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Anatomy and Reproductive Biology of Two Western Atlantic Species of Vitrinellidae, With a Case of Protandrous Hermaphroditism in the Rissoacea

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ABSTRACT

Two western Atlantic vitrinellids, *Cyclostremiscus beauii* (Fischer, 1857) and *Circulus texanus* (Moore, 1965) new combination are redescribed based on a study of live snails from the burrows of the stomatopod crustacean *Lysiosquilla scabricauda* (Lamarck, 1818). Anatomy and reproductive biology are emphasized, with the first recorded description of spawn and larval development in the family. Synonymies are given, and a lectotype is selected for *Cy. beauii*. Literature data concerning anatomy are reviewed for the marine near-planispiral rissoaceans; Vitrinellidae (including *Cyclostremiscus* and *Circulus*, with Circulidae as a synonym) is considered distinct from Tornidae. Unusual morphological aspects of *Cy. beauii* are discussed, including external ciliation patterns, pallial tentacles (which are functionally and morphologically different from each other), and stomach morphology (with a large posterior chamber). Protandrous sequential hermaphroditism in *Cy. beauii* is inferred (for the first time in the Rissoacea) from morphological evidence of sex change correlated with size.

Key words: *Cyclostremiscus*; *Circulus*; Vitrinellidae; Tornidae; Rissoacea; systematics; anatomy; hermaphroditism.

INTRODUCTION

Despite the great number of nominal species assigned to the poorly defined, cosmopolitan, marine rissoacean family Vitrinellidae Bush, 1897, little is known about the biology of its members. Their small size, mostly unknown habitats, poor representation in collections, and frequent confusion with other small-shelled members of groups such as Cyclostrematidae Fischer, 1885, Skeneidae Thiele, 1929, Turbinidae Rafinesque, 1815, and Tornidae Sacco, 1896, may account for the lack of attention paid to this family, and why authors who have attempted revisions (*e.g.*, Tryon, 1888; Bush, 1897; Melvill, 1906; Pilsbry & Olsson, 1945; Pilsbry & McGinty, 1945a,b, 1946a,b, 1950; Laseron, 1958; Moore, 1964; Adam & Knudsen, 1969) relied almost entirely on shell characters to distinguish taxa on all taxonomic levels.

Aside from Pilsbry and McGinty's (1945a, 1946b) sketches of crawling animals of several nominal genera,

and studies on the gross morphology of *Cochliolepis parasitica* Stimpson, 1858 (by Moore, 1972) and *C. albicerata* Ponder, 1966 (by Ponder, 1966), published information on anatomy is available for only one species of this family, *Circulus striatus* (Philippi, 1836) from the eastern Atlantic. Data on *Ci. striatus*, extensively presented by Fretter (1956) and later summarized by Fretter and Graham (1962, 1978), were based on material which Fretter and Graham (1978:228) described as "the only live specimens . . . obtained by Fretter (1956) from the stomach of the starfish *Astropecten* . . . dredged on sandy bottoms 28-30 m deep in the Gulf of Gascony."

Thus, the present concept of vitrinellid anatomy is based mainly on Fretter's description of a single species, *Circulus striatus*, the type species of the name-bearing genus of the nominal family Circulidae (see Discussion, below). Discussions of phylogenetic relationships (or synonymies) between families such as Vitrinellidae and Tornidae have demonstrated the need for anatomical and reproductive data for these groups (*e.g.*, Fretter, 1956; Taylor & Sohl, 1962; Moore, 1965; Golikov & Starobogatov, 1975; Boss, 1982; Graham, 1982; Ponder, in press).

Studies on two species of western Atlantic Vitrinellidae are reported herein. Populations of *Cyclostremiscus beauii* (Fischer, 1857) and *Circulus texanus* (Moore, 1965) were discovered in Florida in sand-flat burrows of the stomatopod crustacean *Lysiosquilla scabricauda* (Lamarck, 1818). These burrows are U-shaped and extend up to 1.5 m into the sediment, with horizontal distances of 6-7 m between the two openings; a pair of stomatopods inhabits each burrow system, maintaining it over long periods of time (Serène, 1954; R. B. Manning, personal communication). *Cyclostremiscus beauii*, with a shell diameter of 6-8 mm, is one of the largest vitrinellids, a fact that facilitated detailed study of its morphology and anatomy and allowed a test of Fretter's hypothesis that some of the characters found in the much smaller (2 mm) *Circulus striatus* are size-related (Fretter, 1956:380).

Special emphasis was placed upon characters of the reproductive system, for which Moore (1964:18) noted "Nothing is known of the reproduction of the family

except that the animals are dioecious, and that the male is provided with a penis." Data presented herein suggest that *Cy. beaultii* is a protandrous sequential hermaphrodite. Only incomplete data are available for *Circulus texanus*, as animals of this species were collected only twice, both times before the actual beginning of this study. However, since gross anatomy, spawn, and developing eggs were observed for this species, available data are presented here.

MATERIAL AND METHODS

Samples were taken from stomatopod burrows in shallow-water sand flats in the Indian River lagoon just inside the Ft. Pierce Inlet, St. Lucie County, eastern Florida (27°28.3'N, 80°17.9'W) using a stainless steel bait pump ("yabby pump") in conjunction with sieves of 1–2 mm mesh. Depths at low tide ranged from less than 0.5 m to supratidal, wherein the water level lay several centimeters below the level of the sand.

Living snails were maintained in finger bowls of seawater at room temperature (24 °C). Carmine and fluorescein sodium particles were used to observe ciliary action and currents produced by the animals. For gross dissections, shells were cracked and animals subsequently relaxed using magnesium sulfate crystals ("epsom salts"). Other anaesthetic chemicals (7% magnesium chloride in distilled water, menthol crystals) were tried but produced little or no effect with gradual addition, or too strong an effect resulting in retraction. Methylene-blue/basic-fuchsin and neutral red were used to better delineate tissues and organs in gross dissections. Structures and organs were measured following in part the outline given by Davis and Carney (1973: fig. 4A). Terminology of the nervous system is after Davis *et al.* (1976).

For histological sectioning, animals were relaxed as above and fixed in either glutaraldehyde-formalin solution (4% formalin, 2.5% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2) or 5% buffered formalin (Humason, 1962:14). Shells were either broken and removed, or dissolved in a 1% solution of ethylene diamine tetraacetic acid (EDTA, adjusted to pH 7.2). Specimens were embedded in paraffin, sectioned at 5–7 μ m and stained with Alcian Blue/Periodic-Acid-Schiff (PAS), counterstained with Harris' Hematoxylin/Eosin (Humason, 1962: 125, 269, 298). Staining reactions described in the text refer to this method unless otherwise noted. Photomicrographs of sections were taken with a Zeiss Photomicroscope-3.

Radulae and jaws were extracted by dissolving the surrounding soft tissue in a solution of 10% sodium hydroxide. Spermatozoa were prepared for SEM by placing a drop of concentrated sperm in seawater onto a coverslip placed in a covered petri dish containing droplets of 25% glutaraldehyde, and passing the coverslip through an ethanol series ending in acetone, and then critical-point drying the sample. Whole animals were fixed, passed through an ethanol series, transferred to amyl acetate, and critical-point dried. These, together with air-dried

shells, radulae, jaws, and opercula were coated with gold/palladium, and scanned using a Zeiss Novascan-30. Figures 1–3 were photographed using a Hitachi S-570 scanning electron microscope. Radular terminology is after Bandel (1984:3).

Protoconch and teleoconch diameters were recorded as the greatest dimension perpendicular to the columellar axis. Teleoconch height was the greatest dimension parallel to the columellar axis, measured from the apex to the base of the aperture. Umbilical diameter was the greatest distance between the columellar lip and the most prominent portion of the umbilical wall, measured in ventral view. Teleoconch whorls were counted from the protoconch II–teleoconch line to the farthest extent of the periphery (= the point on the outer lip used for greatest shell diameter). The number of protoconch whorls was determined by the method of Taylor (1975:10; summarized by Jablonski & Lutz, 1980:332, fig. 4).

Cited repositories are (* indicates location of voucher material):

- ANSP—Academy of Natural Sciences of Philadelphia, PA.
- CAS—California Academy of Sciences, San Francisco.
- *IRCZM—Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution (HBOI), Ft. Pierce, FL.
- MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA.
- MNHN—Muséum National d'Histoire Naturelle, Paris.
- *RSMAS—Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, FL.
- UNC-IMS—Institute of Marine Sciences, University of North Carolina, Morehead City, NC.
- *USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC.

RESULTS

Rissoacea Gray, 1847

= Truncatellacea Gray, 1840, "submission to be made to ICZN to suppress this name" (Ponder, 1985:15).

Vitrinellidae Bush, 1897

Cyclostremiscus Pilsbry & Olsson, 1945:266.

Type species: *Vitrinella panamensis* C. B. Adams, 1852 (by original designation).

Cyclostremiscus beaultii (Fischer, 1857)
(figures 1–52; tables 1, 2)

Adeorbis Beaultii Fischer, 1857a:173 [*nomen nudum*].

Adeorbis Beaultii Fischer, 1857b:286, pl. 10, fig. 12 [Guadeloupe].—Bush, 1897:104.

Cyclostrema Beani [sic].—A. Adams, 1866:251, pl. 255, fig. 25 [after Fischer, 1857b].

Cyclostrema bicarinata Guppy, 1866:291, pl. 17, figs. 5a,b ["Miocene" (Lower Pliocene), Jamaica].

- Skenea sulcata* "Bush" Simpson, 1887:61 [*nomen nudum*; see Moore, 1964:131].
- Adeorbis Beau*i.—Dall, 1889:150; 1892:345.
- Adeorbis Beau*i var. *bicarinata*.—Dall, 1903:1595 ["Oligocene," Jamaica].
- "*Circulus*" *bicarinatus*.—Woodring, 1928:439, pl. 37, figs. 10–12 [neotype designation].
- "*Adeorbis*" *beau*i.—Woodring, 1928:440.
- Circulus strophorus* M. Smith, 1937:67, pl. 6, figs. 2a,b [Pliocene, Florida].
- Cyclostrema angulata*.—Hertlein & Strong, 1951:110 [West Indies].
- Cyclostremiscus (Ponocyclus) beau*i *bicarinatus*.—Pilsbry, 1953:427, pl. 55, figs. 1–1e.
- Vitrinella (Solariorbis) beau*i.—Abbott, 1954:138.
- Vitrinella beau*i.—Wells *et al.*, 1961:267.
- Cyclostremiscus beau*i.—Moore, 1964:131–135.—Morris, 1973:138, pl. 40, fig. 19.—Porter, 1974:143.—Emerson & Jacobson, 1976:64, pl. 18, fig. 21.—Abbott & Dance, 1982:58, text-fig.
- Cyclostremiscus (Ponocyclus) beau*i.—Warmke & Abbott, 1961:60, pl. 11, fig. b.—Humfrey, 1975:76, pl. 3, figs. 11–11a.
- Cyclostremiscus (Ponocyclus) beau*ii.—Abbott, 1974:85, text-fig. 786.—Rios, 1975:38, pl. 10, fig. 131; 1985:41, pl. 16, fig. 177.—Vokes & Vokes, 1983:15, pl. 25, figs. 4–4a.

Material examined: Lectotype (designated herein): 10.5 mm, MNHN unnumbered (Guadeloupe). Neotype of *Cyclostrema bicarinata*: 7.4 mm, USNM 115621 (Pliocene, Jamaica); other material: 60 specimens: NORTH CAROLINA: 1 specimen with dried animal, BEVERIDGE Sta. I (ex *Astropecten*), UNC-IMS. FLORIDA: Ft. Pierce Inlet: 10 March 1987, 1 male, 3 unsexed; 2–3 May 1987, 1 male; 24 June 1987, 3 males; 3 August 1987, 6 males; 31 August 1987, 7 females, 11 males; 14 September 1987, 1 female; 27 September 1987, 3 females, 2 males. Peanut Island, Lake Worth Inlet: 11 August 1987, 1 female, 1 male. Boynton Beach: 1 shell, ANSP 277740. Miami: 1 shell, EOLIS Sta. 311, USNM 449192. Fowey Light: 2 shells, EOLIS Sta. 187, USNM 449193; 1 shell, EOLIS Sta. 129, USNM 449194; 1 shell, EOLIS Sta. 142, USNM 449195; 1 shell, EOLIS Sta. 170, USNM 449196; 1 shell, EOLIS Sta. 355, USNM 449198. Turtle Harbor: 2 shells, EOLIS Sta. 61, USNM 449197. Sand Key: 1 shell, EOLIS Sta. 162, USNM 449199. Key West: 1 shell, EOLIS Sta. 63, USNM 449200. Dry Tortugas: 1 shell, USNM 61114; 1 shell, USNM 271949. Cape San Blas: 1 shell, USBF Sta. 2402, USNM 323914. CARIBBEAN: St. Martin: 1 shell, ANSP 20621. Jamaica: 1 shell, USNM 426872; 1 shell, USNM 442372. SOUTH AMERICA: Coveñas, Colombia: 1 shell, USNM 364409.

DESCRIPTION

Teleoconch (figures 1–3): Shell large for family [usually 2–3 whorls, 6–8 mm diameter (\bar{x} = 6.9, n = 56); height: \bar{x} = 3.8, n = 33; umbilical diameter: \bar{x} = 1.5, n = 30; largest specimen (female): diameter 11.5 mm, height 6.2 mm, umbilicus diameter 2.4 mm, teleoconch whorls 3%, nearly planispiral. Opaque-whitish, with 5–8 strong, concentric ribs on apical side, above peripheral keel. Widely-spaced irregular pustules between ribs (figures

Table 1. Anatomical characters and character states, and habitat types of species in the vitrinellid-tornid complex.

- 1) Projecting snout bilobed, lateral extensions: (a) absent; (b) present.
- 2) Cilia along cephalic tentacles: (a) absent; (b) present.
- 3) Terminal stiff setae on cephalic tentacles: (a) absent; (b) present.
- 4) Number of pallial tentacles.
- 5) Pallial tentacles: (a) all finger-shaped; (b) upper finger-shaped and lower paddle-shaped.
- 6) Upper pallial tentacle: (a) naked; (b) with motile cilia; (c) with stiff setae; (d) with distinct motile cilia and/or stiff setae.
- 7) Lower pallial tentacle: (a) naked; (b) with motile cilia; (c) with stiff setae; (d) with distinct motile cilia and/or stiff setae.
- 8) Gill filaments: (a) projecting from aperture in crawling position; (b) not projecting from aperture in crawling position.
- 9) Anterior foot margin: (a) straight or only weakly indented; (b) cleft.
- 10) Posterior foot margin: (a) simple and rounded or weakly indented; (b) cleft.
- 11) Operculum nucleus: (a) concentric; (b) subcentral.
- 12) Number of whorls on operculum.
- 13) Eyes: (a) distinctly developed; (b) lack nerve supply.
- 14) Osphradium: (a) small, ciliated groove; (b) distinctly developed, paralleling ctenidium.
- 15) Penis: (a) simple, without glandular processes, recurved; (b) with glandular area, directed straight back; (c) with several, finger-like processes.
- 16) Habitat: (a) under rocks; (b) under scales of annelid *Polyodontes lupina* (Stimpson); (c) ? from stomach of starfish; (d) in burrows of stomatopod *Lysiosquilla scabricauda* (Lamarck); (e) sandy mud bottom; (f) under large boulders on well-oxygenated sandy mud.

5–8) on first whorl, becoming more dense and regularly spaced on second whorl. Fields of pustules on body whorl intersected by smaller concentric ridges, 4–6 between major ribs, added first between suture and first major rib, subsequently between peripheral ribs. Strong cords forming sharp peripheral and basal keels, separated by wide flat area, inclined ventrally and marked by growth lines, spiral cords, and pustules. Base widely umbilicate, with 0–5 concentric ribs between basal keel and umbilicus; larger specimens showing decreasing number of ribs with increasing size. Umbilical wall often with 2–4 narrow ribs. Outer lip sinuous, with shallow sutural sinus. Microstructure (figure 4) of 3 layers: 2 thick cross-lamellar layers and 1 thin homogenous outer layer thickened to form spiral ribs.

Protoconch (figures 9–11): Diameter 0.40–0.48 mm (\bar{x} = 0.45, n = 32). Protoconch I (prior to hatching) smooth, of about 1 whorl (diameter \approx 0.23 mm). Protoconch II (after hatching, before settling) of an additional whorl, sculptured with irregular, more-or-less concentric markings (figure 11). Total protoconch of 2 whorls, rather high-spined (spire angle \approx 50°).

Table 2. Summary of anatomical and habitat data for species in the vitrinellid-tornid complex. Characters and character states are listed in table 1. Sources of data listed under each species. ** = type species of genus; * = synonym of type species of genus. *¹ = c according to Moore, 1964:22; d according to Moore, 1964:159. All biological data from Florida, except for *Cochliolepis parasitica* (also South Carolina), *Co. albicerata* (New Zealand), *Circulus striatus* Guernsey, English Channel).

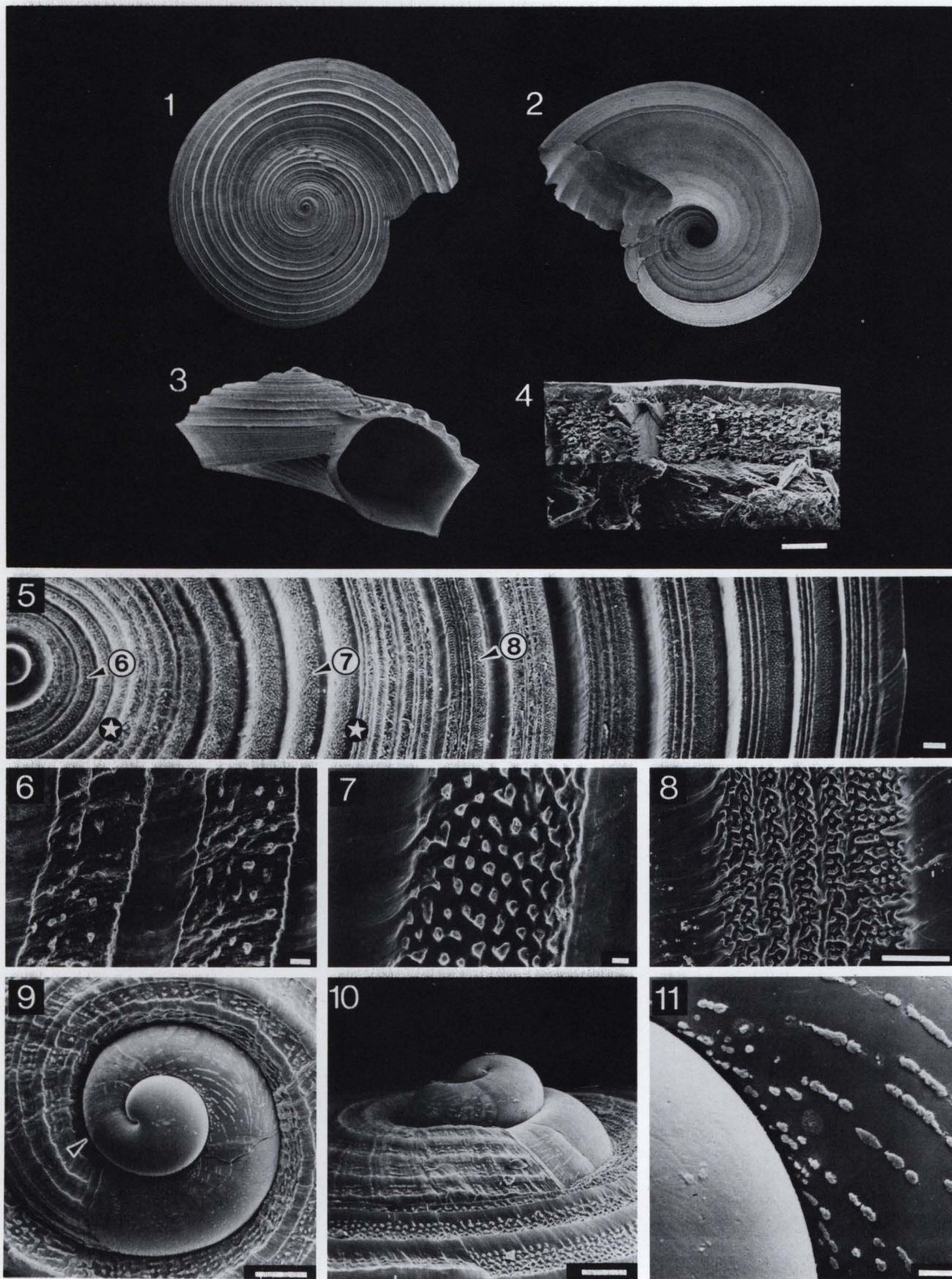
Species	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Group 1																	
** <i>Vitrinella helicoidea</i> C. B. Adams, 1850																	
Pilsbry & McGinty, 1945a: pl. 2, fig. 5; 1946b:13.	a	b	b	2	a	d	a	a	a	a	?	?	a	?	?	a	
* <i>Vitrinella praecox</i> Pilsbry & McGinty, 1946																	
Pilsbry & McGinty, 1945a: pl. 2, fig. 4; 1946b:14.	a	b	b	2	a	a	d	a	a	a	?	?	a	?	?	?	
<i>Teinostoma carinacallus</i> Pilsbry & McGinty, 1946																	
Pilsbry & McGinty, 1946b:17, pl. 2, fig. 6b.	a	b	b	2	a	d	a	a	a	a	?	?	?	?	?	a	
<i>Teinostoma lerema</i> Pilsbry & McGinty, 1945																	
Pilsbry & McGinty, 1945a:6, pl. 2, fig. 1a.	a	b	b	2	a [?]	d	?	a	a	?	?	?	?	?	?	a	
<i>Teinostoma parvicallum</i> Pilsbry & McGinty, 1945																	
Pilsbry & McGinty, 1945a:4, pl. 2, fig. 2.	a	b	b	2	a	d	d	a	a	a	?	?	?	?	?	a	
** <i>Pleuromalaxis balesi</i> (Pilsbry & McGinty, 1945)																	
Pilsbry & McGinty, 1945a:10, pl. 2, fig. 8.	a	b	b	2	a	d	a	a	a	?	?	?	?	?	?	a	
** <i>Cochliolepis parasitica</i> Stimpson, 1858																	
Stimpson, 1858:307ff.; Moore, 1972:100ff.	a	a	b	2	a	a	b	a	a	a	a	?	a	?	a	b	
<i>Cochliolepis albicerata</i> Ponder, 1966																	
Ponder, 1966:38, pl. 5.	a	b	b	1	a	—	a	b	a	a	a	6	a	?	?	a	
* <i>Circulus striatus</i> (Philippi, 1836)																	
Fretter, 1956:369ff.; Fretter & Graham, 1978:227ff.	a	a	b	2	a	c	c	b	a	a	a	12	a	b	a	c	
<i>Circulus texanus</i> (Moore, 1965)																	
This paper.	a	b	b	2	a	c	b	a	a	a	a	8	a	b	a	d	
<i>Cyclostremiscus beauii</i> (Fischer, 1857)																	
This paper.	a	b	b	2	b	c	b	a	a	a	a	7	a	b	a	d	
<i>Cyclostremiscus pentagonus</i> (Gabb, 1873)																	
Bush, 1897:127, pl. 22, figs. 6, 12a–g [as <i>Skenea trilix</i>].	a	?	?	?	?	?	?	?	?	?	?	a	5	a	?	?	e
Group 2																	
** <i>Tomura bicaudata</i> (Pilsbry & McGinty, 1946)																	
Pilsbry & McGinty, 1945a: pl. 2, fig. 9; 1946b:15.	b	a	a	1	a	—	a	b	b	b	b	?	?	?	?	a	
* <i>Parviturboides interruptus</i> (C. B. Adams, 1850)																	
Moore, 1962:695ff., fig. 1B; 1964:21, 156ff.; 1972:106ff., figs. 5, 6.	a	b	b	2	a	* ¹	d	b	a	b	a	?	a	?	b	a	
Group 3																	
** <i>Tornus subcarinatus</i> (Montagu, 1803)																	
Woodward, 1898:140ff., pl. 8, figs. 1–3, 5–7; Fretter & Graham, 1978:229ff.; Graham, 1982:144ff.	a	b	b	2	a	a	a	a	a	a	a	b	?	b	a	c	f

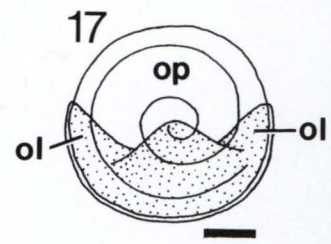
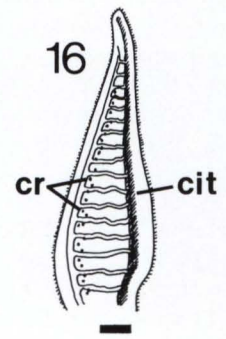
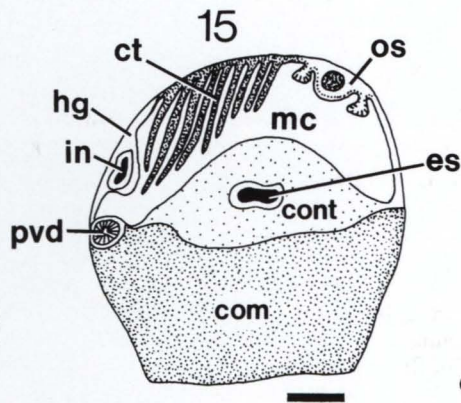
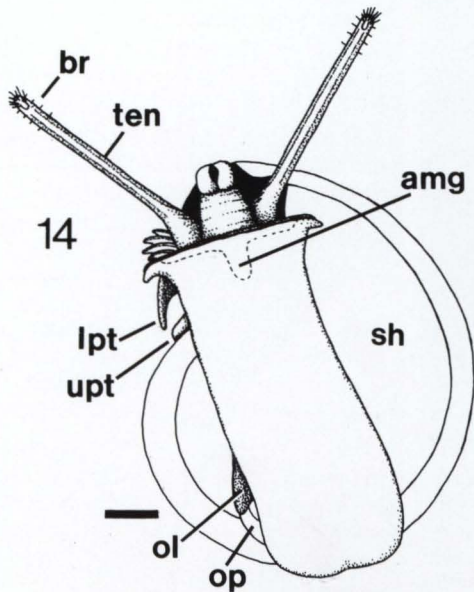
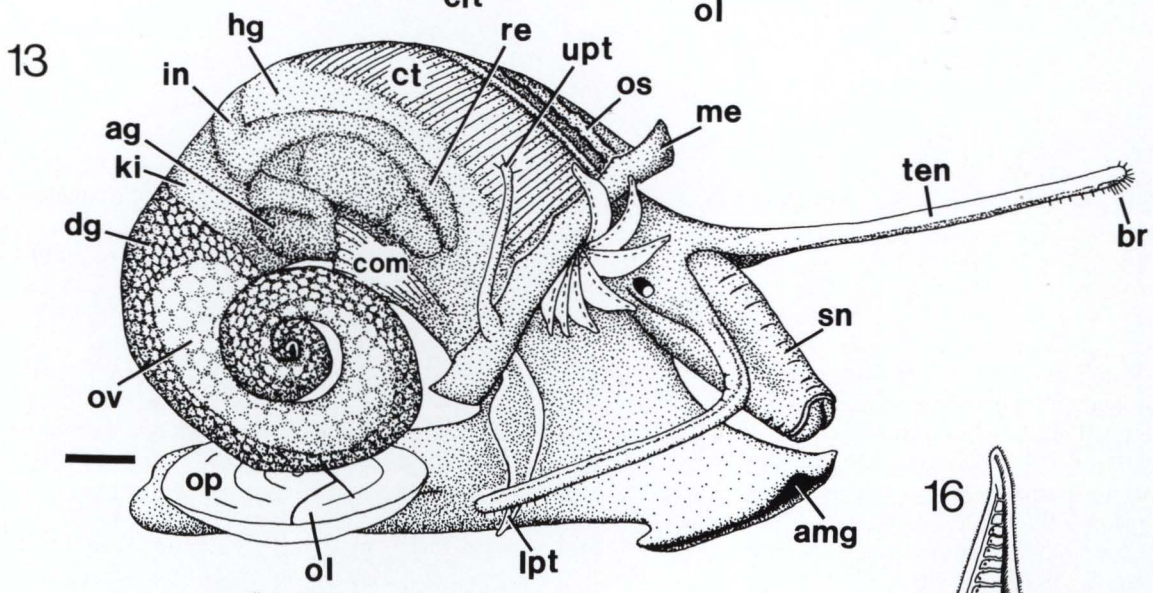
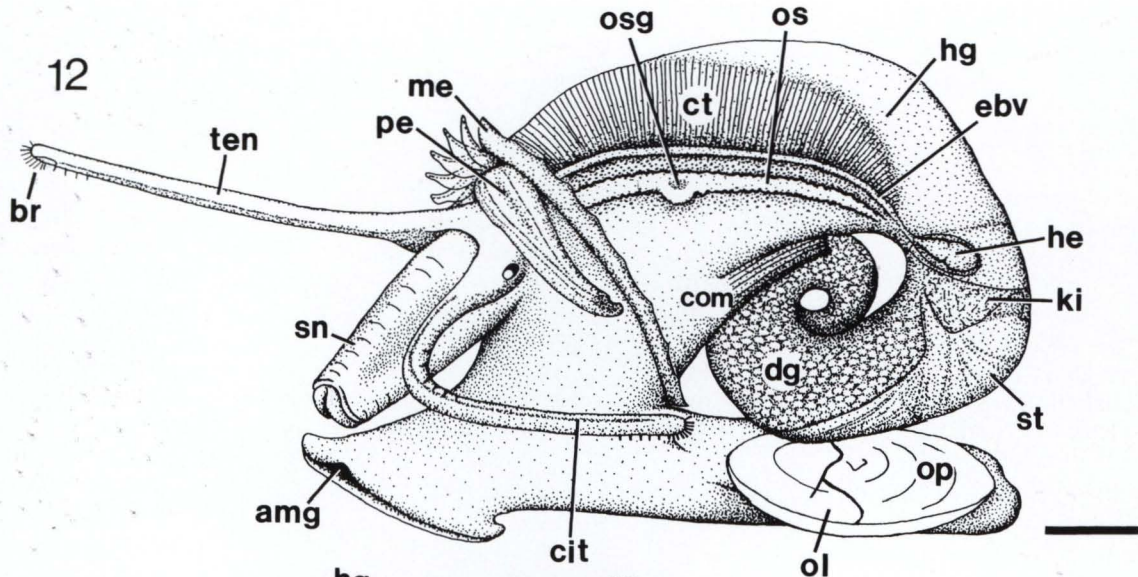
External anatomy and organs of the mantle cavity (figures 12–18, 20–25, 27, 34–37): Living animal translucent yellowish-orange, with buccal mass, anteriormost gill filaments, and tip of penis rose-pink; digestive gland brownish-orange. Base of ctenidial lamellae on osphradial side pigmented white; central area of osphradium white flanked by brown lines on each side, resulting in pattern of parallel lines on left body side (figure 12). Long snout terminating in pair of muscular "lips," separated by vertical slit with mouth opening. Lips sepa-

rated from remainder of snout by strongly ciliated groove. Serial sections revealed 2 narrow longitudinal bands of cilia, situated in grooves on each side, beginning shortly behind tip of snout. Two slender, flexible, cephalic tentacles reaching approximately twice length of snout when fully extended. Left tentacle fitting into shallow notch formed by ventral shell keel (figure 14). Black eyes on outer expanded bases of cephalic tentacles, each equipped with spherical, transparent lens.

Cephalic tentacles exhibiting elaborate pattern of mo-

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Figures 1–11. *Cyclostremiscus beauii*, specimens from Ft. Pierce Inlet, Florida (SEM) (figures 1–3, USNM 846323). **1.** Shell, apical view (8.0 mm diameter). **2.** Shell, umbilical view (5.0 mm diameter). **3.** Shell, apertural view (4.1 mm diameter). **4.** Microstructure of lateral body wall; fracture surface parallel to growing edge. **5.** Teleoconch sculpture, apical view. Circled numbers indicate location of sculptural details in figures 6–8. Stars indicate location of sutures. **6.** Detail of teleoconch sculpture, first whorl. **7.** Detail of teleoconch sculpture, second whorl. **8.** Detail of teleoconch sculpture, third (= body) whorl. **9.** Protoconch, apical view. Arrow indicates sculptural line between protoconchs I and II. **10.** Protoconch, lateral view. **11.** Sculpture of protoconch I (left, smooth) and protoconch II (right, sculptured). Scale bars: 4, 5, 8–10 = 0.1 mm; 6, 7, 11 = 10 μ m.





tile cilia and stiff bristles. Ventral tip of each tentacle with U-shaped, heavily-ciliated groove surrounding smooth area, forming tactile pad (figure 25, tp). Numerous stiff bristles (lost during fixation, therefore not evident in histological or SEM preparations) distal to and just behind pad; additional bristles sparsely distributed over distal quarter of tentacle. Two longitudinal ciliated tracts, situated in grooves, extending from region of pad on ventral side. Near tentacle base, innermost groove sloping dorsally toward dorsal midline; outermost groove ending proximal to expanded tentacle base (figure 20). Flattened base of tentacle facing snout surface covered by additional, irregular, parallel tracts of cilia (figure 20). Third longitudinal ciliated groove on dorsal side of tentacle extending from flattened, triangular area just below eye to near tentacle tip (figure 18). Ciliated grooves usually lined by narrow bands of brown pigment. Cilia fully retractable into grooves. Cilia in grooves with distinct movement pattern (right tentacle: dorsal row—toward tentacle base, inner and outer ventral rows—toward tip; left tentacle: opposite directions). (These movements are easily mistaken for direction of ciliary beating, and therefore current flow. However, further microscopic observation with the aid of carmine and fluorescein sodium particles revealed lateral beating of the individual cilia across the tentacle, away from the snout, indicating that the apparent ciliary movement actually reflects the conduction of nervous impulses along the tentacle.) In cross-section, each tentacle usually with 3 nerves, 1 larger blood sinus, and several smaller blood spaces in central area, especially around nerve cords (figure 24).

Foot (figures 12–14) elongate (just reaching posterior shell margin in crawling animal), flattened, densely and finely ciliated, with anterolaterally recurved corners; broadly rounded posteriorly and slightly indented at posterior terminus. Anterior pedal mucous gland (figure 14, amg) present, opening at center of transverse slit across anterior, leading edge of foot. No posterior mucous gland or metapodial tentacles. Locomotion by ciliary action.

Operculum (figures 17, 34–37) corneous, circular, multispiral, with about 7 whorls and small internal knob, supported by finely ciliated opercular lobes (figure 17, ol) on dorsal side of foot. Lobes simple, unpigmented, without tentacles. Lemon-shaped muscle scar on internal surface of operculum (figure 35).

Mantle edge (figures 12, 13) somewhat scalloped, corresponding to spiral ribs of shell. Large monopectinate

ctenidium, attached along entire length to inner surface of mantle, originating on posterior left, curving over dorsum, terminating just above right eye where last few gill filaments protrude from aperture. Numerous (≤ 180) gill filaments (figures 16, 21) flattened, elongated leaflets, almost finger-like when contracted, forming tapered blades when extended. Filaments longest in central part of gill, decreasing somewhat in size toward both ends. "Supporting rods" lacking; filaments well supplied with blood spaces and muscles (transverse muscle bands giving extended filaments ladder-like appearance; figure 16). Both sides of blade carrying wide band of cilia off-center, closer to left (osphradial) side. Along right side in same relative position, each filament with longitudinal row of small embedded crystals (figure 16, cr). Narrow rim clear, somewhat thinner on "crystal" side, bearing continuous band of cilia. Filaments draining into large efferent branchial vessel leading to heart (figure 12). Filaments hardly reacted to direct physical stimuli, contracting rapidly when either cephalic tentacle or finger-shaped pallial tentacle (see below) touched.

Whitish hypobranchial gland (figures 12, 13) paralleling entire length of rectum, most conspicuous posteriorly. Osphradium (figures 12, 22, 23) paralleling almost entire left side of gill, comprised of wide central area and two strongly developed, heavily ciliated, lateral zones. Central area with irregular chevron-like pattern of tracts of shorter cilia. Osphradial ganglion (figure 12, osg) very conspicuous at point about $\frac{1}{3}$ of total length from mantle edge. Mantle cavity ending immediately behind posterior end of ctenidium.

Two pallial tentacles (figures 13, 27) arising from just inside right mantle edge; upper (= most dorsal) tentacle finger-shaped, unciliated, somewhat closer to mantle edge, curling into shallow sutural sinus, directed dorsally. Lower tentacle paddle-shaped, ciliated at edges (except on narrow stalk) and also across its broad surface; narrow band at tentacle edge unciliated. Single stiff bristles sometimes occurring at tip. Lower tentacle originating at point on mantle edge ventral and slightly more interior to upper finger-shaped tentacle; directed anterolaterally. Stimulation with forceps or needle caused immediate contraction of upper tentacle (followed by contraction of cephalic tentacles and exposed ctenidial filaments). Lower tentacle showed little response to touch and cannot markedly contract (compare tentacles in figure 27). Lower tentacle observed to regulate and enhance water

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Figures 12–17. *Cyclostremiscus beaulti*. **12.** Male, left side, in crawling position (shell removed). Penis reflected anteriorly, out of mantle cavity. **13.** Female, right side, in crawling position (shell removed). Mantle slightly reflected to show relative insertion points of pallial tentacles. **14.** Crawling animal, ventral view. **15.** Diagrammatic cross-section through mantle cavity of male, at level of osphradial ganglion. **16.** Gill filament. **17.** Diagrammatic view of closed operculum, as seen when animal is retracted, showing position of opercular lobes. Scale bars: 12–14 = 1.0 mm; 15 = 0.5 mm; 16 = 0.1 mm.

ag, albumen gland; amg, anterior mucous gland; br, immobile bristles; cit, ciliary tract; com, columellar muscle; cont, connective tissue; cr, crystals; ct, ctenidium; dg, digestive gland; ebv, efferent branchial vessel; es, esophagus; he, heart; hg, hypobranchial gland; in, intestine; ki, kidney; lpt, lower pallial tentacle; mc, mantle cavity; me, mantle edge; ol, opercular lobe; op, operculum; os, osphradium; osg, osphradial ganglion; ov, ovary; pe, penis; pvd, pallial vas deferens; re, rectum; sh, shell; sn, snout; st, stomach; ten, cephalic tentacle; upt, upper pallial tentacle.



flow, by paddle positioning and by strong ciliary action, respectively, in or out of right side of mantle cavity.

Alimentary system: Mouth opening between pair of muscular lips into large buccal mass (figure 42; length 1.3 mm in specimen 8.5 mm shell diameter). Radula protruding from short radular sac (figure 42, ras) extending somewhat behind and to left of buccal mass.

Paired jaws (figure 41) each crescent-shaped, approximately 0.5×0.16 mm (in specimen 7.8 mm shell diameter), composed of interlocking diamond-shaped elements $14 \mu\text{m}$ in length, varying slightly in shape across surface of jaw.

Radula (figures 28–33) taenioglossate, with about 100 rows (max. 138; $n = 7$), length ≈ 1.3 mm, width ≈ 0.2 mm. Rachidian tooth (figure 31) wider than long ($0.40 \mu\text{m}$ wide, $n = 8$), with acute posterior corners projecting laterally, and concave front. Main cusp narrowly-triangular, unserrated, with 4–5 flanking cusps on each side (number of flanking cusps varying within single radula, apparently by splitting and fusion), decreasing laterally in size; base with 1 strong basal denticle per side, midway between posterior corners and central ridge. Lateral tooth (figures 32, 33) with asymmetrical cutting edge, strongly indented at front edge, bearing large, narrowly-triangular, unserrated main cusp and highly variable number of flanking cusps (3–6 inner, 7–8 outer) decreasing in size laterally. Base of lateral tooth with broad central ridge; basal platform long, blade-like. Apex of inner marginal (figures 30, 33) with short, stout main cusp, and 12–14 subequal, inner and outer flanking cusps. Stalk long, blade-like, with robust supporting ridge. Apex of outer marginal (figures 28, 30) with sharp, undulating inner margin (sometimes finely incised into closely-adhering flanking cusps), and smooth, rounded outer margin.

Esophagus opening widely into buccal cavity, without esophageal pouches. Salivary glands (figures 19, 26, 42) narrow, tube-like, emptying into buccal mass at its lateral mid-point, extending posteriorly along esophagus. Position of salivary ducts relative to circumesophageal nerve ring highly variable: some or all passing through ring ($n = 3$; figure 49), stopping just anterior to ring ($n = 4$), or extending past without going through ring ($n = 2$). Relative lengths of salivary glands vary. Anterior part of esophagus, in cross-section (figures 26, 43), bearing 2

muscular, longitudinal, dorsal folds, their lower extensions coiling upwards to form semi-isolated compartments. Anterior esophagus thus divided into strongly ciliated dorsal food channel (figure 26, dfc), larger ventral channel, and two small lateral pockets. Posterior to nerve ring (figure 42), ventral projections into main channel increasing gradually in size, but without clear distinction between anterior and mid-esophageal regions. Food channel remaining dorsal. Dorsal folds and ventral projections gradually decreasing in size, with posterior esophagus as a simple muscular tube.

Stomach (figures 12, 38–40) amber in color, slightly translucent in living animal, approximately 4×1.5 mm (in largest specimen, 11.5 mm shell diameter), lying on exterior surface of visceral coil, appressed to the surface of digestive gland just posterior to heart and kidney, encompassing approximately $\frac{1}{2}$ total length of digestive gland. Stomach consisting of two continuous chambers (figure 39) differing in function: anterior chamber ($\frac{1}{3}$ of total stomach length) containing gastric shield, working end of crystalline style, and all openings into stomach; remaining $\frac{2}{3}$ forming large sorting and storage chamber.

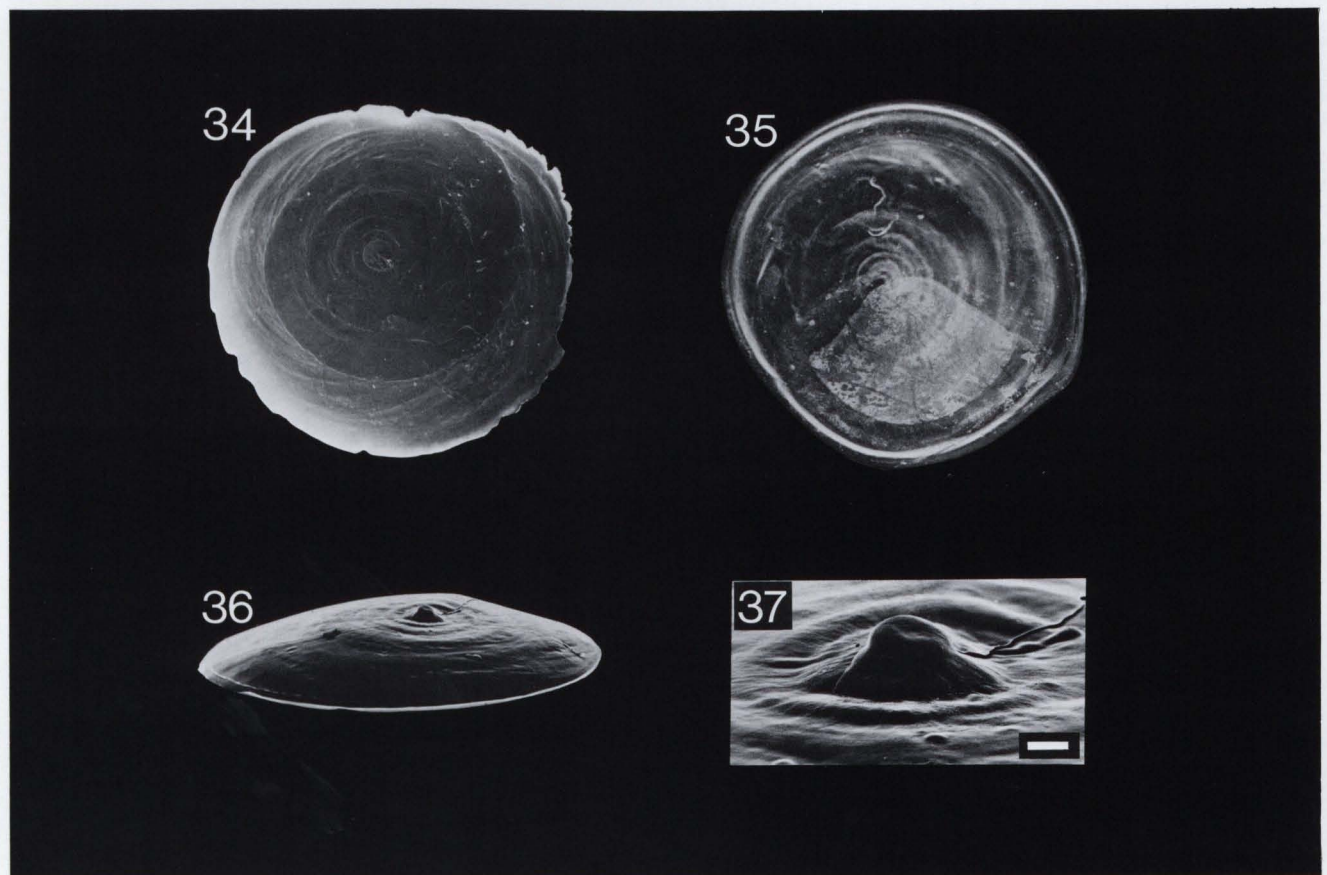
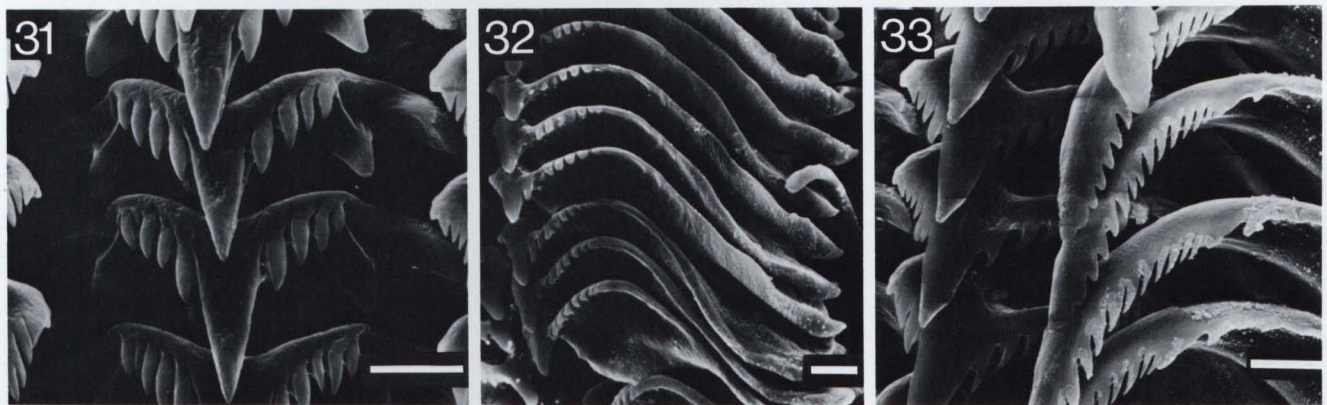
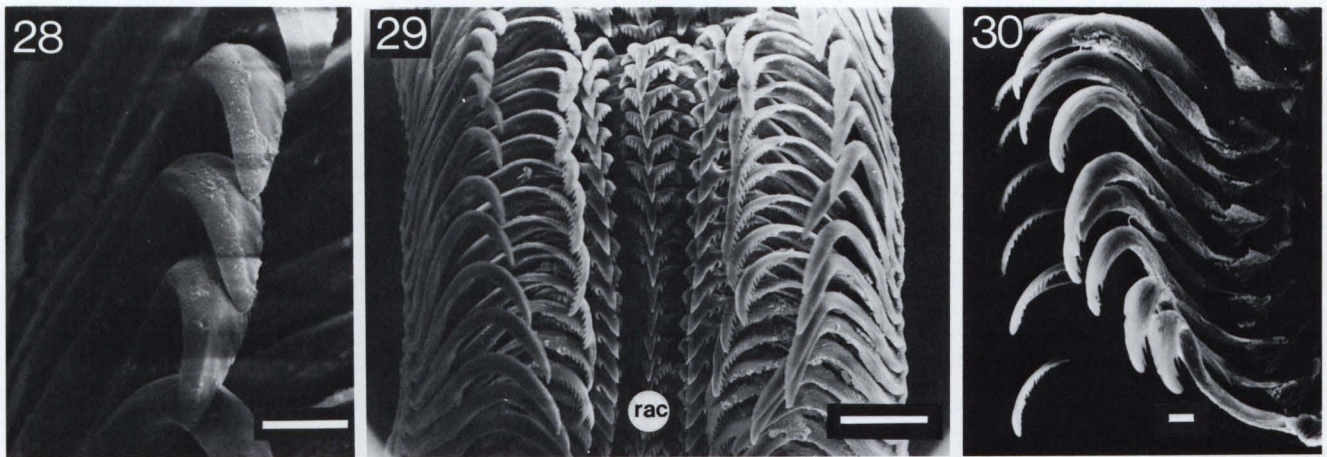
Esophagus entering stomach on left side at junction of anterior and posterior chambers. From this point, series of folds extending transversely across stomach, posteriorly into posterior chamber, and anteriorly toward intestinal opening. Opening to digestive gland lying to right of esophageal opening, between it and gastric shield. Gastric shield (figures 39, 40), with cup-like lateral wing upon which crystalline style rotates, protruding into anterior chamber, and central longitudinal portion with flattened lateral expansion that cradles style, positioning it against cup-like grinding surface.

Style sac and intestine, at anterior end of stomach, usually partially obscured by connective tissue and kidney. Style sac (figure 39, ss) narrow, finger-shaped, approximately $\frac{1}{3}$ length of stomach, not communicating directly with intestine [Johansson's (1940:1) group 3, revised after Mackintosh (1925)]. Style completely transparent, rod-shaped (length 1.8 mm, diameter 0.35 mm), rotating within style sac by action of densely packed cilia on style sac walls, protruding into anterior chamber of stomach through fleshy tube-like structure above gastric shield. Channel extending between digestive gland opening and intestinal opening at anterior terminus of anterior chamber.

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Figures 18–27. *Cyclostremiscus beaulti*, specimens from Ft. Pierce Inlet, Florida (light micrographs or critical-point dried SEM preparations). **18.** Head-foot (male), with mantle edge reflected posteriorly, dorsal view (SEM). **19.** Sagittal section of male through buccal mass and esophageal region. **20.** Anterior view of snout and left cephalic tentacle, showing pattern of ciliated tracts on ventral surface (SEM). **21.** Tip of gill filament (SEM). **22.** Osphradium, anterior to osphradial ganglion (SEM). **23.** Osphradium, cross-section through osphradial ganglion. **24.** Cephalic tentacle, cross-section. **25.** Ventral tip of cephalic tentacle, showing tactile pad (SEM). **26.** Esophagus, cross-section through anterior section, with salivary glands. **27.** Pallial tentacles: upper, finger-shaped tentacle (retracted), and lower, paddle-shaped tentacle (SEM). Scale bars: 18 = 0.5 mm; 22 = $50 \mu\text{m}$; 19, 20, 23, 24, 26, 27 = 0.1 mm; 21, 25 = $20 \mu\text{m}$.

bm, buccal mass; bs, blood space; car, cartilage; cit, ciliary tract; cont, connective tissue; df, dorsal folds of esophagus; dfc, dorsal food channel of esophagus; es, esophagus; lcg, left cerebral ganglion; lpt, lower pallial tentacle; me, mantle edge; ne, nerve; os, osphradium; osg, osphradial ganglion; pe, penis; ra, radula; rs, receptaculum seminis; sag, salivary gland; sn, snout; tp, tactile pad; upt, upper pallial tentacle.



Posterior chamber (figures 39, 47, pch) with irregular longitudinal folds along its left side leading from esophageal opening, and well-defined longitudinal groove on its right side leading toward gastric shield. Central area with series of ciliated transverse folds.

Proximal portion of intestine (figure 39, in) consisting of 3 histologically separate sections: (1) slightly bulging section immediately adjacent to stomach, containing large typhlosole, leading into second section via small loop; (2) very muscular, ball-shaped section passing under style sac to join third section; and (3) moderately ridged intestine proper, initially quite narrow, dilating slightly as it passes, without further loops or undulations, toward rectum in mantle cavity. Anus set back from mantle edge. No special ciliated tracts from anus to mantle edge and exterior.

Observed flow of particles (figure 39, small arrows): Large and small food particles enter stomach through esophagus. Counter-clockwise whirlpool at esophageal opening preliminarily sorts particles according to size. Smaller particles pass laterally to right in groove toward gastric shield and style. Large particles move into posterior chamber along left series of longitudinal folds, passing to far posterior terminus of stomach. From there, particles pass into central area where peristaltic action manipulates and returns large particles to anterior chamber. Concurrently, smaller particles separate and/or break off, and follow transverse folds toward right longitudinal groove, and then anteriorly within groove toward gastric shield. Large particles in central area of sorting chamber continue moving anteriorly to region of esophageal opening, where they pass rapidly by ciliary action directly to intestinal opening. Small particles entering area of gastric shield are manipulated by clockwise-rotating style against cup-shaped flange of gastric shield. Resultant particles move directly left into opening of digestive gland, guided by cuticularized lateral folds near style sac opening. Unacceptable particles and material returning from digestive gland are shunted via longitudinal groove toward intestinal opening. Ball-shaped proximal section of intestine probably serves as a pellet compressor.

Live specimens fed on single-celled algae and detritus scraped from laboratory aquaria walls. Fecal pellets oval, 0.33×0.19 mm ($n = 5$), round in cross-section, with rounded ends.

Renopericardial system: Two-chambered heart and surrounding kidney visible on left surface of visceral coil, posterior to ctenidium and hypobranchial gland (figure 12). Kidney large, with nephridial gland on its outer wall.

Kidney opening at posteriormost end of mantle cavity, without conspicuous ciliated tract associated with opening. No gonopericardial or renogonadial ducts observed.

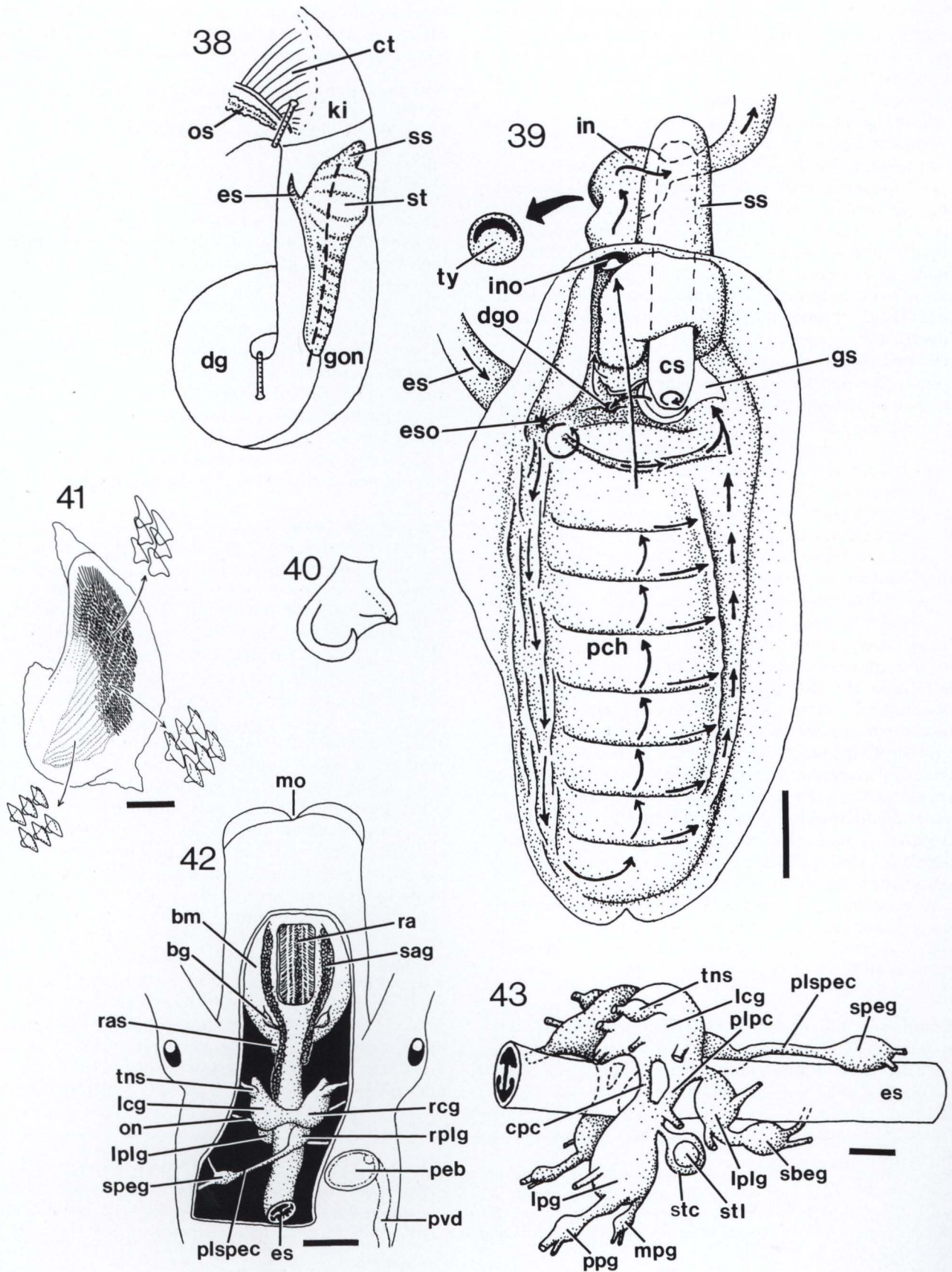
Nervous system: Circumesophageal ganglia (figures 42, 43, 49) moderately concentrated. RPG ratio [Davis *et al.*, 1976:263; defined as length of pleurosupraesophageal connective/(length of connective + length of right pleural ganglion + length of supraesophageal ganglion)] averaged 0.49 ($n = 7$). Cerebral ganglia connected by narrow commissure, each separated from pleural ganglia by constriction. Tentacular nerves with distinct swellings at their bases. Pedal ganglia each with paired connectives, connecting anteriorly to cerebral ganglia, posteriorly to cerebropleurial junctions. Pedal commissure very short, narrow. Subesophageal ganglion somewhat smaller than supraesophageal ganglion; connective to its pleural ganglion much shorter. Statocysts (figure 44, stc) about 110 μ m diameter. Buccal ganglia small, conspicuous, joined by commissure passing beneath esophagus at posterior end of buccal mass.

Highly-vacuolated connective tissue surrounding nerve ring, as well as other organs and areas throughout body.

Reproductive system: Animals in male phase (for discussion of sex change, see below) distinguished from functional females by smaller size and by dark-orange, rather than creamy-orange or beige, gonadial coloration. Penis large (size at rest: length 2.5–3.0 mm, width at midlength 0.4 mm), muscular, somewhat flattened (figures 12, 18, 42, 44) arising just behind and slightly right of bases of cephalic tentacles, coiling counter-clockwise back into mantle cavity. Fully extended penis may be longer than cephalic tentacles (*e.g.*, 4.4 mm *vs.* 3.0 mm). Subcentral penial duct terminating in opening on slightly hooded tip, which, unlike remainder of penis, is unciliated. Long, closed pallial vas deferens extending from penis, along right side of body, to prostate in posterior part of mantle cavity (figure 44). Vas deferens relatively wide (diameter ≈ 0.2 mm), tubular, forming prominent, somewhat undulating ridge that differs from surrounding tissue by its shiny, unciliated surface and by its white appearance caused by heavy internal ciliary action. Prostate orange, egg-shaped, $0.65\text{--}0.90 \times 0.35\text{--}0.48$ mm ($n = 5$), lying ventral to rectum, connected to right pallial wall, its lumen communicating with mantle cavity by slit (≈ 0.35 mm length) at its base (figures 44, 48). Visceral vas deferens much narrower, passing through posterior mantle wall, leading along inner coil of visceral mass, where widened, extensively-coiled portion functions as vesicular seminalis (figure 47, vs) before reaching

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Figures 28–37. *Cyclostremiscus beaulti*, radula and operculum, specimens from Ft. Pierce Inlet, Florida (SEM). **28.** Outer marginal teeth. **29.** Radula, whole mount. **30.** Inner marginal teeth. **31.** Rachidian teeth. **32.** Lateral teeth. **33.** Tips of lateral (left) and inner marginal (right) teeth. **34.** Operculum, outer surface (2.1 mm diameter). **35.** Operculum, inner surface (1.7 mm diameter). **36.** Operculum, oblique lateral view of inner side (2.2 mm diameter). **37.** Opercular peg, oblique lateral view. Scale bars: 28, 30–33 = 10 μ m; 29, 37 = 50 μ m.

rac, rachidian teeth.



testis. Testis simple, elongated sac, yellow to bright orange, along inner right side of visceral coil, totalling 50–60% of its length (figure 44).

Spermatozoon (56–62 μm total length, $n = 3$) with slightly twisted head comprising elongated nucleus and pointed acrosome ($\approx 14\%$ of total length), very long, narrow midpiece ($\approx 58\%$) and long tail ($\approx 28\%$). Atypical sperm not found.

Female reproductive tract (figures 13, 46) adjacent to rectum along right side of mantle cavity. Female opening, about level with anus, situated on muscular papilla hanging freely in mantle cavity at distal end of capsule gland. From there, closed sperm duct leading posteriorly, initially forming very thick-walled muscular vagina (figure 52), with lumen almost filled with large gland cells. Sperm duct giving rise to small, ball-shaped, dorsally-situated sperm pouch with weakly muscular walls. Thin-walled ducts leading from sperm pouch and muscular vagina joining shortly before opening into slit-like lumen of massive capsule gland. Vagina-type muscular wall gradually disappearing, while thin-walled part forms sperm channel ("sperm groove" in "ventral channel" of authors), in communication with gland but partially separated by lateral fold (figure 46, cross-section B, lf). Anterior part of capsule gland with large, turquoise-staining gland cells; remaining capsule gland staining dark blue in sections. [At least in the anterior part, the gland cells are arranged in a complex pattern (see Ponder, in press). A detailed histological description was hampered by the extremely strong staining reaction of the glands.] Posteriorly, glandular mass continuing, with communicating lumina, as albumen gland. Albumen gland massive, thick-walled, with narrow, slit-like lumen, pinkish-orange in living animals, staining turquoise in sections; folded as S-shaped loop on right side of animal, partly in parallel with posterior part of capsule gland. Posteriormost part of albumen gland pressing against, or, in large females, extending beyond posterior mantle wall. Sperm channel separating at junction of capsule and albumen glands, forming closed oviduct, penetrating posterior mantle wall, and forming large, widened, non-glandular coil, containing (from sections and dissected specimens) both sperm and eggs. At its posterior end, coiled oviduct giving rise to 2 proximal sperm pouches, as inconspicuous, subequal, ball-shaped sacs, closely adjacent, and partially hidden under layers of connective tissue and kidney.

In ripe females, unoriented sperm, often in large quantities, found throughout length of sperm channel and in anterior sperm pouch (functional bursa copulatrix). Packed oriented sperm, with heads embedded in walls, found in the two posterior pouches (receptacula seminis).

Visceral oviduct very thin-walled, leading from coiled oviduct to ovary. Ovary situated at right side of visceral mass, structure not grape-like, extending over central 80% of digestive gland, covering half to all of right side of coil (figure 46).

(During copulation, sperm are apparently deposited in the vagina, temporarily stored in the bursa copulatrix and then stored in the two posterior receptacula. Fertilization occurs in the anterior part of the coiled oviduct, after which fertilized eggs pass through the ciliated lumina of the albumen and capsule glands where they are surrounded by capsular and mucous material. Eggs apparently enter the mantle cavity through the vagina, as no other female opening was found.)

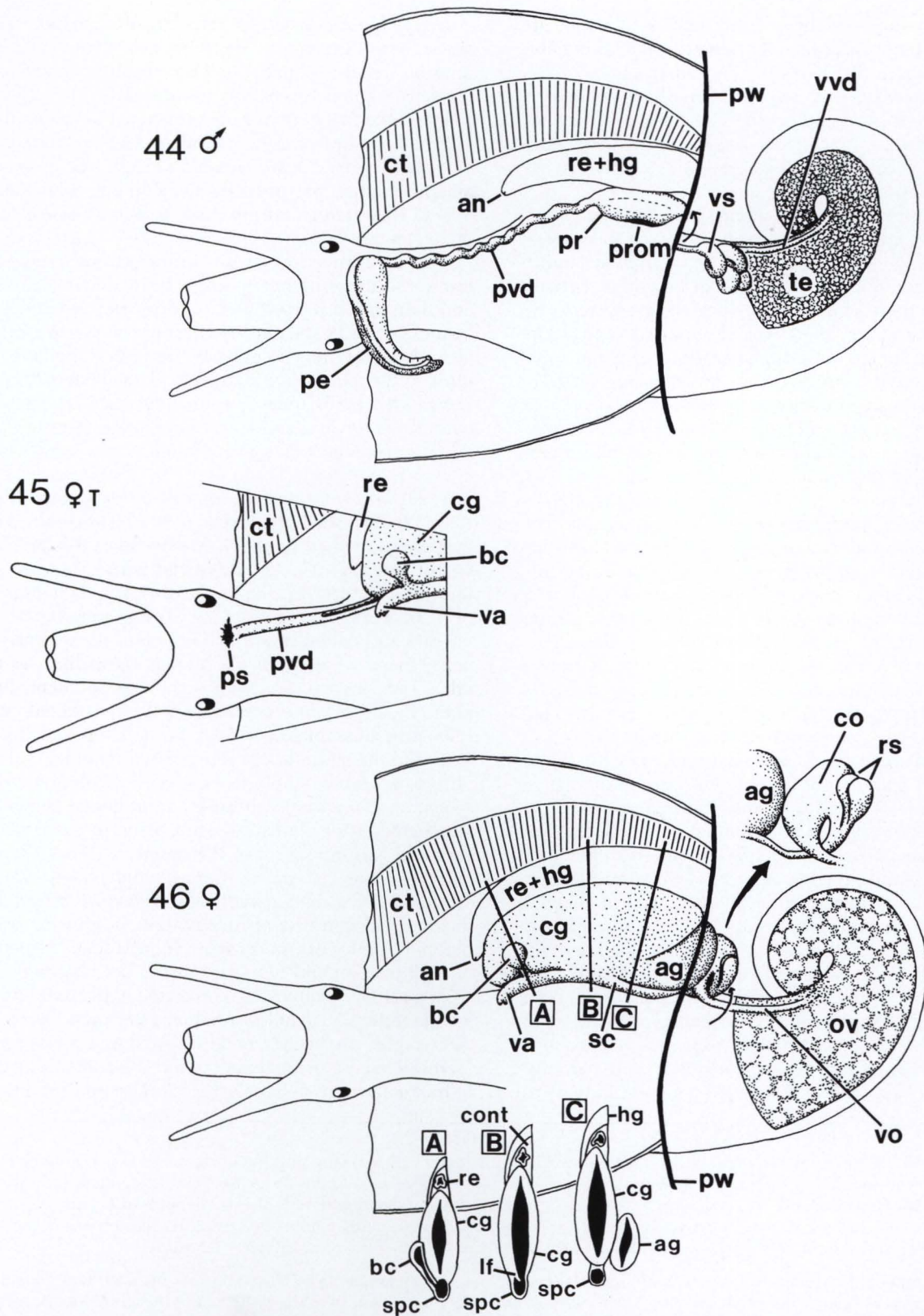
Sex and size relationships (figure 53): Specimens less than 7.6 mm shell diameter ($n = 25$) were all males. Specimens of shell diameter greater than 8.6 mm ($n = 6$) were all fully functional females without male reproductive structures. Specimens 7.8–8.5 mm shell diameter ($n = 6$) were "transitional" in appearance (figure 45); visceral and pallial reproductive organs were clearly female, however, with visible remnant of pallial vas deferens and "wound" (= penis scar) at attachment site of penis. Pallial vas deferens of smallest "transitional" specimen present as unciliated duct, partially opened at proximal end, extending between penis scar and distal end of capsule gland. No positive connections observed. This specimen also with nearly transparent gonad containing small amount of whitish ovarian tissue in early part of coil, and with no sperm in the female system (it apparently had not yet mated in its female phase). Largest "transitional" specimen with fully-developed ovary, faint longitudinal marking on integument in position of vas deferens, and weak penis scar. Simultaneous possession of both ovarian and testicular tissues not observed.

"Transition" somewhat correlated with date of collection (figure 53). Collections made between March and mid-August exclusively male. Fully developed females, "transitional" individuals, and males encountered in each of four collections in later part of August and September.

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Figures 38–43. *Cyclostremiscus beaulti*. **38.** Left lateral view of visceral coil, showing position of stomach. Dashed line indicates location of dorsal incision. **39.** Stomach, dorsal view, opened at incision shown in figure 38. Arrows inside stomach indicate flow of particles. **40.** Gastric shield. **41.** Right jaw, inner side, posterior end up, showing details of jaw elements. **42.** Head with mid-dorsal incision showing buccal mass, circumesophageal nerve ring, and base of penis. Connective tissue and minor nerves removed. **43.** Central nervous system, left side, oblique lateral view. Scale bars: 39, 42 = 0.5 mm; 41, 43 = 0.1 mm.

bg, buccal ganglion; bm, buccal mass; cpc, cerebropedal connective; cs, crystalline style; ct, ctenidium; dg, digestive gland; dgo, opening of digestive gland; es, esophagus; eso, opening of esophagus; gon, gonad; gs, gastric shield; in, intestine; ino, opening of intestine; ki, kidney; leg, left cerebral ganglion; lplg, left pleural ganglion; lpg, left pedal ganglion; mo, mouth; mpg, metapodial ganglion; on, optic nerve; os, osphradium; pch, posterior chamber; peb, base of penis; plpc, pleuropedal connective; plspeg, pleurosopraesophageal connective; ppg, propodial ganglion; pvd, pallial vas deferens; ra, radula; ras, radular sac; reg, right cerebral ganglion; rplg, right pleural ganglion; sag, salivary gland; sbeg, subesophageal ganglion; speg, supraesophageal ganglion; ss, style sac; st, stomach; stc, statocyst; stl, statolith; tns, swelling of tentacular nerve; ty, typhlosole.



Figures 44-46. *Cyclostremiscus beaulti*, reproductive system (semi-diagrammatic). 44. Male phase. 45. "Transitional" female phase. 46. Female phase, with three cross-sections (A, B, C) through female glands. Small arrows indicate reflected organs.

ag, albumen gland; an, anus; bc, bursa copulatrix; cg, capsule gland; co, coiled oviduct; cont, connective tissue; ct, ctenidium; hg, hypobranchial gland; lf, lateral fold; ov, ovary; pe, penis; pr, prostate gland; prom, opening of prostate gland into mantle cavity;

Mating and larval development unknown. Protoconch morphology suggests planktonic veliger stage (see Discussion). Sex change within single individual not observed.

Habits and habitat: To our knowledge, this is the first record of habitat type for this species, *i.e.*, within the burrows of the stomatopod *Lysiosquilla scabricauda*; other published records (see synonymy) refer only to empty shells. Wells *et al.* (1961) recorded *Cyclostremiscus beauii* from the stomachs of *Astropecten articulatus* (Say, 1825), however it is unclear whether the material was alive when swallowed by the starfish. Another specimen from gut contents of *A. articulatus*, in the UNC-IMS collections, from 24 m depth off North Carolina, contained dried animal tissue and is the only other verified live-collected specimen known to the authors. Although burrows of other local species, *e.g.*, callinassid shrimps, polychaetes, hemichordates, and sipunculans, were also sampled, these vitrinellids were not collected in association with any burrower but *Lysiosquilla* during this study.

The snails probably feed on algae, bacterial films and detritus in the burrows. They are capable of handling larger items in their alimentary tract, as evidenced by various shell pieces and foraminiferan shells found in the stomach. From the absence of glandular esophageal pouches and the presence of a crystalline style in the stomach, it can be inferred (Yonge, 1930) that free proteolytic enzymes, capable of digesting animal matter, are not present in this species and would not be expected in this group.

Individuals were almost invariably collected in groups of more than one animal per burrow sample; the maximum number encountered in one burrow sample was seven. *Cyclostremiscus beauii* was twice found crawling openly on sand or seagrass in the vicinity of *Lysiosquilla* burrow openings. In captivity, the animals were active crawlers and were not distracted by light; dark, sheltered areas in the tank (provided by black plastic film containers) were not preferred. During resting periods, all specimens attached themselves to the wall of their container, just above the water level, by means of highly viscous mucus produced by the anterior pedal gland. This behavior was not correlated with food availability or water quality. It might reflect tidal rhythm, but material was not sufficient to test that hypothesis.

Geographical distribution: Western Atlantic, from North Carolina to Brazil (Ceará and Alagoas; *teste* Rios, 1985:41). Recorded from the Pliocene of Jamaica and Florida (see synonymy).

Taxonomic remarks: Fischer (1857b:286), in the original description of *Adeorbis beauii* (in his earlier publication, the name occurred only as a nude list name;

1857a:173), did not give an indication of the number of specimens in the original lot. Moore (1964:132) mentioned a "holotype" in the Paris Museum. However, the single *A. beauii*-specimen in that type collection (MNHN unnumbered, *vidi*) is much smaller than the dimensions given by Fischer (teleoconch diameter 6.3 mm, height 3.5 mm, protoconch diameter 0.42 mm, umbilical diameter 1.1 mm; protoconch whorls 2, teleoconch whorls 2 $\frac{1}{4}$; *vs.* 10.5 mm maximum shell diameter in the original description). The specimen is therefore considered the only remaining syntype of a formerly larger lot, and is here selected as lectotype.

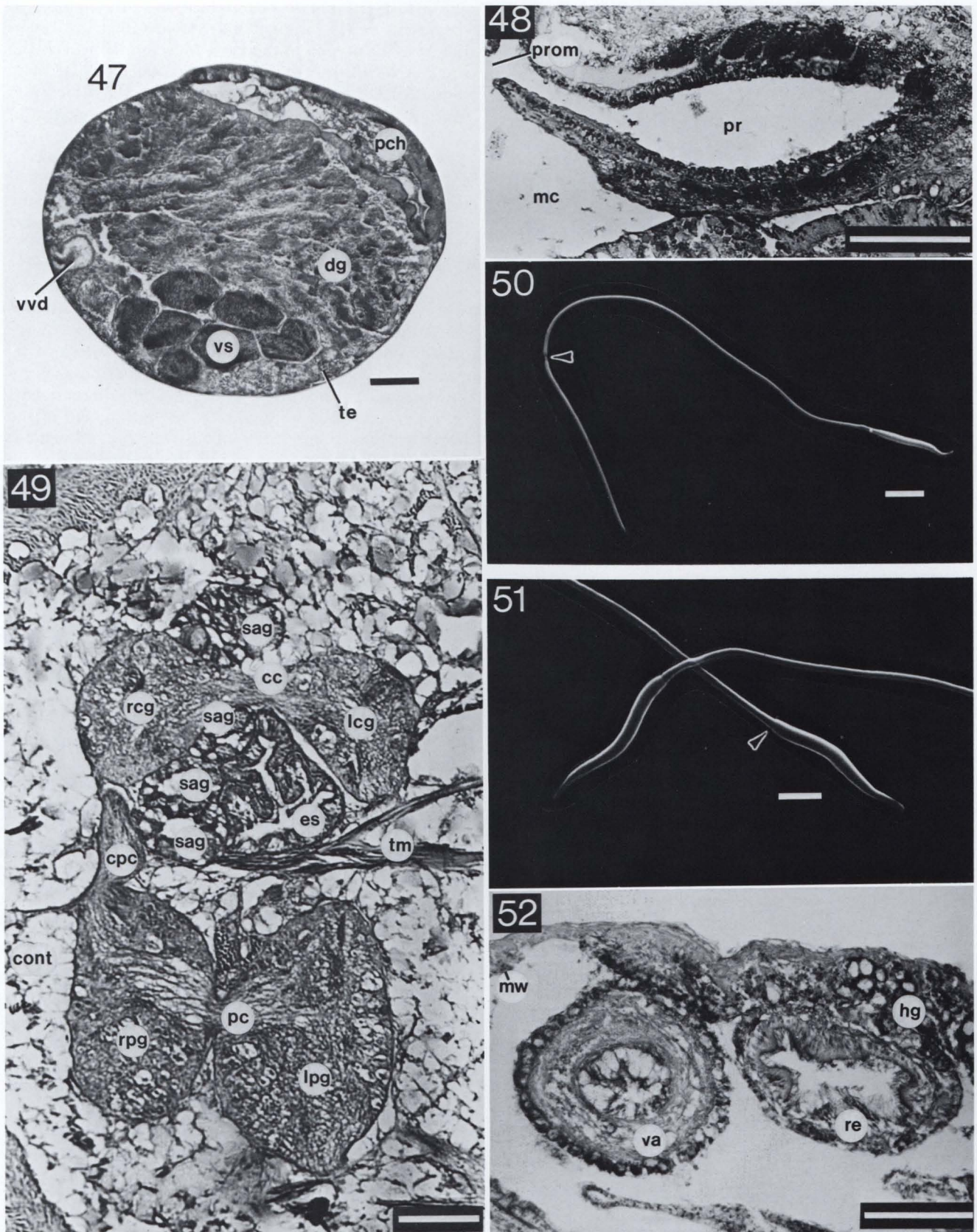
Woodring (1928:440) pointed out the close resemblance between Guppy's (1866) *Cyclostrema bicarinata* and *Adeorbis beauii* Fischer, but separated the two because the latter "has a more strongly sculptured base." Smith (1937:67) in turn separated his new species *Circulus stirophorus* from both "*Circulus bicarinatus* Guppy" and "*Circulus beauii* Fischer," by differing numbers of upper and basal spiral ribs. A re-examination of the neotype (Woodring, 1928) of *Cyclostrema bicarinata* (USNM 115621) and the original description and figure of *Circulus stirophorus* Smith revealed that both fall within the range of variation (partly caused by ontogenetic change of basal sculpture) displayed by the Ft. Pierce population, and both are here synonymized (see also Moore, 1964:131). The holotype of *Circulus stirophorus* could not be located. Although the original author indicated the type to be in the MCZ collection, it was never received by that institution (K. J. Boss, personal communication); it was also not located at the Florida State Museum, Gainesville (F. G. Thompson, personal communication).

Cyclostremiscus beauii is the largest vitrinellid in the western Atlantic. Two Recent Panamic species are very similar in size, shape and sculpture:

Cyclostremiscus major Olsson & Smith (1951:46, pl. 3, figs. 1a,b) from Panama differs from *Cy. beauii* in having more numerous spiral ribs throughout and a more rounded periphery (holotype ANSP 187199; figured by Olsson & Smith, 1951).

Cyclostrema gordana Hertlein & Strong (1951:110, pl. 9, figs. 3, 4, 7; holotype CAS 064803, *vidi*) from the Gulf of California, differs conchologically from *Cyclostremiscus beauii* in having a prominent double spiral rib on the base between the basal keel and the umbilicus (see Pilsbry, 1953: pl. 55). Hertlein and Strong (1951: 110) gave the following measurements for the "unique type": maximum diameter 9.7 mm, minimum diameter 7.0 mm, and height 3.3 mm; our examination of the holotype yielded, respectively, 8.6, 6.8, and 3.9 mm. Hertlein and Strong (1951:110) compared *C. gordana* to "*Cyclostrema angulata* A. Adams [1850] from the West Indies" [following "Pilsbry" (= error for Tryon), 1888:

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ps, penis scar; pvd, pallial vas deferens; pw, posterior pallial wall; re, rectum; rs, receptaculum seminis; sc, sperm channel; spc, sperm channel; te, testis; va, vagina; vo, visceral oviduct; vs, part of visceral vas deferens serving as vesicula seminalis; vvd, visceral vas deferens.



Figures 47-52. *Cyclostremiscus beaulti*, specimens from Ft. Pierce Inlet, Florida (light micrographs or critical-point dried SEM preparations). 47. Cross-section through visceral mass (male), at level of vesicula seminalis. 48. Section through prostate, showing

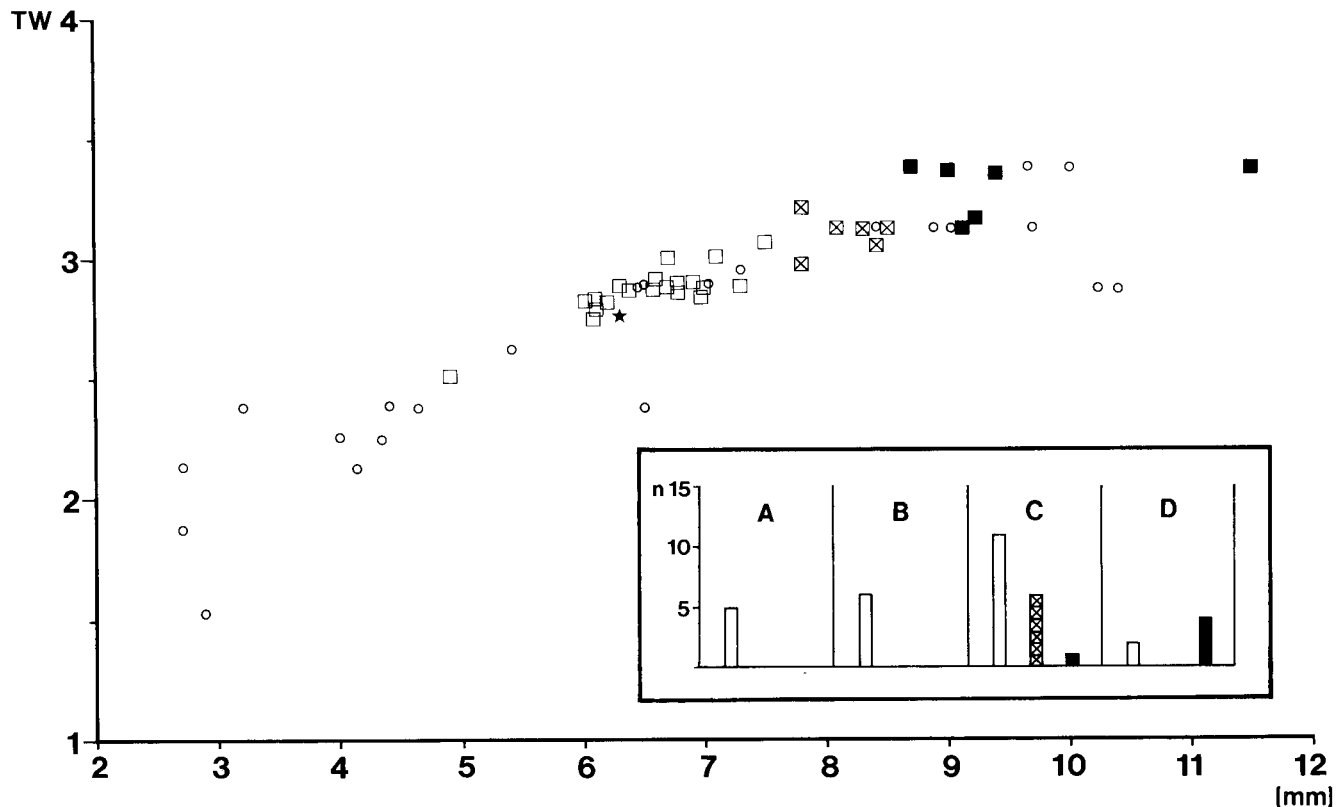


Figure 53. *Cyclostremiscus beaulti*. Plot of maximum shell diameter vs. number of teleoconch whorls (TW). Inset: Histogram summarizing sex distribution of collections, Ft. Pierce Inlet population. A = collecting period March–July, B = August 1–15, C = August 16–31, D = September, 1987. Open circles = empty shells and unsexed specimens. Open squares = functional males. Cross-hatched open squares = “transitional” females with pallial vas deferens and/or penis scar. Solid squares = females without male structures. Star indicates lectotype specimen (MNHN unnumbered).

92, they considered *C. angulata* a senior synonym of *Cyclostremiscus beaulti*—see below] and stated that it differed “principally in the smaller size and more depressed form.” However, a re-examination of the *C. gordana* type showed it to differ principally by a strong, second basal keel surrounding the umbilicus. It definitely belongs in the genus *Cyclostremiscus*, as advocated by Keen (1971).

Tryon (1888), followed by Hertlein and Strong (1951), considered *Cyclostremiscus beaulti* a synonym of *Cyclostrema angulata* A. Adams, 1850: “*C. angulata*, A. Ad. was described as from the Philippines on the authority of Cuming, but as that great collector sometimes made mistakes, the locality needs confirmation. There can be no doubt of the identity with this species of *C.*

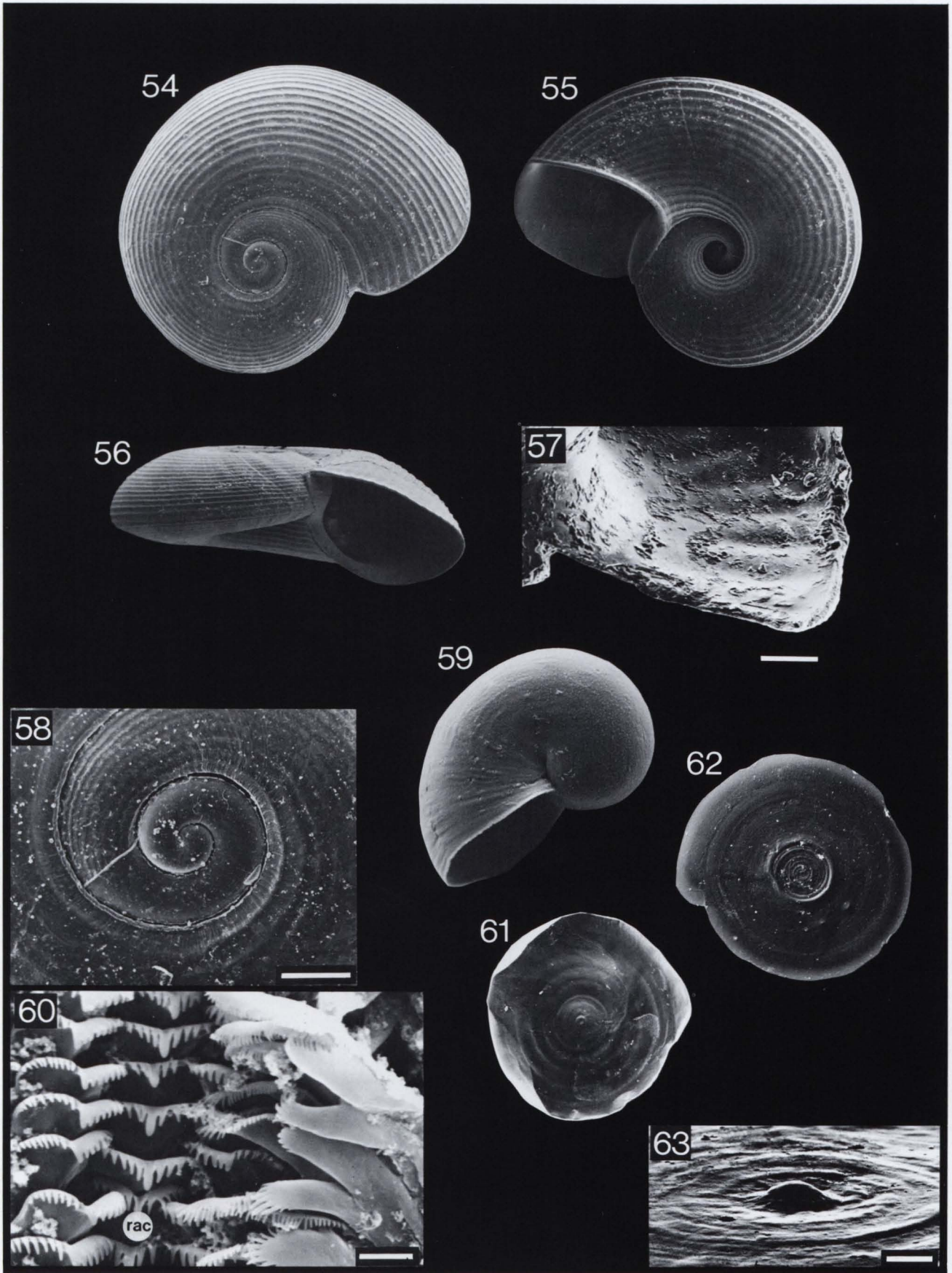
Beaulti, Fischer (fig. 63), a West Indian species” (Tryon, 1888:92–93). Tryon’s figures (1888: pl. 32, figs. 64, 65) may represent *Cyclostremiscus beaulti*. However, as similar species are known from the Indo-Pacific, we feel that the two nominal species should not be synonymized without a re-examination of *Cyclostrema angulata* type material, which could not be located in the British Museum (Natural History) (London) nor in the Redpath Museum (Montreal).

The type species of *Cyclostremiscus*, *Vitrinella panamensis* C. B. Adams, 1852, and several other, similar species (see, e.g., Pilsbry & Olsson, 1945) have distinct axial sculpture which is lacking in *Cy. beaulti*, *Cy. major*, *Cy. gordana*, and a number of other nominal species. Pilsbry (1953) described the subgenus *Ponocyclus* in *Cy-*

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lumen and opening into mantle cavity. **49.** Section through circumesophageal nerve ring, with salivary glands. **50.** Spermatozoon (SEM). Arrow indicates junction of midpiece and tail. **51.** Same, detail of two heads (SEM). Arrow indicates junction between head and midpiece. **52.** Cross-section through vagina (left) and rectum (right). Scale bars: 47–49, 52 = 0.1 mm; 50 = 4 μ m; 51 = 2 μ m.

cc, cerebral commissure; cont, connective tissue; epc, cerebropedal connective; dg, digestive gland; es, esophagus; hg, hypobranchial gland; lcg, left cerebral ganglion; lpg, left pedal ganglion; mc, mantle cavity; mw, mantle wall; pc, pedal commissure; pch, posterior chamber of stomach; pr, prostate gland; prom, opening of prostate gland into mantle cavity; rcg, right cerebral ganglion; re, rectum; rpg, right pedal ganglion; sag, salivary gland; te, testis; tm, transverse muscle band; va, vagina; vs, part of visceral vas deferens serving as vesicula seminalis; vvd, visceral vas deferens.



clostremiscus with *Adeorbis beauii* as the type species, and distinguished it from *Cyclostremiscus* by its lack of axial sculpture. As Pilsbry already pointed out in his description of *Ponocyclus* (1953:426), there are a number of species showing intermediate conditions ("weak traces of axial sculpture") and the name is not used here.

Due to the small number of species studied in the Vitrinellidae, little can be said about anatomical characters on the generic level. Aside from the large and elaborately-sculptured shell, the extensive ciliation of the head-foot, and the paddle-shaped pallial tentacle, *Cyclostremiscus beauii* differs anatomically from *Circulus striatus* (see Fretter, 1956), *Ci. texanus* (see below), and *Cochliolepis parasitica* (see Moore, 1972) in having the pallial portion of the intestine straight and uncoiled.

Circulus Jeffreys, 1865 (page 315)

Type species by monotypy: *Delphinula duminyi* Requier, 1848 (page 64; not "*Trochus duminyi* Requier" as usually cited) [= *Valvata? striata* Philippi, 1836; see Jeffreys, 1865:317, where he used the junior synonym *D. duminyi* only to avoid secondary homonymy with *Trochus striatus* Linné, 1767].

Circulus texanus (Moore, 1965) new combination (figures 54–68; tables 1, 2)

Vitrinella texana Moore, 1964:66 [unpublished dissertation].
Vitrinella texana Moore, 1965:76, pl. 7, figs. 4–6 [Gulf of Mexico].

? *Vitrinella texana* "Moore, 1964"—Andrews, 1971:73–74, text-fig.—Andrews, 1977:887 [citing "1965"], text-fig. [poor figure; = *Vitrinella* sp., *teste* Odé, 1987:35].

Vitrinella (Vitrinella) texana,—Abbott, 1974:83.

Vitridomus texana,—Odé, 1987:37.

Material examined: Holotype: empty shell, 1.8 mm, USNM 636311 (Texas). Other material: 15 specimens. FLORIDA: Ft. Pierce Inlet: 2–3 May 1987, 1 unsexed; 24 June 1987, 14 specimens (4 males, 7 females, 2 unsexed, 1 empty shell).

DESCRIPTION

Teleoconch (figures 54–56): Shell small (1.7–1.8 mm diameter, 0.55–0.65 mm height), with 1½–1¾ teleoconch whorls; almost planispiral, sculptured dorsally and ventrally with about 18 fine spiral ribs; transparent when alive, opaque after death. Ribs slightly stronger, more widely spaced just below suture on dorsum and at periphery, where about 3 ribs form rounded keel below

lateral midline. Suture impressed. Ventral surface below keel less convex, often with 30–40 widely-spaced, low axial ribs which are primarily evident from inside of body whorl (figure 57). Umbilicus wide (\approx 25% of width). Outer lip very slightly reflected; some specimens with one former varix. Aperture at oblique angle to dorso-ventral axis. Sutural sinus shallow. Periostracum thin, transparent, with spiral grooves more numerous than on shell surface.

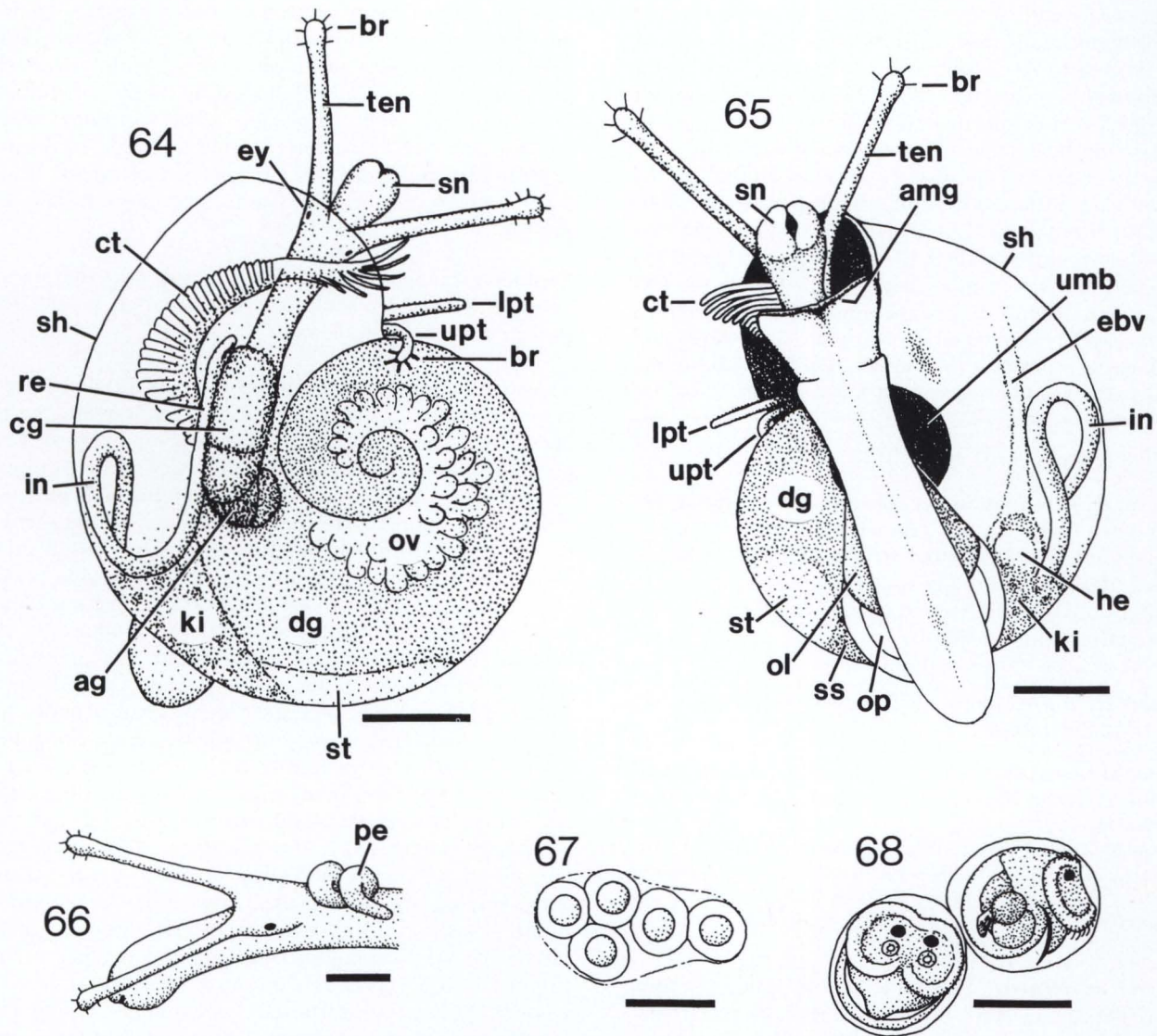
Protoconch (figure 58): Smooth, 0.5 mm diameter, about 2 whorls. No sculptural demarcation separating protoconch I and protoconch II.

External anatomy and organs of the mantle cavity (figures 64–66): Living animal translucent white with buccal mass (visible through proboscis) and protrusible portion of ctenidium rose-pink; digestive gland orange; nerve ring area opaque yellow, visible through integument between eyes. Head with long, extensible snout, rounded and terminally notched at mouth. Ventral side of snout ciliated behind mouth opening, with cilia beating toward mouth. Two long cephalic tentacles with immobile bristles on slightly enlarged tip; motile cilia at least at tip and along side facing snout. Left cephalic tentacle fitting into shallow notch formed by shell keel (figure 65). Eyes black, on slight bulges at base of cephalic tentacles. Neck region very long, slender. Foot elongate, flattened, with anterolaterally recurved corners; finely ciliated sole broadly rounded posteriorly, extending well beyond shell (figure 65). Transverse crease on sole about ½ of total length from anterior edge. Anterior pedal mucous gland (figure 65, amg) opening at slit across entire leading edge; mid-ventral fold evident on posterior quarter of sole, but presence of posterior mucous gland not confirmed. Locomotion by ciliary action. Operculum (figures 61–63) corneous, circular, multispiral (ca. 8 whorls), with small central peg and rounded-triangular muscle scar on inner surface. Operculum supported by opercular lobes (figure 65, ol) on dorsal side of foot. Lobes simple, unpigmented, without tentacles. Epipodial tentacles absent.

Two finger-shaped pallial tentacles (figure 64, lpt, upt) arising separately but adjacently from inner mantle edge, at right side of animal. Upper (= most dorsal) tentacle unciliated, with immobile terminal bristles, curling into shallow sutural sinus, directed dorsally during crawling. Lower tentacle bearing motile cilia, directed anterolaterally. Ctenidium (figures 64, 65, ct) with numerous finger-shaped filaments, attached for most of its length to internal surface of mantle; anteriormost filaments darker

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Figures 54–63. *Circulus texanus*, specimens from Ft. Pierce Inlet, Florida (SEM) (figures 54–56, USNM 846324). **54.** Shell, apical view (2.7 mm diameter). **55.** Shell, umbilical view (2.7 mm diameter). **56.** Shell, apertural view (2.2 mm diameter). **57.** Inside surface of base of body whorl, showing shallow radial grooves. **58.** Protoconch. **59.** Larval shell, left lateral view (167 μ m max. diameter). **60.** Radula. **61.** Operculum, inner surface (0.7 mm diameter). **62.** Operculum, outer surface (0.8 mm diameter). **63.** Operculum, oblique view of inner surface with opercular peg. Scale bars: 57, 58 = 0.2 mm; 60 = 5 μ m; 63 = 50 μ m.

rac, rachidian teeth.



Figures 64–68. *Circulus texanus*. 64. Crawling female, dorsal view, drawn as with transparent shell. 65. Crawling animal, ventral view, drawn as with transparent shell. 66. Head of male, left lateral view, showing penis. 67. Egg mass. 68. Two egg capsules, each with veliger larva shortly before hatching. Scale bars: 64, 65 = 0.5 mm; 66, 67 = 0.25 mm.

ag, albumen gland; amg, anterior mucous gland; br, immobile bristles; cg, capsule gland; ct, ctenidium; dg, digestive gland; ebv, efferent branchial vessel; ey, eye; he, heart; in, intestine; ki, kidney; lpt, lower pallial tentacle; ol, opercular lobe; op, operculum; ov, ovary; pe, penis; re, rectum; sh, shell; sn, snout; ss, style sac; st, stomach; ten, cephalic tentacle; umb, umbilicus; upt, upper pallial tentacle.

in color, not attached to mantle skirt, extending out of aperture at right side of head. Extent of osphradium not ascertained.

Alimentary system: Radula (figure 60) taenioglossate. Rachidian tooth wider than long, with acute posterior corners projecting laterally and concave front. Main cusp narrow, unserrated, with 5–6 slightly smaller flanking cusps on each side (number of flanking cusps varying within single radular ribbon) decreasing laterally in size; base with 1 weak elevation per side (in position of basal denticle), midway between posterior corners and central ridge. Lateral tooth with asymmetrical cutting edge, strongly indented at front edge, with narrow, unserrated

main cusp and subequal flanking cusps (6–7 inner, 9 outer). Apex of inner marginal tooth with numerous long, thin, flanking cusps on either side of similarly-sized main cusp. Apex of outer marginal tooth with long, thin inner flanking cusps, slightly more robust than those of inner marginal tooth; cusps at terminus subequal in size; outer margin with 2–3 cusps decreasing in size, remainder of outer margin smoothly rounded. Jaws composed of elements approximately $4\ \mu\text{m}$ in length.

Stomach transparent, with rotating style often clearly visible through shell. Posterior part of stomach not markedly elongated. Intestine (figures 64, 65, in) forming wide loop in posterior part of mantle cavity. Anus just above anterior end of capsule gland in females. Fecal material

as continuous rods of irregular length, rather than pellets, with no obvious surface sculpture.

Reproductive system: Penis (figure 66, pe) a posteriorly directed, counterclockwise, double coil; base arising posterior to eyes, somewhat right of dorsal midline. Testis orange.

Ovary (figure 64, ov) filling inner side of early whorls with grape-like lobes, lighter in color than digestive gland. Capsule gland and much darker-staining (in methylene blue) albumen gland (figure 64, cg, ag) forming compact mass on right wall of mantle cavity, below rectum, terminating anteriorly at level of anus. Position and number of sperm pouches not ascertained.

No evidence of sexual dimorphism associated with possible sequential hermaphroditism. Males both considerably smaller (1.7 mm diameter at 1% whorls) or larger (1.8 mm diameter at 1½ whorls) than females in same sample (1.74–1.78 mm at 1% whorls). One copulation briefly observed, wherein male paused while crawling over dorsal surface of female, with heads adjacent (male at left) and at angle of about 30°. Position of penis not ascertained.

Eggs and larval development: Three weeks after collecting, 7 females and 4 males were placed into glass bowl with seawater (24 °C). Overnight, 15 egg masses were laid; each mass contained 1–5 eggs, each in clear, flattened, circular capsule (egg diameter 110 µm; capsule diameter 170 µm; n = 20). All eggs found in same developmental stage, uncleaved, completely round, finely granular. Soft capsule walls of eggs laid in groups touching each other; each “mass,” even if consisting of single egg, coated by sticky, clear, gelatinous layer (figure 67). Eighteen additional egg masses were found in glass jar in which specimens had been kept since collecting. Total number of masses (with respective numbers of single-egg-capsules) was: 4 masses with 1 capsule, 4 masses with 2, 13 masses with 3, 9 masses with 4, and 3 masses with 5 capsules.

One mass with 5 eggs followed through development: From beginning of equal, holoblastic 2-celled stage, 60 minutes elapsed to 4-celled stage, 205 minutes to 8-celled stage, 385 minutes to 16-celled stage, respectively. Gastrula-stage discernible after 11 hours; embryos rotating after 17 hours.

Veliger larvae (figure 68) fully developed at 104 hours, intermittently or constantly rotating, with transparent shell, 2 short veliger lobes, black eye spots (not situated on tentacles at this point), statocysts and operculum [much as described for *Caecum glabrum* by Götze (1938:108, text-fig. 33), but with smaller vela]. Periphery of velar lobes bearing long cilia, underlain by row of shorter cilia. Capsule size now approximately 150 × 120 µm, greatest shell diameter 107 µm, longest dimension of veliger with extended vela 133 µm. During entire process, 3 of 5 embryos developed completely synchronously; other 2 initially about 45 minutes, later several hours, behind. First veligers hatched after 130 hours and swam actively. For following 36 hours, veligers observed either swim-

ming or resting on bottom of bowl, with strong ciliary action on extended vela. No further development noted. Added cultures of mixed single-celled green algae apparently not excepted; all larvae died within next 2 days. [From the size difference between these larvae (170 µm) and the protoconchs of adult shells (500 µm), a longer larval stage, with extensive food intake can be predicted.]

Habits and habitat: Habitat as described for *Cyclostremiscus beauii*. In the laboratory, animals of *Circulus texanus* were very active and fed on normally-occurring algal and bacterial surface films.

Geographical distribution: *Circulus texanus* (type locality: Mustang Island, near Port Aransas) was previously reported to be endemic to the northwestern Gulf of Mexico, and has never been reported alive (Moore, 1964:41; Andrews, 1977:87; Odé, 1987:37). No fossil records are known.

Taxonomic remarks: Moore (1965:77) placed this species in the genus *Vitrinella* C. B. Adams, 1850, and pointed out the differences in shell shape and sculpture in comparison to other species. However, members of *Vitrinella* (based on the type species *V. helicoidea* C. B. Adams, 1850; see tables 1, 2) are generally smooth-shelled or weakly sculptured and are usually furnished with a carina bordering the umbilicus (e.g., Keen, 1971:377; Abbott, 1974:82). We feel that this species is better placed in *Circulus sensu lato* because it agrees in shell shape and sculpture with the type species, *Circulus striatus* from the eastern Atlantic. Odé's (1987:37) placement of this species in *Vitridomus* Pilsbry & Olsson, 1945, cannot be accepted: members of *Vitridomus* [a “rather feebly defined genus” (Pilsbry & Olsson, 1952:36), very similar to *Teinostoma* H. & A. Adams, 1853] have the umbilicus partly covered by a callus.

DISCUSSION

Comparison of the anatomical information on *Cyclostremiscus beauii* and *Circulus texanus* with literature data revealed that published information is scarce or misleading, and that genus- as well as family-level taxa of marine near-planispiral Rissoacea are poorly defined. Three nominal families, Vitrinellidae Bush, 1897, Tornidae Sacco, 1896, and Circulidae (for authorship, see below), are currently in use for members of this group, and the lack of comparative data led Ponder (in press) to treat all three families as a single group in a phylogenetic analysis of the Rissoacea. In the following discussion, we (a) review the available data on species of this complex, (b) compare *Cy. beauii* and *Ci. texanus* with these data and with other members of the Rissoacea, (c) suggest a preliminary grouping for the species for which anatomical data are available, (d) demonstrate the differences between Vitrinellidae and Tornidae, (e) evaluate the taxonomic status of the nominal family Circulidae, and (f) discuss some unusual aspects of the anatomy and reproductive biology of *Cy. beauii*, namely ciliation,

tentacle shape, stomach morphology, and hermaphroditism.

(a) Available literature data (see tables 1, 2).

Except for Fretter's (1956) study of *Circulus striatus*, and Woodward's (1898) and Graham's (1982) work on *Tornus subcarinatus*, most of the available data on the anatomy of marine near-planispiral Rissoacea are restricted to descriptions or illustrations of external morphology, especially Pilsbry and McGinty's (1945a, 1946b) sketches of western Atlantic forms. Some of the few published observations on the radular structure and gross morphology of vitrinellid softbodies are misleading (see also Moore, 1964, 1972). Based on the misconception that these species are archaeogastropods, Bush (1897:127, 142, pl. 22, figs. 12a-g) erroneously constructed a rhipidoglossate radula for *Circulus trilix* (Bush, 1885) [= *Cyclostremiscus pentagonus* (Gabb, 1837), *vide* Moore, 1964: 138]. The "supplementary plicated gill" (Stimpson, 1858: 308) of *Cochliolepis parasitica* was not found in that species by Moore (1972:101). Pilsbry (1953:427) mentioned a taenioglossate radula for *Cyclostremiscus beauui*, and added "This will be figured in a paper now in preparation by T.L. McGinty and the author." This work was apparently never published.

(b) Comparison of *Cyclostremiscus beauui* and *Circulus texanus* with other vitrinellids and rissoaceans.

Both *Cyclostremiscus beauui* and *Circulus texanus* display "typical" rissoacean characters (as outlined by Fretter & Graham, 1978:153; Boss, 1982:984; Ponder, 1983, in press) and agree to a large extent with the previous concept of Vitrinellidae (Fretter, 1956; Moore, 1972; see tables 1, 2, Group 1). As in most other vitrinellid species, the cephalic and pallial tentacles bear immobile bristles and/or motile cilia. Tracts of motile cilia on the cephalic tentacles occur in numerous groups in the Rissoacea; for lack of comparative data, it is not yet clear whether the arrangement of these cilia in grooves, as in *Cy. beauui*, is unusual. Photographs of critical-point dried tentacles of a freshwater rissoacean, the hydrobiid *Tryonia clathrata* Stimpson, 1865 (see Hershler & Thompson, 1987: 27, figs. 13-17), show no grooves present in that species.

Cyclostremiscus beauui and *Circulus texanus* have two closely-spaced pallial tentacles on the right side. This arrangement is present in most studied vitrinellids (the exception being *Cochliolepis albiceratus* Ponder, 1966), in the type species of *Tornus* (Tornidae, see below), in *Hydrococcus brazieri* (T. Woods, 1876) (monotypic Hydrococcidae, see Ponder, 1982), and in the rissoid genus *Rissoina* Orbigny, 1840, where some species have either the anterior (right) or posterior (left) pallial tentacle bilobed (Ponder, 1985:78). As described for *Cy. beauui*, the function of the upper tentacle, which usually bears immobile bristles, and is held upright and bent around the aperture, is clearly sensory, while the lower one, often distinctly ciliated and sometimes broadened, controls and/or enhances water flow.

Both species have a small central opercular peg which is probably not homologous with the lateral "neritid-

type" peg in other families of Rissoacea (character considered plesiomorphic in this superfamily), while the circular shape of the vitrinellid operculum is considered derived (Ponder, 1985:5).

The osphradium of *Cyclostremiscus beauui* is very similar to those described for *Circulus striatus* (see Fretter, 1956:372) and for species of the Rissoidae (Johansson, 1939:319, pl. 3, figs. 3, 4, text-fig. 5; Haszprunar, 1985: 476, figs. 7k, 16).

The radulae of the two species studied here have only one pair of basal denticles (or elevations) on the rachidian tooth, a feature known from some other rissoacean families, such as Hydrobiidae (see Bandel, 1984:29, text-fig. 47) and Rissoidae (see Ponder, 1985:10). This character was hypothesized to be primitive in the Rissoacea by Ponder (1985:119).

The position of the salivary glands relative to the circumesophageal nerve ring is often used in family- and superfamily-level discussions (*e.g.*, Ponder, 1983:236, 258; in press). However, as a highly variable character in the populations of *Cyclostremiscus beauui* studied herein, further data on additional species are necessary before it can be reliably utilized to infer phylogenetic relationships of the Vitrinellidae.

The extensive anterior section of the esophagus of *Cyclostremiscus beauui*, with its long, coiled, dorsal folds, is very similar to that of *Hydrococcus brazieri* (see Ponder, 1982:77).

The conspicuous ciliated tract leading from the renal opening to the head of *Circulus striatus* (see Fretter, 1956:372) is lacking in *Cyclostremiscus beauui*.

The presence of markedly vacuolated connective tissue in *Cyclostremiscus beauui* is a character shared by *Circulus striatus* and *Tornus subcarinatus* (see Graham, 1982:147).

The nervous system of vitrinellid species is typically rissoacean and shows moderate (*Cyclostremiscus beauui*) to high (*Circulus striatus*; Fretter, 1956:377) concentration. The RPG ratio of *Cy. beauui*, averaging 0.49, lies within the range of those of members of the rissoacean family Pomatiopsidae (see, *e.g.*, Davis & Mazurkiewicz, 1985:45, table 8).

The structure of the male and female reproductive systems encountered during this study is rissoacean (*e.g.*, Johansson, 1956). As in most other rissoaceans (*e.g.*, Ponder, 1985:6), the albumen and capsule glands form a single, continuous mass [a character not recognizable from Fretter's (1956) description and figures of *Circulus striatus*]. The Vitrinellidae differ from the Rissoidae (*e.g.*, Ponder, 1985: text-fig. 2) wherein a non-homologous structure, an expanded part of the upper oviduct, posterior to the bursa copulatrix and/or receptacula seminis, functions as an albumen gland. This "upper oviduct gland" of the Rissoidae is homologous with the coiled part of the visceral oviducts of the Hydrobiidae (see Johansson, 1956) and Vitrinellidae [Fretter's (1956) "renal oviduct"].

Most members of the Rissoacea have one bursa copulatrix and one receptaculum seminis near the posterior

pallial wall, requiring the sperm to travel the entire length of the sperm channel (vaginal lumen, sperm groove of the ventral channel of authors) immediately after copulation. Others have developed additional, distal sperm pouches (anterior sperm-storage structure, distal blind sac, sac-like vestibule, spermatheca, pseudo-bursa of authors), either in addition to [e.g., *Pusillina inconspicua* (Alder, 1844); see Johansson, 1939:337, text-fig. 22 (as *Rissoa*); Rissoidae], or instead of the proximal bursa copulatrix [e.g., *Hyala vitrea* (Montagu, 1803); see Johansson, 1949: text-fig. 1; Iravadiidae]. These distal sperm pouches are not necessarily homologous with each other and certainly not with the proximal bursa (see, e.g., Slavoshevskaya, 1978). Vitrinellids for which such data are available (*Circulus striatus* and *Cyclostremiscus beauii*) differ from most other rissoaceans in the presence of two more-or-less equally developed, proximal receptacula seminis which, in position and size, look much like the two sperm sacs (i.e., bursa copulatrix and receptaculum seminis) of other Rissoacea (e.g., in the rissoid *Lucidestea* Laseron, 1956; see Ponder, 1985:67, text-fig. 3). Whether the presence of two proximal receptacula seminis is a distinguishing character for Vitrinellidae cannot yet be determined, as accessory receptacula have been demonstrated for members of the genus *Alvania* in the Rissoidae (Johansson, 1956; Ponder, 1985). In both *Circulus striatus* (see Fretter, 1956:377) and *Cyclostremiscus beauii*, the distal end of the coiled oviduct serves as the fertilization area, and not as an additional functional receptaculum as has been reported for some other rissoaceans [e.g., *Alvania subsoluta* (Aradas, 1847), where the distal end contained oriented sperm; Johansson, 1956:380].

The spawn mass of members of the Rissoidae usually has numerous eggs per capsule in planktonic forms, while one-egg-per-capsule is characteristic of "direct" development (see Lebour, 1937; Thorson, 1946). This does not hold true for the spawn of *Circulus texanus*, which generally resembles that of the freshwater rissoacean *Bithynia tentaculata* (Linné, 1758), as described and illustrated by Ankel (1936:164, text-fig. 142B). [The number of eggs there, however, is larger (4–24; Lilly, 1953:104), and hatching occurs at the crawling stage]. Jablonski and Lutz (1980:336; after Taylor, 1975) stated that the Rissoacea "... follow one of two developmental pathways: those that hatch as crawling juveniles from relatively large eggs (140–320 μm) and those that hatch from relatively small eggs (60–130 μm) and spend 2–3 weeks as planktonic veligers." Both species studied here definitely fall into the latter category: veliger shells of *Circulus texanus* (figure 59) were one full whorl smaller than the final larval shells as seen in the adult protoconch (figure 58); the protoconch of *Cyclostremiscus beauii* (figures 9–11) shows a distinct line and change of sculpture between protoconch I and protoconch II, with almost another full whorl of growth before metamorphosis, suggesting several weeks (K. Bandel, personal communication) of planktonic life. In his unpublished revision of western Atlantic Vitrinellidae, Moore (1964:18) inferred that

"most, if not all, species appear to have a planktonic veliger stage of some duration."

The sperm cells of *Cyclostremiscus beauii* are of the general type known for other members of Rissoacea (see Götze, 1938; Franzén, 1955). The twisted acrosome and relative lengths of head, midpiece and tail are similar to those described by Franzén (1955) for *Caecum glabrum* (Montagu, 1803). The head is much shorter than that of the two rissoids previously studied [*Pusillina inconspicua* (Alder, 1844) (as *Rissoa*) and *Onoba striata* (J. Adams, 1797); Franzén, 1955:406–409], and the relative length of the midpiece much greater than in *Hydrobia ulvae* (Pennant, 1777).

Direct communication of the coiled ("renal") oviduct with the kidney (Fretter, 1956), previously considered unique for *Circulus* or the Vitrinellidae, is now also known for other families of the Rissoacea (Tornidae, Graham, 1982; Truncatellidae, Fretter & Graham, 1962).

Anatomical characters of *Circulus striatus*, which Fretter (1956:380) discussed as probably "associated with small size and body form," are equally expressed in the much larger *Cyclostremiscus beauii*, suggesting that Fretter's hypothesis was incorrect.

(c) Preliminary grouping of "vitrinellid-like" species for which anatomical data are available.

The species for which sufficient gross morphological data are available appear to fall into three groups, two of which are here considered of familial rank and one comprising species of *incertae sedis* (tables 1, 2). Members of Group 1, currently placed in the genera *Vitrinella*, *Teinostoma*, *Pleuromalaxis*, *Cochliolepis*, *Circulus* and *Cyclostremiscus*, are here considered to belong to the Vitrinellidae (the placement of the species described as *Cochliolepis albicerata* Ponder, 1966, is somewhat doubtful as it has only one pallial tentacle, and the morphologies of its osphradium and penis are unknown). Some of the characters attributed to the family Vitrinellidae in Moore's dissertation (1964) were based on *Parviturboides interruptus* (C. B. Adams, 1850) (tables 1, 2, Group 2), later considered a species of uncertain systematic position (Moore, 1972:107). This species differs from the other forms here grouped in Vitrinellidae by the following anatomical characters: posterior foot margin with immobile cilia, left cephalic tentacle with four low swellings on proximal posterior border, penis with glandular area and directed straight back. Another species, *Tomura bicaudata* (Pilsbry & McGinty, 1946) differs in many head-foot characters (tables 1, 2, Group 2) and is here also considered as *incertae sedis*. White (1942:92) advocated the inclusion of "*Cyclostrema*" *bushi* Dautzenberg & Fischer, 1907, in the Vitrinellidae/Tornidae complex and published anatomical descriptions and illustrations of that species. While some morphological characters [head with well-developed eyes and terminally ciliated cephalic tentacles, the well-developed osphradium (1942: text-fig. 6), and the circular, multi-spiral operculum (1942: pl. 2, fig. 3)] agree well with the species listed here as vitrinellids, the glandular pouches

in the esophagus and, most of all, the pair of epipodial (not pallial) tentacles on the right side of the animal (White, 1942:90, text-fig. 5), prevent inclusion in Vitrinellidae. *Tornus subcarinatus* (tables 1, 2, Group 3) is here considered a member of a separate family (see below).

(d) Family relationships: Vitrinellidae-Tornidae.

Several attempts have been made to define the key characters of the family Vitrinellidae (e.g., Moore, 1965: 74, 1969:170, 1972:107ff.; Boss, 1982:991). However, because of the small number of species fully studied anatomically, no single synapomorphy defining the family is clear at this time. The most obvious features of the Vitrinellidae are: a low-spined, translucent white shell; long cephalic tentacles equipped with terminal bristles and, in most cases, motile cilia; two closely-spaced pallial tentacles on the right side; a large monopectinate gill often projecting to the right of the head; a large linear osphradium; a foot with simple or only slightly indented anterior and posterior margins; a horny concentric, multi-spiral operculum; and the possession of a non-glandular curved penis in the male. Some of these features (shell shape, pallial tentacles, and projecting gill) have led authors (e.g., Taylor & Sohl, 1962) to synonymize Vitrinellidae and Tornidae, based on Woodward's (1898) work on *Adeorbis* [= *Tornus*] *subcarinatus* (Montagu, 1903). Others (e.g., Adam & Knudsen, 1969; Moore, 1972) have pointed out differences between vitrinellids and *Tornus*/tornids in features of the eyes (functional eyes are lacking in *T. subcarinatus*) and/or the operculum (oval and paucispiral in *T. subcarinatus*) and have separated the two families. In a redescription of the anatomy of *T. subcarinatus*, Graham (1982:147) saw the opercular shape as the "single difference" between the two nominal families and again advocated synonymy.

Additional anatomical characters of Tornidae that warrant separation from Vitrinellidae are: (1) the conspicuous, elongate osphradium of the latter is not present in *Tornus* (Graham, 1982:144, found only "a small ciliated groove, which may be a reduced osphradium"), (2) the attachment of the ctenidial axis to the mantle is short and the axis hardly supplied with blood vessels, and (3) the penis of *T. subcarinatus* bears several finger-like processes which are not known in vitrinellids as delimited here. [Fretter & Graham (1978:231) described the ctenidium of *T. subcarinatus* as "partly bipectinate." This is apparently in error, as both Woodward (1898) and Graham (1982) described and illustrated that gill with only a single row of lamellae.] As *T. subcarinatus* lives in a comparable habitat (under boulders on well-oxygenated sand or mud) and is of about the same size as *Circulus* spp., the drastic difference in osphradial type indicates phylogenetic difference rather than specialization on a low taxonomic level.

Ponder (in press) combined the "tornid-vitrinellid-circulid complex" as family Tornidae for the purpose of his phylogenetic analysis of the Rissoacea. However, most of the characters and character states he attributed to

that complex (metapodial tentacle present, esophageal pouches and glands present, penial glands present, osphradium short, posterior end of foot not simple) do not occur in Vitrinellidae as understood here, and must refer to *Tornus* and other tornid genera studied by Ponder (*Pseudoliotia* Tate, 1898, *Scrupus* Finlay, 1927; unpublished).

Vitrinellidae and Tornidae fit well into the Rissoacea, and an independent grouping of these families as Tornacea (e.g., Kuroda *et al.*, 1971; Golikov & Starobogatov, 1975) is not justified. The family Adeorbidae Monterosato, 1884, used by some authors for members of this complex, is a synonym of Tornidae, since *Adeorbis* S. Wood, 1842, is an objective synonym of *Tornus* Turton & Kingston, 1830 (see Iredale, 1914:172, 1915:344).

(e) The nominal family Circulidae.

The taxonomic status of the nominal family Circulidae remains problematic. The family name "Circulidae" was first used by Fretter and Graham (1962:642, "Appendix I"), in a list of taxa treated in that publication. The text reads merely "Circulidae: *Circulus striatus* (Philippi)." Fretter and Graham (1962) did not state that they intended to create a new family, did not mention the name in the main body of the text, even when the taxonomic position of the genus (1962:550, 618) and the composition of the superfamily (1962: 622-623) were discussed, and in fact never used any family name but Vitrinellidae when they referred to *Ci. striatus* in subsequent publications (Fretter & Graham, 1978:227; Graham, 1982: 147). Lacking any description, definition, or bibliographic reference, a name thus introduced is not taxonomically available (ICZN, 1985: Art. 13). "Circulidae" could therefore be regarded as a *nomen nudum*.

However, Golikov and Starobogatov (1975:211) accepted "Circulidae Fretter & Graham, 1962" as a valid family and stated (1975:218) that "the characteristics of the latter family are found in Fretter (1956:381)," thereby referring to the summary of Fretter's description of *Ci. striatus*. This fulfills the requirement of ICZN (1985) Art. 13(a)iii (Bibliographic Reference to Published Statement) and, unless there are earlier such statements that have escaped us, this makes Golikov and Starobogatov (1975) the authors of Circulidae, with *Circulus* as the name-bearing type. The nominal family Circulidae is, with anatomical descriptions available for *Ci. striatus* and *Ci. texanus*, much better defined than the Vitrinellidae, where our knowledge of *Vitrinella* is based only on shell characters and Pilsbry and McGinty's (1945a, 1946b) sketches of crawling animals (tables 1, 2). All available data suggest synonymy of Vitrinellidae and Circulidae (tables 1, 2; Boss, 1982:991). In any case, the placement of Vitrinellidae and Circulidae in separate superfamilies, or even separate superorders (Golikov & Starobogatov, 1975), is highly exaggerated.

(f) Unusual features of *Cyclostremiscus beaulti*.

The study of *Cyclostremiscus beaulti* revealed a number of features that differ from other members of the Vitrinellidae (and, in part, from the Rissoacea). Most of

these features may be related to either its unusually large size (for a vitrinellid) or its unusual habitat in stomatopod burrows.

Ciliation and tentacle shape: The extensive ciliation of the gills, cephalic tentacles and lower pallial tentacle provides effective respiratory and excretory currents. On the right side of the head, where in- and outgoing currents are present, water flow is controlled by the paddle-shaped tentacle. Low tides and high water temperatures are likely to create anoxic conditions in the burrows, and a large vitrinellid such as *Cyclostremiscus beauii* may be more strongly affected by oxygen deficiencies than, for instance, the smaller *Circulus texanus*, and thus would benefit from an elaborate system to produce and direct currents. The only other known commensal vitrinellid, *Cochliolepis parasitica*, is much smaller, and lives directly on its host [under the scales of the giant scale worm *Polyodontes lupina* (Stimpson, 1856); see Stimpson, 1858; Hartman, 1945:10]. Moore (1972:104) did not find cilia on the gill filaments of *Cochliolepis parasitica*, suggesting that currents produced by the annelid are sufficient to supply the snail. All other species studied live under rocks (table 2).

Stomach: The rissocean stomach does not normally have a caecum or an elongated posterior chamber, as occurs in various other prosobranchs ("it is not possible to see any trace of it in the . . . Rissoacea"; Fretter & Graham, 1962:225). Only a few exceptions are known: Ponder (1985:78) described the stomach of *Rissoina* (Rissoidae) as "very long due to elongation of posterior chamber," and Ponder (in press) listed the character state "posterior gastric chamber not small" for the families Emblandidae, Truncatellidae and Stenothyridae. The presence of a large posterior chamber in *Cyclostremiscus beauii*, similar in relative shape and organization to that of *Pomatias elegans* (Müller, 1774) (Pomatiasidae), as described by Graham (1939:90, fig. 6D), is therefore surprising. It may allow *Cy. beauii* to maintain a regular supply of food particles by regulating fluctuations in the rate of food intake (as suggested by Graham, 1939:93, for *Pomatias*), especially since feeding must be strongly affected by tidal, and therefore water-level, changes within the stomatopod burrows. A relatively large animal such as *Cy. beauii* would be more strongly affected than smaller vitrinellids, e.g., *Circulus texanus*, which were observed to feed in very small pockets of water (personal observation), thus maintaining a more-or-less continuous feeding activity, as has been described, e.g., for a member of the genus *Caecum* (Morton, 1975:14).

Hermaphroditism: The most striking result of this study was the discovery of small functional females in *Cyclostremiscus beauii* with apparently functionless remnants of the male reproductive system. Penial structures are known to occur in various female rissoceans (particularly hydrobiids and rissoids). Thiriot-Quévieux (1977:779ff.) based her hypothesis of sequential hermaphroditism in four species of *Rissoa* on the presence of more-or-less developed penes in immature specimens

and females. However, a later in-depth study (Thiriot-Quévieux, 1982:167ff.) of these species through annual cycles showed a seasonal (and geographical) pattern of penis-size distribution in females, but no evidence of sex change. The survey did "not support the hypothesis of a successive hermaphroditism" (1982:167). In *Cyclostremiscus beauii*, remnants of the male apparatus are only evident in the smallest functional females (figure 53), with a gradual decrease of male structures with size. As outlined above, we take this as evidence for a sex change in this species rather than a simple sexual dimorphism in shell size. During ontogeny, the male reproductive system apparently disappears completely and is replaced by female organs. The anteriormost part of the pinkish-orange female albumen gland is found in the same relative position as the prostate (of similar color and reaction to staining) in the male phase. As no animal was found with a very early stage of development of the albumen gland, it cannot be decided whether these organs, or parts of them, are homologous. [Reid (1986), in a study of *Mainwaringia* Nevill, 1885, the first reported case of protandrous sequential hermaphroditism in the Littorinacea, found both a closed pallial oviduct and an open prostate in the intersexual and female stages, "suggesting that these structures are not strictly homologous" (1986:225). In that littorinid group, small penes are retained in the female phase (1986:237), and the pallial oviduct opens into the also-retained pallial vas deferens, then serving to carry egg capsules (1986:238).] With this admittedly small data set for *Cy. beauii* from only two localities, and the absence of data on individual development and longevity, settlement cues and adult mobility, several scenarios could be constructed. It is, for example, theoretically possible that functional males arrest growth to prolong the male phase, or that the change into the female phase occurs only after successful mating as a male. However, no evidence was found to consider this sex change as labile, i.e., environmentally mediated, as is known for other caenogastropod families such as Calyptraeidae and Stiliferidae (see Hoagland, 1978, for examples and discussion). The data are further insufficient to demonstrate either seasonal or partner-induced change. The sex change in *Cy. beauii* appears to occur only once, at a predetermined size (figure 53; about 8 mm shell diameter, 3 teleoconch whorls), and it apparently affects most, if not all, individuals (as the general shift in gender over time in the Ft. Pierce population suggests).

Thus *Cyclostremiscus beauii* is interpreted as a protandrous sequential hermaphrodite. The term sequential (= consecutive, successive) is important here. In a review of the terms protandry, protogyny and hermaphroditism, Hoagland (1984:86) defined *protandry* as "the functioning of an organism first as male, then as female, with no further sex change. The two sexual phases are separated by a phase in which male primary and secondary sex characters disappear, and the animal re-differentiates as a female." This however omits those species which, after an initial male-only phase, have both male and female

reproductive systems developed and functional (e.g., members of Rissoellidae and Omalogyridae; see below), i.e., protandrous simultaneous hermaphrodites. [Simultaneous hermaphrodites, in our understanding, do not necessarily use "the same gonad to produce both eggs and sperm" as defined by Hoagland (1984:85).]

Although, at this point, we do not know whether protandrous sequential hermaphroditism is the exception, rather than the rule, in this family, the occurrence of hermaphroditism in *Cyclostremiscus beauui* could be interpreted as an adaptation to its peculiar habitat characterized by low density and relative isolation. Protandrous sequential hermaphroditism has an advantage for *Cy. beauui*, as each individual thereby minimizes the age at which it first reproduces and increases the likelihood of finding a compatible mate in a small group. Inbreeding between siblings would also be reduced (see Ghiselin, 1969, for discussion).

Members of the approximately 25 families grouped under Rissoacea are generally described as gonochoristic (see, e.g., Boss, 1982:984), although possibly derived from ancestors that were sequential hermaphrodites (Slavovshevskaya, 1984). Reported cases of hermaphroditism in prosobranchs (e.g., Webber, 1977:10; Fretter, 1984:15) include only two genera that have classically been assigned to this superfamily, *Omalogyra* (Omalogyridae) and *Rissoella* (Rissoellidae). Fretter (1948) described in detail the anatomy and reproductive biology of *O. atomus* (Philippi, 1841) and *R. diaphana* (Alder, 1848). Both species were found to be protandrous simultaneous hermaphrodites, with some likelihood of self-fertilization in *O. atomus* (1948:612, 621, 630; see also Fretter & Graham, 1962:381, and 1978:218, 223). [Fretter & Graham, 1964:134, refer (erroneously?) to the same two species as being "protandrous consecutive hermaphrodites."] Both families have been subsequently removed from the Rissoacea and have been recently placed outside the Caenogastropoda, near (Salvini-Plawen & Haszprunar, 1987) or in (Ponder & Warén, in press) the Allogastropoda (= Heterostropha of authors). Thus, *Cyclostremiscus beauui* is to our knowledge the only species in the superfamily Rissoacea for which protandrous sequential hermaphroditism has been demonstrated. However, as sequential hermaphroditism is not as easily recognized as simultaneous hermaphroditism, it might be more widely distributed in the Vitrinellidae and/or other families of this group. The mismatch in descriptions of the male reproductive system of *Tornus subcarinatus*, where a penis was lacking according to Woodward (1898) and was found by Graham (1982), might find an explanation after all.

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LITERATURE CITED

- Abbott, R. T. 1954. American seashells. D. Van Nostrand Company, Inc., Princeton, NJ, xiv + 541 p., 40 pls.
- Abbott, R. T. 1974. American seashells: the marine Mollusca of the Atlantic and Pacific coasts of North America, 2nd ed. Van Nostrand Reinhold Company, New York, 663 p., 24 pls.
- Abbott, R. T. and S. P. Dance. 1982. Compendium of seashells: a color guide to more than 4,200 of the world's marine shells. E. P. Dutton, New York, x + 411 [+ 1] p., illus.
- Adam, W. and J. Knudsen. 1969. Quelques genres de Mollusques prosobranches marins inconnus ou peu connus de l'Afrique occidentale. Bulletin Institut Royal des Sciences Naturelles de Belgique 44(27):1–69.
- Adams, A. 1850. Monographs of *Cyclostrema*, Marryat, and *Separatista*, Gray; two genera of gasteropodous mollusks. Proceedings of the Zoological Society of London 1850:41–45.
- Adams, A. 1866. Monographs of the genera *Cyclostrema*, *Adeorbis*, and *Teinostoma*. Thesaurus Conchyliorum, Sowerby, G. B. (ed.) 3:249–262, pls. 255–256.
- Andrews, J. 1971. Sea shells of the Texas coast. University of Texas Press, Austin, xvii + 298 p., illus.

- Andrews, J. 1977. Shells and shores of Texas. University of Texas Press, Austin, xx + 365 p., illus.
- Ankel, W. E. 1936. Prosobranchia. In: Grimpe, G. and E. Wagler (eds.). Die Tierwelt der Nord- und Ostsee, Vol. IXb. Akademische Verlagsgesellschaft, Leipzig, p. 1-240.
- Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandlungen No. 214, 188 p., 22 pls.
- Boss, K. J. 1982. Mollusca. In: Parker, S. P. (ed. in chief). Synopsis and classification of living organisms, Vol. 1. McGraw-Hill Book Company, New York, p. 945-1166.
- Bush, K. J. 1897. Revision of the marine gastropods referred to *Cyclostrema*, *Adeorbis*, *Vitrinella*, and related genera; with descriptions of some new genera and species belonging to the Atlantic fauna of America. Transactions of the Connecticut Academy 10:97-144, pls. 22, 23.
- Dall, W. H. 1889. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the south-eastern coast of the United States, with illustrations of many of the species. Bulletin of the United States National Museum 37:221 p., pls. 1-74.
- Dall, W. H. 1892. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene Silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River, II.—Streptodont and other gastropods, concluded. Transactions of the Wagner Free Institute of Science 3(2): 201-448, 1 map, pls. 13-22, p. 459-473.
- Dall, W. H. 1903. Contributions to the Tertiary fauna of Florida with especial reference to the Silex Beds of Tampa and the Pliocene Beds of the Caloosahatchie River including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part VI. Concluding the work. Transactions of the Wagner Free Institute of Science of Philadelphia 3(4):i-xiv, 1219-1654, pls. 48-60.
- Davis, G. M. and W. P. Carney. 1973. Description of *Oncomelania lindoensis*, first intermediate host of *Schistosoma japonicum* in Sulawesi (Celebes). Proceedings of the Academy of Natural Sciences of Philadelphia 125(1):1-34.
- Davis, G. M., V. Kitikoon, and P. Temcharoen. 1976. Monograph on "*Lithoglyphopsis*" *aperta*, the snail host of Mekong River schistosomiasis. Malacologia 15(2):241-287.
- Davis, G. M. and M. Mazurkiewicz. 1985. Systematics of *Cincinnatia winkleyi* (Gastropoda: Hydrobiidae). Proceedings of the Academy of Natural Sciences of Philadelphia 137:28-47.
- Emerson, W. K. and M. K. Jacobson. 1976. The American Museum of Natural History guide to shells: land, freshwater, and marine, from Nova Scotia to Florida. Alfred A. Knopf, New York, 482 p. text + xviii p. index, 47 pls.
- Fischer, P. 1857a. Études sur un groupe de coquilles de la famille des Trochidae (suite). Journal de Conchyliologie 6:168-176.
- Fischer, P. 1857b. Études sur un groupe de coquilles de la famille des Trochidae (fin). Journal de Conchyliologie 6: 284-288, pl. 10.
- Franzén, A. 1955. Comparative morphological investigations into the spermiogenesis among Mollusca. Zoologiska Bidrag från Uppsala 30:399-456, pls. 1, 2.
- Fretter, V. 1948. The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). Journal of the Marine Biological Association of the United Kingdom 27: 597-632.
- Fretter, V. 1956. The anatomy of the prosobranch *Circulus striatus* (Philippi) and a review of its systematic position. Proceedings of the Zoological Society of London 126:369-381.
- Fretter, V. 1984. Prosobranchs. In: Wilbur *et al.* (eds.). The Mollusca, Vol. 7, Reproduction. Academic Press, New York and London, p. 1-45.
- Fretter, V. and A. Graham. 1962. British prosobranch molluscs: their functional anatomy and ecology. Ray Society, London, xvi + 755 p.
- Fretter, V. and A. Graham. 1964. Reproduction. In: Wilbur, K. M. and C. M. Yonge (eds.). Physiology of Mollusca, Vol. 1. Academic Press, New York and London, p. 127-164.
- Fretter, V. and A. Graham. 1978. The prosobranch molluscs of Britain and Denmark. Part 4—Marine Rissoacea. Journal of Molluscan Studies, Supplement 6:153-241.
- Gardner, J. 1948. Mollusca from the Miocene and lower Pliocene of Virginia and North Carolina. Part 2. Scaphopoda and Gastropoda. U.S. Geological Survey Professional Paper 199-B, i-iii, 179-310, pls. 24-38.
- Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. Quarterly Review of Biology 44:189-208.
- Götze, E. 1938. Bau und Leben von *Caecum glabrum* (Montagu). Zoologisches Jahrbuch (Systematik), Jena 71(1-2): 1-190.
- Golikov, A. N. and Y. I. Starabogatov. 1975. Systematics of prosobranch gastropods. Malacologia 15(1):185-232.
- Graham, A. 1939. On the structure of the alimentary canal of style-bearing prosobranchs. Proceedings of the Zoological Society of London (B) 109(1):75-112.
- Graham, A. 1982. *Tornus subcarinatus* (Prosobranchia, Rissoacea), anatomy and relationships. Journal of Molluscan Studies 48:144-147.
- Guppy, R. J. L. 1866. On the Tertiary Mollusca of Jamaica. Quarterly Journal of the Geological Society of London 22(1):281-295, pls. 16-18.
- Hartman, O. 1945. The marine annelids of North Carolina. Bulletin of the Duke University Marine Station 2:1-54, 10 pls., 2 charts.
- Haszprunar, G. 1985. The fine morphology of the osphradial sense organs of the Mollusca. I. Gastropoda, Prosobranchia. Philosophical Transactions of the Royal Society of London, B 307:457-496.
- Hershler, R. and F. G. Thompson. 1987. North American Hydrobiidae (Gastropoda: Rissoacea): redescription and systematic relationships of *Tryonia* Stimpson, 1865 and *Pyrgulopsis* Call and Pilsbry, 1886. The Nautilus 101(1): 25-32.
- Hertlein, L. G. and A. M. Strong. 1951. Eastern Pacific expeditions of the New York Zoological Society. XLIII. Mollusks from the west coast of Mexico and Central America. Part X. Zoologica, Scientific Contributions of the New York Zoological Society 36(2):67-120, pls. 1-11.
- Hoagland, K. E. 1978. Protandry and the evolution of environmentally-mediated sex change: a study of the Mollusca. Malacologia 17(2):365-391.
- Hoagland, K. E. 1984. Sententia. Use of the terms protandry, protogyny, and hermaphroditism in malacology. American Malacological Bulletin 3(1):85-88.
- Humason, G. L. 1962. Animal tissue techniques. W. H. Freeman and Company, San Francisco and London, xv + 468 p.

- Humfrey, M. 1975. Sea shells of the West Indies: a guide to the marine molluscs of the Caribbean. Taplinger Publishing Company, New York, 351 p., 32 pls.
- International Code of Zoological Nomenclature [ICZN]. 1985. Third edition, Ride, W. D. L., C. W. Sabrosky, G. Bernardi, and R. V. Melville (eds.). International Trust for Zoological Nomenclature, London, xx + 338 p.
- Iredale, T. 1914. On some invalid molluscan generic names. Proceedings of the Malacological Society of London 11(2): 170-178.
- Iredale, T. 1915. The nomenclature of British marine Mollusca. Journal of Conchology 14(11):341-346.
- Jablonski, D. and R. A. Lutz. 1980. Molluscan larval shell morphology. Ecological and paleontological applications. In: Rhoads, D. C. and R. A. Lutz (eds.). Skeletal growth of aquatic organisms. Topics in geobiology, Vol. 1. Plenum Press, New York and London, p. 323-377.
- Jeffreys, J. G. 1865. British conchology, or an account of the Mollusca which now inhabit the British Isles and the surrounding seas. Vol. III. Marine shells, comprising the remaining Conchifera, the Solenoconchia, and Gasteropoda as far as *Littorina*. J. van Voorst, London, 393 (+ 1) p., 8 pls. + frontispiece.
- Johansson, J. 1939. Anatomische Studien über die Gastropodenfamilien Rissoidae und Littorinidae. Zoologiska Bidrag från Uppsala 18(1938-40):287-396, pls. 1-11.
- Johansson, J. 1940. Ein Beitrag zur Kenntnis des Kristallstielsackes der Mollusken und der Flimmerbewegung in demselben. Arkiv för Zoologi 33B(3):1-8.
- Johansson, J. 1949. Über die weiblichen Geschlechtsorgane von *Hyala vitrea*, einer von dem *Rissoa*-Typus stark abweichenden Form der Gruppe Rissoacea. Arkiv för Zoologi 42A(7):1-6.
- Johansson, J. 1956. Genital organs of two *Alvania* species, and a comparison with related families (Moll. Pros.). Arkiv för Zoologi 9(16):377-387, pl. 1.
- Keen, A. M. 1971. Sea shells of tropical west America—marine mollusks from Baja California to Peru, 2nd ed. Stanford University Press, Stanford, CA, xiv + 1064 p., 22 pls.
- Kuroda, T., T. Habe, and K. Oyama. 1971. The sea shells of Sagami Bay. Maruzen, Tokyo, xix + 741 p. [in Japanese], pls. 1-121, 489 p. [in English], 51 p., index, map.
- Laseron, C. F. 1958. Liotiidae and allied molluscs from the Dampierian Zoogeographical Province. Records of the Australian Museum 24(11):165-182.
- Lebour, M. V. 1937. The eggs and larvae of the British proso-branches with special reference to those living in the plankton. Journal of the Marine Biological Association of the United Kingdom 22:105-166.
- Lilly, M. M. 1953. The mode of life and the structure and functioning of the reproductive ducts of *Bithynia tentaculata* (L.). Proceedings of the Malacological Society of London 30:87-110.
- Mackintosh, N. A. 1925. The crystalline style in gastropods. Quarterly Journal of Microscopical Science 69:317-342, pls. 20, 21.
- Melvill, J. C. 1906. A revision of the species of Cyclostrematidae and Liotiidae occurring in the Persian Gulf and North Arabian Sea. Proceedings of the Malacological Society of London 7(1):20-28, pl. 3.
- Moore, D. R. 1962. The systematic position of the family Caecidae (Mollusca: Gastropoda). Bulletin of Marine Sciences of the Gulf and Caribbean 12(4):695-701.
- Moore, D. R. 1964. The family Vitrinellidae in South Florida and the Gulf of Mexico. Ph.D. dissertation, University of Miami, Coral Gables, FL, xi + 235 (+ 2) p.
- Moore, D. R. 1965. New species of Vitrinellidae from Gulf of Mexico and adjacent waters. The Nautilus 78(3):73-79, pls. 7, 8.
- Moore, D. R. 1969. *Cyclostrema miranda* Bartsch, a synonym of *Tornus subcarinatus* Montagu. The Veliger 12(2):169-170.
- Moore, D. R. 1972. *Cochliolepis parasitica*, a nonparasitic marine gastropod, and its place in the Vitrinellidae. Bulletin of Marine Science 22(1):100-112.
- Morris, P. A. 1973. A field guide to shells of the Atlantic and Gulf Coasts and the West Indies, 3rd ed. Houghton Mifflin Company, Boston, xxviii + 330 p., 76 pls.
- Morton, J. 1975. Form and habit in some small gastropods of New Zealand boulder beaches. The Veliger 18(1):1-15.
- Odé, H. 1987. Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph) family Vitrinellidae Bush, 1897 (continued). Texas Conchologist 24(1):21-40.
- Olsson, A. A. and M. Smith. 1951. New species of Epitoniidae and Vitrinellidae from Panama City. The Nautilus 65(2): 44-46, pl. 3.
- Pilsbry, H. A. 1953. Vitrinellidae. In: Olsson, A. A. and A. Harbison (eds.). Pliocene Mollusca of southern Florida with special reference to those from north Saint Petersburg. Monographs of the Academy of Natural Sciences of Philadelphia, no. 8, p. 411-438, pls. 49-56.
- Pilsbry, H. A. and T. L. McGinty. 1945a. Cyclostrematidae and Vitrinellidae of Florida—I. The Nautilus 59(1):1-13, pls. 1, 2.
- Pilsbry, H. A. and T. L. McGinty. 1945b. "Cyclostrematidae" and Vitrinellidae of Florida, II. The Nautilus 59(2):52-59, pl. 6.
- Pilsbry, H. A. and T. L. McGinty. 1946a. "Cyclostrematidae" and Vitrinellidae of Florida, Part III. The Nautilus 59(3): 77-83, pl. 8.
- Pilsbry, H. A. and T. L. McGinty. 1946b. Vitrinellidae of Florida, Part 4. The Nautilus 60(1):12-18, pl. 2.
- Pilsbry, H. A. and T. L. McGinty. 1950. Vitrinellidae of Florida: Part 5. The Nautilus 63(3):85-87, pl. 5.
- Pilsbry, H. A. and A. A. Olsson. 1945. Vitrinellidae and similar gastropods of the Panamic Province. Part I. Proceedings of the Academy of Natural Sciences of Philadelphia 97: 249-278, pls. 22-30.
- Pilsbry, H. A. and A. A. Olsson. 1952. Vitrinellidae of the Panamic Province: II. Proceedings of the Academy of Natural Sciences of Philadelphia 104:35-88, pls. 2-13.
- Ponder, W. F. 1966. On a subterranean snail and a tornid from New Zealand. Journal of the Malacological Society of Australia 10:35-40, pls. 4, 5.
- Ponder, W. F. 1982. The anatomy and relationships of *Hydrococcus brazieri* (T. Woods). Journal of Molluscan Studies 48:64-79.
- Ponder, W. F. 1983. Review of the genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea). Records of the Australian Museum 35:231-281.
- Ponder, W. F. 1985. A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). Records of the Australian Museum, Supplement 4:1-221.
- Ponder, W. F. In press. The rissocean radiation—a preliminary phylogeny. Malacological Review, Supplement.
- Ponder, W. F. and A. Warén. In press. Classification of the Caenogastropoda and Heterostropha—a list of the family-

- group names and higher taxa. *Malacological Review*, Supplement.
- Porter, H. J. 1974. The North Carolina marine and estuarine Mollusca—an atlas of occurrence. University of North Carolina, Institute of Marine Sciences, Morehead City, NC, vi + 351 p.
- Reid, D. G. 1986. *Mainwaringia* Nevill, 1885, a littorinid genus from Asiatic mangrove forests, and a case of protandrous hermaphroditism. *Journal of Molluscan Studies* 52:225–242.
- Requien, E. 1848. Catalogue des coquilles de l'Île de Corse. F. Seguin Ainé, Avignon, 109 (+ 2) p.
- Rios, E. C. 1975. Brazilian marine mollusks iconography. Museu Oceanográfico, Fundação Universidade do Rio Grande, Rio Grande, 331 p., 91 pls.
- Rios, E. C. 1985. Seashells of Brazil. Museu Oceanográfico, Fundação Cidade and Universidade do Rio Grande, Rio Grande, 328 [+ 1] p., 102 pls.
- Salvini-Plawen, L. von and G. Haszprunar. 1987. The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *Journal of Zoology*, London 211:747–770.
- Serène, R. 1954. Observations biologiques sur les Stomatopodes. *Mémoires de l'Institut Océanographique de Nhatrang* 8:1–93, 10 pls.
- Simpson, C. T. 1887. Contributions to the Mollusca of Florida. *Proceedings of the Davenport Academy of Natural Sciences* 5:45–72.
- Slavoshevskaya, L. V. 1978. Peculiarities of the genital system of the Rissoacea and their importance for taxonomy in this superfamily. *Malacological Review* 11:112–114.
- Slavoshevskaya, L. V. 1984. An analysis of the organization of the Rissoacea (Mollusca: Gastropoda). 2. The reproductive system. *Zoologicheskii Zhurnal* 63(3):361–372 [in Russian].
- Smith, M. 1937. Further notes upon Tertiary and Recent mollusks from Florida together with descriptions of new species. *The Nautilus* 51(2):65–68, pl. 6.
- Stimpson, W. 1858. [On *Cochliolepis parasiticus*]. *Proceedings of the Boston Society of Natural History* 6:307–309.
- Taylor, D. W. and N. F. Sohl. 1962. An outline of gastropod classification. *Malacologia* 1(1):7–32.
- Taylor, J. B. 1975. Planktonic prosobranch veligers of Kaneohe Bay. Ph.D. thesis, University of Hawaii, Honolulu, 599 p., illus.
- Thiriot-Quévrevreux, C. 1977. Particularité de l'appareil génital de quelques espèces de Rissoïdæ (Mollusca: Mesogastropoda). *Compte Rendu de l'Académie des Sciences, Paris, série D* 285(7):779–781, pl. 1.
- Thiriot-Quévrevreux, C. 1982. Données sur la biologie sexuelle des Rissoïdæ (Mollusca: Prosobranchia). *International Journal of Invertebrate Reproduction* 5:167–180.
- Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound. *Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelse, Serie Plankton*, Vol. 4(1), 523 p., illus.
- Tryon, G. W. 1888. Monograph of the families Neritidae, Neritopsidae, Adeorbidae, Cyclostrematidae, and Liotidae. *Manual of Conchology* 10:3–160, pls. 1–36.
- Vokes, H. E. and E. H. Vokes. 1983. Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico. *Mesoamerican Ecology Institute Monograph 1*, Middle American Research Institute Publication 54, viii + 183 p., 50 pls.
- Warmke, G. L. and R. T. Abbott. 1961. Caribbean seashells: a guide to the marine mollusks of Puerto Rico and other West Indian Islands, Bermuda and the Lower Florida Keys. Livingston Publishing Company, Wynnewood, PA, x + 348 p., 44 pls.
- Webber, H. H. 1977. Gastropoda: Prosobranchia. In: Giese, A. C. and J. S. Pearse (eds.). *Reproduction of marine invertebrates, IV. Molluscs: gastropods and cephalopods*. Academic Press, New York, p. 1–97.
- Wells, H. W., M. J. Wells, and I. E. Gray. 1961. Food of the sea-star *Astropecten articulatus*. *Biological Bulletin* 120: 265–271.
- White, K. M. 1942. The anatomy of *Cyclostrema bushi* D. & F. *Proceedings of the Malacological Society of London* 25:89–94, pl. 2.
- Woodring, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part II: Gastropods and discussion of results. *Carnegie Institution of Washington, Publication* 395:vii + 564 p., 40 pls.
- Woodward, M. F. 1898. On the anatomy of *Adeorbis subcarinatus*, Montagu. *Proceedings of the Malacological Society of London* 3:140–146, pl. 8.
- Yonge, C. M. 1930. The crystalline style of the Mollusca and a carnivorous habit cannot normally co-exist. *Nature, London* 125:444–445.