

Comparison of *Acteocina canaliculata* (Say, 1826), *A. candei* (d'Orbigny, 1841), and *A. atrata* spec. nov. (Gastropoda: Cephalaspidea)

by

PAUL S. MIKKELSEN AND PAULA M. MIKKELSEN

Harbor Branch Foundation, Inc., R.R. 1, Box 196,
Ft. Pierce, Florida 33450

Abstract. The type species of the genus *Acteocina*, *Acteon wetherilli* Lea, 1833, is synonymized with *Volvaria canaliculata* Say, 1826, type species of the genus *Utriculastra*; because *Utriculastra* and *Cylichnella* are synonymous, *Acteocina* is the senior synonym. The systematics of *A. canaliculata* and *A. atrata* spec. nov. are examined, and a neotype is designated for *A. canaliculata*. Descriptions are presented of shell, radular, and gizzard plate morphologies; geographic and bathymetric distributions are re-evaluated based on museum collections. Floridian specimens of *A. canaliculata* have planktotrophic development, hatching in 4 days and settling in 24 days; *A. atrata* has capsular metamorphic development, hatching in 9 days as benthic juveniles. A preliminary review of *Acteocina candei* (d'Orbigny, 1841) is given, and a lectotype is designated. *Acteocina candei* distinctly differs conchologically from *A. canaliculata*, is resurrected from synonymy, and is considered a valid species.

INTRODUCTION

Acteocina canaliculata (Say, 1826) and *A. candei* (d'Orbigny, 1841) are small, cephalaspid gastropods common throughout much of the western Atlantic. Intraspecific variability of shell and radular characters has obscured interspecific differences, making them consistently difficult to distinguish. Publications reporting either species may actually have considered both species simultaneously or confused the two.

Acteocina canaliculata and *A. candei* have been assigned to many genera, most notably *Utriculus* Brown, 1844, *Tornatina* A. Adams, 1850, *Retusa* Brown, 1827, and *Acteocina* Gray, 1847. *Acteocina* has had the most frequent usage in recent years. However, MARCUS (1956:41), MARCUS (1977:2), and CERNOHORSKY (1978:83) advocated restriction of the genus *Acteocina* to fossil forms because (1) the type species, *A. wetherilli* (Lea, 1833), was described as a fossil whose internal anatomy will never be known, and (2) knowledge of internal anatomy is necessary to define cephalaspid genera according to modern standards. Thus, they concluded that fossil species of this group cannot be reliably allocated to Recent genera. Following this reasoning, MARCUS (1977) allocated *A. canaliculata* and *A. candei* (which she synonymized with *A. canaliculata*) to *Utriculastra* Thiele, 1925. RUDMAN (1978)

incorrectly placed *A. canaliculata* (and thus *A. candei*) in the genus *Tornatina*, apparently unaware of MARCUS' (1977) work restricting *Tornatina* on the basis of radular and gizzard plate morphologies, and because he incorrectly believed that the genus *Cylichnella* Gabb, 1873, lacked jaws (see MARCUS, 1956:39; GOSLINER, 1979:88). GOSLINER (1979) determined that *Utriculastra* was a junior synonym of *Cylichnella* based on similar arrangements of the reproductive system. Therefore, according to the more recent literature, *A. canaliculata* and *A. candei* should be placed in the genus *Cylichnella*.

The familial placement of *Acteocina* (as *Cylichnella*, etc.) has likewise been varied; it has most recently been placed (MARCUS, 1977; RUDMAN, 1978; GOSLINER, 1980) in the Scaphandridae G. O. Sars, 1878. This family was considered (ABBOTT, 1974; CERNOHORSKY, 1978), apparently on a conchological basis alone, to be a junior synonym of Cylichnidae H. & A. Adams, 1854 (not of A. Adams, 1850, as stated by ABBOTT, 1974; not of Rudman, 1978). Although RUDMAN (1978:105) incorrectly repropounded Cylichnidae as a new family, he restricted the family to the genus *Cylichna* on the basis of anatomy. Therefore, according to Rudman, Cylichnidae and Scaphandridae are both valid and distinct families. GOSLINER (1980) refuted RUDMAN'S (1978) distinction between Cylichnidae and



Scaphandridae, considering them synonymous. However, Gosliner chose Scaphandridae as the senior synonym, because he incorrectly considered Cylichnidae of Rudman, 1978, rather than of H. & A. Adams, 1854. Cylichnidae H. & A. Adams, 1854, is the proper senior synonym and would be the correct family for *Acteocina* following GOSLINER's (1980) synonymy. Following RUDMAN (1978), Scaphandridae is correct. The family Acteocinidae Pilsbry, 1921, may be valid as well (see CERNOHORSKY, 1978).

In 1962, WELLS & WELLS attempted to distinguish "*Retusa*" *canaliculata* from *Acteocina candei*. The diagnostic characters used were: radular characters (shape and number of denticles for lateral and rachidian teeth), protoconch appearance (degree of protrusion and number of whorls), shell shape (spire height, basal shape, convexity of the whorls, and apertural shape), habitat, and type of larval development. Wells & Wells found direct-developing larvae in field-collected egg masses of "*R.*" *canaliculata*, and assumed planktonic development in *A. candei* from the appearance of the protoconchs of the adults. However, FRANZ (1971a, b) found planktotrophic development in eggs deposited in the laboratory by adults of *A. canaliculata* collected from Connecticut. Franz explained this discrepancy by suggesting (1) that Wells & Wells, using field-collected egg masses from North Carolina, had unknowingly reared some other cephalaspid, (2) that poecilogony (multiple patterns of development within a species) exists for *A. canaliculata*, or (3) that cryptic species were present. GOSLINER's (1979) observations from the estuarine Pictou Harbor, Nova Scotia, also determined planktotrophic development for *A. canaliculata*.

MARCUS (1977:14) examined additional specimens of "*Utriculastra*" *candei* and "*U.*" *canaliculata* and determined that their shell and radular characters were highly variable and overlapping. Although Marcus noted different morphologies in the gizzard plates of each species, these differences were attributed to varying degrees of desiccation, and the plates were considered "identical." Possibly due to WELLS & WELLS' (1962) questionable developmental observations, MARCUS (1977) failed to address Wells & Wells' criterion of developmental type as a distinguishing character between the two species. Based on her observations, and on identical morphologies of the male reproductive structures, Marcus synonymized "*U.*" *candei* with "*U.*" *canaliculata*. This synonymy had been suggested many years earlier by DALL (1889:45).

Fifteen shells and 5 radulae of "*Utriculastra*" *canaliculata* were figured by MARCUS (1977), but no attempt was made to document further the degree of variability. MIKKELSEN & MIKKELSEN (1982) closely examined the shell and radular variability of "*U.*" *canaliculata* (as defined by MARCUS, 1977) and indicated that "*U.*" *candei* is an immature form of "*U.*" *canaliculata*, thus supporting the synonymy of Marcus. MIKKELSEN & MIKKELSEN (1983) noted the presence of two types of larval development in the "single species," "*Cylichnella*" *canaliculata*, and suggested that "*C.*" *candei* be resurrected as valid.

In the present study, embryonic, larval, and postlarval morphological characters, and examination of museum collections are utilized to:

- (1) show that Wells & Wells' "*Retusa canaliculata*" is actually an undescribed species, living sympatrically with *Acteocina canaliculata* in eastern Florida;
- (2) determine the correct generic placement for *A. canaliculata* and *A. candei*;
- (3) examine in detail the postlarval intraspecific variation of the shell, radula, and gizzard plates of *A. canaliculata* and the new species;
- (4) describe the larval development of *A. canaliculata* as well as that of the new species; and
- (5) partially characterize *Acteocina candei*, in contrast with *A. canaliculata* and the new species.

MATERIALS AND METHODS

Collections

The principal study site was the 195 km-long Indian River lagoon, along the central east coast of Florida (Figure 7D). Salinity generally ranged from 18 to 36 ppt, although extremes of 8 and 42 ppt were recorded during the study. Live snails were sieved, using 0.5 mm-mesh screens, from bare or vegetated subtidal sand or mud substrates. Dried or wet-preserved specimens from various museums and private collections were utilized to redetermine geographic and bathymetric distributions. Fossil type specimens were examined for synonymies; however, because additional fossil material was not thoroughly studied, detailed paleontological distributions are not given. Cited repositories and other sources are as follows:

- ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia, PA
 BM(NH)—British Museum (Natural History), London
 CAS—California Academy of Sciences, San Francisco, CA
 ChM—Charleston Museum, Charleston, SC
 D. Franz Collection—Department of Biology, Brooklyn College of the City University of New York, Brooklyn, NY
 HMNS—Houston Museum of Natural Science, Houston, TX
 IRCZM—Indian River Coastal Zone Museum, Harbor Branch Foundation, Ft. Pierce, FL
 MACN—Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
 MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA
 MORG—Museo Oceanográfico, Rio Grande, Brazil
 PRI—Paleontological Research Institution, Ithaca, NY
 ROM1Z—Royal Ontario Museum, Toronto, Ontario, Canada
 R. Van Dolah Collection—South Carolina Marine Resources Research Institute, Charleston, SC
 UNC-IMS—Institute of Marine Sciences, University of North Carolina, Morehead City, NC

USNM—National Museum of Natural History, Washington, DC.

In synonymies, a dagger (†) preceding a species name indicates fossil type specimens. In "Material examined" sections, an "L" indicates that at least some of the specimens in the lot were live-collected and contained soft parts; an "E" indicates that all specimens were empty shells.

Either original figures or type specimens were examined of all western Atlantic *Acteocina canaliculata*-like forms, fossil and Recent, described to date. Types were examined if figures even remotely resembled the species discussed herein. Two exceptions were *Cylichna virginica* Conrad, 1868, and *Tornatina cylindrica* Emmons, 1858, for which no types could be located to clarify the ambiguous original figures.

Postlarval Observations

Specimens with intact protoconchs, collected from various localities throughout the study area, were chosen for statistical analyses. These encompassed a wide range of shell lengths, but excluded specimens not retained by the 0.5 mm-mesh collecting sieve. Each shell was illustrated using a stereomicroscope and camera lucida providing permanent records of shell length, shell width, spire height and angle (Figure 1A), and percent of protoconch protrusion (Figure 1D). Drawings were essential because partial destruction of the shells was necessary to remove the retracted animals.

Percent of protoconch protrusion was determined (Figures 1E–G) utilizing the circle, $(x - h)^2 + (y - k)^2 = r^2$, approximated by the periphery of the protoconch, where (h, k) are the coordinates of the center, (x, y) are the coordinates of any point on the circle, and r is the radius. With the ordinate axis drawn through the center of the circle, and the abscissa through the lateral suture points of the protoconch with the first postnuclear whorl, the y -coordinate (h) of the center equals zero, and the equation reduces to Equation I: $x^2 + (y - k)^2 = r^2$. Measurement of the protoconch's exposed height (b) and width at the suture (2a) yields 3 points on the circle: $(a, 0)$, $(-a, 0)$, and $(0, b)$. For point $(a, 0)$ or $(-a, 0)$, $y = 0$, and Equation I becomes Equation II: $a^2 + k^2 = r^2$. For point $(0, b)$, $x = 0$, and Equation I becomes Equation III: $b^2 - k^2 = r^2$ or Equation IV: $b - k = r$. Subtracting Equation II from Equation III yields Equation V: $k = (b^2 - a^2)/2b$. Using a and b obtained from actual protoconch measurements, Equation V can be solved for k , which is used in Equation IV to determine the radius: $r = b - (b - a)/2b$. The diameter of the circle ($2r$) and the exposed height (b) are then used to determine the percentage (P) of protoconch protrusion: $P = b/2r \times 100\%$.

Radulae and gizzard plates were extracted by dissolving the surrounding soft tissue in a solution of 10% sodium hydroxide at 20°C (LINDBERG, 1977). In addition to suggestions by TURNER (1960) and SOLEM (1972), handling

of small radulae was facilitated by use of a cat's vibrissa mounted on the tip of a probe. Gizzard plates were observed and subsequently stored in 70% ethanol, or dried. Radulae were simultaneously stained and permanently mounted on glass slides, using Turttox CMC-9AF low-viscosity stain-mountant tinted with acid fuchsin (Masters Chemical Co., Inc., Des Plaines, IL). Due to the extremely small size of the radula, this one-step operation eliminated the loss of many radulae. Each radula was mounted so that at least some of the lateral teeth were oriented as in Figure 1B. All slide-mounted radulae were illustrated using a compound microscope and camera lucida. These drawings provided the width, angle, and number of denticles for lateral teeth (Figure 1B), plus the width and number of denticles for rachidian teeth (Figure 1C). Radulae used for scanning electron microscopy were cleaned by sonication, following the method of SOLEM (1972). Radulae and gizzard plates were air dried and scanned using a Zeiss Novascan-30.

Shell terminology is after SMITH (1967a:758–760) and KNIGHT (1952:7–9); radular terminology is after BERTSCH (1977). Providing regressions of various characters follows the initiative of BERTSCH (1976).

Larval Development

Adults were collected during each month of the year from at least one of several locations (Figure 7D). Adults from a single site were left together for about 24 h in a finger bowl with seawater and sand substrate from the collection site. Individuals were then isolated in compartmented plastic trays, each containing filtered seawater and a thin layer of sand. Each compartment was checked daily, for up to 14 days, and egg masses were removed to compartmented plastic trays containing seawater only. Adults and developing egg masses were maintained at ambient laboratory conditions of 22–25°C with variable lighting, or under incubation at 22°C with a daily light cycle of 12 h light/12 h dark.

Planktotrophic larvae were reared using larval culture sieves placed in 300-mL beakers. Each larval sieve consisted of a 4.5-cm section of acrylic tubing, 7.6 cm in diameter, closed at the base by a 33 μm -mesh nitex screen. Larvae from a single egg mass were reared in the same sieve. Survivorship was maximized by adding antibiotics (5 mg/mL streptomycin sulfate plus 5 mg/mL penicillin-G) to 0.5 μm -filtered, 36-ppt seawater (SWITZER-DUNLAP & HADFIELD, 1981:207). Cetyl alcohol flakes were floated on the water to prevent larvae from being trapped by the surface tension (HURST, 1967). Veligers were fed to excess with *Stephanoptera* sp., a 10 μm -diameter, unicellular green alga. Water and food supply were changed every other day.

Direct-developed hatchlings and metamorphosed planktic larvae were transferred to 300-mL beakers of filtered seawater. Amorphous organic material, collected

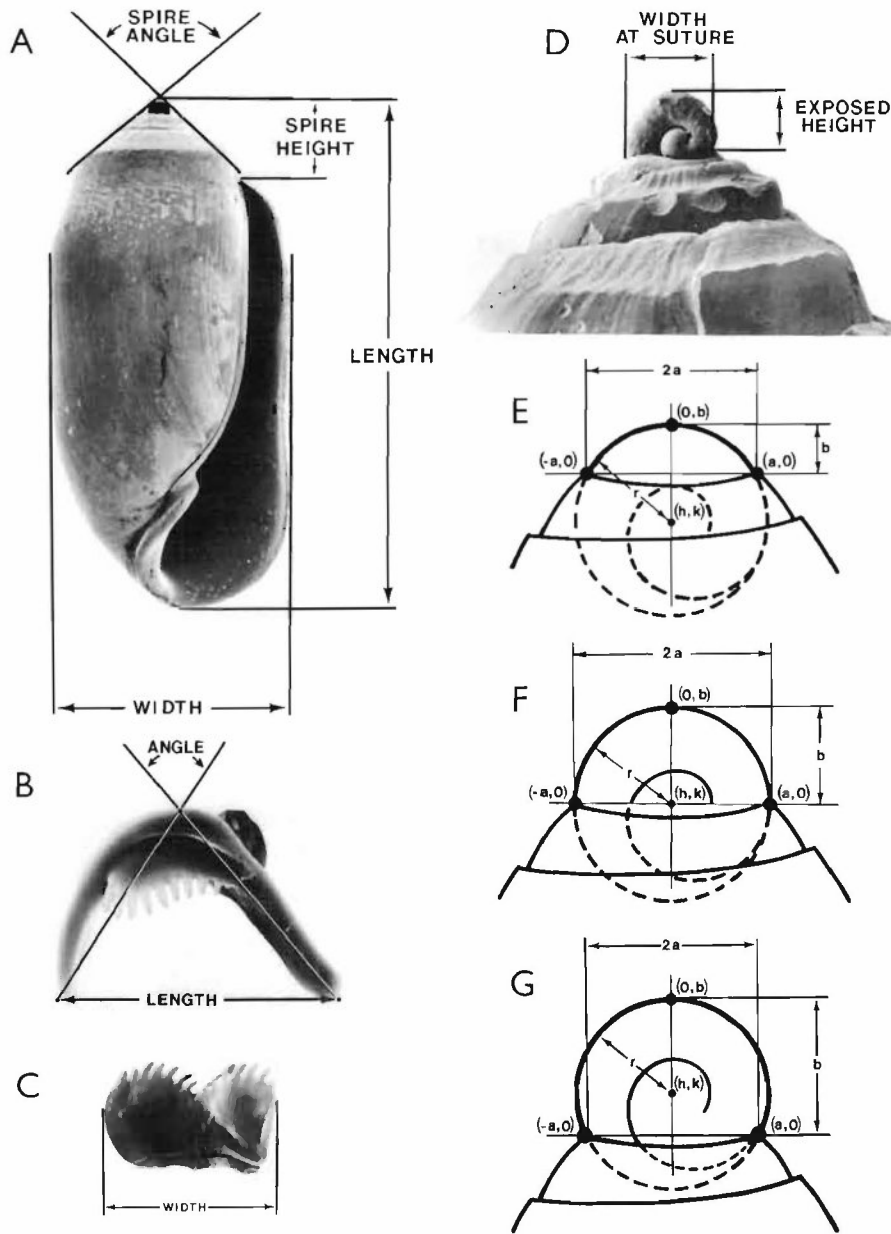


Figure 1

Shell and radular parameters. A. Shell in apertural view. B. Lateral radular tooth. C. Rachidian radular tooth. D. Apical view of protoconch. E, F, and G. Diagrammatic protoconchs of increasing degree of protrusion, showing points and distances used in calculating percent protrusion.

from sedimentary detritus at the collection site or from a laboratory running-seawater system, provided food for the juveniles. After this material was suspended by swirling, the larger particles were allowed to settle and the finer suspended material was decanted off. It was this fine organic material which was added in small quantities to the

beakers containing the juveniles, to form a thin bottom layer of food. Juveniles were visually located and transferred to new seawater and food once a week.

Larval shells were prepared for SEM either by preservation in 80% ethanol or by soaking in a dilute solution of household bleach to remove the soft tissues. The latter

method was considered least desirable because opercula were invariably lost. The larval shells were then dried, mounted, and scanned as described above for the radulae and gizzard plates.

SYSTEMATIC RESULTS

Genus *Acteocina* Gray, 1847

Acteocina GRAY, 1847:160.

Cylichnella GABB, 1873:273-274.

Utriculastra THIELE, 1925:235.

The holotype of *Acteon wetherilli* Lea, 1833 (type species of the genus *Acteocina*) is extremely worn, and lacks its protoconch. The type locality of *A. wetherilli* is Deal, New Jersey, from deposits of Miocene age (RICHARDS, 1968). L. D. Campbell (personal communication, 1983) indicated that the type locality may be as young as Pleistocene.

In all discernible conchological characters, *Acteocina wetherilli* agrees with the Recent species *Volvaria canaliculata* Say, 1826, type species of the genus *Utriculastra*. This synonymy was first suggested by OLSSON & HARBISON (1953) and reiterated by OLSSON & MCGINTY (1958), OLSSON (1964), and CAMPBELL *et al.* (1975). The genus *Acteocina* is therefore applicable to Recent forms (contrary to MARCUS, 1956:41). The anatomical characteristics of *A. canaliculata* may now be assumed to be applicable to the genus. In addition, the genus *Utriculastra* becomes a junior synonym of *Acteocina*.

Utriculastra and *Cylichnella* are presently synonymous, in accordance with the anatomical studies of GOSLINER (1979). Although GOSLINER (1979) additionally included *Tornastra* Marcus, 1977, in this synonymy, we prefer to omit it here because of the distinctive gizzard plate and radular anatomy of *Bulla eximia* Baird, 1863, the type species of *Tornastra* (see MARCUS, 1977). DALL (1908) listed eight additional synonyms of *Cylichnella*, but they are either incorrect or unconfirmed herein.

Our experience has determined that *Acteocina*-like species can be distinguished conchologically. In the case of *Acteocina*, we have conchologically matched its fossil type specimen with a Recent species, and have subsequently defined the genus using the internal characteristics of Recent specimens. This action does not differ from the conchological matching of dead-collected Recent type specimens (of prosobranch and other mollusks) with living individuals, which are then used to redescribe the species, complete with internal anatomy. Although this procedure is followed frequently in malacology, it has been considered inappropriate for cephalaspids (MARCUS, 1956;

MARCUS, 1977). In our opinion, it must be considered acceptable (for example, in the case of *A. candei*).

Until further studies at the species level are complete for *Acteocina* and other closely related genera, resolution of the familial placement of *Acteocina* is not possible.

Acteocina canaliculata (Say, 1826)

(Figures 2 to 5)

Volvaria canaliculata SAY, 1826:211.

[non *Bulla canaliculata* D'Orbigny, 1841:133-134; 1842: pl. 4 bis, figs. 21-24.]

Bullina canaliculata: SAY, 1832:pl. 39.

†*Acteon wetherilli* LEA, 1833:213, pl. 6, fig. 224.

Bulla obstricta GOULD, 1840:196.

†*Acteocina chowanensis* RICHARDS, 1947:34, pl. 11, fig. 10.

Acteocina canaliculata: FRANZ, 1971a:68-69; 1971b:174-182.

Utriculastra canaliculata: MARCUS, 1977:14-17 (in part), figs. 36-38, 40, 42.

Utriculastra canaliculata: MIKKELSEN & MIKKELSEN, 1982: 38.

Cylichnella candei: MIKKELSEN & MIKKELSEN, 1983:91.

Material examined

Neotype (designated herein): 3.80 mm, ANSP A9721A.

Specimens collected with the neotype: 11L, ANSP A9721B; 9L, IRCZM 65:1910; 2L, IRCZM 65:1911; radula slide, IRCZM 65:MØ55; 11L, USNM 836099; 10L, ChM IN 19869; 10L, MCZ 272599.

Type material of synonyms:

†*Acteon wetherilli* Lea, 1833: holotype, ANSP 14431. Miocene (?Pleistocene), New Jersey.

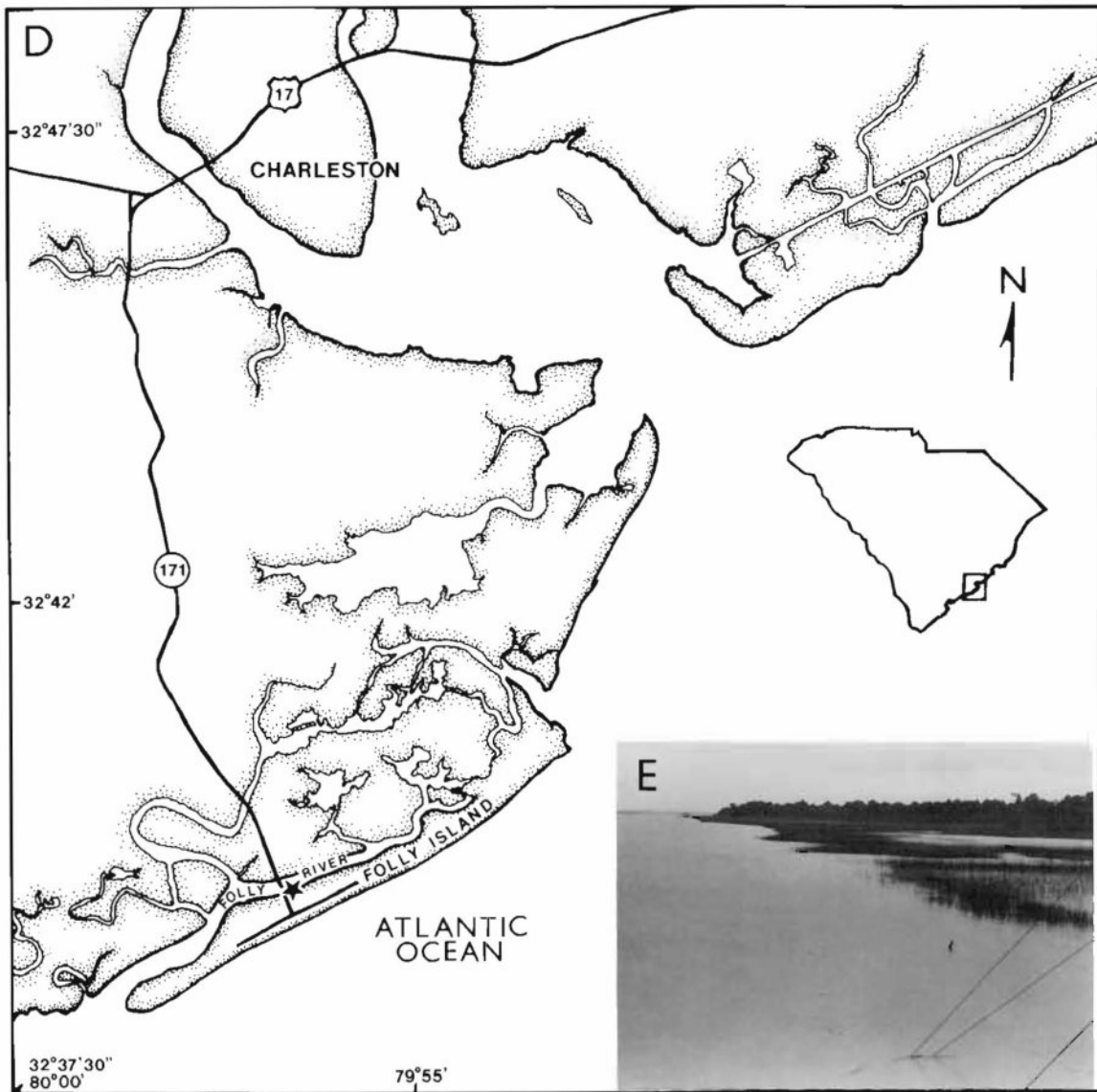
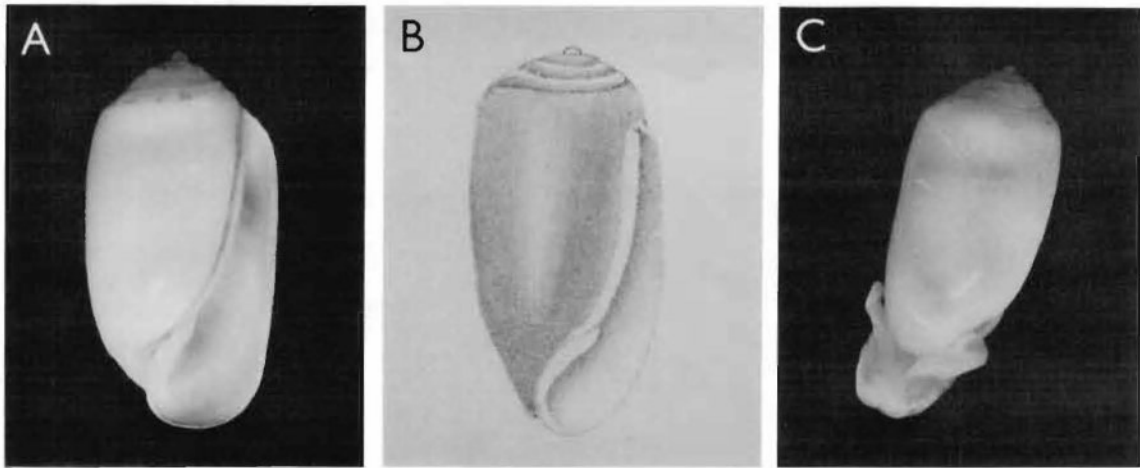
Bulla obstricta Gould, 1840: 14 syntypes (+4 shell fragments), MCZ 216773. New Bedford, Massachusetts.

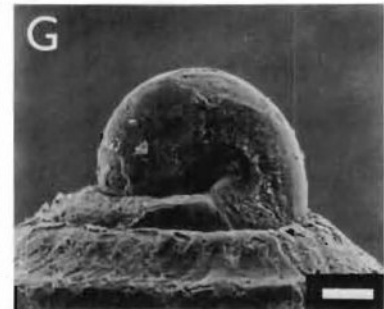
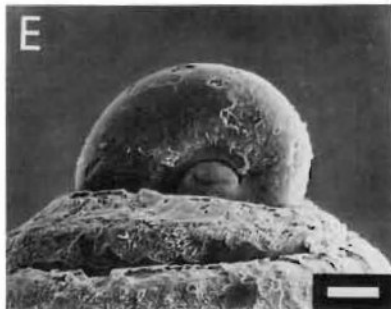
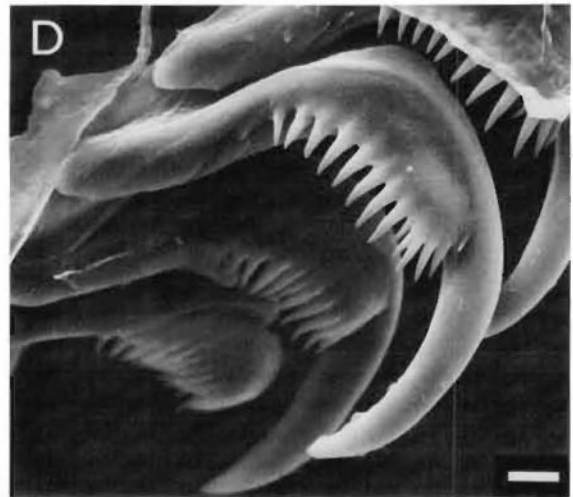
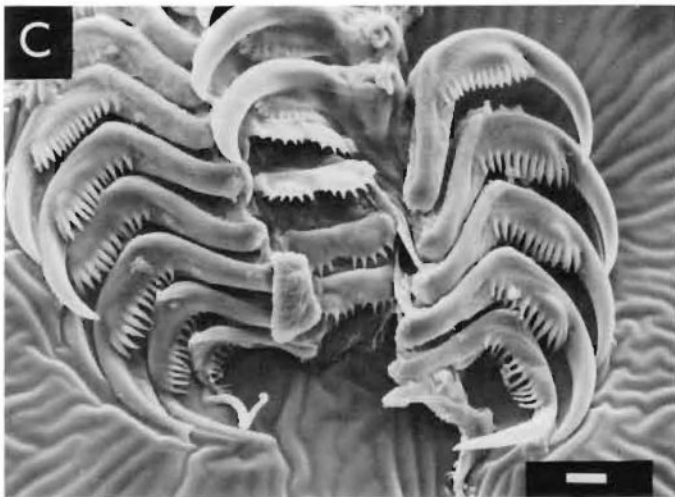
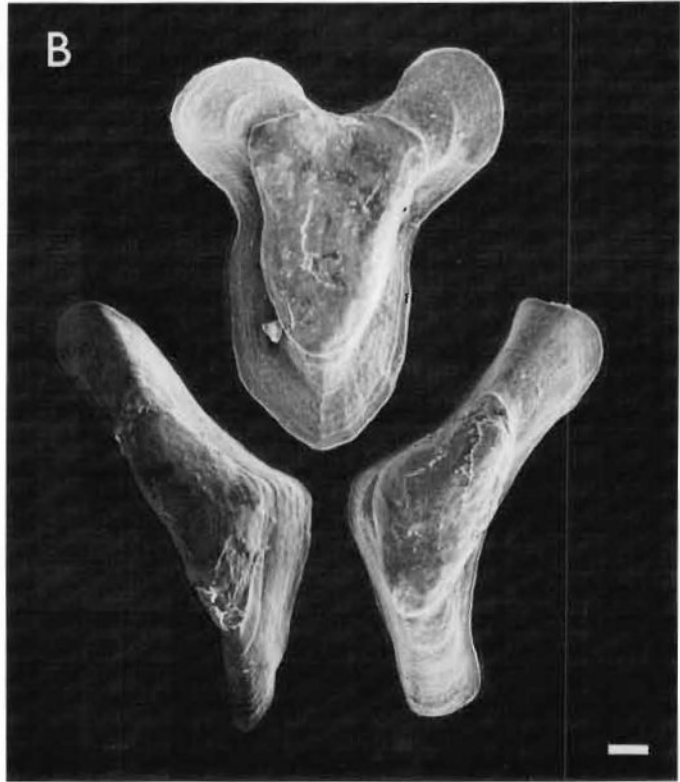
†*Acteocina chowanensis* Richards, 1947: holotype, ANSP 16754. Yorktown Formation, Miocene, North Carolina.

Other material: *Prince Edward Island:* 34L, MCZ 38870.—*Maine:* Isle au Haut(?): 10E, MCZ ex.14531 (in part).—*Massachusetts:* Duxbury: 76L, USNM 358256.—*New Bedford:* 24L, USNM 57310.—*Rhode Island:* Westerly: 200+L, USNM 358281.—*Connecticut:* Noank (Beebe Cove), 20L, D. Franz Collection.—*New Jersey:* Little Egg Harbor: 8E, D. Franz Collection.—*Maryland:* Point No Point: 100+L, USNM 379507.—*North Carolina:* Cape Hatteras: 3L, D. Franz Collection.—off Cape Lookout: 500+L, USNM 523583.—*Neuse River:* 51L, UNC-IMS 9859.1-51.—*South Carolina:* Charleston Harbor: 3E, ChM 30.183.11.—*Georgia:* Jekyll Island: 12E, UNC-IMS 8074.1-12.—*Florida:* St. Augustine: 18E, USNM 358292 (in part).—*Cape Canaveral:* 4E, ChM 43.28.4734.—*Merritt Island* (Pleistocene fossils): 6E, IRCZM 65:2000.—*Turnbull Creek* (vouchers): 14L,

Figure 2

Acteocina canaliculata. A. Neotype, 3.80 mm, ANSP A9721A. B. SAY's (1832) original figure. C. Neotype, crawling animal. D. Map of Charleston, SC, area showing Folly River collection site for the neotype. E. Folly River site at high tide.





USNM 804403; 22L, IRCZM 65:1671.—Round Island (vouchers): 50L, ROM1Z B2462; 10L, ROM1Z B2464; 10L, USNM 804404; 10L, IRCZM 65:1672.—Lantana: 86E, ANSP 180523 (in part).—Miami: 224E, USNM 270719 (in part).—Rabbit Key, Monroe Co.: 4E, ANSP 105428.—Cape Romano: 8E, ANSP 92061.—Sanibel Island: 84L, MCZ 84334.—Charlotte Harbor: 68L, USNM 83763.—Clearwater Bay: 117L, ANSP 9446.—Cedar Keys: 39L, MCZ 242896.—St. Joseph Bay: 3L, ANSP 83771.—off Ft. Walton: 7L, MCZ 145871.—Louisiana: Timbalier Island: 27L, HMNS 9231.—Texas: Galveston: 27L, HMNS 8134.—Matagorda Bay: 64L, HMNS 9238.—Corpus Christi: 10E, USNM 125553.

Original description

Acteocina canaliculata was originally described from specimens taken from the coast of South Carolina. The type locality is believed to be in the vicinity of Charleston, where the collector, Mr. Stephen Elliott, lived (MAZYCK, 1913) and probably did the majority of his collecting. SAY (1826:211) briefly described the species: "Shell whitish, immaculate, cylindrical, with very minute obsolete wrinkles; spire convex, very little elevated, mammillated at the tip; volutions above five, with their shoulder very obtusely grooved; labrum with the edge arcuated; labium over-spread with a calcareous lamina, and with a single oblique fold or small tooth near the base." Say also stated that "the arcuated form of the edge of the labrum is only perceived when the part is viewed in profile." Although a figure did not accompany the original description, the species was figured later (as *Bullina canaliculata* in "American Conchology" (SAY, 1832:pl. 39) and is reproduced herein (Figure 2B).

Type material

A series of 25 specimens of *Acteocina canaliculata* labeled as syntypes was procured from the Academy of Natural Sciences of Philadelphia (ANSP 57312). However, these are probably not type specimens because: (1) the specimen label reads "*T. canaliculata*," indicating the genus *Tornatina*, (2) the cited locality is "Georgia," and (3) "J. S. Phillips" is recorded as donor of the lot. Thus, the status of ANSP 57312 as a type lot is questionable.

A search (by ANSP personnel) of the remaining lots of *Acteocina canaliculata* and related species in the ANSP collections failed to yield the original type material. Historical information obtained from Virginia O. Maes (personal communication, 1982) indicates that the types were probably destroyed. According to her, Say removed his

molluscan collections from the ANSP to New Harmony, Indiana in 1825 where much of his material was subsequently lost in a fire. Long after Say's death in 1884, his wife returned whatever was salvaged of Say's collections to Dr. H. A. Pilsbry at the ANSP. Unfortunately, no records exist of the species involved in these transactions, and we conclude that the types of *Volvaria canaliculata* were probably destroyed in the New Harmony fire. To the best of our knowledge, a neotype has not been designated.

Lacking any type specimens, one must rely entirely upon the original description by Say and his subsequent illustration. Unfortunately, the description and figures could apply to any of several species of *Acteocina*. However, a survey of South Carolina material in museum collections (USNM, ANSP, MCZ, ChM) and from Dr. L. Campbell (University of South Carolina at Spartanburg) included only one species living in shallow, estuarine waters (equivalent to SAY's [1826] "coast of South Carolina"). This species closely approximates Say's original illustration. In addition, the majority of specimens labeled as *A. canaliculata* in early museum collections were also of this same form. We take this as sufficient evidence to consider the species in South Carolina estuaries to be Say's *Volvaria canaliculata*.

Following the determination of Say's *Volvaria canaliculata*, designation of a neotype was necessary to avoid future confusion. On December 3, 1982, specimens of *Acteocina canaliculata* were collected by the authors from soft, subtidal mud, below zones of *Spartina* and oysters in the Folly River, an estuarine channel just south of Charleston Harbor, Charleston County, South Carolina (Figures 2D–E). The site was located adjacent to the State Route 171 bridge over the Folly River. Salinity ranged (on an incoming tide) from 27 to 30 ppt during collection of the specimens. The neotype and specimens collected with it were distributed to various repositories (see Material examined, above).

A redescription of *Acteocina canaliculata* follows, based primarily on our observations of Indian River specimens, but consistent with material from South Carolina.

Diagnosis

Teleroconch thick-walled, cylindrical to pyriform. Shoulder rounded; subsutural sculptural band indistinct. Spire height variable, but usually less than 20% of total shell length. Protoconch distinctly tapered toward its origin, showing strongly coiled sutures in lateral view. Lat-

Figure 3

Acteocina canaliculata, adults. A. Shell, from Indian River lagoon, in apertural view, 4.58 mm. B. Gizzard plates, view of grinding surfaces. C. Radula with lateral teeth reflected to expose rachidians. D. Lateral teeth, showing wing-like expansion with denticles. E, F, and G. Protoconch: E. "Apical" view. F. "Posterior" view. G. "Umbilical" view. Scales: B = 100 μ m; C = 10 μ m; D = 5 μ m; E, F, and G = 50 μ m.

eral radular teeth with wing-like expansion bearing one row of denticles. Unpaired gizzard plate T-shaped. Tissues of gizzard, pallial caecum, and Hancock's organs light orange to pink in live material.

Distribution

Prince Edward Island, Canada; Maine (dead shells only); Massachusetts to peninsular Florida and entire Gulf coast to Texas; intertidal to 40 m.

Description

Shell characters

The orthostrophic, dextral teleoconch of adult *Acteocina canaliculata* is smooth and cylindrical, and has up to three whorls (Figure 3A). Large specimens tend toward a pyriform shape, *i.e.*, with greater shell width at the posterior end. The aperture is narrow posteriorly and flares anteriorly; it extends from 80 to 94% of the shell length. The parietal area bears a slight callus, ending in a columella with a single fold. The shell walls are porcelaneous white and thick, approximately 175 μm at the midpoint of the body whorl of adults. The shoulder is somewhat keeled in young to immature individuals, becoming more rounded with maturity, with an indistinct, impressed, subsutural sculptural band. Indian River specimens attained a shell length and width of 5.0 mm and 2.3 mm respectively; the specimens varied in spire angle from 76 to 142 degrees and in spire height from 6 to 20%. The periostracum is thin and transparent, unless environmentally stained, in which case it is often spirally banded.

The sutures of the smooth, hyperstrophic, sinistral protoconch (Figures 3E, G) are strongly curved in both "lateral" views (*i.e.*, from the larval shell's umbilical or apical aspect), appearing slightly umbilicate in "umbilical" view. In its "posterior" view (Figure 3F), the protoconch tapers toward its distal end, or origin. The percent of protoconch protrusion varied from 25 to 74%.

Correlation coefficients (r) were calculated for shell length versus the four other characters measured (Table 1). Shell length versus shell width showed the strongest r -value, while percent of protoconch protrusion, percent spire height, and spire angle yielded very low coefficients. Percent spire height versus spire angle showed a fairly strong negative coefficient.

Radular characters

The radular formula of *Acteocina canaliculata* is 1-R-1 (Figure 3C), with 11-19 rows in specimens 2 mm or more in length. The rachidian teeth ranged in width from 17 to 34 μm and are centrally notched, with each rounded half bearing 4-11 sharply pointed denticles. The lateral teeth (Figure 3D) are sickle-shaped and unicuspid, with the cusp bearing a wing-like expansion supporting one row of several denticles. A blunt, basal tubercle is present for articulation with adjoining lateral teeth. Ontogenetic

increases were noted in the lateral teeth in number of denticles from 6 to 18, in width from 41.6 to 71.9 μm , and in angle from 79 to 104 degrees. Variation in number of lateral tooth denticles within a single radula was also noted (Figure 3C). Shortly after metamorphosis, lateral teeth of juveniles were about 15 μm in length, and smooth; faint traces of denticles were evident on some lateral teeth at 7-9 days post-metamorphosis.

Correlation coefficients (r) for shell length versus radular characters (Table 1) were generally low, with the exception of lateral and rachidian tooth widths. Lateral tooth width versus lateral tooth angle ($r = 0.06$) and shell length versus lateral tooth angle ($r = 0.01$) were particularly low.

Other features

The extended, living animal of *Acteocina canaliculata* is of typical cephalaspid form (Figure 2C). The foot and mantle are translucent white in color, with scattered opaque white dots. Although the shell walls are thick and porcelaneous, they are translucent enough to allow limited observation of the internal anatomy. The gizzard, pallial caecum, and Hancock's organs are light orange to pink in color.

The calcified portion of the gizzard of *Acteocina canaliculata* consists of three plates (Figure 3B): a "pair" of non-identical, but similarly elongated, plates opposing a larger "unpaired" plate. The unpaired plate is most dorsal in the crawling animal and is distinctly T-shaped, regardless of the method of extraction, preparation, or degree of desiccation.

The reproductive system did not differ in gross arrangement from that described by MARCUS (1977) or GOSLINER (1979).

Oviposition

Oviposition in the laboratory occurred at all hours except those between 1800 and 2400. Egg masses were usually deposited within the first few days after collection of the adults. Spawning occurred monthly in the field and in the laboratory, giving no indication of reproductive seasonality in the Indian River Lagoon animals.

Egg mass

The egg mass of *Acteocina canaliculata* (Figure 4A) corresponds to "type C" of HURST's (1967) opisthobranch egg mass forms. It is gelatinous and ovoid, ranging in maximum diameter from 1.9 to 6.4 mm (mean = 3.7 mm). It is firmly anchored at the sediment surface by a mucous thread, up to 60 mm long, which may bifurcate one or more times. Fresh egg masses were usually coated with sand grains, although most fell off within the first few hours after deposition. Uncleaved egg diameters ranged from 63.2 to 85.4 μm (mean = 77.5 μm). The number of eggs per mass ranged from 189 to 1293 (mean = 631 eggs/

Table 1

Statistical analysis of characteristics examined in *Acteocina canaliculata* and *A. atrata* spec. nov.; r , correlation coefficient; $y = mx + b$, regression line equation; n , number of cases; **, not applicable.

Character x	vs.	Character y	<i>Acteocina canaliculata</i>			<i>Acteocina atrata</i>		
			r	$y = mx + b$	n	r	$y = mx + b$	n
Shell length	vs.	Shell width	0.93	$y = 0.445x + 0.163$	56	0.98	$y = 0.490x + 0.0534$	49
Shell length	vs.	Percent spire height	0.09	$y = 0.358x + 13.6$	56	0.27	$y = 1.30x + 8.16$	49
Shell length	vs.	Spire angle	-0.23	$y = -4.05x + 114$	56	-0.57	$y = -11.6x + 153$	49
Shell length	vs.	Percent protoconch protrusion	0.10	$y = 1.31x + 52.1$	56	0.20	$y = 2.03x + 49.0$	49
Shell length	vs.	Radular rows	0.20	$y = 0.506x + 12.7$	56	0.52	$y = 0.975x + 12.2$	49
Shell length	vs.	Lateral tooth denticles	0.48	$y = 1.83x + 5.08$	56	0.18	$y = 0.638x + 17.2$	49
Shell length	vs.	Rachidian tooth denticles	0.46	$y = 0.775x + 3.82$	56	0.52	$y = 0.797x + 4.46$	49
Shell length	vs.	Lateral tooth width	0.85	$y = 8.79x + 25.5$	56	0.92	$y = 13.5x + 18.4$	49
Shell length	vs.	Rachidian tooth width	0.76	$y = 3.91x + 11.1$	56	0.79	$y = 3.83x + 15.5$	49
Shell length	vs.	Lateral tooth angle	0.01	$y = -0.07x + 92.6$	56	0.54	$y = 4.33x + 92.9$	49
Lateral tooth width	vs.	Lateral tooth angle	0.06	$y = 0.047x + 89.8$	56	0.60	$y = 0.326x + 86.6$	49
Lateral tooth width	vs.	Lateral tooth denticles	0.52	$y = 0.190x + 0.79$	56	0.60	$y = 0.0526x + 15.9$	49
Lateral tooth width	vs.	Rachidian tooth width	0.76	$y = 0.374x + 3.70$	56	0.82	$y = 0.270x + 11.2$	49
Rachidian tooth width	vs.	Rachidian tooth denticles	0.55	$y = 0.185x + 1.96$	56	0.58	$y = 0.181x + 2.02$	49
Percent spire height	vs.	Spire angle	-0.77	$y = -3.54x + 153$	56	-0.82	$y = -3.49x + 156$	49
Shell length	vs.	Number of eggs	0.90	$y = 393x - 801$	32	0.55	$y = 38.2x - 56.6$	54
Shell length	vs.	Egg mass diameter	0.88	$y = 1.42x - 1.46$	32	0.41	$y = 0.534x + 1.42$	54
Shell length	vs.	Egg tube diameter	**	**	**	0.42	$y = 92.3x + 256$	26
Shell length	vs.	Egg diameter	0.72	$y = 10.4x + 39.9$	7	0.22	$y = 5.19x + 131$	15
Shell length	vs.	Egg capsule length	-0.10	$y = -2.46x + 163$	15	0.02	$y = 0.91x + 317$	21
Shell length	vs.	Egg capsule width	-0.50	$y = -6.36x + 150$	15	-0.30	$y = -8.39x + 294$	21
Egg capsule length	vs.	Egg capsule width	0.56	$y = 0.302x + 83.7$	15	0.60	$y = 0.373x + 143$	21

mass). Each egg was encased in an oval capsule, about $155 \times 130 \mu\text{m}$ (range: $141\text{--}174 \times 121\text{--}139 \mu\text{m}$); capsules were interconnected by chalazal material. No internal transparent tubes, nurse eggs, or auxiliary yolk-like material were present. Statistical analyses showed high correlation coefficients (r) for maternal shell length versus egg diameter, egg mass diameter, and number of eggs per mass (Table 1).

Larval development

Acteocina canaliculata exhibits planktotrophic development. Pre-hatching development was rapid and consistent between egg masses. The first two cleavages, to 2 cells at 2.5 h and to 4 cells at 3.5 h, are total, spiral and equal, after which they are unequal and form distinct animal and vegetal poles. The 8-celled stage appears at 4.5 h followed by the 16-celled stage at 5 h into development. Further development proceeds rapidly to a multicelled or blastula stage, and by 23 h to a heart-shaped gastrula with its slit-like blastopore clearly visible.

The trochophore stage forms, and it begins to spin on its lateral axis (effectively doing "backwards somersaults") at about 28.5 h into development. The mouth, metapodial rudiment, and prototroch bearing fine cilia are clearly visible at this stage, and the vegetal pole appears as an undifferentiated spherical mass. Two anal cells appear on the lower right surface of the visceral hump.

The third day of development is characterized by the appearance of the rapidly spinning veliger stage (Figure 4B). By then, the larva has switched to an antero-posterior axis of rotation. A well-developed velum with long cilia, a subvelum, two otocysts, a paucispiral operculum beneath a pointed metapodium, a ciliated median metapodial band, and a spherical embryonic shell approximately $85 \mu\text{m}$ in diameter are present. As with other opisthobranchs, torsion does not occur as a larval process, except in the migrating anal cells, and the viscera differentiate in their post-torsional positions. On the 4th day of development, the veliger (Figure 4C) has a large, well-formed right eye. Its shell averages $140 \mu\text{m}$ long, and is nearly symmetrical, being only slightly skewed to the larval left. A colorless, larval kidney is prominent adjacent to the anus, and cilia are visible within the lumen of the midgut. Hatching can be mechanically stimulated by handling or rupturing the egg mass at about 90 h, but if not induced, will occur by 100–110 h after deposition. Hatching is rapid and nearly synchronous, being completed (*i.e.*, the entire mass emptied) within 10 to 20 min.

Post-hatching development depended greatly on the de-

gree of feeding by individual larvae. A large proportion (77.4%) of the hatched veligers in our most successful culture did not metamorphose, most of these were apparently unable to feed, as evidenced by their colorless digestive systems and little or no growth. The remaining individuals (22.6%) began feeding immediately, as evidenced by the bright green coloration of their guts, and developed rapidly. Acquisition of juvenile characteristics after hatching was a function of the degree of growth, expressed as shell length, rather than age of the specimen. The degree of development among the individuals in a culture was also highly variable.

When larvae were not fed, many individuals survived for two weeks although no shell growth was observed. Although the left eye appeared in some individuals after four days, it remained smaller than the first-formed right eye. The left digestive diverticulum noticeably decreased in size during this period. All starved larvae died by the third week after hatching.

In feeding individuals, the left eye appeared, and equaled the right in size, by the fourth post-hatching day at $163 \mu\text{m}$ shell length. By $270 \mu\text{m}$ shell length, the propodium began to swell, the right side of the mantle opened, and the larval heart began pulsating.

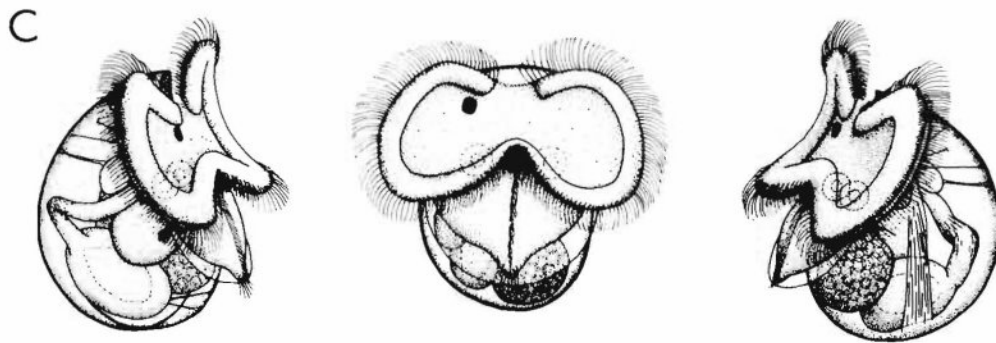
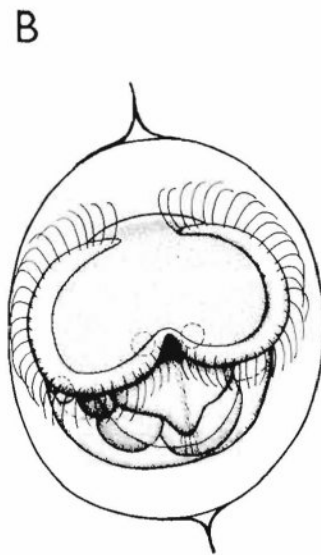
Metamorphosis at $300 \mu\text{m}$ shell length (Figures 5A–C) began after 14 to 20 days, independent of any special substrate. In newly metamorphosed individuals, both larval and adult hearts beat actively, and the nearly umbilicate aspect of the shell was visible from the larval right (Figure 5A). Immediately after metamorphosis, shell growth accelerated at the larval right, beginning the change in direction of coiling. Shells of juveniles approximately one week post-metamorphosis are shown in Figures 5D and E. Attempts at rearing *A. canaliculata* juveniles past this stage of development were unsuccessful.

Remarks

Specimens of *Acteocina canaliculata* show a strong resemblance to those of *Retusa obtusa* (Montagu, 1803), especially in New England where the two species overlap in distribution. Living or live-collected material of *R. obtusa* may be distinguished from *A. canaliculata* by the presence of a much thinner shell and by the absence of eyes and a radula. In the chalky condition often found in dead shells, however, the two species are more similar in appearance, and one must rely upon conchological characters alone. The bulbous protoconch of *R. obtusa*, indicating direct development, is the most reliable feature in these

Figure 4

Acteocina canaliculata, larval development. A. Egg mass. B and C. Larval stages showing appearance of larvae and corresponding larval shells. B. Early veliger in egg capsule, three days post-deposition. C. One-eyed veliger at hatching, four days post-deposition. Scales: B and C = $20 \mu\text{m}$.



cases. *Retusa obtusa* also usually exhibits an umbilical chink and a weaker or absent columellar fold.

The maximum shell length of 9 mm for *Acteocina canaliculata*, given by MARCUS (1977:14) and others, is in error, being attributable to *Bulla canaliculata* d'Orbigny, 1841, a probable synonym of *Tornatella bullata* Kiener, 1834.

Although current literature (ABBOTT, 1974) characterizes *Acteocina canaliculata* as a shallow-water, estuarine species, this viewpoint was derived from the incorrect results of WELLS & WELLS (1962). Our examination of live-collected museum specimens determined wider ecological and bathymetric ranges—from estuarine to oceanic, and from intertidal to a depth of 40 m.

Acteocina chowanensis Richards, 1947, is herein synonymized with *A. canaliculata* for the first time, based on examination of type material. *Tornatina coixlachryma* Guppy, 1867, is herein removed from synonymy with *A. wetherilli* (= *A. canaliculata*), as stated by DALL (1890) and PILSBRY (1921). The neotype of *T. coixlachryma* (USNM 369322), designated by WOODRING (1928), has a protoconch indicating direct development and spiral striae over the entire teleoconch; it does not agree in morphology with any of the species discussed herein.

In his synonymy of *Bulla* (*Tornatina*) *Wetherilli* [sic], DE GREGORIO (1890) listed “=?(1887. *Tornatina crassiplica* Conr. Meyer . . .).” This refers to *Bulla crassiplica* Conrad, 1847, and to MEYER's (1887) listing and figure of that species. Both Meyer's figure and the lectotype (ANSP 13412) and paralectotypes (ANSP 13413) of *B. crassiplica* exhibit cylindrical shells with keeled shoulders around low to nearly involute spires. This is very different from *A. wetherilli*; therefore, we also remove *B. crassiplica* from synonymy with *A. wetherilli*.

FRANZ's (1971b) observations on larval development of *Acteocina canaliculata* from Connecticut compare well with our observations from eastern Florida. Franz noted oviposition only at night, while Florida specimens oviposited from 2400 to 1800; he also noted a smaller range (250–700) in the number of eggs per mass. Franz found sand grains adhering to the newly deposited egg mass; we observed this also, but found that most of the sand grains fell off within a few hours after deposition. Floridian *A. canaliculata* egg capsules were generally smaller, as was the diameter of the uncleaved ovum. The larval shell, at hatching, was also slightly smaller in Floridian specimens. Shell length at metamorphosis in Florida was identical to that found in Connecticut; however, metamorphosis occurred after 14 to 20 days post-hatching in Florida, twice as long as in Connecticut.

Acteocina candei (d'Orbigny, 1841)

(Figure 6)

- Bulla candei* D'ORBIGNY, 1841:128–129; 1842:pl. 4 bis, figs. 1–4.
 †*Acteocina anetaspira* WOODRING, 1928:121–122, pl. 2, fig. 6.
 †*Acteocina canaliculata vaughani* GARDNER, 1948:278–279, pl. 38, figs. 5–6.
Acteocina candei: WELLS & WELLS, 1962:87–93 (in part); figs. 4, 7–10, 12.
 †*Acteocina elachista* WOODRING, 1970:418, pl. 62, figs. 1–2.

Material examined

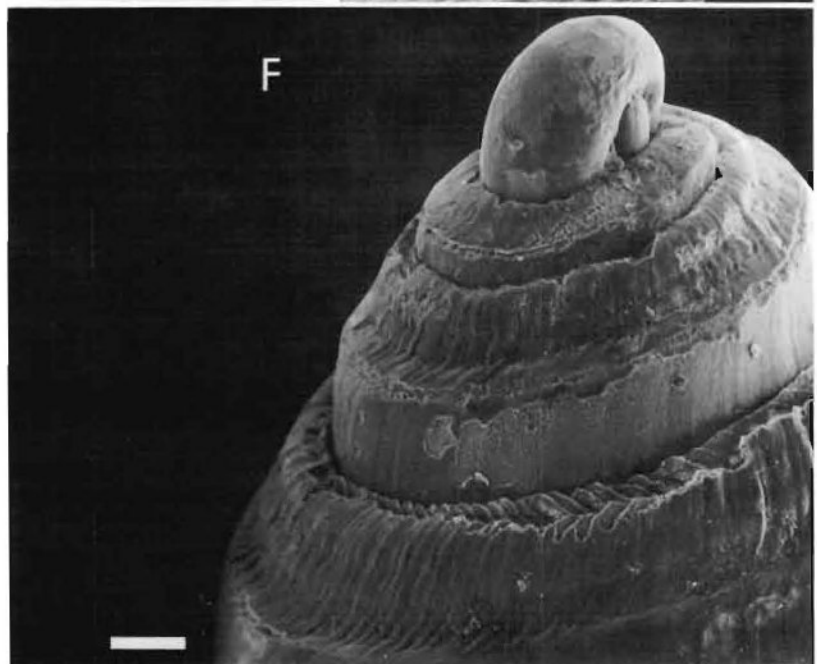
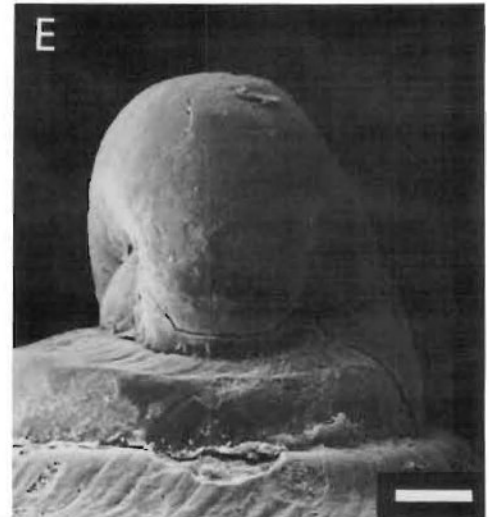
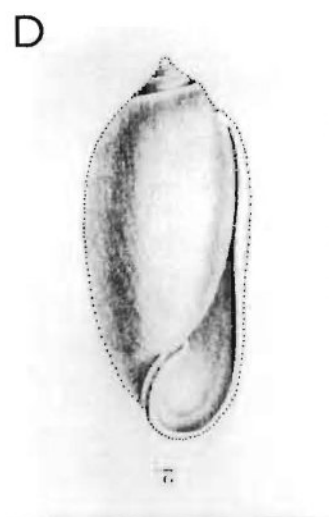
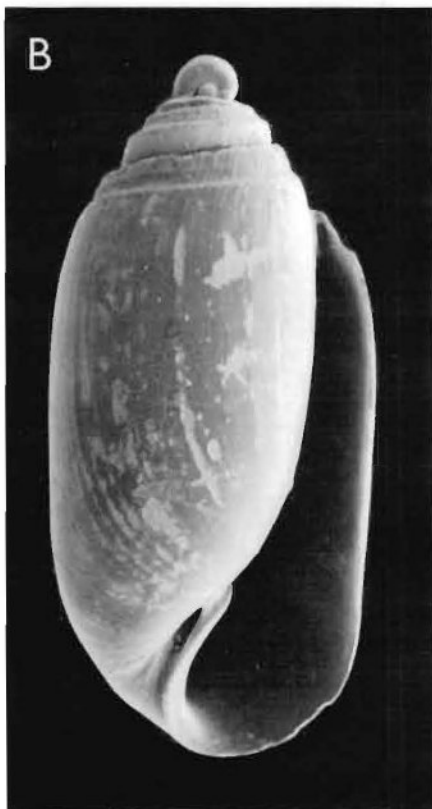
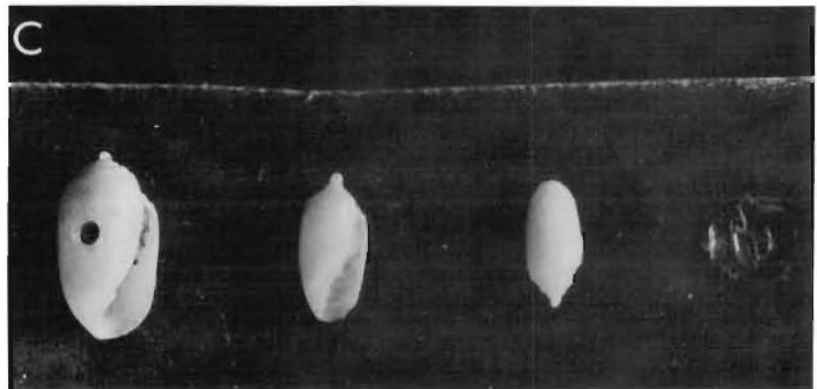
- Lectotype** (designated herein): 3.28 mm specimen, BM(NH) 1854.10.4.17 (in part).
Paralectotypes (designated herein): 2.61 mm and 2.25 mm specimens, BM(NH) 1854.10.4.17 (in part).
Type material of synonyms:
 †*Acteocina anetaspira* Woodring, 1928: holotype, USNM 369321. Bowden Formation, Miocene, Jamaica.
 †*Acteocina canaliculata vaughani* Gardner, 1948: holotype, USNM 497059. Waccamaw Formation, Pliocene, North Carolina.
 †*Acteocina elachista* Woodring, 1970: holotype, USNM 646052. Gatun Formation, Miocene, Canal Zone.
Other material: *North Carolina:* off Cape Hatteras: 14E, USNM 322831.—off Cape Lookout: 4L, UNC-IMS 9278.1–4.—*South Carolina:* 5L, R. Van Dolah Collection.—*Georgia:* off Savannah: 7E, UNC-IMS 7544.1–7.—*Florida:* off St. Augustine: 1E, IRCZM 65:1943.—off Miami: 2E, USNM 358309 (in part).—‘Tortugas’: 26L, USNM 358304 (in part).—off Sanibel Island: 4E, MCZ 245063.—off Calhoun County: 7E, ANSP 83825.—*Alabama:* off Mobile: 4E, USNM 323745.—*Texas:* off Galveston: 1L, HMNS 8133; 3E, HMNS 9266.—*Greater Antilles:* Northwest Cuba: 76L, USNM 358210 (in part).—Jamaica: 11E, USNM 442626.—Haiti: 2E, USNM 383220 (in part).—*Lesser Antilles:* British Virgin Islands: 6L, ANSP 338601.—Antigua: 23E, USNM 500363 (in part).—Barbados: 17E, USNM 500360 (in part).—Grenada: 24E, ANSP 296954.—Bonaire: 7E, ANSP 351033.—*Central America:* Yucatan: 6E, USNM 323195.—Belize: 1E, ANSP 20656.—Limon Bay, Panama: 1E, USNM 760350.—*South America:* Cabo Orange, Brazil: 13E, MORG 21.811.—Fernando de Noronha, Brazil: 12E, MORG 20.608.—Sao Paulo, Brazil: 31L, MORG 21.743.—Uruguay: 8E, MORG 20.070.—San Antonio, Argentina: 17E, MORG 17.917.

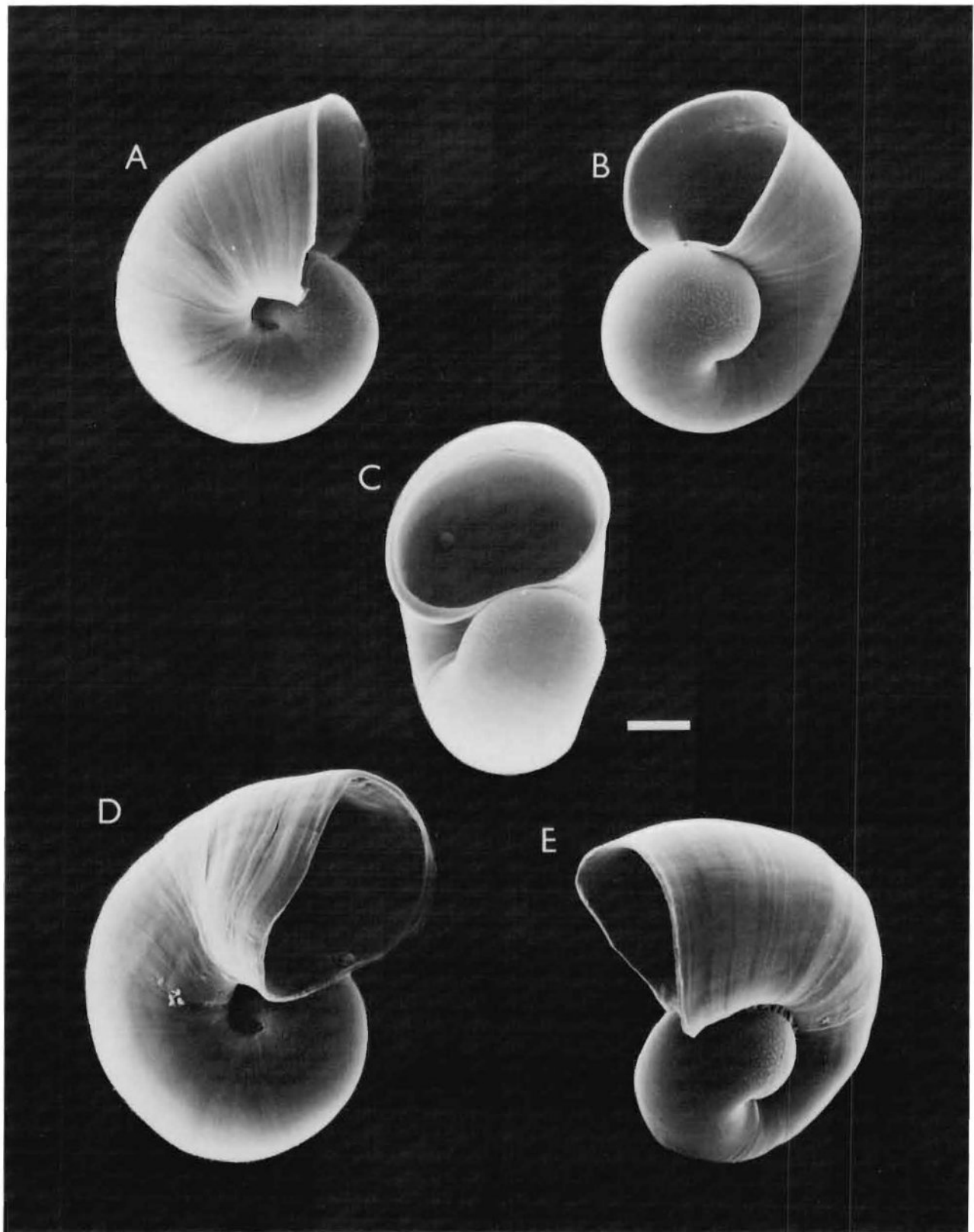
Original description

D'ORBIGNY (1841:128–129) originally described shells of *Bulla candei* as “oval, oblong, thick, slightly narrowing

Figure 5

Acteocina canaliculata, post-larval development. A, B, and C. Shell at metamorphosis. D and E. Shells at approximately one week post-metamorphosis. Scale = 50 μ m.





anteriorly, smooth, bright, marked slightly by a few lines of growth. Spire prominent, conical, canaliculate on the suture, aperture narrow, ending in a point posteriorly, very enlarged anteriorly, and supplied, on the columella, with a ridge resembling a tooth. Color uniformly white." d'Orbigny also described the general appearance of the hyperstrophic protoconch. No distinction was made between *B. candei* and the earlier described *Volvaria canaliculata*.

Type material

The type material of *Bulla candei* (Figures 6A, C) consists of three specimens (3.1, 2.5, and 2.1 mm lengths) glued to a strip of black paper. All three have intact protoconchs and appear to have been dead-collected. A fourth specimen originally part of the lot was found to be missing in 1982 by BM(NH) personnel, but is believed to have been the smallest of the four based on the size of its impression in the glue. We herein designate the largest specimen of the remaining three as lectotype (Figure 6A), because it most closely approximates d'Orbigny's illustration (1842:pl. IV bis, figs. 1-4; reproduced herein, Figure 6D) as well as the dimensions (3 mm long by 2 mm wide) given in the original description (D'ORBIGNY, 1841). The two smaller specimens are herein designated as paralectotypes. The type locality was given as the "Antilles."

Diagnosis

Shell, radula and gizzard plates as in *Acteocina canaliculata*, except: subsutural sculptural band strongly impressed with distinct axial ribbing; spire height usually greater than 20% of total shell length; shell shape more uniformly cylindrical.

Distribution

Cape Hatteras to peninsular Florida and entire Gulf coast to Texas; throughout the Caribbean, including the Greater and Lesser Antilles, coasts of Central America and South America to San Antonio, Argentina; recorded from 3 to 42 m.

Remarks

Acteocina candei is primarily an offshore species. From the appearance of its protoconch, it is probably planktic-developing. The adult shell is extremely similar to that of the planktic-developing, congener *A. canaliculata*. We are unable to distinguish the two species on the basis of shell

thickness, radula, gizzard plates, or gross reproductive anatomy. The only consistent diagnostic character for *A. candei* is the presence of a strongly impressed, and usually ribbed, subsutural band of sculpture (Figure 6F), apparently what D'ORBIGNY (1841) meant by "canaliculate on the suture." This subsutural band of sculpture is as reliable a conchological character to separate *A. candei* from *A. canaliculata* as are the involute spire and double columellar fold used to distinguish *A. bidentata* (D'ORBIGNY, 1841) from either *A. candei* or *A. canaliculata* (all three species have extremely similar radulae and gizzard plates). *Acteocina candei* also usually exhibits a more uniformly cylindrical (*i.e.*, less pyriform) shell shape, greater spire height, and a more highly protruded protoconch.

Acteocina candei and *A. canaliculata* were synonymized by MARCUS (1977). According to her illustrations, MARCUS (1977:figs. 39, 42a), also included a third species (described as new below). Whether both *A. canaliculata* and *A. candei* were actually present in Marcus' material cannot be reliably determined from her text or illustrations. The subsutural sculptural band below the suture in *A. candei* is distinct, consistent, and comprises a good specific character in our opinion. This is perhaps the same feature noted by D'ORBIGNY (1841) as "canaliculate on the suture," and by DALL (1922:96) as "channel at the suture." However, Dall probably considered specimens of both *A. candei* and *A. canaliculata* in observing that the "channel" varied from "clear-cut and sharp" (= *A. candei*) to "obsolete" (= *A. canaliculata*). Because of this distinct sculptural feature, we resurrect *A. candei* from synonymy, giving it full specific status. Until living specimens of *A. candei* can be further studied, the relationship between it and *A. canaliculata* is uncertain. Therefore, only a preliminarily revised diagnosis and distribution for *A. candei* are given herein; detailed description awaits more complete study.

Based on examination of their type material, the following fossil species are herein synonymized with *Acteocina candei*: *Acteocina anetaspira* Woodring, 1928 (synonymy previously suggested by WOODRING [1970]); *Acteocina canaliculata vaughani* Gardner, 1948; and *Acteocina elachista* Woodring, 1970.

Acteocina atrata

Mikkelsen & Mikkelsen, spec. nov.

(Figures 7-10)

Retusa canaliculata: WELLS & WELLS, 1962:87-93.

Utriculastra canaliculata: MARCUS, 1977:14-17 (in part), figs. 39, 42a.

Figure 6

Acteocina candei. A. Lectotype, 3.28 mm, BM(NH) 1854.10.4.17 (in part). B. Shell from offshore of Indian River region, 2.89 mm. C. Syntypes, BM(NH) 1854.10.4.17, glued to a strip of black paper; lectotype is at extreme left. D. D'ORBIGNY's (1842) original illustration. E. Same as B, "apical" view of protoconch. F. Same as B, posterolateral view of shoulder, showing sculptured subsutural band. Scales: E = 50 μ m; F = 100 μ m.

Utriculostra canaliculata: MIKKELSEN & MIKKELSEN, 1982: 38 (in part).

Cylichnella canaliculata: MIKKELSEN & MIKKELSEN, 1983: 91.

Material examined

Holotype: (Figures 7A, B), 3.72 mm, USNM 838029.

Paratypes: 25 each to USNM 838030, ANSP A 10112, MCZ 294223, IRCZM 65:1996, BM(NH) 1983098, UNC-IMS 9860.1-25, HMNS 13002, CAS 035945, and MORG 22.549.

Type locality: Indian River lagoon, Indian River County, Florida; in shallow, subtidal mud east of Round Island, on the eastern side of the lagoon (Figures 7C, D), 27°33.53'N latitude, 80°09.91'W longitude. Salinity at the time of collection was 17 ppt.

Other material: *Florida:* St. Augustine: 10E, USNM 358292 (in part).—Turnbull Creek (vouchers): 11L, USNM 836098; 3L, IRCZM 65:2001.—Haulover Canal area (vouchers): 10L, ROM1Z B2463.—Merritt Island (Pleistocene fossils): 8E, USNM 371722; 8E, IRCZM 65:1999; 8E, PRI 30017a-h.—Round Island (vouchers): 24L, ROM1Z B2461.—Lantana: 61E, ANSP 357893.—Miami area: 193E, USNM 270719 (in part).—Sanibel Island: 70E, MCZ 282080-b.—Sarasota: 7E, USNM 36019.—Clearwater area: 2L, ANSP 357892.—Tampa Bay: 21E, ANSP 356485.—Cedar Keys: 13L, USNM 36020 (in part).—off Ft. Walton: 3E, MCZ 282779.—*Bahamas:* Great Abaco: 2E, ANSP 299498.

Diagnosis

Teleoconch thin-walled, cylindrical. Shoulder keeled, with a distinct subsutural, sculptural band. Protoconch globose, showing nearly straight suture in lateral view. Lateral radular teeth with one row of denticles directly on inner carinate edge of cusp. Unpaired gizzard plate heart-shaped. Tissues of gizzard, pallial caecum, and Hancock's organs black.

Etymology

The specific name *atrata*, from the Latin *atratus*, means "clothed in black" and refers to the black pigment present on various tissues of the living animal.

Distribution

Both sides of peninsular Florida; Bahamas (one record of dead shells from Great Abaco); less than 2 m. Uncon-

firmed literature record from Pamlico Sound, North Carolina (WELLS & WELLS, 1962).

Description

Shell characters

The heterostrophic shell of *Acteocina atrata* (Figure 8A) consists of a smooth, hyperstrophic, sinistral protoconch, followed by a cylindrical, orthostrophic, dextral teleoconch with up to three whorls in adults. The teleoconch is off-white, smooth, translucent, and more thinly shelled than that of *A. canaliculata*, with the shell wall approximately 112 μ m thick at the midpoint of the adult body whorl. The shell is angulate or keeled at the shoulder, and shows a prominent subsutural sculptural band. The aperture extends from 78 to 97% of the shell length, and flares widely at the rounded to truncate anterior end. In Indian River material, the shells reached a maximum length and width of 5.4 mm and 2.7 mm respectively, and varied in spire angle from 80 to 160 degrees and in spire height from 3 to 22%. Large shells (3 mm and over) showed a strong tendency for the last whorl to be set at an abnormally high level on the body whorl, thus decreasing the expected final spire height and increasing the expected final spire angle. Periostracum as in *A. canaliculata*. The protoconch (Figures 8E-G), when viewed "laterally" (either from the larval shell's umbilical or apical aspect) exhibits an only slightly curved suture. From its posterior view (Figure 8F), the protoconch is globose and does not taper. The percent of protoconch protrusion varied from 27 to 70%.

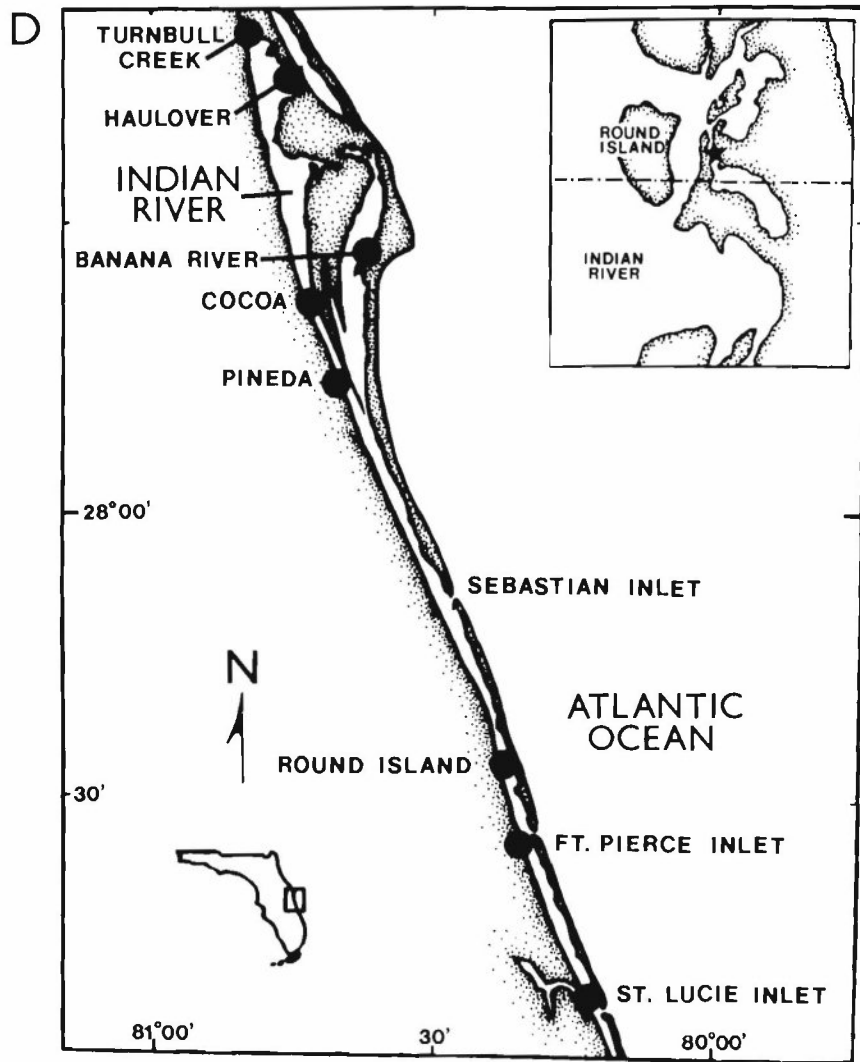
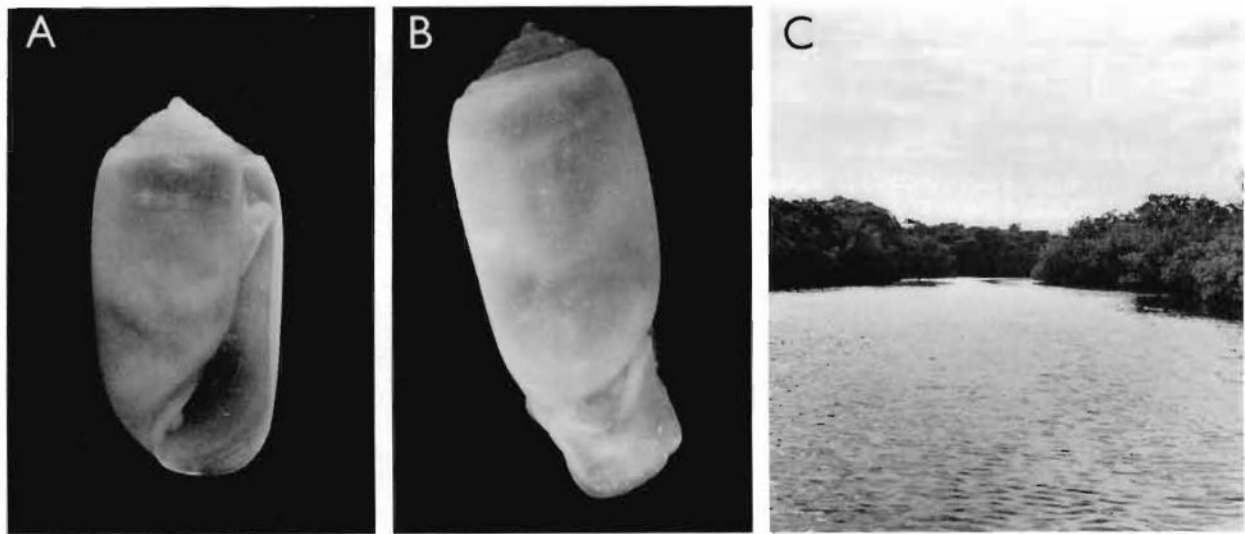
Correlation coefficients (r) for shell characters (Table 1) followed a pattern similar to those for *Acteocina canaliculata*.

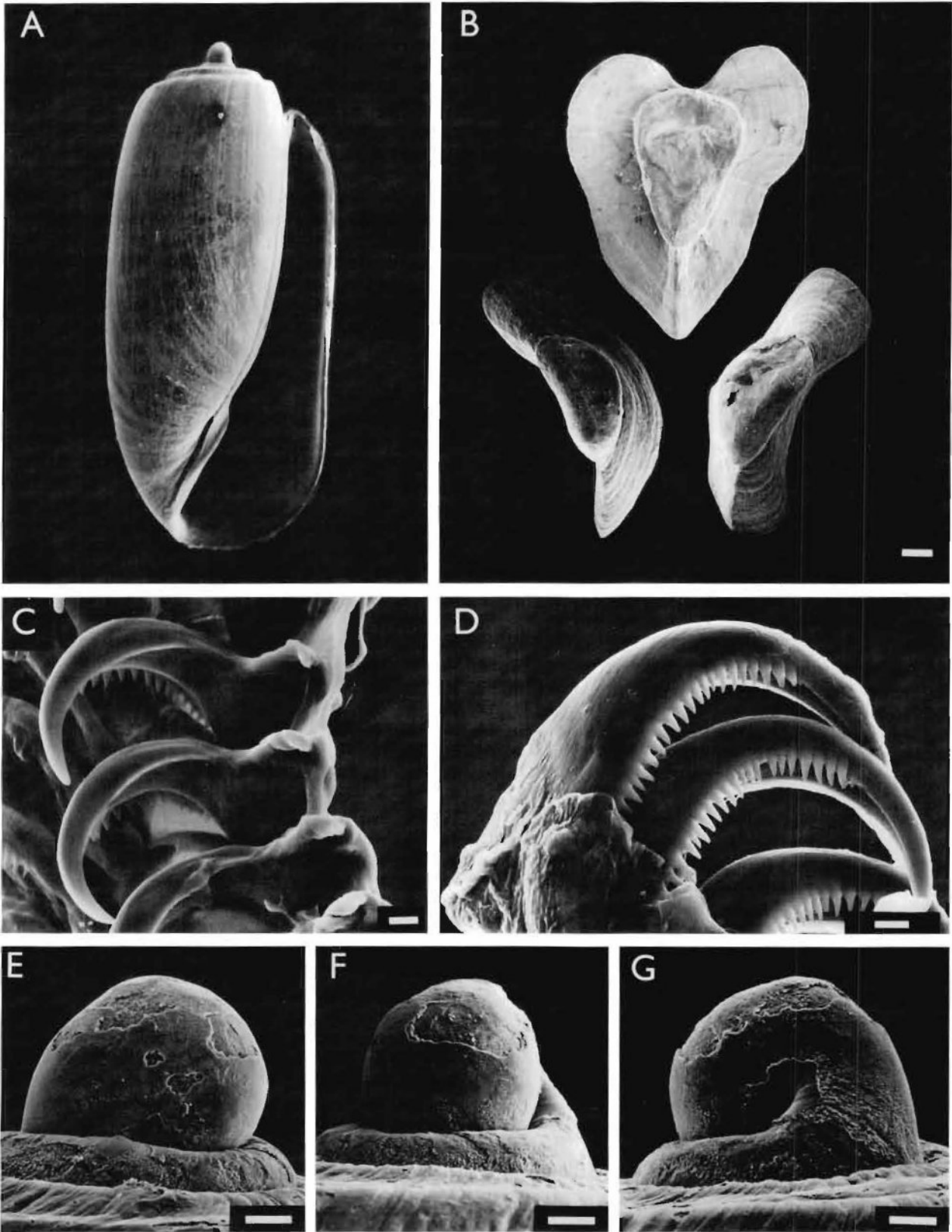
Radular characters

The radular formula of *Acteocina atrata* is 1-R-1, with 14-19 rows in specimens 2 mm or more in length. The rachidian teeth are centrally notched, with each rounded half bearing 5-11 sharply pointed denticles. The width of the rachidian teeth ranged from 24 to 39 μ m. The lateral teeth (Figures 8C, D) are distinct from *A. canaliculata*, being sickle-shaped, unicuspid, and bearing one row of finer denticles directly on the cusp's inner carinate edge. A blunt basal tubercle is present for articulation with adjoining lateral teeth. The lateral teeth varied ontogenetically in number of denticles from 14 to 25, in width from 46.8 to 97.8 μ m, and in angle from 98 to 125 degrees.

Figure 7

Acteocina atrata, spec. nov. A. Holotype, 3.72 mm, USNM 838029. B. Same as A, crawling animal. C. Round Island cove, the type locality of *A. atrata*. D. Map of the central east coast of Florida, showing primary collection sites (dots); detailed insert shows type locality (star), east of Round Island and north of the Indian River County/St. Lucie County line.





Variation within a single radula was also noted, especially in number of lateral tooth denticles. Hatchlings possessed radulae with 4–5 denticles per lateral tooth, increasing to 6 denticles in 14–20 days. These denticles are of the same form as those in the adult specimens, located directly on the inner carinate edge of the cusp; no wing-like expansion supporting the denticles, as is present in *A. canaliculata*, was seen at any stage of development.

Correlation coefficients (r) for shell length versus radular characters (Table 1) were generally low, with the exception of lateral and rachidian tooth widths, as in *Acteocina canaliculata*. However, lateral tooth width versus lateral tooth angle ($r = 0.60$) was an order of magnitude higher than in *A. canaliculata*; shell length versus lateral tooth angle was also notably higher.

Other features

The foot and mantle coloration in living *Acteocina atrata* is similar to *A. canaliculata*. The thinly walled adult shell of *A. atrata* allows visual observation of a portion of the internal anatomy, enhanced in this species by the presence of black pigment (absent in *A. canaliculata*) in the tissue over the gizzard and the pallial caecum (Figure 7B). Black pigment is also visible in the lateral groove between the cephalic shield and the propodium, in the vicinity of Hancock's organs.

The gizzard plates of *Acteocina atrata* are similar to those of *A. canaliculata*, except that the unpaired plate is distinctly heart-shaped (regardless of method of extraction, preparation, or degree of desiccation).

Gross reproductive anatomy was examined and found not to differ from that described by MARCUS (1977) and GOSLINER (1979) for *Acteocina canaliculata*. Preliminary observations by T. M. Gosliner (personal communication, 1983) determined differences in penial morphology between *A. atrata* and *A. canaliculata*.

Oviposition

Oviposition occurred in a time frame identical to that of *Acteocina canaliculata*. Spawning occurred monthly in the field and in the laboratory, giving no indication of reproductive seasonality in the Indian River lagoon.

Egg mass

The egg mass of *Acteocina atrata* (Figures 9A, A') is very similar in general shape and size to that of *A. canaliculata*. It is also gelatinous, ovoid to spherical (from 2.3

to 5.0 mm in maximum diameter, mean = 3.5 mm), and is anchored at the sediment surface by a mucous thread. When freshly deposited, the egg masses were always heavily coated with sand grains, which persisted for most of the developmental period, but most of which dropped off during the last 1–2 days before hatching. The un-cleaved egg diameter ranged from 132.3 to 175.9 μm (mean = 151.6 μm), and each mass contained from 23 to 148 eggs (mean = 91.1 eggs/mass). Each egg was enclosed in an oval capsule about $320 \times 262 \mu\text{m}$ (range: $268\text{--}347 \mu\text{m} \times 235\text{--}288 \mu\text{m}$). The capsules were interconnected by chalazal material, and were also loosely packed into transparent tubes, $427.0\text{--}807.7 \mu\text{m}$ in diameter (mean = 609.4 μm), irregularly coiled within the egg mass. There were no nurse eggs or auxiliary yolk-like material.

In contrast to *Acteocina canaliculata*, statistical analyses showed low correlation coefficients (r) for shell length versus egg diameter, mass diameter, and number of eggs/mass (Table 1).

Larval development

Acteocina atrata exhibits capsular metamorphic development (as defined by BONAR, 1978). Although the time between developmental stages varied among egg masses, development within an individual mass was well synchronized. Early cleavages resulted in a 2-celled stage at 3 h, 4 cells at 4 h, 8 cells at 5 h, and 16 cells at 6 h. Further development proceeded rapidly to a multicelled or blastula stage, and then to the heart-shaped gastrula by 20 to 25 h into development.

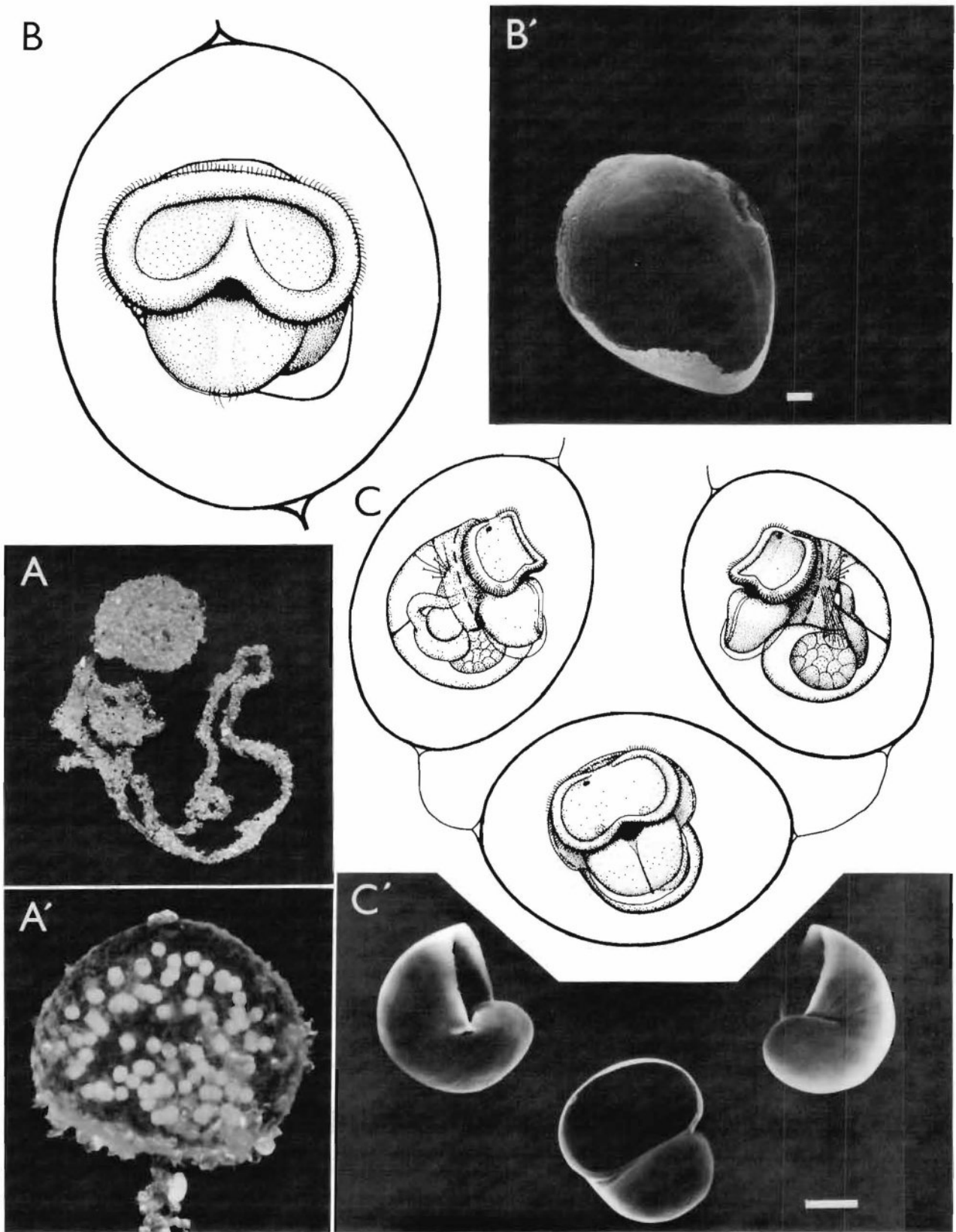
During the second 24-h period, the trochophore stage appears and begins to spin on its antero-posterior axis, 40–45 h into development. The mouth, metapodial rudiment, and prototroch bearing fine cilia are clearly visible at this stage; the vegetal pole appears as an undifferentiated spherical mass. Two anal cells are present on the lower right surface of the visceral hump.

The third day after deposition is characterized by a rapidly spinning, early veliger stage (Figures 9B, B'). A cone-shaped shell, 177 μm in length, has formed with its apex at the veliger's left. The velum is well formed, with a strong median elevation. The anal cells have migrated to a position below the lower right edge of the velum. A median ridge is evident on the rounded metapodium, and the operculum is visible at the edge of the foot. The viscera have begun to separate within the visceral hump.

By the fourth day, continued growth has modified the conical aspect of the larval shell, seemingly decreasing its

Figure 8

Acteocina atrata, spec. nov., adults. A. Shell from Indian River lagoon in apertural view, 4.18 mm. B. Gizzard plates, view of grinding surfaces. C. Outer edge of lateral radular teeth showing basal tubercle. D. Inner edge of lateral teeth showing denticles. E, F, and G. Protoconch: E. "Apical" view. F. "Posterior" view. G. "Umbilical" view. Scales: B = 100 μm ; C and D = 5 μm ; E, F, and G = 50 μm .



length to 165 μm . The direction of coiling from this point onward is decidedly skewed to the larval right. Spinning has slowed from the previous day, but continues steadily. The propodium has begun to expand. The digestive organs are clearly differentiated, as is a large, and now fully functional, retractor muscle on the larval left. The torsional process is represented solely by the migration of the anal cells, as in *Acteocina canaliculata*.

On day five, motion has slowed drastically although the larvae (Figures 9C, C') continue to turn, now frequently changing direction of rotation. The velar lobes are still fully extended, with the single row of fine preoral cilia erect and beating. No postoral band, or subvelum, has developed nor will develop in this species. The propodium has continued to develop and the median metapodial band is now a strong keel. A pair of otocysts has appeared in the base of the foot. A small right eye is visible.

The continued decrease of spinning movement and the appearance of the left eye, initially smaller than the right, occur on day six. As the larva stops rotation by day seven, the larval heart (at the center of the larva, just dorsal to the foregut) begins to pump. A mantle opening appears to the right of the cephalic area; at its edges beat cilia longer than those of the velum. Also as rotation ceases, the velum becomes reduced to form the cephalic shield of the juvenile snail, with its row of fine cilia still visible. The propodium is well inflated and nearly equal in size to the metapodium.

The larva of eight days, with a shell length of 260 μm , nearly fills its egg capsule, and spends much time fully retracted. A radula of four rows is present, with about four denticles on each lateral tooth. The osphradium and the two-chambered adult heart have formed in the mantle, appressed to the interior right side of the shell. As the continuous crawling movements that precede hatching begin on day nine, 200–210 h after deposition, the adult heart begins to beat. The egg capsules appear thin and weakened by this time, and the larvae break through them to crawl freely within the egg tubes. Nearly all of the larvae will have hatched from their capsules before breaks in the tubes and mass are located and benthic life can begin. At hatching (Figures 10A–D), shell length is 300 μm , the larval retractor muscle and operculum are still present, and there is no evidence of gizzard plates. In lateral view (Figure 10D), the short and only slightly curved suture line of the larval shell is distinct.

Immediately after hatching, shell growth becomes accelerated at the larval right, beginning the change in direction of coiling. The teleoconch first appears within the

apertural edge of the protoconch, creating a distinct suture. At the larval left, the leading edge of the teleoconch is still internal four days after hatching (Figures 10E, F). Starved hatchlings of similar age showed no trace of teleoconch growth. The operculum is lost during the second post-hatching week, and the black pigment characteristic of *Acteocina atrata* appears during the sixth week, at 0.75 mm shell length.

During the first 2–3 weeks after hatching, when the transition from sinistral to dextral coiling takes place, the increase in shell length is slow, gaining only about 0.01 mm/week. When this transitional phase of growth is completed, shell length increases at a mean rate of 0.11 mm/week under laboratory conditions; this rate of growth continues until a shell length of about 2.5 mm has been attained, approximately 23 weeks after hatching. At this time, increase in shell length again slows considerably.

Remarks

There is a possibility that *Acteocina atrata* is not properly placed in the genus *Acteocina*, because of distinct differences in the lateral radular teeth, specifically the absence of the denticle-bearing "wing." In this regard, the lateral teeth of *A. atrata* more closely approximate those of the types of *Tornastra* and *Paracteocina* Minichev, 1966 (see MARCUS, 1977), than they do those of the type of *Acteocina*. Therefore, generic placement of *A. atrata* in *Acteocina* may be tentative, pending generic revision of the group.

Fossil specimens of *Acteocina atrata* have been recently discovered at a canal excavation site on Merritt Island, Brevard County, Florida. The Pleistocene fossiliferous layer was approximately 1.8 m under the surface. The specimens were found with roughly equal numbers of *A. canaliculata*. The venerid bivalve *Parastarte triquetra* (Conrad, 1846) was also present in great numbers, paralleling Recent conditions in the Indian River lagoon.

The development of *Acteocina atrata* is similar to that of *Retusa obtusa*, the only other cephalaspid with well-documented capsular metamorphic development (see SMITH, 1967a, b; BONAR, 1978). However, there are notable differences (*A. atrata* versus *R. obtusa*): a smaller egg diameter (151.6 versus 245 μm) and a greater number of eggs per mass (means of 91.1 versus 33 eggs, and maxima of 148 versus 46). In *A. atrata*, the entire developmental progression toward hatching is greatly accelerated at all stages. Hatching in *A. atrata* occurs 3.2 times faster: 9 days versus 29 in *R. obtusa*. Several anatomical differ-

Figure 9

Acteocina atrata, spec. nov., larval development. A. Egg mass with sand coating. A'. Same as A, enlarged slightly, with sand removed. B and C. Larval stages showing appearance of larvae corresponding to larval shells. B. Early veliger in egg capsule, three days post-deposition. B'. Same as B, shell only. C. One-eyed veligers in capsules, five days post-deposition. C'. Same as C, shells only. Scales: B and B' = 15 μm ; C and C' = 50 μm .

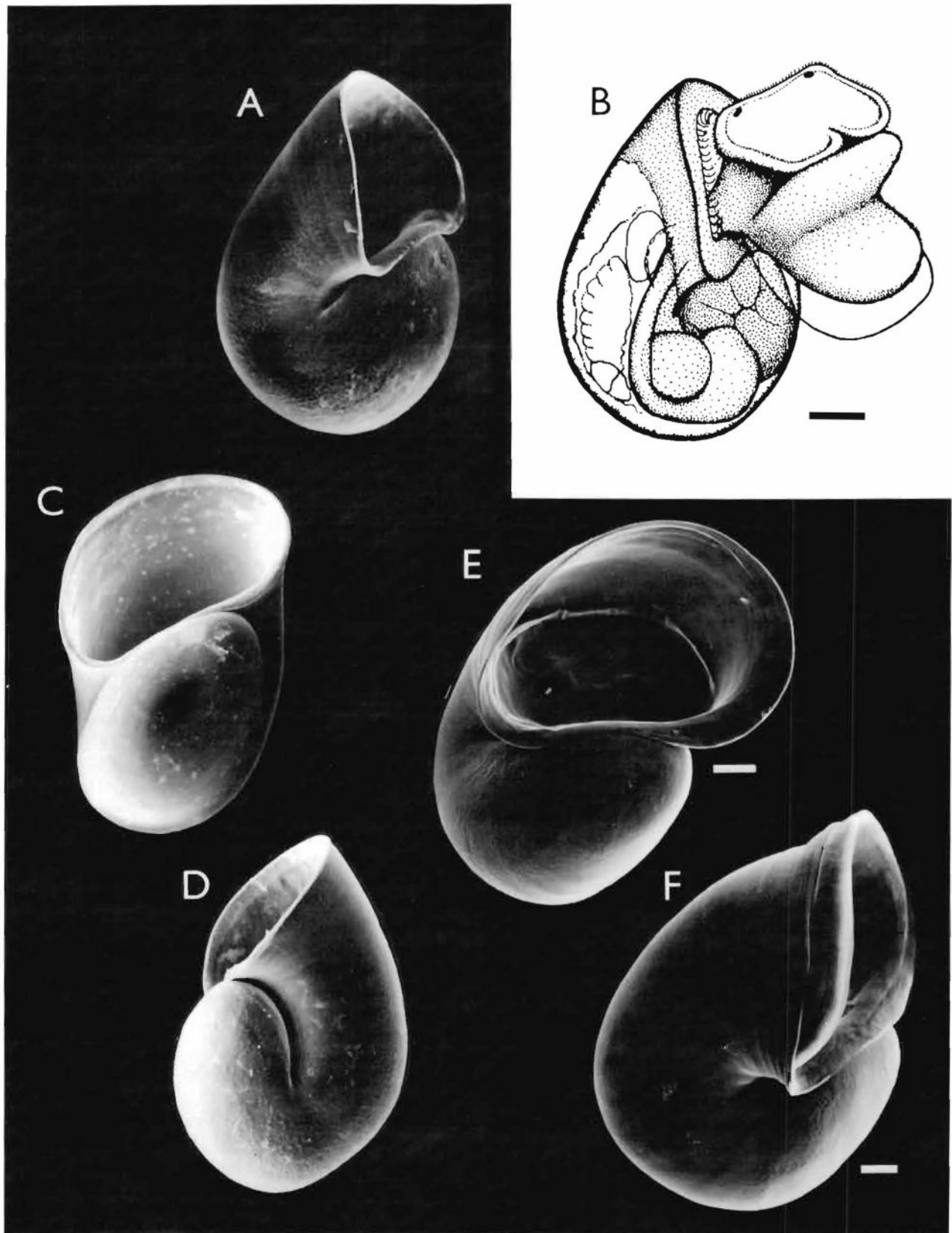


Table 2
Distinguishing characteristics of *Acteocina canaliculata*, *A. atrata* spec. nov., and *A. candei*.

	<i>Acteocina canaliculata</i>	<i>Acteocina atrata</i>	<i>Acteocina candei</i>
Egg mass	Sand-free Tubes absent Many (>150) small eggs	Sand-covered Tubes present Few (<150) large eggs	? ? ?
Development	Planktotrophic Florida: Hatch on day 4, settle on day 24 Connecticut: Hatch on day 4, settle on day 14-20	Capsular metamorphic Hatch on day 9, as benthic juveniles	Planktic (?) ?
Trochophore	Spins on lateral axis	Spins on antero-posterior axis	?
Veliger	Spherical early embryonic shell Pointed foot Subvelum present Long velar cilia	Cone-shaped early embryonic shell Rounded foot Subvelum absent Short velar cilia	? ? ? ?
Shell	Pyriform Rounded shoulder Thick-walled (175 μ m)	Cylindrical Keel shoulder Thin-walled (112 μ m)	Cylindrical Sculptured shoulder Thick-walled
Protoconch	Tapered Curved suture	Globular Straight suture	Tapered Curved suture
Gizzard	Pink-pigmented T-shaped unpaired plate	Black-pigmented Heart-shaped unpaired plate	Not pigmented (?) T-shaped unpaired plate
Lateral radular teeth	Denticles on wing of cusp Few denticles: 6-18 in adults	Denticles directly on cusp edge Many finer denticles: 14-25 in adults	Denticles on wing of cusp Few denticles

ences are also apparent. The initial appearance of the shell in the *R. obtusa* veliger is rounded and globular (SMITH, 1967b), not distinctly cone-shaped as in *A. atrata*. The larval kidney adjacent to the anus and the ciliated mid-velar groove of *R. obtusa* are both absent from *A. atrata* larvae. Also, the right larval retractor muscle of *R. obtusa*, composed of various muscle fibers to the right posterior interior of the shell, was not noted in *A. atrata*, although numerous small bundles attached to various dorsal and posterior locations were present. In addition, the prominent eyes, presence of a radula, pulsating larval heart, and median metapodial keel of *A. atrata* were not noted by SMITH (1967b) for *R. obtusa*.

Although we once considered the possibility of poecilogony for *Acteocina canaliculata*, the consistent differences in egg, larval, and adult characters (Tables 2, 3) indicate the definite presence of two distinct species. Preliminary electrophoretic examination (unpublished data, M. J. Harszewych, January 1983) of *A. canaliculata* and *A. atrata* has shown strong and consistent differences in their esterase systems, with strong tendencies in other enzyme systems as well.

DISCUSSION

Because most lots of *Acteocina canaliculata* in early museum collections are now known to have been correctly identified, the recent taxonomic confusion between *A. canaliculata* and *A. candei* apparently stems from WELLS & WELLS (1962). Although their conception of *A. candei* was correct, their "*Retusa canaliculata*" was in fact *A. atrata*; the true *A. canaliculata* seems to have been excluded entirely. FRANZ (1971b:181) was correct in his identification as well as in his belief that Wells & Wells' observations of direct development in *A. canaliculata* were for "some other cephalaspid." Our own earlier work reflects the taxonomic problems initiated by WELLS & WELLS (1962) and augmented by MARCUS (1977), who considered *Acteocina canaliculata*, *A. candei*, and *A. atrata*, all as a single species. While considering Marcus' synonymy valid, we (MIKKELSEN & MIKKELSEN, 1982) determined "*A. candei*" (actually *A. canaliculata*) to be a juvenile form of "*A. canaliculata*" (actually *A. atrata*). This incorrect result is now known to have been influenced by the coincidental lack at that time of large specimens of *A. atrata*. After

Figure 10

Acteocina atrata, spec. nov., post-larval development. A, C, and D. Shell at hatching. B. Appearance of hatchling corresponding to shell in A. E and F. Shells at four days post-hatching, showing unequal growth of teleoconch. Scales: A-D = 50 μ m (marker at B); E and F = 25 μ m.

Table 3

Results of *t*-tests to determine distinctness of the means of character distributions between *Acteocina canaliculata* and *A. atrata* spec. nov. (* indicates characters useful in distinguishing these species).

Significantly distinct		Significantly indistinct	
Character	P<	Character	P<
Spire angle	0.0001	Shell length	0.7627
Spire height	0.0022	Shell width	0.1755
Radular rows	0.0003	% Protoconch protrusion	0.7895
Lateral tooth denticles	0.0000	Egg mass diameter	0.2929
Rachidian tooth denticles	0.0010		
Lateral tooth width	0.0000		
Rachidian tooth width	0.0000		
Lateral tooth angle	0.0000		
*Number of eggs	0.0000		
*Egg capsule length	0.0000		
*Egg capsule width	0.0000		
*Egg diameter	0.0000		

larval development studies had convinced us of the presence of two distinct species (while still confusing the names), we suggested the resurrection of *A. candei* as a valid species (MIKKELSEN & MIKKELSEN, 1983). It was not until type material was examined that we determined the distinct characteristics for these species, and the correct identifications of our specimens.

Our search for previous names for *Acteocina atrata* included investigation of *Bulla pusilla* Pfeiffer, 1840. Personnel of the British Museum (Natural History) and the Museum für Naturkunde der Humboldt-Universität zu Berlin agreed that Pfeiffer's types were probably destroyed in the Stettin museum during World War II. This opinion was also held by DANCE (1966:197, 285). The Humboldt museum located a lot of 33 specimens of "*Bulla pusilla*" from Cuba in R. W. Dunker's collection, which were presumably obtained from Pfeiffer. This lot included 32 specimens of *Acteocina candei* and one specimen of a species of *Acteon*. However, in view of the uncertain status of this lot, the lack of definite type material, and the ambiguity of the original description, it is unknown what Pfeiffer intended to be called *Bulla pusilla* and the name must be considered a *nomen dubium*.

Analysis of *Acteocina canaliculata* and *A. atrata* from the Indian River lagoon showed overlap of all shell and radular meristic and morphometric characters (Figures 11, 12). Results of *t*-tests (Table 3) showed some significantly distinct means of the character distributions; how-

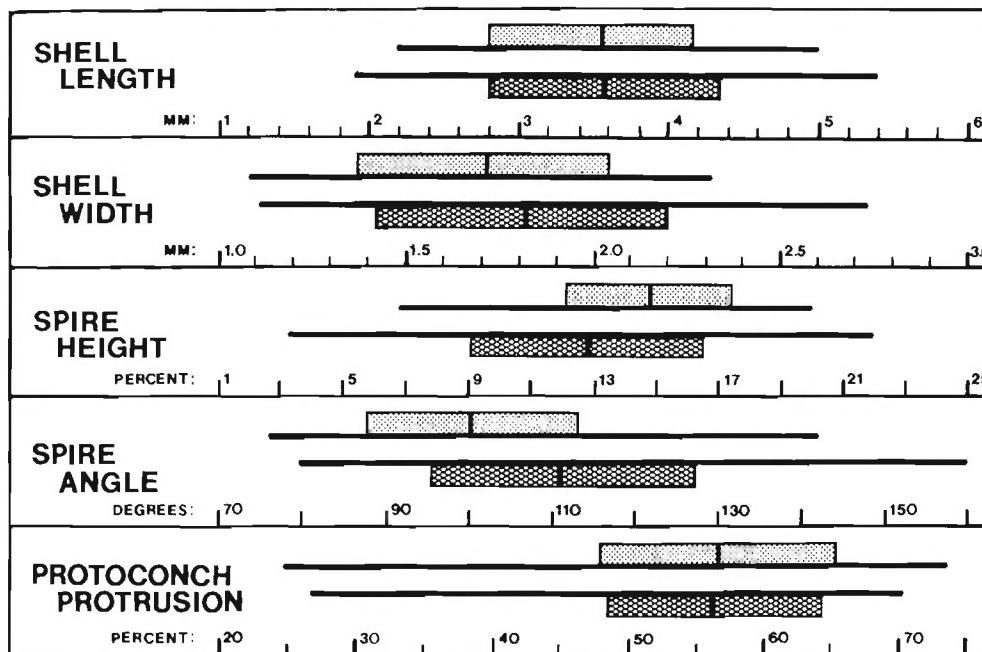


Figure 11

Variation in shell characters of *Acteocina canaliculata* (stippled; n = 56) and *A. atrata* (cross-hatched; n = 49). Ranges (horizontal solid line), means (vertical mid-point of pattern), and \pm SD (pattern) are plotted.

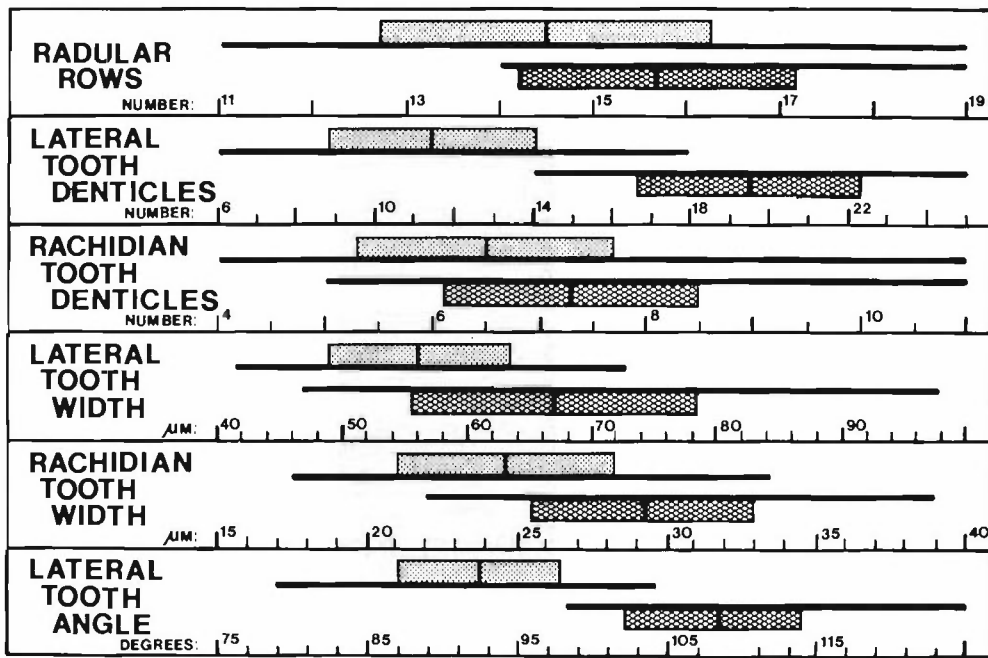


Figure 12

Variation in radular characters of *Acteocina canaliculata* (stippled; n = 56) and *A. atrata* (cross-hatched; n = 49). Symbols as in Figure 11.

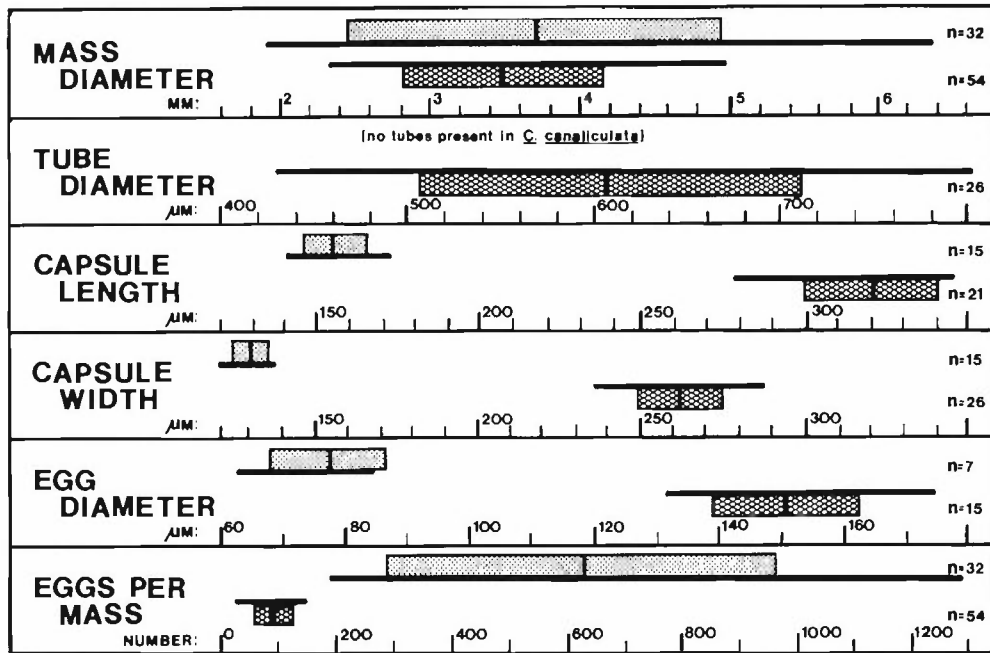


Figure 13

Variation in eggs and egg mass characteristics of *Acteocina canaliculata* (stippled) and *A. atrata* (cross-hatched). Symbols as in Figure 11.

ever, because of the overlap of the ranges, these characters cannot be reliably used in specimen identification. Consistent subjective differences do exist in the sculpture of the shoulder, the shape of the protoconch, the presence or absence of black pigment on the animal, the placement of lateral tooth denticles, and the shape of the unpaired gizzard plates. However, distinct meristic and morphometric differences exist in the characteristics of the eggs and egg capsules (Figure 13, Table 3).

The distinguishing characters for *Acteocina canaliculata*, *A. atrata*, and *A. candei* are summarized in Table 2. The most useful of these in the routine sorting of samples are the shape of the protoconch, features of the shoulder, and the presence or absence of black pigment on portions of the animal. Caution is advised, however, in the frequent cases where the protoconch is either worn or absent, or where the tissue has been stained or preserved. Also, potentially misleading black coloration may occur in the digestive gland of individuals of *A. canaliculata* that have been feeding on a blackish food source. This coloration, however, is restricted to the digestive gland and does not affect the areas of the gizzard, pallial caecum, or Hancock's organs.

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