidae (*sensu* Wenz, 1943) are poorly defined, and the assignment of many species to genera remain tentative.

Among the taxa listed by Bouchet and Warén (1986) as "insufficiently known" is *Metula fusiformis* Clench and Aguayo, 1941. The placement of this species in *Metula* was disputed by Olsson and Bayer (1972) who suggested that it had affinities with *Fusinus* or a fusiform buccinid. Abbott (1974) referred this species to the genus *Bartschia*. Bouchet and Warén (1986) considered it to be a buccinid, and commented on its conchological resemblance to *Euthriostoma*.

During a recent dive aboard the research submersible Johnson-Sea-Link I off Navassa Island, situated off the southwestern peninsula of Haiti, the author had the opportunity to observe and collect several living specimens of "*Metula*" *fusiformis*. These observations, together with data from additional material discovered in the USNM

collections, form the basis of this report, the first in a series on enigmatic deep-water buccinid taxa.

MATERIALS AND METHODS

Five specimens of "*Metula*" *fusiformis* Clench and Aguayo, 1941 were observed, recorded on videotape and collected either in (1 specimen) or within 2 meters (4 specimens) of a bucket baited with decomposing octopus and set on an ooze-covered area (slope about 20°) off the west coast of Navassa Island (18°24'42"N, 75°03'00"W) at a depth of 578 m for 50 hours. The specimens, which were moribund upon reaching the surface, were fixed in 10% neutral buffered formalin and stored in 70% ethanol until dissection.

Phenetic analyses were used to assess the relationships of three conchologically similar taxa, each proposed on the basis of a single specimen. All specimens listed in the "material examined" section, as well as the holotype of *Buccinofusus surinamensis* Okutani, 1982 and two specimens of a southern variant of *Buccinum canetae* Clench and Aguayo, 1944, described as *Plicifusus jamarci* Okutani, 1982, were scored for the 11 shell characters listed in table 1. These data were standardized (mean = 0, standard deviation = 1), a Euclidean distance matrix calculated, and a phenogram based on the UPGMA clustering algorithm was produced using SYSTAT version 4.0 (Wilkinson, 1988). A Principle Component Analysis using the same data matrix (25 specimens × 11 characters) was performed, also using SYSTAT, and the individuals plotted using the first two principal components as axes.

Repositories of examined specimens are indicated by the following abbreviations:

MCZ—Museum of Comparative Zoology, Harvard University

NSMT—National Science Museum, Tokyo

USNM—National Museum of Natural History, Smithsonian Institution

SYSTEMATICS

Family Buccinidae Rafinesque, 1815
Genus *Manaria* E. A. Smith, 1906

Manaria fusiformis (Clench & Aguayo, 1941)
(figures 1–5, 7–17)

Metula fusiformis Clench & Aguayo, 1941:179, pl. 14, fig. 1; Bouchet & Warén, 1986:485, fig. 116.
"*Metula*" *fusiformis* Clench & Aguayo.—Olsson & Bayer, 1972: 925.
Bartschia fusiformis (Clench & Aguayo).—Abbott, 1974:217.
Mohnia kaicherae Petuch, 1987:103, pl. 21, figs. 8, 9.

Shell morphology: Shell (figures 1, 3, 4, 5) to 69 mm, thick, biconical, fusiform. Protoconch badly eroded or missing on all adult specimens examined. Protoconch of juvenile specimen (figures 7, 8) just over one smooth whorl, with a diameter of 0.75 mm. Transition to teleo-

Table 1. Shell characters used for phenetic analysis. Characters 1 through 8 describe the geometry of the generalized shell form (Harasewych, 1982).

1. Shape of the generating curve of the body cavity (Sbc).
2. Shape of the generating curve of the siphonal canal (Ssc).
3. Relative siphonal length (Rsl).
4. Siphonal angle (β).
5. Angle of the generating curve (θ).
6. Rate of whorl expansion (W).
7. Position of the generating curve relative to the axis (D).
8. Rate of whorl translation (T).
9. Spire angle (α).
10. Number of axial ribs on fourth teleoconch whorl (no. rib).
11. Number of spiral cords on fourth teleoconch whorl (no. cord).

conch gradual, marked by formation of axial ribs, followed within ½ whorl by the formation of six fine spiral cords. Teleoconch of up to 8¾ convex whorls, rounded at first, becoming sharply shouldered by the fifth postnuclear whorl. Suture broadly adpressed. Axial sculpture of broad, rounded, regularly-spaced, axial to slightly prosocline ribs that do not extend onto the anteriormost portions of the body whorl or the siphonal canal. Axial ribs number 11–12 on the first and 11–16 on the penultimate whorl. Spiral sculpture of strong cords, as broad or broader than intervening spaces, that overlay axial ribs. Cords number 12–13 between suture and shoulder, 19–21 between shoulder and siphonal canal, 16–18 on siphonal canal. Sixteen to 21 cords remain exposed on penultimate whorl. Aperture elliptical, tapering posteriorly beneath suture to form anal sulcus. Outer lip with 18–23 thin spiral lirae pronounced beneath axial ribs and weak or absent between. Inner lip smooth, with thin, porcellaneous inductura. Columella solid, sinuate, lacking folds. Siphonal canal broad, slightly shorter than aperture, crossing coiling axis. Siphonal fasciole weak, adjacent to columellar edge of siphon. Exterior surface of shell dull ivory to light amber, aperture and columella white. Periostracum (figure 9) thick, straw-colored to brown, consisting of thin, axial blades that are broadest between spiral cords and abraded along their surfaces. Operculum (figures 2, 13, op) thick, elongate, with terminal nucleus (usually abraded), attached along slightly less that ½ of its inner surface, glazed along posterior and left inner margins, fills aperture ¼ whorl from outer lip.

Shell ultrastructure: (figure 10) Shell composed of three layers of crossed-lamellar crystals and an outermost prismatic layer. Innermost layer ($\simeq$200 μm) with crystal faces oriented at approximately a 35° angle to growing edge of the shell; crystal faces of next layer ($\simeq$250 μm) perpendicular to growing edge; outermost crossed-lamellar layer ($\simeq$625 μm) parallel to growing edge. Prismatic layer of varying thickness (50–200 μm) outermost, comprising the spiral cords and contains all of the shell color. Inner three layers white.
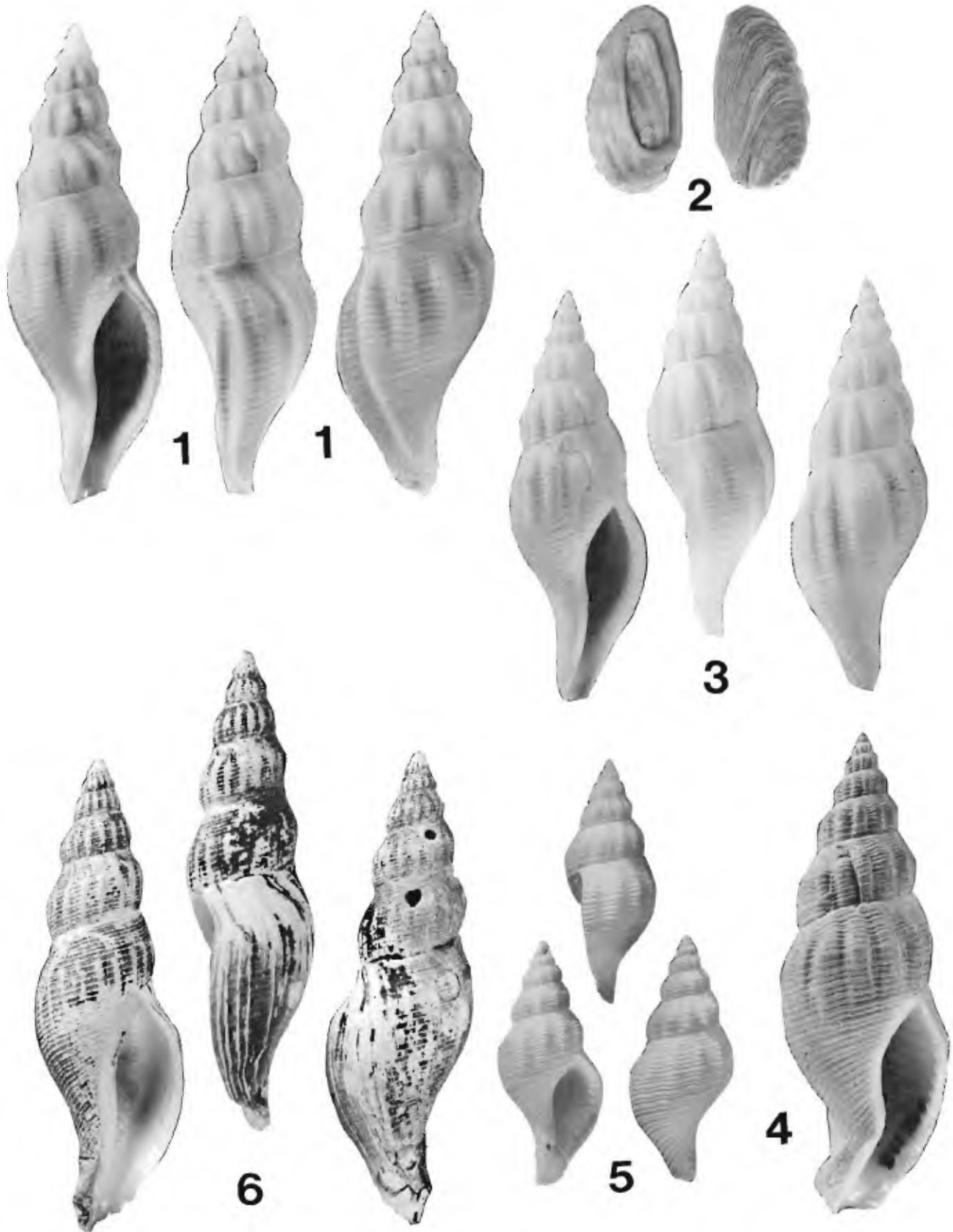
External anatomy: (figure 13) Soft tissues comprise 3½–4 whorls, mantle cavity spans ⅔ whorl, kidney ¼ whorl, digestive gland 2½–3 whorls. Columellar muscle long, narrow, attaching to shell 1⅓ whorl behind mantle edge. Foot small, rectangular (L/W = 1.4) with thin, deep propodial groove along leading edge of sole. Animal uniform khaki to tan in color. Head small, with pair of thin, tapering cephalic tentacles with round black eyes at their bases. Siphon (figure 13, s) short, muscular.

Mantle cavity: Arrangement of mantle cavity organs similar to that of *Buccinum undatum* Linné, 1758 (Fretter & Graham, 1962: fig. 180B). Mantle with thick, muscular band (figure 13, mb) along edge, thin, transparent posteriorly. Osphradium bipectinate, large, dark brown, with 70–80 filaments above ganglion and 62–68 below. Ctenidium, twice as long and slightly narrower than osphradium, sharply tapered along anterior edge. Hypobranchial gland (figure 13, hg) broad, thick, viscous and clear in water, solid and opaque in alcohol.

Alimentary system: Proboscis (figure 14, pb) long (1.5 × shell aperture length), narrow (1.2 mm), pleurombolic, retracts to rear of cephalic hemocoel, overlying salivary glands anteriorly and gland of Leiblein posteriorly. Buccal mass, as long as introverted proboscis, with radular sac extending slightly from its posterior margin. Radula (figure 12) short (6.0–7.9 mm, n = 3), composed of 102–108 rows of teeth. Rachidian tooth with three cusps of equal length located on central portion of broad, basal plate. Lateral teeth with two cusps, outer cusp 1.5 times as long and broad at its base as inner cusp. Salivary glands (figure 14, sg) large, irregular, with ducts becoming embedded in wall of esophagus (within dorsal folds) anterior to valve of Leiblein (figure 14, vl). Gland of Leiblein (figure 14, gl) long, convoluted, posteriorly tapering, filling posterior ⅔ of cephalic hemocoel, emptying via a thin duct into the posterior region of the mid-esophagus. Stomach (figures 13, 14, sto) simple, U-shaped, with two widely separated ducts to digestive glands. Intestine thin, tubular, with longitudinal folds, rectum (figure 14, r) little expanded, simple. Anal gland absent.

Female reproductive system: A narrow oviduct leads from the large yellow-orange ovary to the albumen gland, which lies along the anterior right wall of the kidney. The pallial portion of the female gonoduct (figure 15) consists of a large sperm ingesting gland (figure 15, ig), long, narrow capsule gland (figure 15, cg) and a muscular bursa copulatrix (figure 15, bc) with the female opening (figure 15, fo) situated ventral to the anus (figure 15, a).

Male reproductive system: Testis (figures 13, 16, te) orange tan, along right side of digestive gland. Testicular duct (figure 16, td) tubular, about 0.3 mm in diameter, becomes convoluted along adaxial wall of kidney to form seminal vesicle (figure 16, sv). Duct straightens before passing along wall of pericardium and entering rear of mantle cavity (figure 16, rmc). The prostate gland (figure 16, pr) is narrow, and runs along the right wall of the mantle cavity, ventral to the rectum. The tubular vas deferens (figure 16, vd) runs from the prostate gland anteriorly along the floor of the mantle cavity to the base of the penis (figure 16, pen), which is approximately ¾ the length of the mantle cavity, dorsoventrally compressed, truncated, and with a terminal papilla (figure 16, pap) emanating from a depression along its distal lateral wall.

Material examined: Holotype, MCZ 135290, Atlantis sta. 3344, trawled off Cienfuegos, Cuba (21°38′N, 80°12′W), in 1,440 fms (2,633 m); Holotype of *Mohnia kaicherae* Petuch, 1987, USNM 859855, off Los Monges Islands, off mouth of Gulf of Venezuela, Venezuela, in 200 m; USNM 875112, Johnson-Sea-Link 1 sta. 2321, off west coast of Navassa Island (18°24′42″N, 75°03′00″W), in or near carrion-baited bucket left in 570 m for 50 hours [5 specimens]; USNM 854016, Johnson-Sea-Link 1 sta. 2320, off Lulu Bay, Navassa Island (18°22′42″N, 75°02′44″W), on small tree branch in 530 m [2 juvenile specimens]; USNM 832953, off Long Point, south shore of St. Croix, US Virgin Islands, in 160 fms (293 m) [10 specimens]; USNM 832954, off Salt River Canyon, north shore St. Croix, US Virgin Islands, in 230 fms (420 m) [2 specimens]; USNM 811332, R/V Oregon sta. 4225, 150 miles north of Sao Luís, Maranhao, Brazil (00°18′N, 44°23′W), in 100 fms (183 m) [1 empty shell].

Ecology: Like many buccinids, this species is attracted to carrion, and is at least a facultative scavenger. The five specimens of *Manaria fusiformis* were the only gastropods collected in or near the baited trap. Also present in the trap were several dozen isopods (*Booralana tricarinata* Camp & Heard, 1988). The two juvenile specimens were collected from a single fragment of sunken wood that was also inhabited by three chitons, about 20 skeneiform trochids, and that contained teredinids and burrowing sipunculans. Water temperatures at the two Johnson-Sea-Link stations at which this species was collected were 9.7° C (JSL-I-2320) and 9.9° C (JSL-I-2321). Gut contents of three adult specimens were examined, but did not reveal identifiable remains. The bathymetric range of all live-collected specimens was 293–578 m.

Geographic range: (figure 17) This species is presently known only from the northern and eastern Caribbean Sea, and from along the northern coast of South America.

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Figures 1–5. *Manaria fusiformis* (Clench & Aguayo, 1941). **1.** USNM 875112, JSL-I sta. 2321, off west coast of Navassa Island. 1.5 ×. **2.** Operculum of specimen in figure 1. 3.0 ×. **3.** Holotype of *Metula fusiformis* Clench & Aguayo, MCZ 135290, Atlantis sta. 3344, off Cienfuegos, Cuba in 2,633 m. 1.5 ×. **4.** USNM 811332, 150 miles north of Sao Luís, Maranhao, Brazil in 183 m. 1.5 ×. **5.** Holotype of *Mohnia kaicherae* Petuch, 1987, USNM 859855, off Los Monges Islands, off mouth of Gulf of Venezuela, Venezuela, 200 m. 1.5 ×. **Figure 6.** *Buccinofussus surinamensis* Okutani, 1982. Holotype NSMT Mo 60028, off Surinam. 1.0 ×.
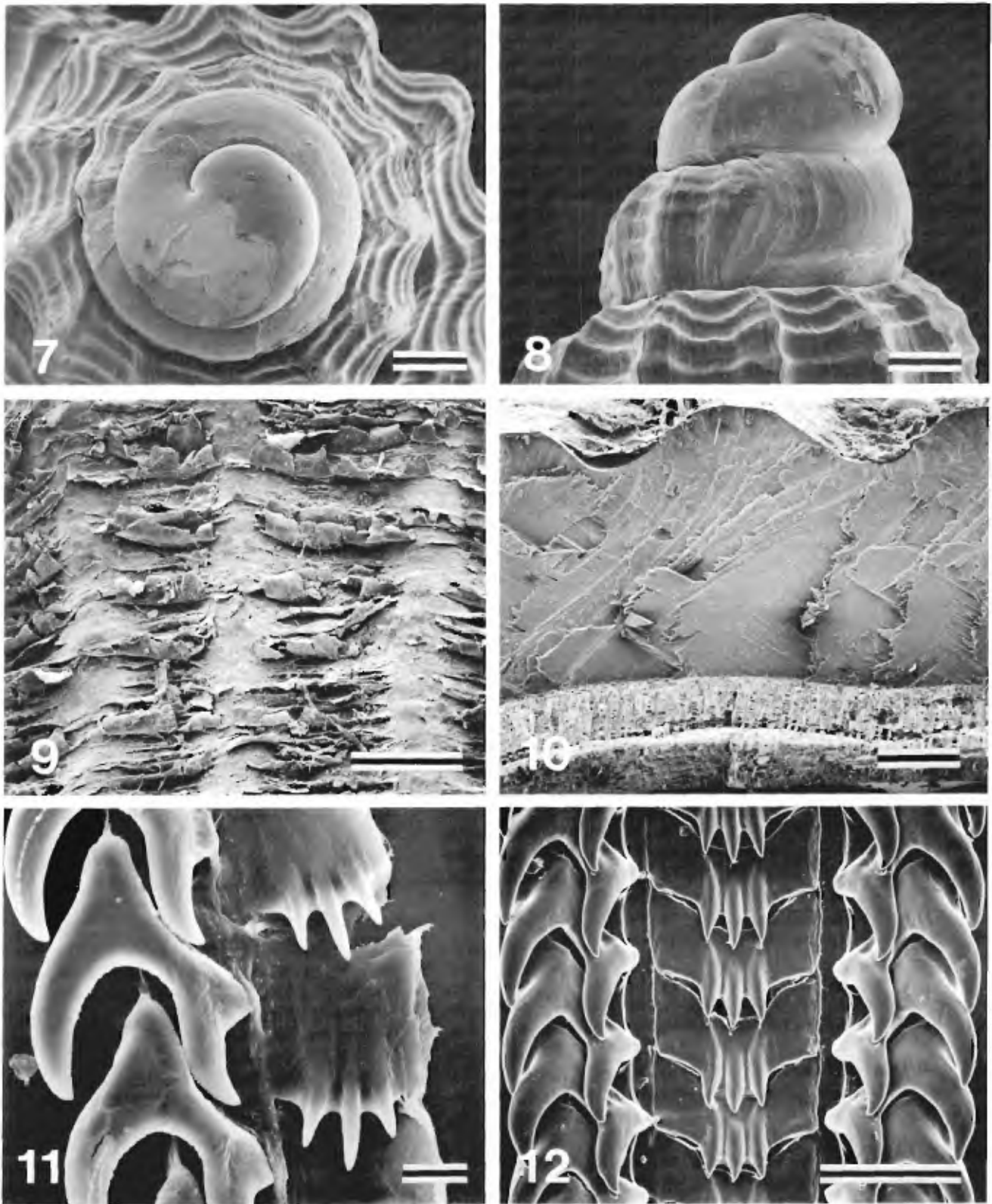
Figures 7–12. *Metula fusiformis* Clench & Aguayo. 7. Axial view of protoconch of juvenile specimen (USNM 854016). Scale bar = 200 μm. 8. Lateral view of same protoconch. Scale bar = 200 μm. 9. Periostracum. Scale bar = 500 μm. 10. Shell ultrastructure, fracture surface parallel to growing edge, ½ whorl behind lip. Scale bar = 250 μm. 11. Radular ribbon of juvenile specimen (USNM 854016), lateral teeth removed from right side. Scale bar = 5 μm. 12. Radular ribbon of adult specimen (specimen in figure 1). Scale bar = 100 μm.
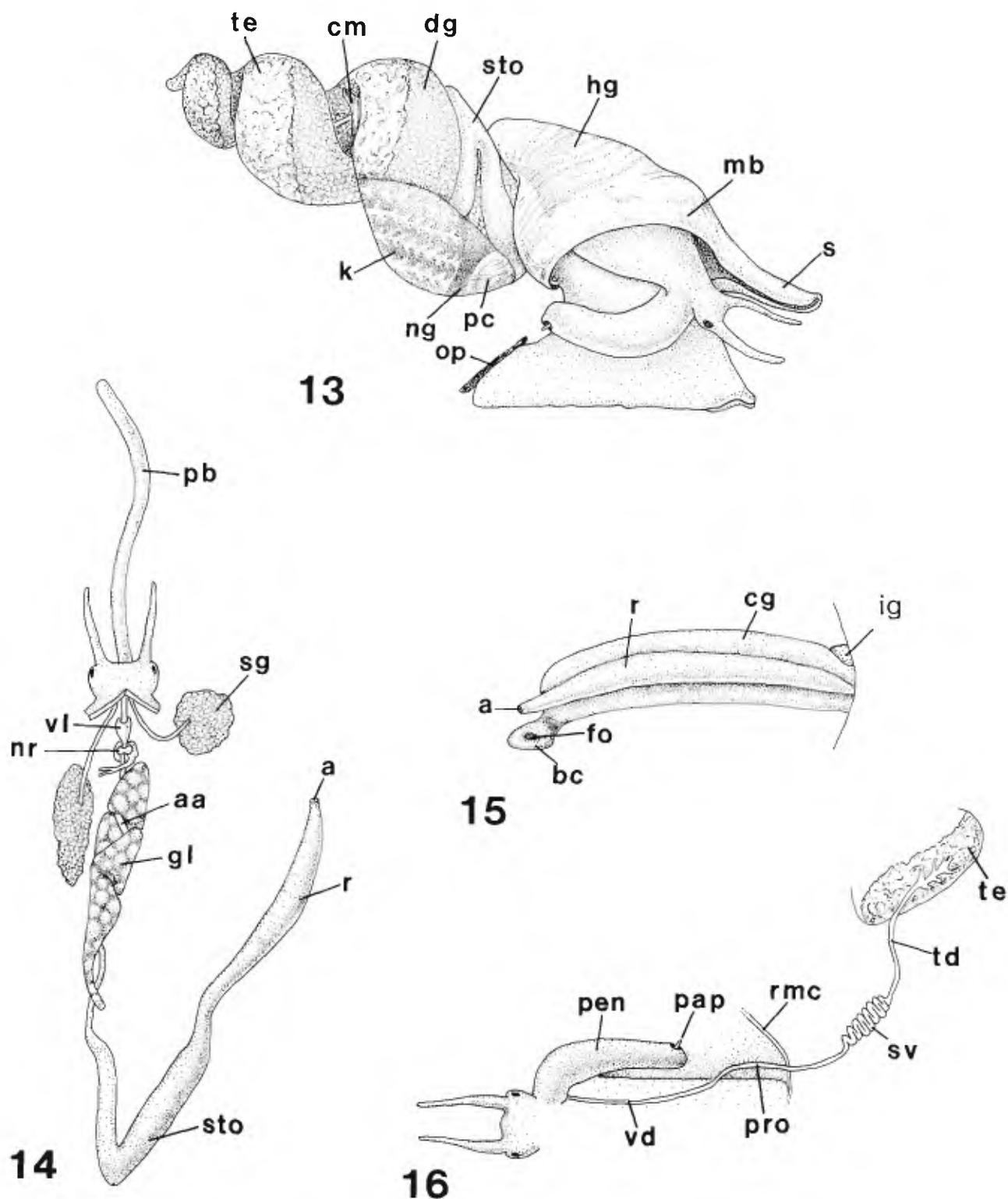
Figures 13–16. Anatomical features of *Manaria fusiformis* (Clench and Aguayo). **13.** Male specimen, lateral view. **14.** Alimentary system. **15.** Female reproductive system. **16.** Male reproductive system. a, anus; aa, anterior aorta; bc, bursa copulatrix; cg, capsule gland; cm, columellar muscle; dg, digestive gland; fo, female opening; gl, gland of Leiblein; hg, hypobranchial gland; ig, ingesting gland; k, kidney; mb, muscular band of mantle; ng, nephridial gland; nr, nerve ring; op, operculum; pap, papilla; pb, proboscis; pc, pericardium; pen, penis; pro, prostate gland; r, rectum; s, siphon; sg, salivary gland; sto, stomach; sv, seminal vesicle; td, testicular duct; te, testes; vd, vas deferens; vl, valve of Leiblein.

Figure 17. Geographic distribution of *Metula fusiformis*. Solid star denotes type locality. Open star denotes type locality of *Mohnia kaicherae*.

DISCUSSION

Although originally described in the genus *Metula,* the generic placement of *M. fusiformis* Clench and Aguayo, 1941 has undergone considerable, if speculative, peregrination during the intervening decades. The radula of this species, with three-cusped rachidian teeth and two-cusped lateral teeth (figures 11, 12), differs from that of *Metula* H. and A. Adams, 1853 (Bouchet, 1988: fig. 1), and precludes the suggested affinities with *Fusinus* or any fasciolariid (Olsson & Bayer, 1972:925), or with *Euthriostoma* (Bouchet & Warén, 1986:485). This radula most closely resembles those of species in the genera *Eosipho* Thiele, 1929 and *Manaria* Smith, 1906 (Bouchet & Warén, 1986: figs. 13–17, 19–24). Ontogenetic changes in the morphology of the rachidian tooth of *M. fusiformis* include the broadening and lateral expansion of the basal plate, as well as the thickening and redirection of the cusps to a parallel orientation (figures 11, 12). Similar ontogenetic changes in *Manaria lirata* Kuroda and Habe, 1961 have been illustrated (Bouchet & Warén, 1985: figs. 20, 23). The presence of pronounced axial ribs overlaid by thick spiral cords, a spire that is more than half the shell length, and a well differentiated siphonal canal in *M. fusiformis*, in *Manaria thurstoni* Smith, 1906 (the type species of *Manaria*), and in several Japanese species of *Manaria*, as well as the lack of these features in *Eosipho smithi* (the type species of *Eosipho*) support the transfer of *Metula fusiformis* to the genus *Manaria*.

A UPGMA phenogram (figure 18) of the 21 available specimens (including the holotype) of *Manaria fusiformis*, the holotypes of *Buccinofusus surinamensis* Okutani, 1982 and *Mohnia kaicherae* Petuch, 1987, as well as two specimens of *Buccinum canetae (jamarci* form), together with a plot of scores of the first two principal components for these specimens (figure 19) indicate that the holotype of *Mohnia kaicherae* falls within the range of variation of *Manaria fusiformis*. This holotype (figure 5, 18K, 19K), which has six teleoconch whorls, is intermediate in morphology between the two juvenile specimens of *Manaria fusiformis* (figures 18e, 19e), which
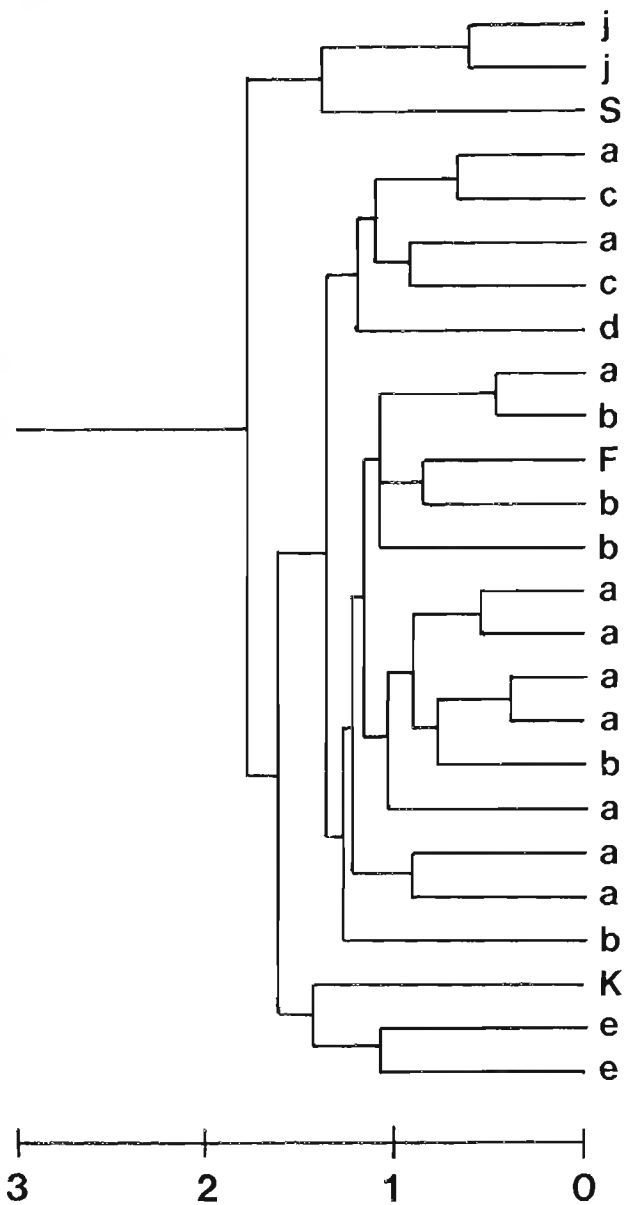
Figure 18. Phenogram of UPGMA clustering of Euclidean distances using standardized data. a–e. *Manaria fusiformis*. **a.** USNM 832953, St. Croix [10 specimens]. **b.** USNM 875112, Navassa [5 specimens]. **c.** USNM 832954, St. Croix [2 specimens]. **d.** USNM 811332, Brazil. **e.** USNM 854016, Navassa [2 juvenile specimens]. **F.** Holotype of *Metula fusiformis* Clench & Aguayo. **j.** Southern variant of *Buccinum canetae* described as *Plicifusus jamarci.* **K.** Holotype of *Mohnia kaicherae* Petuch. **S.** Holotype of *Buccinofusus surinamensis* Okutani.

have 3.8 and 4.0 teleoconch whorls, and the remaining adult specimens (figures 18, 19a–d), which have between 8.0 and 8.75 whorls. Thus, *Manaria fusiformis* can be seen to undergo allometric growth in shell and radular form.

The holotype of *Buccinofusus surinamensis* Okutani,

Table 2. Survey of the subfamilies of Buccinidae (according to Ponder & Warén, 1988) for morphologies of the gland of Leiblein (gL), sperm ingesting gland (ig), and number of cusps on rachidian teeth (rach). gL: 0 = absent, 1 = reduced, flaccid; 2 = large, glandular. ig: + = present; − = absent; ? = unknown.

	gL	ig	rach
Buccinidae			
Manaria fusiformis (herein)	2	+	3
Penion (Ponder, 1973)	2	+	3
Serratifusus (Harasewych, 1990)	2	+	3
Buccinum undatum (Dakin, 1912; Fretter, 1941)	1	+	>3
Neptunea (Golikov, 1963)	1	−	2, 3, >3
Retifusus tenuis (Kosuge, 1967)	?	+	3
Tacita arnoldi (Lus, 1981)	2	?	4
Volutopsius (Kantor, 1990)	0	?	1, 3, >3
Thalassoplanes moerchi (Lus, 1973)	0	?	1
Nassariinae			
Illyanassa obsoleta (Brown, 1969; Fretter, 1941)	1	+	>5
Melongeninae			
Busycon carica (Harasewych, 1982a)	1	−	4–8
Melongena corona (Harasewych, 1982a)	0	−	3
Fasciolariinae			
Leucozonia nassa (Marcus & Marcus, 1962)	2	+	3
Microfulgur carinatus (Ponder, 1970)	2	−	3

1982, a species synonymized with *M. fusiformis* by Bouchet and Warén (1986:485), is more similar in shell morphology to *Plicifusus jamarci* Okutani, 1982 than to any specimens of *M. fusiformis*, and is therefore removed from the synonymy of *M. fusiformis*. In addition to being separable on the basis of the continuous characters listed in table 1, both *Buccinofusus surinamensis* and *P. jamarci* differ from *Manaria fusiformis* in having a substantially larger, chalky, white shell with deeply receding spiral lirae along the outer lip of the aperture.

The presence of a large, well-developed gland of Leiblein, simple, three-cusped rachidian teeth, and a female reproductive system with a distinct sperm ingesting gland between the albumen gland and the capsule gland in *Manaria* (herein), *Penion* (Ponder, 1973), and *Serratifusus* (Harasewych, 1990), represents a combination of characters uncommon within Buccinidae (table 2). Each of these features occurs widely throughout the Muricoidea (table 3), suggesting that these are plesiomorphic characters, and that the fusiform buccinids are among the more primitive members of the family Buccinidae.

Finally, it is suggested that the depth at which the holotype of *M. fusiformis* was collected (2,633 m) falls outside the bathymetric range of the species, and represents *post-mortem* transport of the shell into greater depths. All living specimens of *Manaria fusiformis* were taken between 183 m and 578 m, indicating that this species is a member of upper slope communities. Bathymetric zonation along the continental slope has been well documented (*e.g.,* Okutani, 1968), and bathymetric ranges of species have been found to be narrower on the upper slope than on the middle slope (Hecker, 1990).

Table 3. Survey of the families of Muricoidea (according to Ponder & Warén, 1988) for morphologies of the gland of Leiblein (gL), sperm ingesting gland (ig), and number of cusps on rachidian teeth (rach). gL: 0 = absent, 1 = reduced or modified; 2 = large, glandular. ig: + = present; − = absent. Reported features are present in some, but not necessarily in all, members of the listed families.

	gL	ig	rach
Muricidae (Houston, 1976; Harasewych, 1984)	2	+	3 major + minor
Turbinellidae (Harasewych, 1987)	2	+	3
Buccinidae	see table 2		
Columbellidae (Marcus & Marcus, 1962a; Houston, 1976)	1	−	0
Volutidae (Ponder, 1970a)	2	+	3
Olividae (Marcus & Marcus, 1959; Ponder & Darragh, 1975)	2	+	3
Harpidae (Bergh, 1901)	0	+	3
Marginellidae (Ponder, 1970b)	1	+	1–20+
Mitridae (Ponder, 1972, 1973a)	0	+	3 or more
Volutomitridae (Ponder, 1972, 1973a)	1	+	1
Costellariidae (Ponder, 1972, 1973a)	2	+	3 or more

Figure 19. Plot of scores of first two principal components. Abbreviations as in figure 18.

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