

Anatomy and Systematic Position of *Fastigiella carinata* Reeve (Cerithiidae: Prosobranchia)

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ABSTRACT

Fastigiella carinata is placed in the family Cerithiidae, close to the genus *Pseudovertagus* Vignal on the basis of conchological, radular, and anatomical characters. *Fastigiella* has a shell sculptured with three strong spiral cords, an aperture with a distinct anterior canal, a pseudumbilicus, missing in juveniles, and a siphonal fasciole. The operculum is ovate, corneous, and paucispiral with an eccentric nucleus, and the radula is taenioglossate. The animal has an unusual hypobranchial gland comprised of many transverse leaflets, a ridge dividing the anterior oviductal groove, and an open pallial oviduct with the seminal receptacle in the medial lamina of the posterior oviduct.

INTRODUCTION

The systematic relationship of *Fastigiella carinata* Reeve, 1848 to other prosobranchs has been uncertain and speculative since its description nearly 140 years ago. The genus has been thought to include only one living species and until now was known only from empty shells from the central Bahamas and northwestern Cuba. Even its familial relationships have been in doubt.

Fastigiella Reeve has been a puzzle to many workers. Reeve (1848) remarked in the original description that the shell is intermediate between *Turritella* Lamarck and *Cerithium* Bruguière, but he hinted that *Fastigiella* might be a *Buccinum*-like carnivore (*i.e.*, what would now be called a neogastropod). Reeve placed *Fastigiella* in the catch-all "family Canalifera" because of its characteristic anterior canal. Woodward (1851:129) placed it with a query after "*Nerinaea*" in the family "Cerithiadae" (= Cerithiidae *sensu lato*). H. Adams and A. Adams first placed *Fastigiella* in the Fascioliariidae (1853:155) but later in the Cerithiidae (1858:655). Chenu (1859:182) also assigned *Fastigiella* to the Fascioliariidae.

Most later malacologists have followed Woodward and H. Adams and A. Adams in placing *Fastigiella* near *Cerithium* in the Cerithiidae, albeit in some cases with doubts indicated. Concepts of the genus *Cerithium* and of the family Cerithiidae have been various and generally

broad. Opinions on the relationships of *Fastigiella* within the superfamily Cerithiacea and related superfamilies (as presently conceived) have also been varied. For example, Mörch (1877:209), although placing *Fastigiella* near *Cerithium* (*sensu lato*), stated that *Fastigiella* is closest to a Recent "*Triphoris*" (= *Triphora* Blainville; Triphoridae) and to a Pliocene "*Cerithium*" (assigned by Wenz, 1940, to the Potamididae). More orthodox discussions and placements of *Fastigiella* are those of Fischer (1884:679), Tryon (1887:115,149), Thiele (1929:214), Pérez Farfante (1940:71), Wenz (1943:770), and Sarasúa and Espinosa (1977:2). Ford (1944:8) considered *Cerithidea* Swainson, 1840 (Potamididae) a subgenus of *Fastigiella*, which is incorrect nomenclaturally (*Cerithidea* having priority over *Fastigiella*). Moore (1971:1-2), on the basis of its rarity and the presence of a siphonal fasciole and prominent varices on the shell, suggested that *Fastigiella* is a neogastropod, probably belonging to the Fascioliariidae. Abbott (1974:105), while assigning *Fastigiella* to the Cerithiidae, wrote that "it may prove to be in a totally different family, possibly the Pyramidellidae."

Approximately 100 specimens are now found in museums and private collections. Hugh Cuming possessed the first known specimen as early as 1847, but recorded no locality data. Dr. C. M. Poulsen obtained an immature specimen from Eleuthera prior to 1877 (*F. poulseni* Mörch, 1877; herein regarded as a synonym). The American Museum of Natural History has a dataless specimen from a collection catalogued prior to 1900. The Rev. P. D. Ford collected several specimens in 1943 along the north coast of New Providence Island. From 1953 through 1986 several dozen specimens have been reported in the literature or have been collected by amateur conchologists. All collectors have found dead specimens from beach drift or in water less than 3 m in depth.

Recently, a living *Fastigiella* was collected by Joseph Lleidá at New Providence Island, Bahamas, and preserved in alcohol. This specimen (USNM 859097), although not preserved well enough for histological study, was a mature female that provided an operculum, radula and preserved soft parts suitable for general anatomical study.

MATERIALS AND METHODS

The senior author studied the anatomy, radula, and operculum of a live-collected snail and also assembled some distribution records. Conchological studies, nomenclatural history, and geographic data are by the junior authors, Robert Robertson and R. Tucker Abbott.

The following abbreviations are used throughout the text: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; DMNH, Delaware Museum of Natural History; BM(NH), British Museum (Natural History); LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History, U.S. National Museum, Washington, DC.

Material examined: BAHAMAS: Nassau, New Providence Id. (LACM S1855); Brown's Point, Nassau, New Providence Id. (DMNH 65992, 65993; USNM 707161, 859097); Silver Cay and Hog Id., off Nassau, New Providence Id. (*vide* G. Fehling); Delaports Point, Clifton Pier, east end of Goulding Cay, New Providence Id. (D. Cosman, *leg.*); South West Reef, 7 mi south of New Providence Id. (D. Cosman, *leg.*); Cable Beach, New Providence Id.; Holms Cay, Berry Ids. (J. Cordy collection); mouth of Stafford Creek, east Andros Id. (DMNH 49248); off Small Hope Bay, east Andros Id. (DMNH 29236, 40987, Sue Abbott, *leg.*); Cowrie Reef, Andros Id. (DMNH 51344); Cave Cay, Exumas (D. Cosman, *leg.*); Guana Cay, Exumas (D. Cosman, *leg.*); Highburn Cay (J. Cordy, *leg.*); Sail Cay (G. Duffy, *leg.*); Wemys Bight, Eleuthera (AMNH); Millars, Eleuthera (M. McNeilus, *leg.*); Berry Islands, Eleuthera (*vide* R. Houbrick); Windemere Id., Eleuthera (AMNH); Governor's Harbour, Eleuthera (AMNH); Bottle Cay, Schooner Cays, Eleuthera (ANSP 189519); Powell's Point, Eleuthera (DMNH 51837); west coast of Cat Island (W. G. Lyons, *in litt.*). CUBA: Cárdenas (USNM 434792); off Havana (Jaume collection); Santa Fe, 8 km west of Marianao, Havana (I. Pérez Farfante, *leg.*); Comacho Beach, 4 mi west of Varadero, Matanzas (J. Finlay, *leg.*); (DMNH 105578); Varadero Beach, Matanzas (J. Finlay collection; Museo Poey, *vide* Jaume & Sarasúa, 1943; ANSP 316919); Camarioca Reef area, Matanzas (J. Finlay, *leg.*); Bahía de Matanzas (R. Burquete, *leg.*).

A live-collected, mature, female snail was collected May, 1986 by Joseph Lleida at Brown's Point, New Providence, Bahamas, where it was found living in shallow water. The specimen, which had a shell 32.1 mm long and 11 mm wide, was preserved in 70% EtOH. It was

kindly given to one of us, R. Tucker Abbott, and sent to the senior author for anatomical studies. The soft parts were extracted by breaking the shell in a small vise. The animal was dissected under a binocular dissecting microscope. Shell pieces, apex, operculum, and radula were examined using a Zeiss Novascan-30 scanning electron microscope. This specimen and its parts (USNM 859097) are deposited in the National Museum of Natural History, Smithsonian Institution.

RESULTS

SYSTEMATIC DESCRIPTION

Family **Cerithiidae** Fleming, 1822

Subfamily **Cerithiinae** Fleming, 1822

Genus *Fastigiella* Reeve, 1848

Genus *Fastigiella* Reeve, 1848:14–15. Type-species: *Fastigiella carinata* Reeve, 1848, by monotypy.

Diagnosis: Shell large, turreted, high spired, sculptured with 3 major, strong, raised spiral cords per whorl, exclusive of body whorl. Aperture ovate, about ¼ the shell length, and with short, recurved anterior canal. Pseudumbilicus and siphonal fasciole present on mature adults. Taenioglossate radula with lateral teeth having large basal plate and long lateral extension; marginal teeth long, hook-like. Paired salivary glands in front of nerve ring. Hypobranchial gland comprised of many transverse leaflets. Strong longitudinal ridge bisects distal oviductal groove of pallial oviduct.

Remarks: Various fossil species have been referred to *Fastigiella* (*e.g.*, by Cossmann, 1906:93–95). The only one appearing to us as possibly belonging in the genus is "*Cerithium*" *rugosum* Lamarck, 1804, of the Middle Eocene of France. *Mellewillia* Cossmann, 1889, named as a Lower Eocene "section" of *Fastigiella* from France, has none of the characteristics of the genus. The Eocene fossil, *Zefallacia australis* (Suter, 1919) somewhat resembles *Fastigiella*.

Fastigiella is a monotypic genus restricted to a small area of the western Atlantic, *i.e.*, the central Bahamas and northwestern Cuba. Its closest relatives appear to be in the cerithiid genus *Pseudovertagus* Vignal, which is now confined to the Indo-Pacific. "*Fastigiella*" *squamulosa* Pease, 1868, from the Tuamotus (Polynesia), is a high-spired Recent *Coralliophila* species.

Figures 1–5. *Fastigiella carinata* Reeve from Holms Cay, Berry Islands, Bahamas. Note light tan spiral band adjacent to suture. Length 44.4 mm (J. Cordy collection). **1.** Apertural view showing anal fasciole and pseudumbilicus. **2.** Lateral view, showing configuration of outer lip. **3.** Basal view, showing reflected anterior canal and basal sculpture. **4.** Dorsal view. **5.** Dorsal view of shell whitened with ammonium chloride to enhance sculptural details. **Figures 6–8.** *Fastigiella carinata*, juvenile from Nassau, New Providence Id., Bahamas. Length 12 mm (J. Lleida collection). **6.** Scanning electron micrograph of early whorl sculpture of specimen in figure 8 (protoconch missing). **7.** Detail of midwhorl sculpture of shell in figure 8. **9.** Upper whorls of *Pseudovertagus aluco* Vignal, showing early sculpture similar to that of adult *Fastigiella*. Total shell length 79 mm. **Figures 10, 11.** Scanning electron micrographs showing microscopic spiral striae (fragments of USNM 859097). **10.** Scale bar = 200 μ m. **11.** Close up of spiral striae showing microscopic cancellate sculpture of striae. Photograph turned 90 degrees; scale bar = 600 μ m.



Fastigiella carinata Reeve

Fastigiella carinata Reeve, 1848:15, 1 fig. Type-locality unknown; subsequently selected: Eleuthera, Bahamas (Sarasúa and Espinosa, 1977:4); two syntypes: BM(NH) 1986272; 1860:122-123, Woodward, 1851:129; H. Adams and A. Adams, 1853:155,655, pl. 16, fig. 7; Chenu, 1859:182, fig. 916; Tryon, 1882:249, pl. 70, fig. 64; pl. 10, fig. 46; Thiele, 1929:214; Wenz, 1943:770, fig. 2230; Pilsbry, 1953:77-78, pl. 6, figs. 2, 3; Kline, 1953:142; Jensen, 1968:6-7, fig.; Abbott, 1974:105, fig. 1009; Sarasúa and Espinosa, 1977: 1-11, fig. 1; Abbott and Dance, 1982:68, fig. 6.

Fastigiella poulsenii Mörch, 1877:207-208. (Type-locality: Eleuthera, Bahamas; holotype: an immature shell without a pseudumbilicus.) Poulsen, 1878:9, no. 533; Pérez Farfante, 1940:71, pl. 13, fig. 3; Jaime and Sarasúa, 1943:57.

Fastigiella (Cerithidea) carinata Reeve. Ford, 1945:8.

Description: *Shell description (figures 1-8, 10, 11):* Shell length 11.2-48.4 mm [mean 33.0 mm; n = 16; observed up to 53.2 mm in Cuba (Sarasúa & Espinosa, 1977:5, 11)]. Spire high; spire angle 25-35 degrees (mean 28 degrees). Shell fairly thin to thick, white, sometimes with brownish orange or light tan spiral band (figures 1, 2, 4). Periostracum inconspicuous, but scale-like when viewed microscopically (figures 10, 11). Protoconch unavailable (shell prone to decollation). Teleoconch whorls 11.7+. Teleoconch initially with a subsutural ramp and 3 spiral cords, the uppermost forming a slight shoulder (figures 6, 7). Upper whorl cords with slight nodes or prickles caused by weak, regularly spaced axial growth wrinkles. Lower whorls of large shells with increasing number of spiral cords (figures 1-5), the new ones beginning as intercalations. Subsutural ramp becoming a wide, slightly raised cord accompanied below by a smaller cord. All other cords larger and about equal-sized on large shells. Counting all 3 kinds of cords, there are 11-14 on last whorl of large shells. Fine spiral threads on all cords and interspaces (figure 10). Pair of subperipheral keels absent on small shells. Suture slightly impressed. Several irregularly spaced faint varices present on lower whorls of large shells (figure 3). A short, somewhat recurved but deeply incised anterior canal present (figures 1, 3, 8). On small shells its left edge is a slightly raised spiral fold joining the columella distally; on large shells a faint swelling in its place (figure 1). Anterior canal variable in width (averaging fairly wide) and, after shell attains length of about 25 mm, leaving a spiral siphonal fasciole with strong growth lines (figure 3). A pseudumbilicus (figure 1) of variable width (up to 1.3 mm) and morphology develops after shell reaches length of about 25-35 mm. Parietal callus thin, conforming with underlying cords on small shells; on large shells callus thick and not conforming, so that there can be 1-3 false umbilical chinks

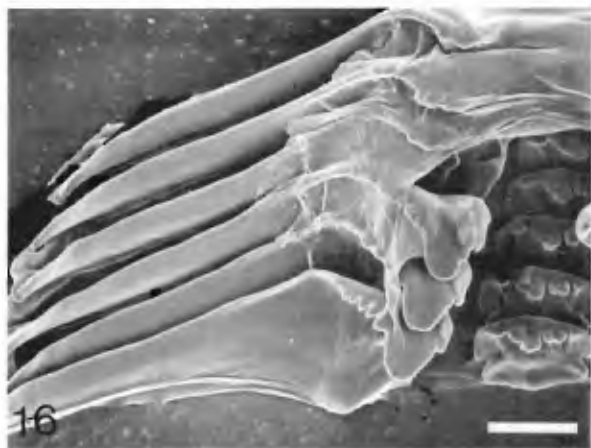
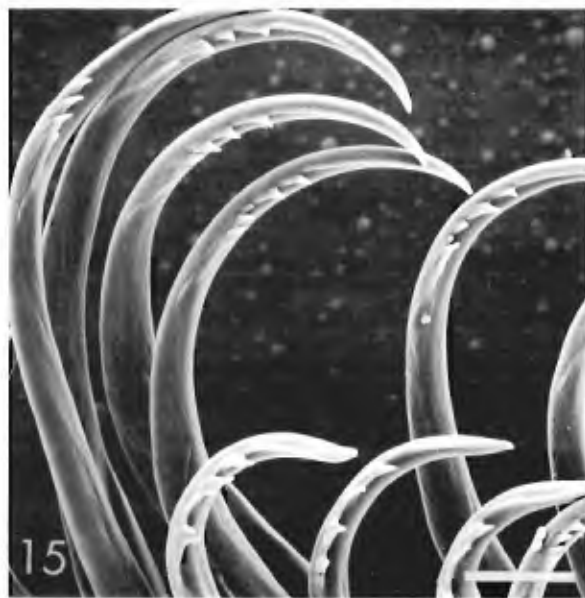
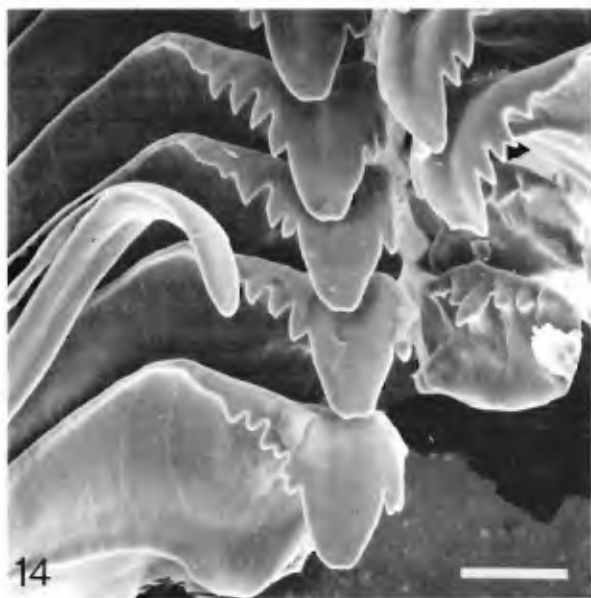
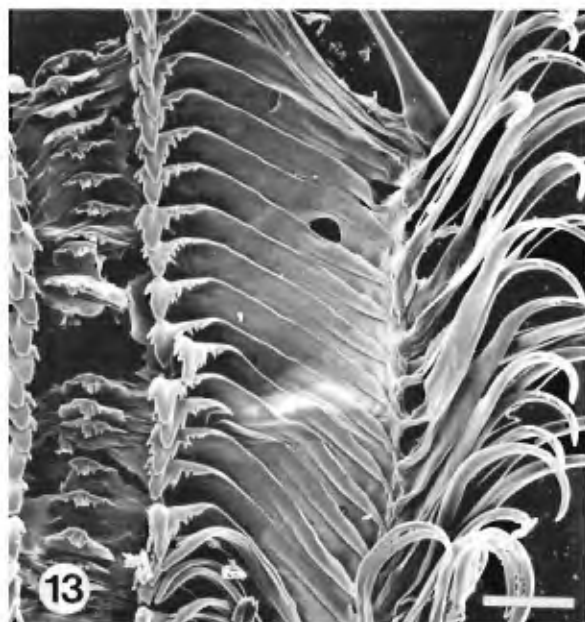
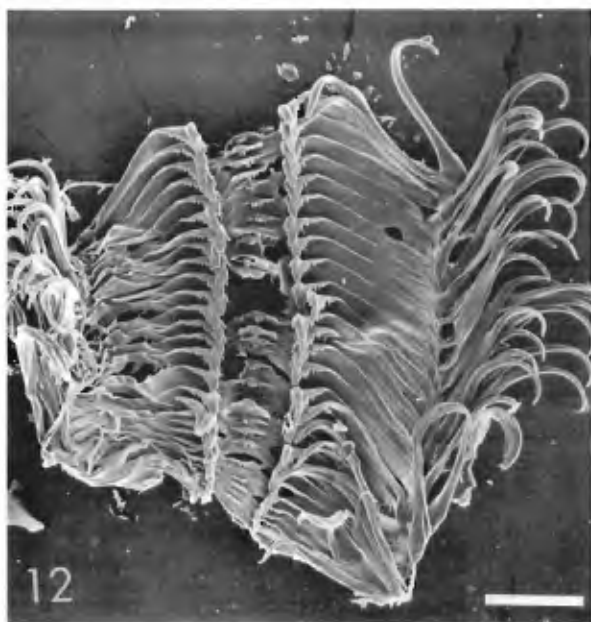
formed by cord interspaces to produce a siphonal fasciole. Faint, wide posterior canal present on large shells, viewed aperturally (figure 1). Columella roundly concave. Outer lip thin in juveniles and thick on large shells; no thick peritreme callus, eversion of outer lip, or up-turned suture near outer lip.

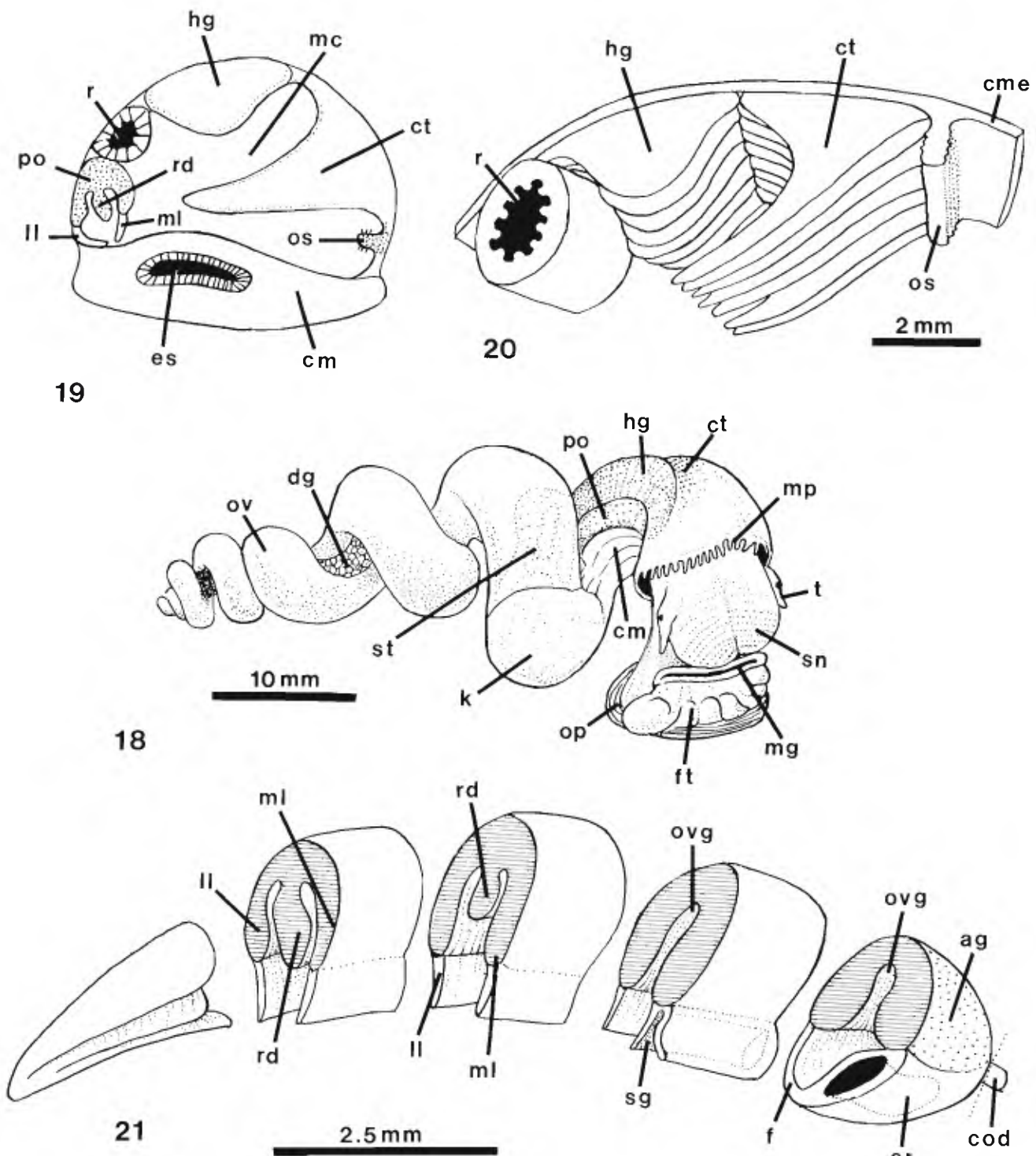
External anatomy (figure 18): Adult female (shell 32 mm long) body slender, tapering, and comprising 6 or 7 whorls. Animal whitish with tiny red dots on head-foot. Head has conspicuously large, broad, spade-shaped snout, bilobed at the tip (figure 18, sn). Pair of stubby cephalic tentacles and tiny black eye at peduncular base of each tentacle (figure 18, t). Foot thick and muscular. Propodial mucus gland (figure 18, mg) is a deep slit along leading edge of anterior sole. Sole composed of thick, hard, yellowish tissue thrown into lumps. Large, dark brown, horny operculum (figure 17) thick, ovate, paucispiral with subcentral nucleus and filling the shell aperture. Columellar muscle (figure 18, cm) thick and short, about ½ mantle cavity length. Mantle edge thick and dorsally fringed with short papillae (figure 18, mp). Inhalant and exhalant siphons inconspicuous except for slight thickening of mantle edge. Posterior 5 whorls comprise digestive gland (figure 18, dg), which is overlain by ovary (figure 18, ov). The 2 whorls above body whorl accommodate the kidney (figure 18, k) and stomach (figure 18, st), respectively.

Mantle cavity: Mantle cavity deep and spacious, occupying about 2.5 whorls. Osphradium (figures 19, 20, os) a raised ridge, squarish in cross section, darkly pigmented and probably highly ciliated on each side. Osphradium begins about 2 mm behind distal end of ctenidium and extends for ¾ ctenidial length. It lies closely adjacent to ctenidium, but deviates from it in region of inhalant siphon. Ctenidium (figures 19, 20, ct) a narrow, large, well-developed organ comprising long, triangular filaments with finger-like tips. Each filament has a supporting rod along its leading edge. Hypobranchial gland (figures 19, 20, hg) a highly developed, thick organ comprising a series of thin, transparent, semicircular leaflets that run adjacent to ctenidium and extend length of mantle cavity. Spaces between each leaflet filled with flocculent, acellular mucus-like material that may be secreted by epithelial lining of leaflets. Rectum (figures 19, 20, r) tubular and thick, filled with rod-shaped fecal pellets without sand and consisting of detritus.

Alimentary tract: Broad, spade-shaped snout (figure 18, sn) highly muscular and bearing relatively large buccal mass. Pair of small, semilunar, chitinous jaws comprising many small, overlapping scales at tip of buccal mass.

Figures 12-17. Scanning electron micrographs of radula and operculum of *Fastigiella carinata* (USNM 859097). **12.** View of part of radular ribbon with marginal teeth spread out. Scale bar = 125 µm. **13.** Half row of teeth showing long lateral tooth and narrow hooklike marginal teeth. Scale bar = 63 µm. **14.** Detail of rachidian tooth, showing basal plate and cusps of rachidian and lateral teeth. Scale bar = 25 µm. **15.** Tips of marginal teeth showing small denticles. Scale bar = 19 µm. **16.** Rachidian and lateral teeth showing long lateral-basal extensions of lateral teeth. Scale bar = 43 µm. **17.** Operculum. Length 8.4 mm.





Figures 18–21. Anatomical features of *Fastigiella carinata*. **18.** External features of female viewed from the right. **19.** Schematic representation of cross section behind nerve ring showing morphological relationships of major mantle cavity organs. **20.** Schematic representation of section of mantle cavity organs exclusive of pallial gonoduct showing relationship of hypobranchial gland leaflets to rectum and ctenidium. **21.** Schematic representation of pallial oviduct and its internal components. ag = albumin gland; cm = columellar muscle; cme = cut mantle edge; cod = coelomic oviduct; ct = ctenidium; dg = digestive gland; es = esophagus; f = fusion of lateral and medial laminae; ft = foot; hg = hypobranchial gland; k = kidney; ll = lateral lamina; mc = mantle cavity; mg = mucus gland; ml = medial lamina; mp = mantle papillae; op = operculum; os = osphradium; ov = ovary; ovg = oviductal groove; po = pallial oviduct; r = rectum; rd = central ridge dividing anterior oviductal groove; sg = sperm gutter; sn = snout; sr = seminal receptacle; st = stomach; t = cephalic tentacle.

Buccal mass has long odontophore. Salivary glands consist of pair of weakly coiled tubes that originate in front of nerve ring and empty at dorsal anterior part of buccal mass near jaws. Salivary glands thicker anteriorly. Mid-esophagus slightly expanded and has large dorsal food channel. Large stomach occupies about 1.5 whorls and comprises short style sac, hyaline gastric shield, large central pad-like ridge, and enormous sorting area.

Radula (figures 12–16): Taenioglossate radula short, about $\frac{1}{16}$ shell length ($L = 2.2$ mm), and comprises around 280 transverse rows of teeth. Rachidian tooth wider than high, with convex tip and squat, hourglass-shaped basal plate (figure 14). Cutting edge of rachidian tooth comprises central cusp flanked on each side by 3 smaller denticles. Lateral tooth conspicuously large with very long lateral extension of basal plate and weak central buttress that extends posteriorly (figure 16). Cutting edge of lateral tooth serrated with 2 or 3 inner denticles, a large, pointed central cusp, and 4–6 outer denticles (figure 14). The two marginal teeth (figures 13, 15) are narrow, elongate, curved hooks with pointed tips and are wider where attached to basal radular membrane. Outer marginal tooth slightly larger and less hooked than inner one. Marginal teeth serrated near their distal outer sides with 3–5 tiny, sharp denticles (figure 15).

Reproductive tract: Large, acinous ovary (figure 18, ov) overlies digestive gland and occupies the first 4 or 5 whorls. It appears to consist of large cells. Female pallial oviduct (figures 19, 21) a very long open tube, comprising lateral (figures 19, 21, ll) and medial (figures 19, 21, ml) laminae connected to mantle floor along their dorsal margins. Posterior end of pallial oviduct has thickened walls and is closed by fusion of the 2 laminae (figure 21, f). Thick albumen gland (figure 21, ag) at posterior end of pallial oviduct. Seminal receptacle (figure 21, sr) and sperm gutter (figure 21, sg) lie near posterior end of medial lamina. Oviductal groove (figure 21, ovg) formed at thick, glandular, connecting bases of these 2 laminae. Oviductal groove divided along its length by large, central ridge (figure 21, rd) that begins anteriorly and extends back a little past midpoint of pallial oviduct. Ridge tapers and ends just anterior to opening of sperm gutter to seminal receptacle on medial lamina. This ridge effectively divides anterior and median parts of the oviduct into 2 open chambers, 1 of which may function as spermatophore bursa. Male gonoduct unknown.

Nervous system: Nervous system epiathroid. Cerebral ganglia joined by short, but distinct, connective. Right pleural ganglion joined to right cerebral ganglion by short connective.

DISTRIBUTION AND ECOLOGY

Distribution (figure 22): *Fastigiella carinata* is known only from the Great Bahama Bank and the northwestern coast of Cuba. The known distribution in Cuba is from Santa Fe, 8 km west of Marianao, Habana, west to Cardenas (Pérez Farfante, 1940:71, pl. 13, fig. 3; Sarasúa &



Figure 22. Geographical distribution of *Fastigiella carinata* based on available records, showing disjunct range.

Espinosa, 1977; USNM 434792), a coastline only about 140 km long that is not the nearest part of Cuba to the Bahamas. Although previously published Bahamian records were from Andros and Eleuthera only, *Fastigiella* has been found on the eastern coast of Andros Island; the northern coast of New Providence Island; the Berry Islands; the southwestern coast of Eleuthera and the nearby Schooner Cays; Cat Island; Exuma Cays. This species appears to be absent from the Little Bahama Bank.

Fastigiella carinata seems to be fairly rare in the localities discussed above, but may occur in other parts of the Bahamas and Cuba that are not as conchologically well known. Sarasúa and Espinosa (1977), who knew of 13 Cuban and only three Bahamian shells, stated that the species is more common in Cuba than in the Bahamas. We have been able to study many Bahamian and only 3 Cuban shells. Like such other shallow water species as *Cittarium pica* (Linnaeus) and *Turbinella angulata* (Lightfoot), this Bahamas-Cuba species has not been reported in Florida or Bermuda.

Ecology: Not much can be said about the ecology of *Fastigiella*. All of the shells available to us are slightly to moderately decollated (figures 6, 7), with not even part of a protoconch present. As the smallest intact whorl width is 0.7 mm, larval development could be planktotrophic or lecithotrophic. Although spawn and larvae remain unknown, the restricted geographic range suggests lecithotrophy or direct development.

The single, live-collected female described herein was found after a five-day blow, intertidally in a small hole on a rocky shelf bordering deeper sand and grass banks. As only one living specimen has been found, it is not certain that this is the normal habitat. Frequently, empty shells are inhabited by hermit crabs which also occur in other shallow water species such as *Tegula fasciata* (Born) and *Cerithium litteratum* (Born). The alimentary tract and fecal pellets indicate typical cerithiacean algal-detrital herbivory.

DISCUSSION

Shell variation: This species does not display the morphological variation that is so common among cerithiid genera such as *Cerithium*, *Clypeomorus* Jousseaume, and *Rhinoclavis* Swainson. Nevertheless, there are some variations that should be noted. Newly dead specimens may have a light tan spiral band adjacent to the suture (figures 1, 2, 4). Sarasúa and Espinosa (1977:6-7) recorded remnants of a brownish orange color pattern on some Cuban shells.

Differences between fully grown and immature shells are most pronounced in the columellar and siphonal areas of the body whorl. Immature shells (figure 8) lack the pseudumbilicus and siphonal fasciole that is present in fully grown specimens (figures 1-3). The narrow pseudumbilicus, which varies in width, and the siphonal fasciole develop after the shell reaches a length of 25-35 mm, as noted by Jensen (1967).

Several Cuban shells reach a length of 52-60 mm, while the largest Bahamian specimens observed are 45-48.4 mm. Fully mature specimens from Cuba, exceeding 35 mm in length and having a deep, narrow pseudumbilicus, differ in having six or seven evenly-sized spiral cords on the penultimate whorl, while those from the Bahamas have only three or four cords. We do not believe that this geographical difference is worthy of subspecific recognition. Cuming's specimen, illustrated by Reeve (1848:15) and copied by Woodward (1851), Tryon (1882), Wenz (1943), and others, is evidently a Bahamian specimen.

Comparative conchology: Before the live-collected specimen became available for study, one of us (Robertson) noted similarities between the shells of full-grown *Fastigiella* and young *Pseudovertagus* Vignal, a genus that has been monographed by Houbriek (1978:99-120). In the Recent fauna, *Pseudovertagus* is restricted to the tropical Indo-Pacific, where there are four species. Houbriek classified *Pseudovertagus* in the family Cerithiidae, subfamily Cerithiinae. Although full-grown shells of *Pseudovertagus* and *Fastigiella* are dissimilar, the sculpture of their upper whorls is very similar. The upper whorls of *Fastigiella carinata* (figures 6, 7) and *Pseudovertagus aluco* (Linné) (figure 9) are illustrated here. Both have three or four main spiral cords per whorl; the cords are prickly or noded; a subsutural ramp is faint to well-developed, and the whorls may or may not be slightly shouldered by one of the cords. *Pseudovertagus* and *Fastigiella* are the only living cerithiaceans known by us to have this apical sculpture. *Cerithium nodulosum* Bruguière, 1792, of the Indo-Pacific, is anomalous within its genus by having apical sculpture intermediate between that of *Cerithium sensu stricto* and those of *Pseudovertagus* and *Fastigiella*. This suggests that these three genera may be fairly closely related.

Pseudovertagus undergoes much greater ontogenetic sculptural change than *Fastigiella*. *Fastigiella* may be a neotenus relative to *Pseudovertagus*. Adults of the two genera both lack a prominent fold on the middle of the

columella such as is present in species of *Rhinoclavis*, an Indo-Pacific genus close to *Pseudovertagus* (see Houbriek, 1978). The outer lip (viewed laterally) is not sinuous in either *Fastigiella* (figure 2) or *Pseudovertagus*, as it is in *Clavocerithium* Cossmann, another genus close to *Pseudovertagus* (see Houbriek, 1978). *Pseudovertagus* is not congeneric with *Fastigiella* as there are a number of conchological and anatomical autapomorphies distinguishing the latter taxon (see "Conclusion").

There are a few vague resemblances between *Fastigiella* and *Campanile* Fischer (Cerithiacea: Campanilidae), of which one relict species occurs in southwest Australia (Houbriek, 1981a). There are two Eocene species of *Pseudovertagus* in France, and two Miocene and Pliocene species in Florida (Houbriek, 1978:116-120), close to *Fastigiella*'s range.

Comparative anatomy: Study of the radula and anatomy has done much to clarify the systematic position of *Fastigiella*. Although only a single, poorly preserved specimen was studied, it was a sexually mature female and provided most of the important characters essential for comparison with other cerithiacean taxa.

Externally, the snail removed from its shell looks very much like some members of the Cerithiidae, such as *Cerithium*, *Rhinoclavis*, and *Pseudovertagus*. Notable features are the broad, bilobed snout, small cephalic tentacles, and tiny eyes (figure 18). The broad snout, contracted by preservation, is probably long and extensible in a living snail. In its contracted state it resembles those observed in *Diastoma* (Houbriek, 1981b:603, fig. 2) and *Campanile* Deshayes (Houbriek, 1981a:269, fig. 3, a, b), some *Cerithium* species, and especially *Pseudovertagus*. The mantle edge, fringed with small papillae (figure 18, mp), and the large, thick operculum (figure 17) are typical of those observed in cerithiids. The sole of the foot, particularly the anterior portion, was composed of thick, yellowish, hard tissue. This may be an unusual feature of *Fastigiella* foot morphology but is more likely an artifact of preservation. Many cerithiaceans have a ciliated groove or ovipositor on the right side of the foot, but no trace of these structures was seen in *Fastigiella*.

The mantle cavity is quite deep and typically cerithiacean in organization. The osphradium appears to be a raised ridge with wrinkled sides. It does not resemble the osphradium of cerithiid species of comparable size, but is more like those seen in potamidids, modulids, and thiarids. An important character is the unusual hypobranchial gland, which comprises a long row of transverse, thin, transparent leaflets and resembles a secondary ctenidium (figure 20, hg). Between the leaflets is thick mucus-like, flocculent, granular material. Due to the poor preservation of the animal, it was not determined if this material was formed by a breakdown of the epithelial lining of the leaflets or was merely hypobranchial gland secretion. The hypobranchial gland is unlike those of all other known cerithiaceans except *Pseudovertagus* species (family Cerithiidae), which have a nearly identical hypobranchial gland (Houbriek, personal observation). The hypobranchial gland of *Cerithium nodulosum* has prom-

inent raised transverse ridges and may be a transitional stage before the development of leaflets as found in *Fastigiella* and *Pseudovertagus* (Houbrick, personal observation). The hypobranchial gland of *Campanile* also has leaflets, but they are tiny and comprise many parallel rows (Houbrick, 1981a:274, fig. 4, A, lhg). This gland is thus a much different structure in *Campanile* and its leaflet structure is not considered homologous with that seen in *Fastigiella*.

The pallial oviduct is a typically cerithiacean open duct. There is no spermatophore bursa, but its function may be taken over by the large closed portion of the posterior pallial oviduct. A spermatophore bursa in the outer or inner laminae of the pallial oviduct is a common feature in most cerithiids and its absence in *Fastigiella* is noteworthy. This pallial oviduct is very similar to those described for many cerithiids, potamidids, and *Diastoma* (see Houbrick, 1974, 1978, 1981b). The posterior end of the pallial oviduct is closed by fusion of the edges of the two laminae (figure 21, f). The pallial oviduct of *Fastigiella* differs from all other known cerithiacean pallial oviducts in having a large, swollen central ridge (figure 21, rd) at the base of the anterior oviductal groove. This ridge diminishes in size and disappears about midway along the pallial oviduct effectively forming two anterior oviductal grooves that merge past the middle of the pallial oviduct to form the main posterior oviductal groove. The function of this apomorphic structure is unknown. The ovary is large and differs from other observed cerithiid ovaries in being highly acinous. Males remain unknown but, on the basis of female anatomy, are expected to be aphallate and have open pallial gonoducts.

The alimentary tract is indicative of a microphagous, herbivorous mesogastropod. The short radula is different from that of most cerithiids in having long lateral teeth with conspicuous platelike lateral extensions (figure 16) and long hooklike marginals with microscopic serrations near their tips (figure 15). Similar lateral and marginal teeth occur in the cerithiids *Clavocerithium taeniatum* (Quoy & Gaimard) and *Rhinoclavis sordidula* (Gould) (Houbrick, 1975:101, figs. 9–12; 1978:71, pl. 40). Some planaxid radulae have similar lateral teeth (Houbrick, 1987). Although the salivary glands, or at least the left salivary gland, pass through the nerve ring in most cerithiids, the salivary glands of *Fastigiella* originate in front of the nerve ring. The esophagus widens behind the nerve ring, but there is no trace of an esophageal gland. A large dorsal food groove is present. The large, complex stomach with its extensive sorting area and large, raised central ridge (pad) is not unlike stomachs described for many other cerithiacean taxa. The number of openings to the digestive gland was not ascertained.

CONCLUSIONS

On the basis of the presence of a taenioglossate radula, proboscis structure and alimentary tract anatomy, we can confidently state that *Fastigiella* is a mesogastropod

(order Caenogastropoda Cox, 1959). The open pallial oviduct and internal arrangement of the seminal receptacle and spermatophore bursa in the medial lamina strongly support an assignment to the superfamily Cerithiacea. Other external anatomical structures such as the head and snout, fringed mantle edge, corneous, ovate, paucispiral operculum, and propodial mucus gland are characters common in many cerithiacean families. Internal anatomical structures of the alimentary tract are likewise consistent with the cerithiacean anatomical organization.

Most characters, including those of the shell, indicate the family Cerithiidae as a suitable assignment for *Fastigiella*. Ontogenetic shell characters and a few anatomical characters suggest a close relationship to the genus *Pseudovertagus* Vignal, 1904. The unusual shell sculpture of three or four main spiral cords per whorl on the post-nuclear and upper whorls of *Fastigiella* is very similar to that seen in *Pseudovertagus* species. The broad snout is a character shared with *Pseudovertagus*. The hypobranchial gland comprised of transverse leaflets is likewise a synapomorphic character found only in *Pseudovertagus* and *Fastigiella*.

The pseudumbilicus and siphonal fasciole with one to three false umbilical chinks formed by cord interspaces in large shells are autapomorphic characters clearly defining *Fastigiella*. Other shell characters identifying the axon are the strong spiral sculpture of three or four rounded cords per whorl, and the short, slightly reflected siphonal canal.

The unusual, large ridge bisecting the anterior oviductal groove of the pallial oviduct is an autapomorphy that sets *Fastigiella* aside as a good genus. Other non-apomorphic anatomical characters including placement and origin of the salivary glands anterior to the nerve ring, the shape of the lateral and marginal teeth, and the unusual leaflets of the hypobranchial gland, are more equivocal, but together provide a distinctive set of characters defining this taxon as a separate genus.

No radular or anatomical characters have emerged from this study to suggest that *Fastigiella* should be given a higher than generic status. *Fastigiella* is a relictual, and geographically disjunct genus (at least on the basis of available material). We assign this genus in the Cerithiidae, close to the genus *Pseudovertagus*. Although it is unlikely that this assignment is incorrect, further study of males, other females, eggs, and larvae may provide more characters supportive of this classification. The systematic position advocated herein is based on knowledge of a single female snail and is tentative until more is known about this rare animal.

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Note added in proof:

Another live specimen of *Fastigiella* was recently collected by Kevan Sunderland in 1m depth on a patch reef, half buried on sand, at Marsh Harbour, Abaco, Bahamas.