REVISION OF HIGHER TAXA IN GENUS *CERITHIDEA* (MESOGASTROPODA: POTAMIDIDAE) BASED ON COMPARATIVE MORPHOLOGY AND BIOLOGICAL DATA

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ABSTRACT

A cladistic analysis of *Cerithidea* subgenera based on morphological studies of *Cerithidea* species is presented. The morphology of *Cerithidea (Cerithideopsis) scalariformis* Say, 1825 is described and compared with observations and published accounts of other species in the genus. An account of the reproduction, spawn, development and growth of this species along with ecological observations are presented and compared with other *Cerithidea* taxa in order to summarize what is known of the biology of the genus, to develop a holistic, less arbitrary classification, and to formulate systematic definitions of the subgenera comprising it. A detailed description of the siphonal eye is given and a survey made of similar structures in other cerithiacean groups. The genus *Cerithidea*, sensu lato, is an estuarine group characterized by turreted shells with dominant axial sculpture, wide apertures, thick outer lips, and short anterior canals. The taenioglossate radula is short and all teeth bear cusps. The operculum is thin, corneous, multispiral and has a central nucleus. The ctenidium is either reduced or of broad low filaments. A simple ridge-like osphradium is present. The alimentary tract includes a pair of anterior salivary glands, a mid-esophageal crop, and a long style sac. Females have an ovipositor, a spermatophore bursa in the outer lamina and a seminal receptacle in the inner lamina of the proximal pallial oviduct. Males are aphallate. Both direct and indirect modes of development occur and growth of juveniles is rapid. Three Recent subgenera are recognized: *Cerithidea* s.s., *Cerithideopsis* and *Cerithideopsilla*, the latter subgenus being considered the most generalized (primitive).

Mesogastropods of the family Potamididae H. and A. Adams, 1854 are common intertidal snails, many of which lead an amphibious existence in muddy, estuarine habiats. Largely confined to tropical and subtropical regions, they are conspicuous members of the fauna of mangrove swamps and salt marshes where they graze on detritus and microalgae. The family represents the estuarine radiation of the superfamily Cerithiacea and is morphologically similar to the large family Cerithiidae Fleming, 1828, which has exploited intertidal and shallow water marine habitats. Both groups tend to be confined to shallow water or intertidal zones and both have an impressive fossil record extending back to the late Cretaceous. Both the Potamididae and Cerithiidae underwent an extensive adaptive radiation in the Tethys Sea during the early Tertiary.

The family Potamididae comprises numerous genera of many diverse shell forms. Members of some genera, such as *Telescopium* Montfort, 1910, *Pyrazus* Montfort, 1910 and *Terebralia* Swainson, 1840, are relatively large snails. Other genera, such as *Batillaria* Benson, 1842 and *Cerithidea* Swainson, 1840, comprise numerous species of smaller snails. Most species are common and occur in large, sometimes enormous, populations that are easily sampled. Although the ecology of a number of species of various genera has been studied, little is known of their comparative anatomies or life histories and almost all generic and higher taxa are defined on shell and radular characters alone. Clearly, the higher taxa assigned to the family Potamididae have not received adequate systematic attention and remain poorly defined.

The family Potamididae is divided into two subfamilies, the Potamidinae and the Batillariinae (Thiele, 1929; Wenz, 1938). Members of the latter live mainly in temperate or subtropical areas while the former group is largely tropical in distribution. The subfamilies are traditionally distinguished by radular structures: the Batillariinae have cusps on the lower basal plate of the rachidian tooth while the Potamidinae lack this feature. Bishop (1987:76) found that the Potamidinae exhibited a greater degree of heterogeneity of both shell and radular characters than the Batillariinae and suggested

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that the former group was probably polyphyletic. Within the subfamily Potamidinae, the genus *Cerithidea* is the largest group.

The main purpose of this paper is to establish reliable morphological characters defining the taxa *Cerithidea* Swainson, 1840, and the three subgenera comprising it: *Cerithidea* s.s., *Cerithideopsis* Thiele, 1929, and *Cerithideopsilla* Thiele, 1929. This allows establishment of homologies and development of hypotheses about polarization of character states and construction of phylogenetic trees. To this end, I describe in detail the shell, radula, soft parts and spawn of selected *Cerithidea* species, concentrating on *Cerithidea scalariformis* (Say, 1825), but employing characters noted in other species. This paper begins with a detailed description of *Cerithidea scalariformis* followed by an account of its reproductive biology and ecology. A discussion incorporates comparative observations on the anatomy, reproduction, growth and ecology of other *Cerithidea* species. Systematic conclusions based on these observations, the fossil record and cladistic analysis of the characters follow.

MATERIALS AND METHODS

I studied *Cerithidea scalariformis* at the Smithsonian Marine Station at Ft. Pierce, Florida. This facility is located on the mid-eastern coast of Florida along the Indian River estuary. A large population was studied on various occasions over a three year period at Big Starvation Cove, across the Indian River from Link Port, Florida (voucher specimens USNM 806783). Although observations were not continuous, I was able to determine the reproductive biology and growth of this population and had adequate material for dissection and morphometric studies. Morphological studies and field observations were also made on *Cerithidea californica* (Haldeman, 1840) from Anaheim Bay, Los Angeles, California. In addition, I briefly observed populations of *Cerithidea costata* (da Costa, 1778) at New Port Richie, Florida (USNM 770694), and *C. pliculosa* (Menke, 1820) at El Zacatal, Laguna de Terminos, Campeche, Mexico (USNM 702904). Preserved material of *C. obtusa* (Lamarck, 1822) [USNM 777233, Rayong, Thailand], *C. quadrata* Sowerby, 1855 [USNM 777651, Satahib Chonburi, Thailand], *C. decollata* (Linnaeus, 1767) [USNM 63348, Ambataloaka, SW Nossi Bé, Madagascar], *C. cingulata* (Gmelin, 1807) [USNM 776696, Ban Ampoe, Satahip, Chonburi, Thailand; USNM 794168, Bais Bay, Negros Oriental, Philippines], and *C. montagnei* (Orbigny, 1841) [USNM 809164, Barra de Navidad, Jalisco, Mexico] from collections in the USNM was dissected for comparative purposes.

Dissections of living material were made using animals relaxed in a 7.5% magnesium chloride solution. Carmine particles were used to determine ciliary tracts and an aqueous solution of methylene blue was used to enhance glandular and nervous tissues in preserved specimens. Animals were fixed in Bouin's fluid, embedded in paraffin, sectioned at 9 μm, stained with Harris' Hematoxylin and counterstained with eosin Y. Scanning electron micrographs were taken on a Mark II Stereoscan Microscope. Eggs and embryos were maintained in sea water in covered petri dishes.

Random samples of the Big Starvation Cove population of *Cerithidea scalariformis* were taken throughout a year-long period in 1980–81. Shell lengths were measured and histograms made to determine the growth pattern of the population. Dissection of various age classes of snails were also made to follow reproductive tract ontogeny.

A cladistic analysis of the *Cerithidea* subgenera using 19 characters comprising 38 character states was made using the Wagner 78 algorithm (Farris, 1970; Wiley, 1981:178–192). This program produced computer generated cladograms that were tested against the fossil record, developmental data, and ecological information to derive a phylogenetic classification incorporating all available evidence. Throughout this analysis I endeavored to discount results derived solely by rigid adherence to methodology but attempted to produce a classification based upon all the information at hand. Polarity was established primarily by out group comparison of presumed homologous structures derived from shell, animal and radula. *Batillaria* was chosen as the out group because it was the only other potamidid group that was relatively well known. Characters and scoring of character states are presented in Table 5, and a more detailed account of the cladistic methodology is presented in the "Systematic Conclusions" section of this paper.

RESULTS

BIOLOGY OF *CERITHIDEA SCALARIFORMIS*

Cerithidea scalariformis (Say, 1825) is a common, estuarine, amphibious snail that lives along the edges of muddy tidal creeks in salt marsh and mangrove habitats. It is assigned to the subfamily Potamidinae H. and A. Adams, 1854, genus *Cerithidea* Swainson, 1840, subgenus *Cerithideopsis* Thiele, 1929. Its geographic range is Georgia, both coasts of Florida, and Cuba.

MORPHOLOGY: *Shell description* (Fig. 1, A–B, E–G). Shell turreted, elongate, thin, comprising about 12 inflated whorls, ranging from 18–30 mm in length and 7–10.5 mm in width, having apical angle of 25 degrees. Shells of females significantly larger than males (see Table 1). Embryonic whorls (protoconch one) smooth, bulbous, forming about one and a half whorls (Fig. 1, E–G). Juvenile (post-embryonic) whorls have axial riblets and are angular in outline due to dominant median spiral cord that diminishes in size and disappears on fifth whorl. Teleoconch (adult) whorls each sculptured with about 26 concave axial ribs and a single, basal, spiral cord at the suture. Axial ribs become more numerous on penultimate and body whorls. Body whorl with about five strong, spiral cords on its lower half. Early whorls usually eroded or decollate in adults (Fig. 3, D). Aperture nearly one-fifth the length of the shell, circular; columella

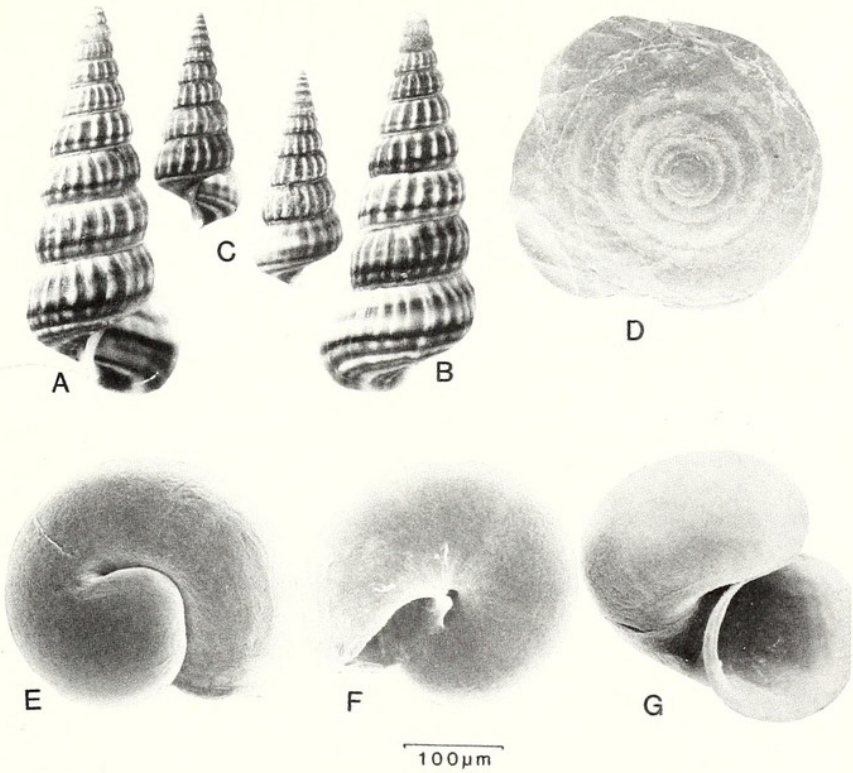

Fig. 1. *Cerithidea scalariformis* from Big Starvation Cove, Indian River, Ft. Pierce, Florida. **A,B)** Shell of adult female (28.5 mm length); **C)** Immature snail lacking thickened outer lip (10.11 mm length); **D)** Scanning electron micrograph of operculum showing central nucleus and multispiral growth lines (2.8 mm diameter); **E–G)** Scanning electron micrographs of shells of newly hatched snails showing aspects of protoconch and aperture.

Table 1. Sexual dimorphism in the shell of *Cerithidea scalariformis* ("t" test, df = 2, ** = $p < 0.01$).

Statistic		$\bar{x}$	sd	Range	n
shell length	females	24.39	2.26	22–30	12
t = 4.13**	males	20.55	1.48	18–22.1	10
shell width	females	8.95	0.68	8–10.5	12
t = 3.25**	males	7.78	0.49	7–8.4	10
aperture length	females	6.7	0.51	5.5–7.2	12
t = 5.46**	males	5.5	0.53	4.7–6.2	10
aperture width	females	5.90	0.42	5–6.4	12
t = 3.82**	males	5.25	0.36	4.5–5.6	10

concave; no anal canal present. Outer lip smooth, convex, slightly flared and with thickened varix at its edge. Anterior siphonal canal reduced; base of outer lip broady depressed in this area. Suture incised. Shell color brownish with tan base. Thick spiral brown band on base of each whorl and several thinner, spiral, brown bands present on mid-portion of whorls. Axial ribs white.

Operculum (Fig. 1,D). Operculum corneous, thin, circular and multispiral with central nucleus. Periphery of operculum flared, slightly reflected when animal withdrawn into shell aperture, providing complete closure.

Animal; External features (Fig. 2, B–C). When removed from the shell, animal has about six whorls. Base color of head-foot cream-yellow, flecked and striped with brown. Foot whitish and mantle bright green. Head large with long, extensible, shovel-shaped snout having transverse wrinkles and a bilobed tip. Cephalic tentacles moderately long, bearing single black eye on outer edge of peduncular stalk. Foot long, crescent shaped at front and tapering posteriorly. Anterior pedal gland a thin, deep furrow at edge of propodium, ending at mesopodium. Sole of foot with slight longitudinal folds. Median right side of foot of females has deeply embedded, ciliated groove leading from genital opening to large whitish bulbous ovipositor lying dorsal to groove (Figure 2, B, *ovp*). Males lack groove. Mantle edge turned slightly back, smooth and yellow. Mantle thin, pigmented green. Major mantle organs visible through mantle wall. Long, narrow, one-lobed kidney of green-white color present. Gonads overlay brown digestive gland on anterior of each upper whorl. Inhalant siphon on left mantle edge bears single eye, black at center, covered with round lens and surrounded by orange pigment cup. When animal withdraws into shell, pallial eye may be protruded at anterior siphonal canal of

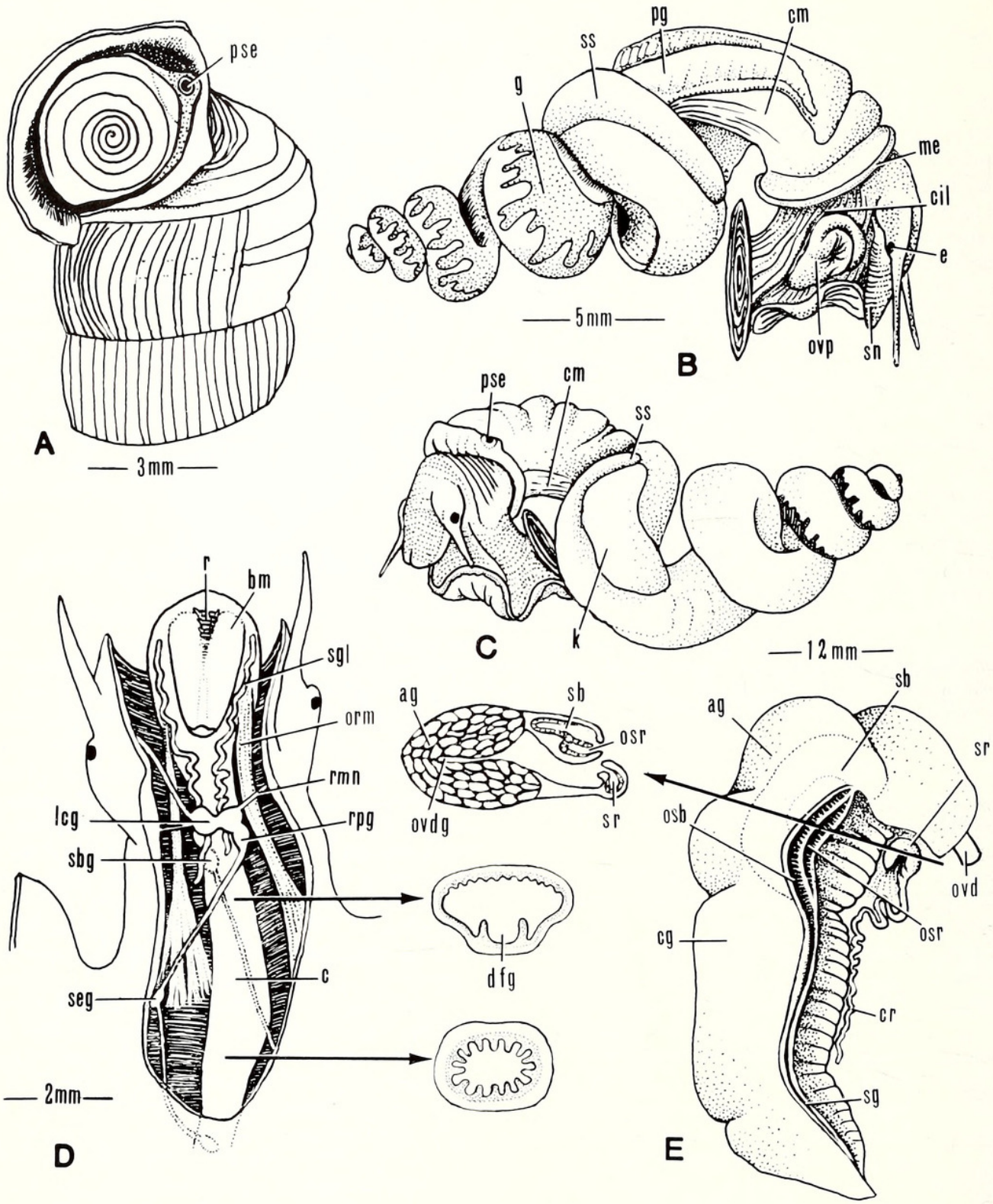

Fig. 2. A) View of shell aperture showing retracted animal of *Cerithidea scalariformis* with pallial eye exposed in anterior canal of shell; **B)** Female removed from shell; **C)** Male, showing pallial eye at mantle edge; **D)** Diagrammatic representation of anterior alimentary tract and nerve ring exposed by dorsal longitudinal cut with sections through mid and posterior esophagus (large arrows); **E)** Female pallial oviduct showing major anatomical features and cross section through seminal receptacle and spermatophore bursa (large arrow). Abbreviations: *ag,* albumen gland; *bm,* buccal mass; *c,* crop; *cg,* capsule gland; *cil,* ciliated groove; *cm,* columellar muscle; *dfg,* dorsal food groove; *e,* eye; *g,* gonad; *k,* kidney; *lcg,* left cerebral ganglion; *me,* mantle edge; *orm,* odontophore retractor muscle; *osb,* opening to spermatophore bursa; *osr,* opening to seminal receptacle; *ovd,* oviduct; *ovdg,* oviducal groove; *ovp,* ovipositor; *pg,* pallial gonoduct; *pse,* pallial siphonal eye; *r,* radula; *rmn,* right mantle nerve; *rpg,* right pleural ganglion; *sb,* spermatophore bursa; *sbg,* subesophageal ganglion; *seg,* supraesophageal ganglion; *sg,* sperm gutter; *sgl,* salivary gland; *sn,* snout; *sr,* seminal receptacle; *ss,* style sac.

shell under opercular edge (Fig. 2, A, *pse*). Portion of operculum covering pallial eye somewhat transparent.

Pallial siphonal eye (Fig. 3, A–C). The pallial eye, located at the edge of the inner surface of the inhalant siphon (Fig. 2, A,C, *pse*), is surronded by pigmented epithelium. The outer area is bright orange but black pigment surrounds the lens. The pigmented epithelium appears to consist of pigment and sensory cells. The pigment cells (Fig. 3, C, *pc*) have darkly stained granules concentrated at the epithelial surface. A thin layer of tiny cells derived from mantle epithelium forms the cornea over the lens. The corneal cells extend around the lens and appear to be joined with the mantle epithelium. The lens is ovate and comprised of a single layer of very long, narrow, rod-like cells (Fig. 3, C, *l*) that stain red in eosin. The basal nuclei of the lens cells stain more darkly and are separated from the vitreous body by a thin basement membrane. The portion of the lens cells nearest the surface corneal layer stains a light pink color. Beneath the lens is a clear, large, vitreous body (Fig. 3, C, *vh*) which stains lightly and does not have a continuous cell structure. There are faint traces of disorganized cell walls and a few isolated, large, vacuolated cells with tiny dark nuclei scattered throughout the vitreous body. These are like the detached sensory cells depicted by Pflugfelder (1930:281) in the vitreous body of the pallial eye of *Cerithidea obtusa*. The entire structure of the vitreous body is disorganized and is difficult to interpret. The retina (Figs. 2–3, B, C, *rc*) seems to derive from the epithelium which has sunk in from the surface and lies beneath the vitreous body. It is characterized by a discrete layer of irregularly arranged, rounded sensory cells, each containing a light staining body that fills the cell and bears a darkly stained nucleus. Nuclei are concentrated at the bases of the cells adjacent to the vitreous body. Beneath the retina lies a thicker layer of larger, irregularly arranged pigment cells, most of which are granulose interiorly. Some of the cells stain weakly with hematoxolin. The function of all the cells in this area was not determined, but most are probably sensory cells of the retina because nerve fibers appear to penetrate the pigment cells and terminate in this loosely organized portion beneath the retina. The entire retinal area lies within tissue composed of elongated, darkly staining cells that form the pigment cup (Fig. 3, C, *pc*). Pigment cells contain tiny dark granules and are irregulary dispersed beneath the retina and sensory cells. A sensory nerve (Fig. 3, B, *n*) emerges from a ganglion in the pallial siphon and extends to the eye where it divides into smaller fibers that appear to penetrate the pigment cup. The manner of innervation of the retina was not discerned.

Mantle cavity and associated organs (Fig. 2, D). The mantle edge is slightly thickened at the undersurface of the inhalant siphon. The mantle skirt in this area is weakly pustulate anterior to the ctenidium and hypobranchial gland. The mantle cavity occupies about three-fourths of a body whorl and is relatively spacious but not particulary deep. The osphradium (Fig. 3, A) is a simple thin, black ridge bearing basal cilia on both sides that begins distally a few millimeters behind the mantle edge adjacent to the ctenidium. It is not quite one-half the length of the ctenidium and terminates at the mid point of the ctenidial axis. The monopectinate ctenidium is gray, broad and low, and extends back into the mantle cavity ending at the pericardium. The gill filaments extend across the mantle roof and lack supporting rods. The hypobranchial gland is a thin sheet of weak, transversely folded tissue that secretes great amounts of mucus. It is not well-defined and extends over the rectum where it assumes a white, fuzzy appearance and is heavily ciliated. The rectum is a wide, spacious tube through which may be seen numerous rod-like fecal pellets. The pallial gonoducts are open slit tubes that extend the length of the mantle cavity. They are wide and glandular in both sexes but particularly so in females. Males are aphallate.

Alimentary system (Fig. 2, D). Mouth lies between lobes of snout tip. Jaws (about 0.8 mm long) very thin, nearly transparent, composed of microscopic scales arranged in shingle-like pattern. Buccal mass moderate in size and taeniglossate radula (Fig. 3, H–J) short in relation to shell length, comprising about 98 rows of teeth and one-ninth length of shell. Rachidian tooth, although asymmetrical, (Fig. 3, J) somewhat pentagonal in shape and concave dorsally. Cutting edge bears five cusps: a long, central, pointed one flanked on each side by pair of smaller, pointed denticles. Basal plate of rachidian tooth flat and with central basal projection (glabrella). Lateral tooth (Fig. 3, I) rhomboidal with long, tapering lateral projection inserting onto basal radular membrane. Top of lateral tooth convex, cutting edge bearing four to five cusps: a small pointed denticle, a large elongate cusp and two to three smaller cusps, respectively. Beneath cutting edge of lateral tooth the basal plate is flat and squarish. Marginal teeth (Fig. 3, H) long, curving and spatulate at tips. Marginals fold over central portion of radular ribbon when not in use. Tips of inner marginal tooth serrated with four broad, nearly fused, cusps; outer marginal tooth has five small pointed cusps.

A pair of large odontophore retractor muscles (Fig. 2, D, *orm*) extends from their insertion on the posterior ventral portion of the buccal mass to each side of the wall of the cephalic cavity, posterior to the nerve ring. The radula sac originates at the ventral-median portion of the buccal mass and extends dorsally. The paired salivary glands (Fig. 2, D, *sgl*) are thick, convoluted tubes that originate slightly behind the nerve ring although they lie mostly anterior to it. The salivary glands taper at their proximal ends, pass through the nerve ring (Fig. 2, D) and each empties into the anterior lateral portion of the buccal cavity. The anterior esophagus has a typical dorsal food channel that twists as it passes through the nerve ring. Posterior to the nerve ring is the large swollen "crop" portion of the esophagus (Fig. 2, D, *c*) encased in very thin tissue. There is no evidence of an esophageal gland. Sections of the midesophagus reveal a deep ventral food channel (Fig. 2, D, *dfg*) and several dorsal longitudinal folds. The food groove is gradually lost in the posterior esophagus (Fig. 2, D, 2) which, in section, has many longitudinal folds. The stomach is a large organ, about one and a half whorls long. The oesphagus opens into it mid-

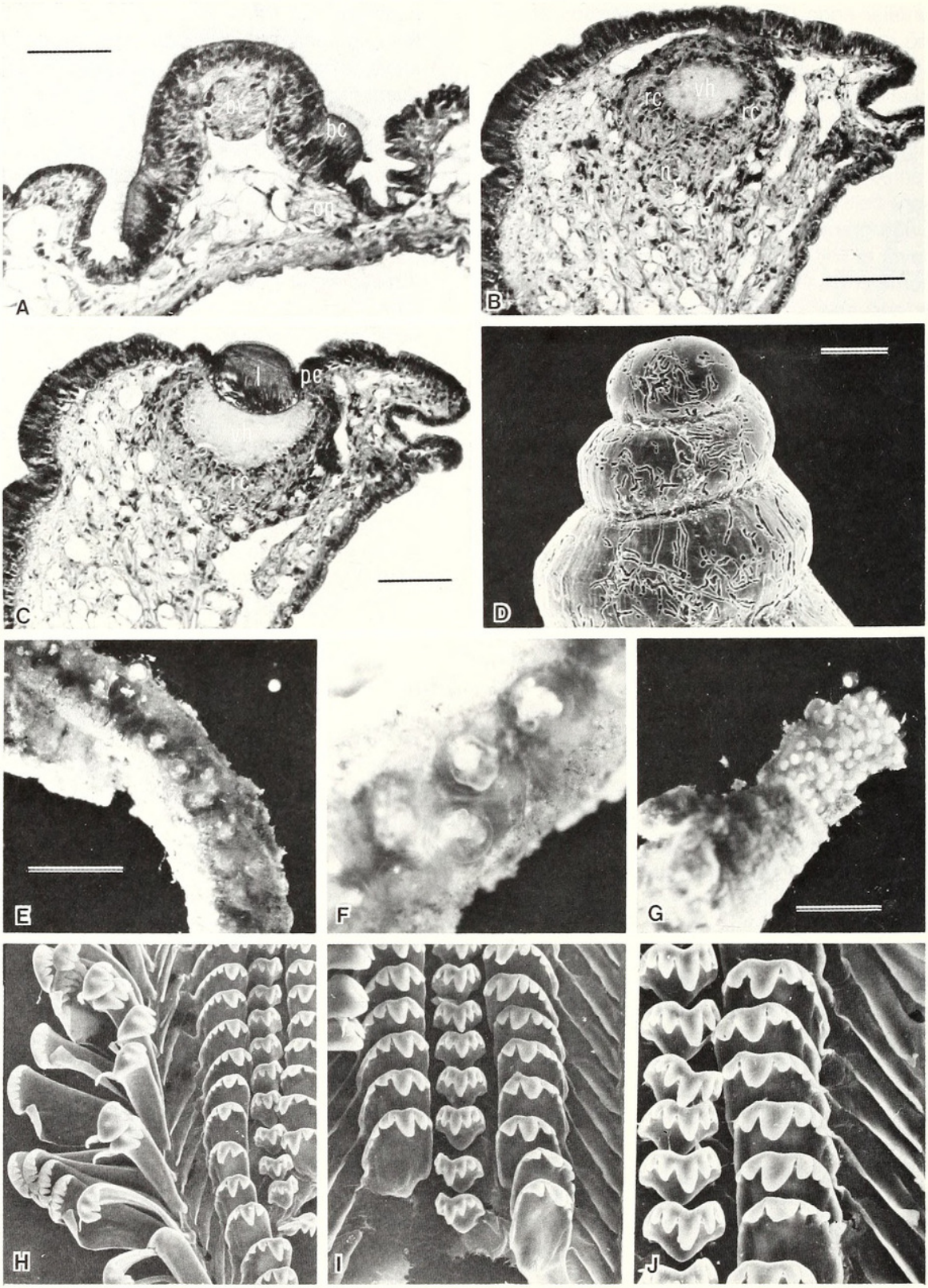

Fig. 3. *Cerithidea scalariformis* (exclusive of G). **A)** Histological section through osphradium showing basal cilia (*bc*), osphradial nerve (*on*) and blood vessel (*bv*) (bar = 0.05 mm); **B)** Histological section of edge of pallial eye showing vitreous humor (*vh*) surrounded by retinal cells (*rc*) and nerve fibers (*n*) (bar = 0.05 mm); **C)** Section through center of pallial eye showing cornea, lens (*l*), vitreous humor (*vh*), retinal (*rc*) and subretinal cells, pigment cells (*pc*) and optic nerve fibers (bar = 0.05 mm); **D)** Early whorls of juvenile snail showing etching of shell surface by fungus (bar = 0.5 mm); **E)** Strand of spawn mass of *Cerithidea scalariformis* showing sandy outer covering of jelly string and veliger stage embryos within individual egg capsules (bar = 2.5 mm); **F)** Detail of embryos in egg mass (capsule diameter 0.38 mm); **G)** Portion of egg mass of *Cerithidea californica* with detritus removed from one end to expose embryos within jelly string (bar = .25 mm); **H–J)** Scanning electron micrographs of *Cerithidea scalariformis* radula: **H)** Marginal teeth (note numerous cusps and wide flange on outer marginal tooth and larger, fewer cusps on tip of inner marginal tooth; **I)** Detail of lateral and rachidian teeth showing flat basal plate and long, lateral extension of lateral tooth; **J)** Detail of rachidian tooth showing cusps and basal plate.

ventrally and empties into a finely folded sorting area. A pad-like ridge lies between the esophagus opening and the two liver ducts. A prominent, cuticularized gastric shield is present as well as a very long style sac which bears an equally long crystalline style, nearly one-half the snail's length (about 10 mm in length in an average snail 22 mm long). The style sac may be clearly seen on the exterior of the animal through the mantle wall (Fig. 2, B,C, *ss*). The intestinal opening lies at the anterior ventral part of the stomach at the base of the style sac. A prominent ventral fold runs along the intestine to the mantle. This is the pellet compacting area. The pallial rectum widens and has a dorsal fold and numerous transverse internal folds that become almost leaflet-like. In section, this area appears to be glandular and may secrete additional mucus to bind fecal pellets together. This part of the intestine holds numerous rod-shaped fecal pellets, each about 1.4 mm long and composed of very fine detrital particles. The fecal pellets are arranged in stacks. The anus is papillate, slightly detached from mantle wall, and opens near the exhalant siphon at the right mantle edge. The lobate digestive gland is made up of numerous small ovate diverticula arranged in clusters like grapes. Each diverticulum is filled with small dark brown spherical bodies.

Nervous system (Fig. 2, D). *Cerithidea scalariformis* has an epiathroid nervous system that is somewhat loosely condensed. The RPG ratio as defiend by Davis *et al.* (1976:263; length of the pleuro-supraesophageal connective divided by the sum of the lengths of the supraesophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion), is 0.79 indicating a looser condition than those recorded for members of the Cerithiidae (0.59) but close to the 0.77 value recorded by *Batillaria minima* (see Houbrick, 1980a:138). The cerebral commissure is short, thick and the ganglia are almost fused to each other. The connectives between the cerebral and pleural ganglia are also short and thick. The subesophageal ganglion (Fig. 2, D, *seg*) is almost joined to the left pleural ganglion. The supraesophageal connective is very long and the supraesophageal ganglion sends out nerves that are connected to the long, left mantle nerve by a dialyneury. The pedal ganglia are deeply embedded in the muscular tissue of the foot. A pair of large statocysts is embedded adjacent to the posterior portion of the pedal ganglia. The visceral loop is very long and the visceral ganglion lies close to the base of the kidney and the posterior pallial gonoduct.

Reproductive system (Fig. 2, B,C,E). Sexes separate, pallial gonoducts open, forming slit tube that comprises outer (left) lamina and inner (right) lamina, which are fused to mantle wall overlying collumellar muscle. Males aphallate and produce spermatophores. Females tend to be larger than males (see Table 1) and have ovipositor in form of deep pit with lobe bordering it anteriorly (Fig. 2, B, *ovp*). Some snails are parasitized by trematodes with single-tailed cercaria. These individuals are difficult to sex because parasitized snails have reduced pallial gonoducts and tend to lose all secondary sexual characters. Parasitized snails are easily distinguished by the white color of their gonads due to the large numbers of sporocysts, rediae and metacercariae in the gonadal tissue.

Male reproductive tract. Males are distinguished from females by the lack of an ovipositor on the median right side of the foot and by their bright yellow testis. Adult males have smaller shells than females (see Table 1): some immature snails that lack a fully developed outer shell lip are males and have sperm in the vas deferens and vas efferens of the testis, but there is no evidence of protandry. The pallial gonoduct of males is composed of two thin laminae that internally bear many transverse, glandular folds. The distal portion of the pallial gonoduct is nearly transparent while the proximal third is white, thick and, in sections, more glandular. This is probably the prostate-spermatophore forming gland. The bright yellow testis overlies the digestive gland on the anterior portion of the upper whorls. Both eupyrene and multiflagellate apyrene sperm are present.

Female reproductive tract (Fig. 2, E). The female gonad is whitish-green. The pallial oviduct is a more complex structure than the gonoduct of the male. The oviducal groove (Fig. 2, E, *ovdg*), down which fertilized eggs move, lies between the two laminae that are fused to the mantle wall. Both inner and outer lamina are highly glandular and internally bear thick transverse folds along their entire lengths. The outer lamina (left) is thick but simple at its distal end (Fig. 2, E). The free edge of the outer lamina has a sperm collecting gutter (Fig. 2, E, *sg*) that begins distally and widens as it approaches the proximal third of the lamina. Here it bifurcates into a left bursa (Fig. 2, E, *sb*) that accommodates spermatophores and a right chamber (Fig. 2, E, *osr*) that may be a seminal receptacle or a storage area for sperm. Both the bursa and seminal receptacle are internally lined with tiny longitudinal folds and are heavily ciliated. The proximal end of the pallial oviduct is an opaque white color and functions as the albumen gland (Fig. 2, E, *ag*). At the edge of the proximal part of the inner lamina is a folded, flap-like, highly ciliated tissue that folds like an envelope and contains numerous oriented sperm. This structure is the seminal receptacle (Fig. 2, E, *sr*) and lies adjacent to and fits into the opening on the edge of the outer lamina which houses the bursa and seminal chamber. Together, these structures form a working unit that functions as the seminal recepacle but their exact functional relationship to each other as regards fertilization of eggs was not determined. The portion of the pallial oviduct that houses the bursa and seminal receptacle is not as opaque as the albumin gland which lies posterior to it. The central portion of the pallial oviduct is highly glandular, thick and is an opaque, white color. This is probably the capsule gland (Fig. 2, E, *cg*).

Excretory and Circulatory systems. The kidney (Fig. 2, C, *k*) is a long, relatively narrow, greenish-white organ easily seen on the exterior of the animal. It is one-lobed and bears both a renopericardial duct and a kidney opening. The heart and circulatory system are typically monotocardian.

REPRODUCTION AND GROWTH: The Potamididiae are aphallate, as are all marine cerithiaceans, and although

pairing was not observed, it probably occurs as described in *Cerithium* Bruguière and *Modulus* Linnaeus (Houbrick, 1973; 1980a), with transfer of spermatophores from male to female via the siphons. Spermatophores are held in the spermatophore bursa (Fig. 2, E, *sb*), which may be homologous with the bursa copulatrix of phallate prosobranchs. After spermatophore disintegration, freed sperm move to the seminal receptacle by ciliary tracts in the laminae of the pallial oviduct. The exact mechanism of this transfer is unknown. The seminal receptacle lies at the distal end of the inner lamina adjacent to the opening of the ovicuct into the pallial cavity. Eggs are fertilized, pass through the albumin and capsule glands and emerge as long jelly strings. The mechanism of jelly string formation and oviposition were not observed, but the ovipositor is connected to the genital opening by a ciliated groove (Fig. 2, B, *cil*). In section, it is comprised of highly glandular mucous cells as determined by cytomorphology and probably secretes the jelly as well as molding the string as it is cemented to the substrate.

Spawn of *Cerithidea scalariformis* (Fig. 3, E–F) was deposited in the field from late September through November. Hatchlings were found in the field during these same months over a three year period of sampling, indicating that the spawning period for this species is during the autumn. A few cases of spawning were noted outside this period but these appear to be random and insignificant. Development is direct and hatching occurs about three weeks after deposition of spawn. The bulbous embryonic shell of few whorls and its smooth outer lip (Fig. 1, E–G) are typical of prosobranchs with direct development. The narrow geographic range and patchy distribution of populations indicate that this species is a poor larval disperser.

Spawn (Fig. 3). *Cerithidea scalariformis* deposits long, detritus covered jelly strings (Fig. 3, E–F) about 51 mm long and 1.13 mm in diameter. Jelly strings are transparent and sticky when first emerging from the female but the surface becomes covered with detritus and is parchment-like after exposure to water. Spawn masses are laid on bark, decaying wood and leaves and are cryptic in the natural habitat. Each jelly string is round in cross section but flat where it is attached to the substratum. Spawn masses vary in length and configuration and contain about 350 eggs per mass. Egg capsules are transparent, about 0.37 mm in diameter and contain albumin and a single egg about 0.28 mm in diameter (see Table 2 for spawn statistics). Egg capsules are arranged in a loose spiral within the jelly string and are packed about three deep in cross section. Each capsule is embedded in a sticky jelly matrix and separated from adjacent capsules by a clear, thin walled partition (Fig. 3, F). No nurse eggs are present. The bright green eggs undergo cleavage quckly after deposition. Early embryonic stages are also green but become lighter colored by the time the veliger stage is reached (about five days after deposition). The green pigment is then concentrated in the yolk and digestive gland. Veliger stage embryos rotate slowly within their albumin filled capsules. They have eye spots, small velar lobes with short cilia and a large larval shell typical of direct developing larvae. The larvae are very similar to what I have described for *Cerithium lutosum* (Menke), *Cerithium muscarum* Say and *Modulus modulus* (Houbrick 1973, 1974). Larval shells (Fig. 1, E–G) have a brownish-red cast around the lip margin and columella and are about 0.31 mm in diameter. Hatching occurs 18–22 days after deposition. Hachlings retain the velar lobes for a day or two but tend to crawl on the substratum using velar cilia only occasionally. No planktonic stage or swimming was observed. Hatchlings undergo rapid metamorphosis and become tiny snails within one to two days.

Table 2. Parameters of *Cerithidea scalariformis* spawn (measurements in mm).

Statistic	$\bar{x}$	Range
length (n=4)	50.25	40–67
width (n=4)	1.11	1.0–1.4
no. eggs/mass (n=4)	372.5	276–502
capsule diameter (n=5)	0.36	0.35–0.38
embryo diameter (n=5)	0.28	0.28

Table 3. Shell length statistics of *Cerithidea scalariformis* from transect of tidal creek (3 1/10 meter square samples) in January.

	n	Range	$\bar{x}$	sd
HWM	59	3.57–22.80	11.22	7.05
MWM	246	2.08–21.8	5.64	2.67
LWM	142	1.20– 7.60	4.31	1.43

Growth. Growth is rapid: thousands of immature snails ranging in length from 1.1–13.0 mm appeared in the field four to five weeks after hatching and in greatest numbers during October and November. There are several cohorts of young due to the extended spawning period, direct development, and rapid growth but a single large cohort comprising all of these smaller groups is clearly discernable (see Fig. 4). Growth continues throughout the winter and by late January millions of subadults, from 2–8 mm in length, appear in the tidal creeks while the larger, older adults begin to die. Most adults had badly eroded shells and were heavily infested with trematode parasites. Immature snails tend to stay in the water where they crawl in the flocculant detritus, while adults are along creek banks or well above the water on plants (see Table 3). In general, adults tend to be amphibious and only occasionally crawl in water. Three 1/10 m^2 samples taken in a tidal creek at the high, mid and low tidal marks clearly demonstrated this segregation of age classes (Table 3).

By early spring, young snails were about half grown but not sexually mature. A few young males were detected but none were producing sperm. Several females showed signs of early egg production but none of these had fully developed ovipositors and their pallial oviducts were largely undifferentiated. The older generation of adults was almost completely gone at this time. Older snails were easily recog-

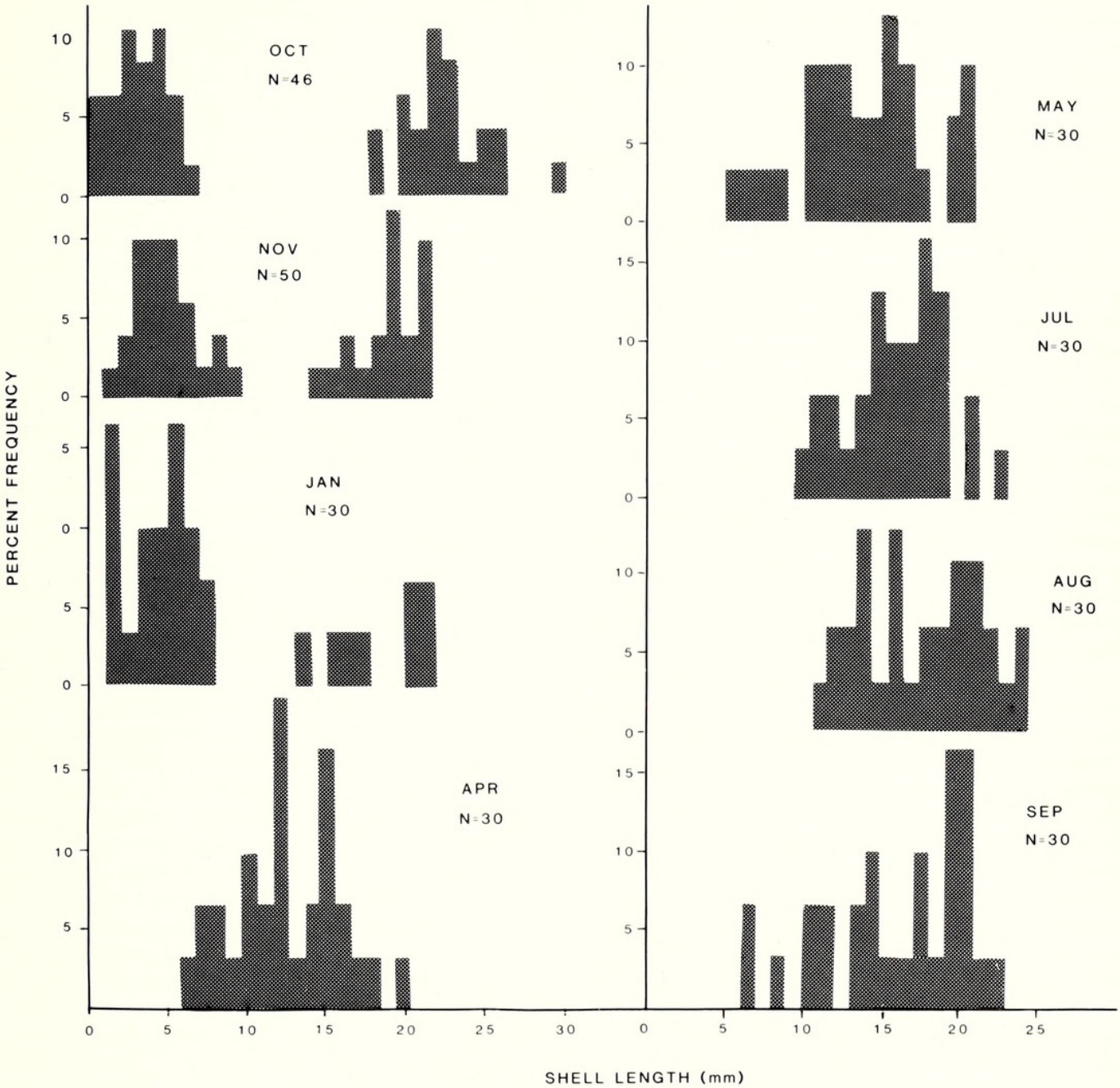

Fig. 4. Monthly percent length-frequency histograms of shells of *Cerithidea scalariformis* from Big Starvation Cove, Indian River, Ft. Pierce, Florida, covering one reproductive year, 1980–81.

nized by their badly eroded, chalky appearance. Monthly samples show that the new cohort achieves adult size and sexual maturity by early summer but the outer shell lips of these individuals have not yet become completely thickened. In August and September, most snails had achieved reproductive maturity and had thickened outer shell lips. Figure 4 illustrates growth over a year's period. It appears that adults live from one to two years.

HABITS AND HABITATS: *Cerithidea scalariformis* lives on muddy-sandy substrata in intertidal and supratidal estuarine habitats. The Big Starvation Cove population occurs along the banks and in shallow tidal creeks created by a mosquito impoundment area in a mangrove swamp along the Indian River. This is a somewhat artificial habitat subject to deliberate draining and flooding, but snails are exceedingly abundant here, numbering in the millions and comprising two size classes during the winter: large adult snails and juveniles of several size groups. These groups represent the adult reproductive population and its progeny. Although most snails are immersed in water during very high tides, adults tend to stay above the high water mark and may be found almost a meter above the high tide zone where they lie beneath or crawl up the vegetation bordering the water. Climbing response to escape immersion and predators as recorded in other *Cerithidea* species such as *Cerithidea*

decollata (Linnaeus) (Cockcroft and Forbes, 1981b:8; Berry, 1972) and *Cerithidea obtusata* (Lamarck) (Sasekumar, 1974) is less pronounced in *Cerithidea scalariformis*. Normally, only a few snails climb vegetation although when the area is completely flooded most adults climb on *Salicornia* and mangroves just above the water level. Haros (1976) made the same observation on the population of *Cerithidea scalariformis* he studied and suggested that the climbing response is not strongly selected for. The dominant plant along the banks of the tidal creeks with which the *Cerithidea* population is associated is *Salicornia*. *Cerithidea scalariformis* had a wide tolerance to temperature, salinity and desiccation. Salinity is normally 33‰ but varies considerably during the year due to periods of drought and heavy rainfall. The entire site is rich in detritus and microalgae that form a flocculent mass at the water-substratum interface. Temperatures at the substratum surface vary considerably with season and exposure to the sun. Winter frosts may occur and extremely high temperatures are attained in the summer sun. Tidal levels fluctuate from 50 cm to 0.5 m depth and may be heavly influenced by rainfall. Larger snails tend to follow the tides while juveniles are more likely to be permanently immersed in the tidal creek where sediments and detrital particles are finer. Tidal creeks range in width from 1–3 m and have an average depth of about 50 cm. During low tides the creeks may be nearly dry exposing up to three meters of bank. At these periods, juveniles and some adults remain partially buried in the detritus. When the area is flooded by exceptional high tides, snails disperse everywhere.

I found no evidence of predation such as drilled or crab-cracked shells. Many wading birds, raccoons and opossums occur at the site but none were observed preying on *Cerithidea*. In May, many of the younger, subadult snails had the tips of their tentacles bitten off suggesting killifish predation. With the exception of *Uca*, no crabs were ever observed in the tidal creeks.

COMPARISON WITH OTHER CERITHIDEA TAXA

COMPARATIVE ANATOMY: The most thorough anatomical studies on *Cerithidea* are those on *C. californica* by Bright (1958) and Driscoll (1972), the latter writer concentrating on the alimentary tract. Aside from a few differences such as the structure of the pallial eye, the basic morphology of *C. scalariformis* and *C. californica* is similar, indicating a close relationship. However, species of other subgenera may differ considerably in the morphology of some organ systems, such as the respiratory, alimentary, and reproductive tracts.

Externally, *Cerithidea* females may be distinguished by the presence of a distinct, bulbous ovipositor on the right side of the foot (Fig. 2, B, *ovp*). Among the cerithiacea, a similar ovipositor occurs in *Cerithidea californica, Batillaria minima, Batillaria zonalis,* among *Cerithium* species (Cerithiidae) (Marcus and Marcus, 1964:507), and in *Modulus modulus* (Modulidae) (Houbrick, 1980a:121), and among the freshwater Melanopsidae, in *Melanopsis* and *Zemelanopsis* (Belgin, 1973). Bright (1960:13) apparently did not notice the ovipositor in *Cerithidea californica* because he stated that there was no sexual dimorphism in that species. He obviously misinterpreted the anatomical layout of the reproductive system and erroneously recorded a penis in males. His sections likewise indicate a total misunderstanding of the functional anatomy of the pallial gonoducts.

The outer lamina of the pallial oviduct of *Cerithidea* bears a long sperm collecting gutter (Fig. 2, E, *sg*) that widens in the proximal end to form the spermatophore bursa (Fig. 2, E, *sb*) which is possibly homologous with the bursa copulatrix of other prosobranchs, and a sperm pouch (Fig. 2, E, *sr*) that may function as a seminal receptacle. This is not unlike the condition in *Tympanotonus* (subfamily Potamidinae) described by Johansson (1956:160). According to his account, *Tympanotonus* has a ciliated ridge in the outer lamina but not a seminal receptacle. I believe the inner pouch depicted by him in the inner lamina of *Tympanotonus* is a seminal receptacle. *Cerithidea* also has another seminal receptacle in the proximal end of the inner lamina similar to the envelope-like receptacle found in the proximal inner lamina of *Modulus* (family Modulidae) (Houbrick, 1980a). A similar case of two seminal receptacles, one in each of the laminae, is described in *Bittium* (family Cerithiidae) by Fretter and Graham (1962:367). I have noted a seminal receptacle at the distal end of the inner lamina of *Cerithium nodulosum* (Houbrick, 1971). It appears that the seminal receptacle in the inner lamina is the larger of the two and that it may represent the "true" receptacle.

Pelseneer (1895:358) was the first to record the presence of a pallial eye in *Cerithidea*. He studied *C. obtusa* (Lamarck, 1822) and made sections of the pallial eye (1895:plate 15, figure 9). The structure of the eye described by Pelseneer (1895) closely resembles the eye of *C. scalariformis*. Pflugfelder (1930) made a more thorough study of the mantle eye of *C. obtusa* (cited as *Potamides obtusus*) in which he described the histology of the eye in detail. His sections are remarkably similar to those I made of *C. scalariformis*. The large nerve depicted by Pelseneer (1895:358) and Pflugfelder (1930:279) innervating the eye of *C. obtusa* and subdividing into branches which pass through the pigment cup and retina was not seen as clearly in my sections of *C. scalariformis*. Van Benthem Jutting (1956:435) was the only worker since Pfugfelder to note the presence of a pallial eye in *C. obtusa*.

The presence of a well-developed pallial siphonal eye has been overlooked in American *Cerithidea* species. Although significant anatomical and ecological work has been done on *C. californica*, no mention of its pallial eye occurs in the literature. I observed a pit-like pallial eye in *C. californica* from Anaheim Bay, Los Angeles, California. The mantle edge adjacent to the eye comprises several transparent bulb-like structures that are filled with white spherules. The function of these structures is unknown but they may gather and concentrate light. The pallial eye comprises a large pit bordered by darker pigment which, in cross section, lies in a dark orange pigment cup embedded in the mantle wall. Preserved specimens of *C. cingulata* (Gmelin) from

Thailand have a pit-like, small black pallial eye on the inner edge of the inhalant siphon. The outer surface bears small spherical bodies that appear to concentrate light and are similar to structures observed on the inner surface of the pallial siphon of *C. californica*. This kind of pallial eye differs from those observed in *C. scalariformis, C. costata,* and *C. pliculosa*. These species have a lens and cornea and are referred to the subgenus *Cerithideopsis* Thiele, 1929. I examined preserved specimens of *Cerithidea montagnei* (Orbigny) (= *reevianum* C. B. Adams) from the Canal Zone, Panama (LACM 70-64) and noted that this species also has a pallial eye similar to that of *C. californica*. I have also seen what appears to be a pit-like pallial eye in poorly preserved specimens of *Cerithidea quadrata* Sowerby. It appears likely that all *Cerithidea* species have some kind of pallial eye and that this organ is an important generic character.

Pflugfelder (1930:277) showed that the pallial eye of *Cerithidea obtusa* was located at the mantle edge and protruded into the anterior canal in living snails, which he claimed were only active at night. He observed the same kind of an eye in *Cerithidea quadrata* (cited as *Potamides quadratus*) but mentioned that he did not find pallial eyes in any other representatives of the "family of Cerithidea." It is unclear what he understood by this taxon, which has no validity. Pflugfelder probably meant the family Potamididae rather than the generic taxon *Cerithidea*, because all members of the genus *Cerithidea* appear to have pallial eyes.

The functional significance of the pallial eye in *Cerithidea* species is not clear. Presumably, this eye assists an amphibious snail to observe the immediate environment of the aperture prior to extruding the more vulnerable head-foot. Pflugfelder (1930) suggested that amphibious snails that are more active at night would have need of this eye to avoid predators during the day but it is unclear what these predators would be and how such an eye would help. Crabs are undoubtedly a danger to the *Cerithidea* species of Indo-Pacific swamps but do not appear to be a threat to *C. scalariformis*. The pallial eye may be more important to juvenile snails which live submerged in water where fish may nibble the extended cephalic tentacles.

The only other published account of a siphonal pallial eye in a potamidid is that of Johansson (1956) who described an eye located at the inner edge of the inhalant siphon of *Tympanotonus fuscatus* (Linnaeus). It consists of a black, bulging structure with a round white spot in the center. The pallial eye of *Tympanotonus* has a cornea of a single layer of high narrow cells with basal nuclei that form a weak lens. The pigment cup is penetrated by branches of the sensory nerve and the inner surface of the cup is covered with a retina. This eye differs from Pelseneer's (1895) description of the pallial eye of *Cerithidea obtusata* in that the retina of that species is penetrated by branches of the sensory nerve and the cornea does not form a lens. Some potamidids appear to have sensory structures other than eyes located in the same area of the mantle edge. For example, Pflugfelder (1977:248–249) mentioned that *Potamides telescopium* (probably *Terebralia palustris*, judging from the figure), a mangrove snail, had sensory areas on its mantle edge. Tenison-Woods (1888:175) recorded that the mantle edge of *Pyrazus ebininus* (Bruguière, 1792) [cited as *Cerithium ebininum*] was "studded with innumerable minute rounded bodies which refract light very brightly." He also noted rounded eye-like bodies in semilunar chambers with a distinct nerve supply in the same area and suggested that these are compound eyes. These observations need to be reconfirmed, preferably on living animals. If present, these are probably convergent structures similar to other pallial eyes such as those found in some cerithiids.

Among the Cerithiidae, I have described a pallial siphonal eye in *Gourmya gourmyi* (Crosse, 1861) (Houbrick, 1981b:5–6), which has numerous ocelli at the inner edge of the inhalant siphon. I have also observed a pit-like siphonal eye similar to that of *Cerithidea californica* in *Rhinoclavis (Proclava) kochii* (Philippi, 1848). I documented inhalant siphonal pigmented sensory areas in *Rhinoclavis* species (Houbrick, 1978) which I suggested might be specialized sensory or light sensitive organs. These structures all appear to be, at best, analogaous light sensory organs independently evolved from ectodermal epithelium. I agree with Johansson (1956:152) that they probably represent a convergent evolution. Nevertheless, their presence in members of different cerithiacean lineages may also suggest that they should be recognized as plesiomorphic characters. All examined *Cerithidea* species have pallial siphonal eyes located in the same area of the mantle. With the exception of *Tympanotonus*, all other potamidids lack this organ; thus, within the genus *Cerithidea*, pallial ocelli are probably homologous and useful as phylogenetic characters.

All *Cerithidea* species I examined have a low, broad ctenidium which extends the length of the mantle cavity. Individual filaments lack supporting rods. Pelseneer (1898) stated that *C. obtusa*, a species that lives almost entirely on dry land in the mangroves, has a reduced ctenidium and a network of blood vessels in the mantle roof. I have observed preserved specimens of *C. obtusa* and confirm his observation. This does not seem to be the only species with a reduced ctenidium. I found no trace of a ctenidium in *C. quadrata* Sowerby, but the specimens I examined were poorly preserved and the ctenidia may have been destroyed. Pelseneer (1895) suggested that the low, broad gill filaments seen in *Littorina* and some potamidid genera were an adaptation to terrestrial life and that *C. obtusa* was the most advanced form in this regard. Johansson (1956:150) supported Pelseneer's view and described a ctenidium similar to what I have recorded for *C. scalariformis* in *Tympanotonus fuscatus* (Linnaeus).

The osphradium in *Cerithidea* and all other potamidids examined is a simple ridge extending the length of the mantle cavity. It is reduced or absent in *Cerithidea*, s.s., species. It thus differs from the well developed bipectinate osphradium found in members of the Cerithiidae (Houbrick, 1974, 1978), Modulidae (Houbrick, 1980a), Diastomatidae (Houbrick, 1981b), and Campanilidae (Houbrick, 1981a). The potamidid osphradium is similar in structure to that of *Planaxis* (per-

sonal observation), *Littorina* and *Rissoa* (Johansson, 1956:150) and may be regarded as a primitive structure in this state. According to Pelseneer (1895), the osphradium of *Cerithidea obtusa* is absent, but I noted a tiny ridged structure in a poorly preserved specimen of that species suggesting that there is a vestigial osphradium and that Pelseneer's observation needs reconfirmation.

The radula differs among *Cerithidea* species, particularly in the configuration of the rachidian tooth and the outer lateral tooth (see Bishop, 1979:31, figures 3-1,d–f). The subgenera are partially defind by differences of the rachidian tooth. Cerff (1981:95–96) depicted scanning electron micrographs of *Cerithidea decollata* but showed only the cusps on the tips of the teeth. Cerff obviously misunderstood the entire configuration of the taenioglossate radula, because he described three lateral teeth and only one marginal tooth. His pictures indicate a spatulate, cuspless outer marginal tooth, an inner marginal tooth with rake-like denticles and a lateral tooth with six, relatively large, pointed denticles. He did not show the basal plate and glabrella of the rachidian tooth.

The rachidian tooth of members of the *Cerithideopsis* group as described and depicted herein is distinctive. It somewhat resembles that of *C. (Cerithideopsilla) cingulata* in general configuration but has fewer cusps. It differs considerably from the rachidian tooth of *Cerithidea* s.s. species such as *C. obtusa, C. decollata* and *C. kieneri* (see Bishop, 1979: figures). The rachidian tooth in true *Cerithidea* species is narrow, has an elongate, tear-shaped basal plate and bears a long, narrow central cusp.

One of the striking features of the alimentary system of *Cerithidea* is the long style sac. In all species I examined, the style sac projects anteriorly from the stomach to the pericardial sac (Fig. 2, C, *ss*). The style itself is nearly one-half the shell length in *C. scalariformis.* Driscoll (1972:384) suggested a functional relationship between style length and composition of ingested food. The rich, flocculent organic detritus ingested by *C. scalariformis* is extremely fine. The short radula, complex sorting area of the stomach and long style all indicate that the alimentary morphology of *Cerithidea* species is well adapted for feeding on fine particulate matter.

There seems to be minor variability in the layout of the nervous system of *Cerithidea* species and other potamidids. Bright (1958:16) does not show the dialyneury between the supraesophageal ganglion and the left mantle nerve that I record in *C. scalariformis.* Bouvier (1887:plate 7, figure 29) noted a similar dialyneury in *C. obtusa.* He also showed a zygoneury between the right pleural and subesophageal ganglia which I did not see in *C. scalariformis.* Bright (1958:10–11) made no mention of zygoneury in *C. californica.* Bouvier (1887) depicted other potamidids such as *Terebralia sulcata* (Bruguière) (cited as *Pyrazus sulcatus*) and *Pyrazus ebininus* (cited as *Potamides ebininus*) as having a similar zygoneury.

COMPARATIVE REPRODUCTIVE BIOLOGY: Both direct and indirect modes of development occur in *Cerithidea* species. It would appear that all *Cerithideopsis* species have direct (lecithotrophic) development. As mentioned above, *C. scalariformis* undergoes direct development and is a poor larval disperser with a limited geographic distribution. MacDonald (1967) made the same observation on *C. californica* although Race (1982) noted that the juvenile floating behavior indicates that it does have access to other habitats and is not completely restricted by lack of dispersal abilities. In contrast to *C. scalariformis,* which has a peak spawning period in September through November, MacDonald (1967) found mating pairs of *C. californica* common in May and spawn masses present from May to October with greatest abundance in July and August. The spawn of *C. californica* which I examined, consists of long, detritus-covered jelly strings within which are held the individual egg capsules. Jelly strings vary in length but five randomly collected strings had a mean length of 60 mm and a width of 2.5 mm. Jelly strands are tear shaped in cross section with the thin portion adhering to the substrate. Egg capsules are packed three to four deep within the jelly strands. There are about 540 egg capsules per spawn. An individual egg capsule is 0.4 mm in diameter and contains a single egg 0.28 mm in diameter. No nurse eggs are present. Advanced embryos were not observed. According to MacDonald (1967), the emerging veliger larvae settle immediately upon hatching, but Race (1982:344) stated that they undergo complete development without a planktonic stage. The eggs of *C. californica,* in mud covered strings, are laid on the substratum in the summer and fragile shelled juveniles emerge in high densities throughout this period. The latter observation is more than likely the correct one since it matches what I have seen in *C. scalariformis.* The protoconch is typical of a direct developing larva.

Habe (1955:204) described the egg masses of two species, *C. (Cerithideopsilla) djadjariensis* and *C. (Cerithidea) rhizophorarum.* The former species lays its eggs in a long jelly string 50–90 mm long and 3–3.5 mm wide. Habe's figure shows an elongate egg string filled with small eggs arranged in tight spirals. The spawn has an axial attachment surface, presumably flat. The small egg capsules (0.2 mm) and wide geographic dispersion of this species indicate a free swimming larval stage. *C. (Cerithidea) rhizophorarum* excavates a hole in the substratum and deposits its spawn in the bottom. The spawn mass consists of a sticky mass of jelly strings about 20 mm wide and 15 mm deep. Individual eggs are 0.35 mm in diameter, suggesting direct development. The spawn and larvae of *C. (Cerithideopsilla) fluviatilis* (Potiez and Michaud), which may be synonymous with *C. cingulata*, was described by Natarajan (1958:174–175), who showed that this species undergoes indirect development and hatches after a four day incubation period. He recorded an average of 4,800 eggs per spawn and small egg capsules 0.25 mm in diameter. Panikkar and Aiyar (1939) have also described the spawn of this species from Madras and Sadasivan (1948) gave an account of the growth rate, duration of the breeding season and age at maturity of this species. Amio (1963:304) depicted the spawn masses of *C.*

Table 4. Comparative measurements of *Cerithidea* spawn, eggs, and larvae (all measurements in mm and expressed as mean values calculated from present study and literature).

Species	Spawn length	Spawn width	No. eggs per mass	Capsule diameter	Embryo diameter	Citation
scalariformis	50.6	1.13	352.6	0.37	0.28	this study
californica	60	2.5	540	0.40	0.28	this study
rhizophorarum	20	14.5	—	0.35	—	Habe, 1955
djadjariensis	70	3.4	—	0.20	—	Habe, 1955
cingulata	80	—	—	0.21	0.11	Amio, 1963
fluviatilis	123	2.5	4,800	0.25	0.14	Natarajan, 1958

(Cerithidiopsilla) cingulata (Gmelin) and demonstrated indirect development with free swimming veliger larvae. The egg capsules are small (0.20–0.22 mm) and there is an incubation period of seven days prior to hatching.

A summary of the kinds of *Cerithidea* spawn, eggs and larvae is given in Table 4. From available published reports, it would appear that tree-dwelling and high tidal, amphibious species tend to have direct development and narrow, patchy geographic ranges while intertidal, widely dispersed species have free swimming veliger larvae. Direct and indirect modes of development have also been shown to occur in the cerithiid genus *Cerithium* (Houbrick, 1973, 1974).

A few published reports on growth patterns of *Cerithidea* species all show some basic similarities. There are differences in life spans, but adults do not increase their length by addition of new whorls once sexual maturity is attained but rather expand and strengthen their shell lips. As erosion of older shells increases, their decollate condition may become more acute and a pronounced reduction in length may occur. Life spans of direct developing snails are difficult to estimate when new subgroups constantly arise during the spawning season. On the basis of three years' observation, I suspect a life span in *C. scalariformis* of one to three years. However, my observations were cursory and not based on growth curves of marked cohorts. As seen in Figure 4, maximum growth rate occurs in juveniles (less than 10 mm). I rarely found adults that survived more than one to two years and these were obvious due to their badly eroded shells. Once adult stage is attained, there is little or no growth in shell length. The outer lip is strengthened and the shell color is lost due to erosion. MacDonald (1967) recorded maximum growth rates in *C. californica* 4–8 mm long and little or no growth in snails over 20 mm long. He observed that some snails do not grow every season and that varix counts underestimate an animal's true age. A maximum life span for *C. californica* was calculated to be seven years, considerably longer than what I estimate for *C. scalariformis*. Cockcroft and Forbes (1981a) found that growth in *C. (Cerithidea) decollata*, a tropical species, was also seasonal, showing an acceleration during summer months and a depression during winter. Summer growth decreases as size increases, while winter growth is relatively constant for all sizes. They estimated that it took three years for *C. decollata* to attain modal size (12–12.9 mm) and that maximum width was attained in excess of nine years. Snails of less than 10 mm width expanded and consolidated their shell lips rather than adding new whorls.

To my knowledge, no one has documented sexual dimorphism in the shells of *Cerithidea* and other potamidid species. Differences in the shell dimensions of males and females of *C. scalariformis* were highly significant (see Table 1), females having the larger shells. This is not surprising since the large pallial oviducts of females occupy more mantle cavity space than the smaller pallial gonoducts of males.

COMPARATIVE ECOLOGY: All *Cerithidea* species are surface animals that occur in dense aggregations and are easily collected because of their high intertidal habitat. The highest densities I observed in a population of *C. scalariformis* was 1,100 snails/m^2. MacDonald (1967) found *C. californica* to occur in densities as high as 13,800 snails/m^2.

I found few empty shells of *C. scalariformis* after death and disappearance of spawning adults. This species has a life span of about one to two years and it is surprising that so few dead shells occur. There are no hermit crabs to carry away shells in the Big Starvation Cove habitat and one rarely finds shells buried in the sediment. This is probably because shells of dead animals quickly become decalcified and break up. MacDonald (1967) observed the same phenomenon in *C. californica* populations and noted that dissolution of shells occurs before burial in the estuarine environments probably as a result of low pH.

A number of papers have been published on ecological zonation and tidal activity rhythms of this genus. Incidental notes about *Cerithidea* also occur in publications of mangrove ecology. Each of the three *Cerithidea* subgenera appears to have its own generalized habitat. This adds support to the subgeneric classification arrived at by analysis of morphological character states.

Cerithidea s.s. species appear to comprise a tree dwelling group. Brown (1971) found that *C. (Cerithidea) decollata* formed dense aggregations on mangrove tree trunks, between 1–2 meters from the ground, but that it fed for short periods on the mud surface of the substratum. He observed a general movement of the snails from the bases of trees to the mud after spring tides. This species, when not

feeding, is attached to tree trunks at its aperture by dried mucus. Cockcroft and Forbes (1981b) showed that descent of *C. decollata* to the substratum was associated with feeding. They found that snails descended at low tide periods and ascended the trees before the following high tide and suggested that tree-climbing was a predator avoidance response. Berry (1972) also suggested that this species was primarily a tree-dweller that feeds on epiphytic algae and descends to browse on the mud when the mangrove is not flooded for several days. *Cerithidea (Cerithidea) quadrata* lives on mangrove roots but also occurs on the mud surface (Berry, 1963). According to Brandt (1974), this species feeds on algae growing at the roots and stems of mangroves. Likewise, *C. (Cerithidea) obtusa* occurs mainly on trees from 50–175 cm above the substratum (Houlihan, 1979; Sasekumar, 1970; 1974), but is occasionally found on the substratum. The *Cerithidea* s.s. group thus differs ecologically from other *Cerithidea* subgeneric taxa that do not spend appreciable time in the trees.

Members of the subgenus *Cerithideopsilla* live mainly on the substratum in intertidal mud flats. *Cerithidea (Cerithideopsilla) cingulata* is a wide-spread Indian Ocean species that is common on the surface of sandy flats in mangrove swamps or estuarine areas. Although Murty and Rao (1977) recorded that this species is abundant on the substratum and climbs mangrove roots with rising tides, it does not seem to be a tree dwelling species in the sense that *Cerithidea* s.s. species are. Basson *et al.* (1977) found dense aggregations of *C. cingulata* on the tidal flats of the western Persian Gulf. These populations were not associated with mangroves. Berry (1972) noted that *C. cingulata* was common on the soil surface of mangrove swamps in west Malaysia. In Singapore, Vohra (1970; 1971) noted that this species was not limited by particle size in its distribution but that it avoided clean, well-drained sand and was confined to regions of low salinity and pH. Vohra (1970) found no evidence for vertical migration with the tide but observed a seasonal migration, controlled perhaps by internal physiological rhythms. *Cerithidea cingulata* also showed segregation by size in relation to tidal levels, the largest, oldest individuals occurring upshore. My observations on size segregation of *C. scalariformis* are similar. Three other *Cerithideopsilla* species, *alata* (Philippi), *microptera* (Kiener) and *djadjariensis* (Martin), are reported by Brandt (1974) to live on mud flats.

Cerithideopsis species are all confined to the New World and the ecology of only a few is known. An account of the ecology of *C. (Cerithideopsis) scalariformis* has been presented earlier in this paper. *Cerithidea (Cerithideopsis) costata, C. (C.) californica,* and *C. (C.) pliculosa* all live primarily on muddy substratum and only occasionally climb trees or vegetation. This supratidal substratum group thus differs from *Cerithidea* s.s. species in ecology. The only thorough work on *C. scalariformis* of which I am aware is an unpublished master's thesis at Florida State University by Harlos (1976). He studied the environmental distribution of this species in a tidal marsh at Wakulla Beach, Apalachee Bay, Florida. His study site is not directly comparable to mine in that the Indian River site is a mosquito impoundment in which the water level is sometimes artificially regulated. Harlos found that *C. scalariformis* preferred a salinity substratum of 28‰ and that its vertical distribution along the shore can be predicted by substrata salinities. He concluded that predator influences in its distribution and behavior are insignificant. As in my study, Harlos found the highest densities of *Cerithidea* in the *Salicornia* zones. Predation was highest in small snails. Harlos (1976) found that snails under 8 mm in length were preyed upon by *Fundulus* fishes. Although I did not see this kind of predation, the only fish present in tidal creeeks at the Indian River site are *Fundulus* species. Harlos also observed the xanthid crab, *Panopeus herbstii* (Milne-Edwards), feeding on *Cerithidea* and suggested the clapper rail, *Rallus crepitans* (Gmelin), as another possible predator. I did not see any crabs in the tidal creeks at my study site, and although several kinds of wading birds are very common there, I never saw them feeding on snails. I found no evidence of predation such as drilled or crab-cracked shells. Many wading birds, racoons and opossums occur at the site but none were observed eating *Cerithidea*. MacDonald (1976) found that whole and fragmented shells of *C. californica* were not uncommon in shore bird droppings. He also recorded crab predation in this species and suggested that bottom fish that enter marsh creeks at high tides prey on *Cerithidea*.

The ecology of *C. (Cerithideopsis) californica* has been the subject of several papers (Race, 1982; Whitlatch and Obrebski, 1980; MacDonald, 1967, unpublished dissertation). This species differs from its other American congeners in having a geographic distribution in essentially temperate climates. It also displays a wide range of physiological tolerances. It can survive up to four hours' immersion in 40°C seawater and, in dry conditions, 65% of a population can survive exposure between 11–15 days (Race, 1982:345). Race (1982) studied the interaction between the endemic *C. californica* and its introduced Atlantic ecological equivalent, *Ilyanassa obsoleta* (Say, 1822) in San Francisco Bay. The latter species is an omnivore that preys on the eggs and young of *C. californica* which it has displaced in much of its former habitats. During the summer, *C. californica* attains densities of 1,000 snails per square meter. It appears to be immersed in water more often than *C. scalariformis.* Race (1982:342) found that during low tide, about two-thirds of the snails were on tidal creek bottoms and one-third out of the water. On cold days most were burrowed into mud on creek bottoms. My observations of *C. scalariformis* showed that it tends to remain out of water except during very high tides or when spawning. I did not find burrowing to be common, even during cold spells. MacDonald (1967) recorded predation on *C. californica* by shore birds and suspected that bottom fishes also preyed on them during high tides. Large individuals were eaten by the crab, *Pachygrapsus crassipes.*

SYSTEMATIC CONCLUSIONS

Genus *CERITHIDEA* Swainson

Cerithidea Swainson, 1840:198,203,342. Type-species: *Melania lineolata* Griffith and Pidgeon, 1934, *non Strombus lineolatus* Gray, 1828 (= *Cerithium obtusum* Lamarck, 1822), by subsequent designation of Pilsbry and Harbison, 1933.—Adams, A., 1854:292–293;—Tryon, 1882:251;—Fischer, 1887:682;—Cossmann, 1906:113;—Thiele, 1929:206–207;—Wenz, 1938:742;—Bequaert, 1942a:20;—1942b:1;—Olsson and Harbison, 1953:290–291;—Van Benthem Jutting, 1956:428–429;—MacNeil, 1960:39;—Ladd, 1972:39.

Phaenommia Mörch, 1860:80. Type-species: *Cerithidea Charbonieri* Petit (= *Cerithium charbonieri* Petit de la Saussaye, 1851), by monotypy.

Aphanistylus Fischer, 1884:682. Type-species: *Cerithidea Charbonniere* (sic) Petit (= *Cerithium charbonnieri* Petit de la Saussaye, 1851), by monotypy.

Diagnosis: Members of genus *Cerithidea* s.l., characterized by elongate, turreted shells of thin to moderate texture sculptured with spiral ridges and prominent axial ribs, sometimes with thick varices. Apeture large, oval with smooth outer lip and short anterior canal. Lower lip projects beyond columella base (Fig. 5, C). Radular ribbon short, all teeth have cusps, and shafts of maginal teeth have flaring, flattened process. Operculum thin, corneous, circular and multispiral with central nucleus. Animal with moderately long tentacles, eyes at their swollen bases. Mantle edge smooth, all species have pallial siphonal eye. Ctenidium reduced, filaments low and broad, osphradium narrow and ridge-like. Hypobranchial gland broad and extends from ctenidium over roof of pallial cavity to cover rectum. Pair of salivary glands passes through nerve ring and large swollen crop present posterior to nerve ring. Stomach has numerous sorting ridges and large gastric shield. Long style sac and style advance from stomach and terminate at pericardium. Females have ovipositor on right side of foot. Spermatophore bursa and sperm pouch lie in proximal outer lamina of pallial oviduct and seminal receptacle in proximal inner lamina. Males aphallate, sperm dimorphic. Spawn deposited in jelly strings which contain egg capsules. Development planktotrophic or lecithotrophic. Amphibious adults live in intertidal environments. Most species tend to avoid rising tide and undergo seasonal migrations.

Remarks: Thiele (1929:206) divided the genus *Cerithidea* Swainson, 1840 into two subgenera, *Cerithidea* s.s. and *Cerithideopsis*. He split the latter taxon into two sections, *Cerithideopsis* s.s. and *Cerithideopsilla*. Wenz (1938:742) considered the genus *Cerithidea* to comprise four subgenera, *Cerithidea* s.s., *Cerithideopsis*, *Cerithideopsilla* and, for a fossil species, *Cerithideops* Pilsbry and Harbison, 1933. According to Bequaert (1942a:20), his citation of *Cerithidea decollata* (Linnaeus, 1767), on the authority of Makiyama (1936), as the type-species of the genus is incorrect. *Cerithidea decollata* is credited to Bruguière (1838). *Cerithium obtusum* Lamarck, 1822 was desginated the type-species of *Cerithidea* by Pilsbry and Harbison (1933:115). Bequaert (1942a:20–21) has thoroughly reviewed the history of the selection of a type-species for this genus and may be consulted for more details. Shell characters, radular morphology and ecological differences appear to warrant Wenz's (1938) recognition of the three Recent subgenera within the genus. Neither Bequaert (1940:1) nor Van Benthem Jutting (1959:428) recognized the subgeneric taxa proposed by Thiele (1929), but included all species in *Cerithidea*. Retgeren Altena (1940), in his revision of some Indo-West-Pacific *Cerithidea* species, recognized the subgeneric status of *Cerithideopsilla* and assigned four living species to it. Following Thiele (1929), he later (1942:7) referred *Cerithideopsilla* to a "Section" under the subgenus *Cerithideopsis*, but gave no reason for this change of status.

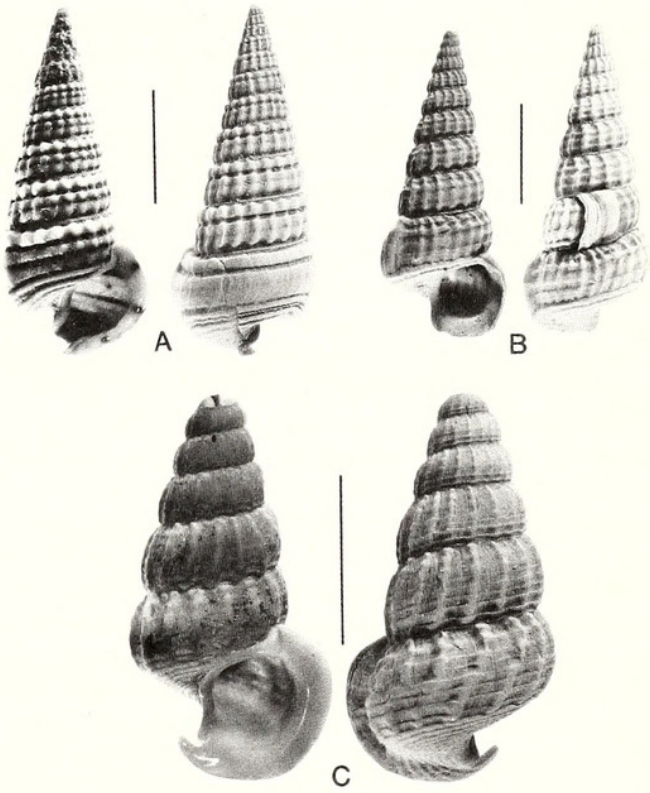

Fig. 5. Type-species of *Cerithidea* subgenera: **A)** *Cerithidea (Cerithideopsilla) cingulata* from Ras Tanura, Saudi Arabia (USNM 622154; 27.4 mm); **B)** *Cerithidea (Cerithideopsis) pliculosa* from El Zacatal, Campeche, Mexico (USNM 702909, 22.6 mm); **C)** *Cerithidea (Cerithidea) obtusa* from Kuala Selangor, Malaysia (USNM 778778, 39.7 mm).

The subgenus *Phaenommia* Mörch, 1860 was pro-

posed to accommodate *Cerithidea charabonnieri* Petit de la Saussayse, 1851. The shell of this species does not seem to differ significantly from those of *Cerithidea* s.s. species and since nothing is known of the radula or soft parts of this species I am synonymizing it with *Cerithidea* s.s. pending further information.

Cerithidea largillierti Philippi, 1849, heretofore referred to *Cerithidea*, does not seem to fit the limits of any subgenera recognized in this study. I agree with Bishop (1979:77), who suggested that it might better be referred to a new genus. More material and anatomical work on this uncommon species are needed before a sound taxonomic decision is reached.

According to Cossmann (1906:113–114), the genus *Cerithidea* occurs as far back in the fossil record as the Maastrichtian of the Cretaceous. Members of this group are common in the Eocene of the Paris Basin indicating that they were abundant in the Tethys Sea.

Three Recent subgenera are herein recognized: *Cerithidea* s.s., *Cerithideopsilla*, and *Cerithideopsis*. The type-species of each of these taxa are depicted in Figure 5.

C. (Cerithidea) Swainson, 1840 [Type-species: *Cerithidea obtusa* (Lamarck, 1822), by s.d.]

Diagnosis: Species characterized by thin textured shells, some markedly decollate, having prominent axial ribs with or without spiral sulci, wide mouthed apertures, smooth rounded outer lips and rudimentary anterior canals (Fig. 5, C). Ctenidium rudimentary. Network of blood vessels in mantle roof functions like pulmonate lung (Pelseneer, 1895). Osphradium either lacking (Pelseneer, 1896) or much reduced. Rachidian tooth of radula narrow with small central cusp. Outer marginal tooth lacks cusps and has wide flange on outer side of basal shaft.

Remarks: Cerithidea s.s. species tend to live on mangroves well above the tide mark and have an Indo-West-Pacific distribution. They are frequently found attached to leaves and branches by glutinous threads. Development may be planktotrophic or lecithotrophic. Although Cossmann (1906:113–114) traced this genus back to the Maastrichtian of the Cretaceous and described many species from the Eocene of the Paris Basin, it is unlikely that these forms are the same as Recent *Cerithidea* s.s. Ladd (1972:27) recorded fossils of *Cerithidea obtusa* from the Miocene of Saipan. Figures of his samples do not look like the living species but are undoubtedly referred to *Cerithidea* s.s. MacNeil (1960:39) recorded fossil *Cerithidea rhizophorarum* A. Adams, 1854 from the Pleistocene of Okinawa and Regteren Altena (1942) cited it from the Pliocene of Java. It would thus appear that *Cerithidea* s.s. dates at least as far back as the Pliocene.

C. (Cerithdeopsilla) Thiele, 1929 [Type-species: *Cerithidea fluviatilis* (Potiez and Michaud, 1838); = *Cerithidea cingulata* (Gmelin, 1790), by o.d.];—Regteren Altena, 1942:212.

Diagnosis: Species distinguished by shells sculptured with axial ribs crossed by spiral grooves and generally divided into three spiral rows of tubercles. Posterior extension of angular outer lip forms flaring, wing-like process extending nearly halfway up penultimate whorl. Anterior extension of outer lip partially crosses over narrow, deeply notched, anterior canal. Aperture narrow, oval and peristome in adults continuous (Fig. 5, A). Rachidian tooth of radula wide, rounded and convex at top, pentagonal, and has small, equal sized cusps. Base broad, bearing long, wide glabrella. Lateral tooth has long twisted lateral extension while outer marginal tooth has numerous small cusps and lacks wide basal flange seen in *Cerithidea* s.s.

Remarks: Species have an Indo-Pacific distribution and live on intertidal, muddy, sandy estuarine flats, frequently near mangroves and sometimes on their roots. The type-species of the subgenus undergoes planktotrophic development. This subgenus is recorded from the Miocene of the Philippines, India, Japan, and Taiwan and has also been cited from the Pliocene of the Philippines, Java, Sumatra, and Japan (Regteren Altena, 1942). Although some of these identifications may be wrong, *Cerithideopsilla* may be reasonably traced back to the Miocene and appears to be the earliest subgenus found in the fossil record.

C. (Cerithideopsis) Thiele, 1929 [type-species: *Cerithidea iostoma* (Pfeiffer, 1839); = *Cerithidea pliculosa* (Menke, 1892), by o.d.].

Diagnosis: Shell moderately decollate, characterized by thickened varices and straight columella. Short, wide anterior canal, thick outer lip. Axial sulpture dominant with few spiral grooves and cords (Fig. 5, B). Rachidian tooth of radula broad, pentagonal, and has concave top and long, central cusp flanked by two denticles on each side. Base of tooth wide bearing long glabrella. Lateral tooth has long, twisted, lateral extension. Outer marginal tooth bears numerous small cusps and has wide flange on basal shaft.

Remarks: Species are amphibious and restricted to New World estuaries where they live on sandy, muddy flats in salt marshes and mangroves, on *Spartina* and *Juncus* grasses and on *Salicornia* bushes at the high intertidal zone. Some species live in the temperate zone and all species examined have lecithotrophic development. The Western Atlantic species of this group were monographed by Bequaert (1924b). *Cerithideopsis* is known from the Pliocene of Florida (Olsson and Harbison, 1953:291).

PHYLOGENY: Cladistic analysis of 19 characters comprising 38 character states (Table 5) derived from shell morphology, anatomy and patterns of radular dentition distributed among four taxa provided the cladogram shown in Figure 6. Six cladograms, derived from a reshuffling of taxa, showed identical trees. Each was derived with a total of 21 character changes among the 19 characters. Of these 21 changes, two (5 and 6) are reversals. The outgroup (ancestor) used was *Batillaria*, subfamily Batillariinae. It would

Table 5. Comparison of three subgenera of *Cerithidea* using 19 characters and 38 character states (outgroup is *Batillaria*).

Character	Taxa			
	Cerithidea	*Cerithideopsis*	*Cerithideopsilla*	Outgroup
SHELL				
1. shell thickness				
strong (0)				
thin (1)	1	1	0	0
2. decollation				
absent (0)				
present (1)	1	0	0	0
3. spiral sculpture				
weak (1)				
strong (0)	1	1	0	0
4. outer lip extension				
absent (0)				
present (1)	0	1	1	0
5. outer lip				
thickened (1)				
not thickened (0)	1	1	0	0
6. prominent varices				
absent (1)				
present (0)	1	0	1	0
7. anal canal				
absent (1)				
present (0)	1	1	0	0
8. anterior canal				
wide (1)				
narrow (0)	0	1	0	0
9. peristome				
rounded (0)				
not rounded (1)	0	0	1	0
ANIMAL				
10. ctenidium				
rudimentary (0)				
developed (1)	1	0	0	0
11. osphradium				
reduced (1)				
not reduced (0)	1	0	0	0
12. pallial eye				
present (1)				
absent (0)	1	1	1	0
13. crystalline style				
long (1)				
short (0)	1	1	1	0
RADULA				
14. rachidian narrow with single cusp (1); with many cusps (0)	1	0	0	0
15. rachidian with long basal plate (1); without long basal plate (0)	1	0	0	0
16. rachidian with cusps on basal plate (0); without cusps on basal plate (1)	1	1	1	0
17. lateral tooth with long twisted extension (0); without extension (1)	0	0	1	0
18. outer marginal with broad basal flange (0); without flange (1)	0	0	1	0
19. outer marginal with many cusps (0); without many cusps (1)	1	0	0	0

have been better to have used a closer sister group in the subfamily Potamidinae but no comparable anatomical and radular studies of species within this group exist.

Polarities of shell characters (characters 1–9) are either difficult to determine or suspect because of possible parallelisms and reversals. As Davis (1979:34) noted, convergence is an underestimated phenomenon in the evolution of shell morphology. Accordingly, the polarities determined for this set of shell characters are based mainly on outgroup comparison (see Table 5). Other evidence for determining polarity and a discussion of some of these characters are given below:

Character 1. A strong heavy shell is usually associated with the larger, more highly sculptured species, especially some of the fossil ones in the Potamidinae. A thinner, decollate shell is better adapted to tree climbing and is probably a derived trait brought about by radiation into the supratidal mangrove habitat where fish and crab predation are not as important.

Character 2. Marked decollation is known only among the tree dwelling *Cerithidea* s.s., and is not common among other potamidids. A minor degree of decollation exists in *Cerithideopsis* species, but this is frequently due to severe erosion of the earlier whorls. Consequently, the decollate condition appears to be a derived character.

Few anatomical characters were used because of the lack of information about comparable structures and tracts in all of the taxa, especially in *Cerithideopsilla*. This is particularly true of the pallial gonoducts. Comments on anatomical characters follow:

Characters 10, 11. A well developed ctenidium and osphradium occur in nearly all potamidid species. Their rudimentary condition in *Cerithidea* s.s. is considered a derived feature that is probably due to their unusual tree dwelling habit.

Character 12. With the exceptions of *Tympanotonus* and *Pyrazus ebininus*, a pallial eye is not found in other potamidid genera and the presence of this structure in all *Cerithidea* species is surely a derived condition. The pallial eyes of the other taxa are probably not homologous with those of *Cerithidea* and are here attributed to convergence.

Character 13. A short crystalline style is found in *Batillaria* (Driscoll, 1972) and probably in other members of the Batillariinae, but it is a prominent feature of *Cerithidea*.

Polarities of radular characters were established by outgroup comparison. There have probably been parallelisms and reversals in the evolution of radular dentition because these structures seem to be closely correlated with the types of food eaten; therefore, they may not be reliable characters for establishing polarities. The characters and states are listed under characters 14, 15, and 19 (Table 5) may reflect a change of diet due to life in the mangroves.

Not enough is presently known of the developmental biology of *Cerithidea* species to make any meaningful systematic comparisons. A summary of available information appears in Table 4. Both planktotrophic and lecithotrophic development are known in *Cerithidea* s.s. and *Cerithideopsilla*. As mentioned earlier, it appears that widely dispersed, intertidal species tend to have planktotrophic larvae, but it is not now possible to suggest polarity of developmental types.

As regards ecology, *Cerithidea* s.s species have moved into the mangroves, well above the high tide mark and are obviously derived from ancestors who lived in the water. They are essentially a tropical group. The New World *Cerithideopsis* group live mainly at the high tide mark and some species are adapted for life in the semitropical or temperate zones. The Potamididae evolved in tropical seas and movement into temperate zones is probably a new development.

Using the characters discussed above, a hypothesis of the relationships among *Cerithidea* species is presented in Figure 6. According to this cladogram, the taxa *Cerithidea* and *Cerithideopsis* are more removed from the outgroup and share more synapomorphies with each other than with *Cerithideopsilla*. This last taxon, therefore, could be ranked differently than the other two. *Cerithideopsilla* has the most generalized characters and, in this respect, is regarded as the more primitive group. This subgenus also has the longest known fossil record, extending back to the Miocene (Regteren Altena, 1942). *Cerithideopsilla* species tend to live on muddy, sandy substrata as do *Batillaria* species. A direct conversion of the cladogram shown in Figure 6 to a classification that reflects the true phylogeny of this group is unwise. It is obvious that criteria for determining polarity in the transformation series of characters used in this analysis are weak and in many cases established solely on the basis of presence in the outgroup. We know too little of other potamidid groups to make comparisons that will provide clues about polarity. Moreover, the potential for convergence within the Potamididae and specifically in *Cerithidea* is, in my opinion, high. For example, many shell characters such as those seen in the aperture and lip are undoubtedly related to habitat, and supratidal species living in trees will have different shells than those confined to mud flats. It is also probable that more than one clade has radiated into a tree-climbing mode of existence with subsequent return of some species to

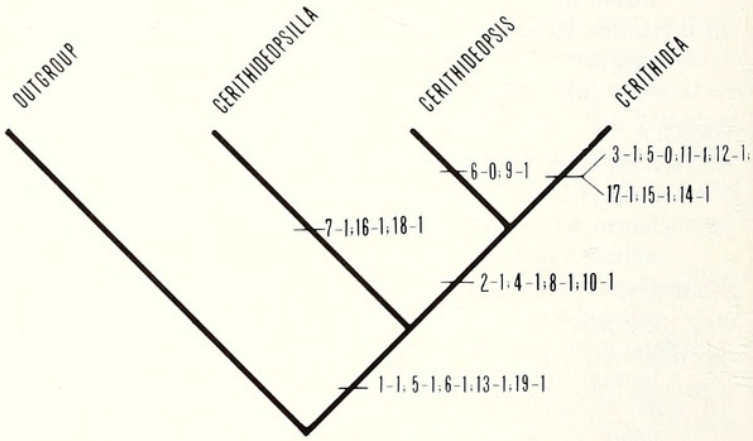

Fig. 6. A hypothesis of the relationships among *Cerithidea* subgenera based on a cladistic analysis of characters. Hyphonated numbers refer to characters and changes in character states, respectively.

the muddy substrate. Accordingly, I give the three taxa equal rank as subgenera of *Cerithidea*. Thus the classification given above should be used with caution and will undoubtedly change as more is known about the anatomy of other higher taxa. It would have been better to have a member of the subfamily Potamidinae as an outgroup, but no comparable anatomical study has been done on members of this group that would serve this purpose. An exception is *Tympanotonus*, but that study concerned the pallial gonoducts.

A survey of fossil and Recent potamidids shows an overall tendency within the Potamididae toward reduction of the expanded, sinuated outer lip, which in many fossil groups and some Recent ones is elaborate and variously produced. Indeed, many extinct higher taxa comprise species with elaborate outer lip morphology, and strong, highly sculptured shells such as seen in *Potamides* and *Pyrazus* species. The Batillariinae are more cerithiid-like in shell morphology than are the Potamidinae and exemplify the familial evolutionary trend to become more "streamlined." In this respect, *Cerithideopsilla* is indeed a more "primitive" *Cerithidea* taxon, having a pronounced expansion and sinus on the posterior outer lip adjacent to the anal canal.

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