

OBSERVATIONS ON THE ANATOMY AND LIFE HISTORY OF  
*MODULUS MODULUS* (PROSOBRANCHIA: MODULIDAE)

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## ABSTRACT

*Modulus modulus* (Linnaeus), family Modulidae, is a style-bearing marine prosobranch in the superfamily Cerithiacea. It differs from other cerithiaceans by its turbinate shell and certain anatomical features. The basic anatomy of *Modulus* is that of a typical mesogastropod but the open pallial gonoducts are similar to those of other cerithiaceans. Characteristic anatomical features are the large hypobranchial gland, aphyallic males, open pallial oviduct with complex inner ducts, and the forward position of the salivary glands relative to the nerve ring.

*Modulus modulus* lives on marine angiosperm grasses and feeds primarily on diatoms.

Fertilization is internal and is effected by spermatophores that contain eupyrene and apyrene sperms. The life cycle of a population from Fort Pierce, Florida lasts about one year. Mating occurs in early winter and spawning in spring. Females have complex pallial oviducts and ovipositors. Spawn masses are cylindrical, comprised of gelatinous tubes and deposited on marine grasses. Development is direct. Young snails emerge after three weeks of incubation.

Within the Cerithiacea, the Modulidae are phylogenetically close to the Cerithiidae and Potamididae.

## INTRODUCTION

The family Modulidae Fischer consists of a single genus, *Modulus* Gray, 1842, and about six species that are largely confined to the shallow waters of tropical and subtropical regions. These prosobranchs are epifaunal, style-bearing, microphagous herbivores and are moderately small animals, having shells 10-25 mm in length. *Modulus* species occur in the fossil record back to the Cretaceous (Dall, 1892). Historically, the family Modulidae has been assigned to the large mesogastropodan superfamily Cerithiacea Fleming, which is comprised of numerous families of herbivorous snails, having open pallial gonoducts, aphyallic males, and shells that are usually high-spired and elongate. Members of the Modulidae, however, differ strikingly from all other cerithiaceans by their top-shaped, trochiform shells. Although the family Modulidae has been included in most of the classic iconographies and the western Atlantic species have recently been monographed by Abbott (1944), there have been no serious anatomical or life history studies of the group. Its standing as a valid family and relationship to other higher taxa in the superfamily has been conjectural.

This paper addresses the functional mor-

phology, developmental biology and aspects of the life history of *Modulus modulus* (Linnaeus, 1758), the type-species of the genus. On the basis of these data, the relationship of the Modulidae to other families of the Cerithiacea will be considered.

## HISTORICAL REVIEW

The family Modulidae has been reviewed by A. Adams (1851), Sowerby (1855), Reeve (1865), Tryon (1887) and more recently by Abbott (1944), who limited his work to the western Atlantic. The older monographs were confined to strict conchological taxonomy and did not address relationships above the alpha level.

The anatomy of *Modulus* was first described by Risbec (1927), who dealt with *Modulus candidus* Petit, 1853 [= *M. tectum* (Gmelin, 1791)]. He placed the Modulidae between the Strombidae and Cerithiidae. Although Risbec (1927) noted the aphyallic condition of males, he did not adequately study the reproductive tract and neglected to describe the complex pallial gonoducts. His other anatomical observations are sketchy and sometimes erroneous. Abbott (1944) figured and described the external soft parts of

the head and foot of *Modulus modulus* and presented a few brief notes on its ecology.

To my knowledge, only two papers have considered the developmental biology of *Modulus*: Lebour (1945: 470–471) has described the spawn and larvae of *Modulus modulus*, and more recently Bandel (1976: 258–259) described and figured the spawn and larvae of *Modulus modulus* and *Modulus carchedonius* (Lamarck, 1822). Both of these descriptions are brief and the taxonomic identity of the species is questionable. This will be discussed in more detail later in this paper.

Mook (1977) is the only author to have written anything about the ecology of *Modulus*. His study was concerned with the role of *Modulus modulus* as a control of fouling organisms on marine angiosperm grasses and did not consider the ecology of *Modulus*.

To my knowledge, nothing more has been published about the biology of *Modulus* species, despite the fact that some species, such as *Modulus modulus*, commonly occur in great numbers and are easily collected and observed.

#### MATERIALS AND METHODS

*Modulus modulus* specimens were obtained from a large population in a seagrass bed north of Link Port on the west bank of the Indian River lagoon near Fort Pierce, Florida (27°32.1'N, 80°20.9'W). For a more detailed description of this site, see Young et al. (1976). The subtidal site consisted of dense stands of *Halodule wrightii* Ascherson and occasional beds of *Thalassia testudinum* König & Sims interspersed with sandy patches. Snails from this population were studied during January, February, May and September of 1978 and in January of 1979. Living animals were studied in the field and in sea water aquaria or petri dishes placed under a Wild M-5 stereo dissecting microscope. Animals were extracted from their shells and relaxed in a 7.5 percent solution of

MgCl<sub>2</sub>, and dissected in an anesthetized state. Carmine particles were used to determine ciliary tracts and a one percent Methylene Blue aqueous solution was used as a vital stain. Stomach contents and fecal pellets were studied under a compound microscope to determine the algae that were ingested. Animals were fixed in Bouin's fluid, embedded in paraffin, sectioned at 9.0 μm, and stained with Basic Fuchsin Picric Indigo Carmine for histological studies. Photomicrographs of sections were taken with a Zeiss photomicroscope-3. Spermatozoa were fixed in a 2.5 percent glutaraldehyde solution in 0.2 molar Mellonig's phosphate buffer and were brought up to 50 percent EtOH and air dried on cover slips prior to SEM studies. Spermatozoa, eggs and embryos were prepared for critical point drying by fixation in 2.5 percent glutaraldehyde in 0.2 molar Mellonig's phosphate buffer at pH 7.4. Material was rinsed in distilled water, dehydrated and the critical point drying was done with liquid CO<sub>2</sub>. Spermatozoa, spermatozoa, eggs, embryos, radulae and embryonic shells were studied with a Nova-Scan SEM. Observations on pairing, spawning and feeding were made in the field and in the lab. Eggs and embryos were maintained in culture dishes with daily sea water changes until hatching. Measurements of eggs and embryos were made with an ocular micrometer.

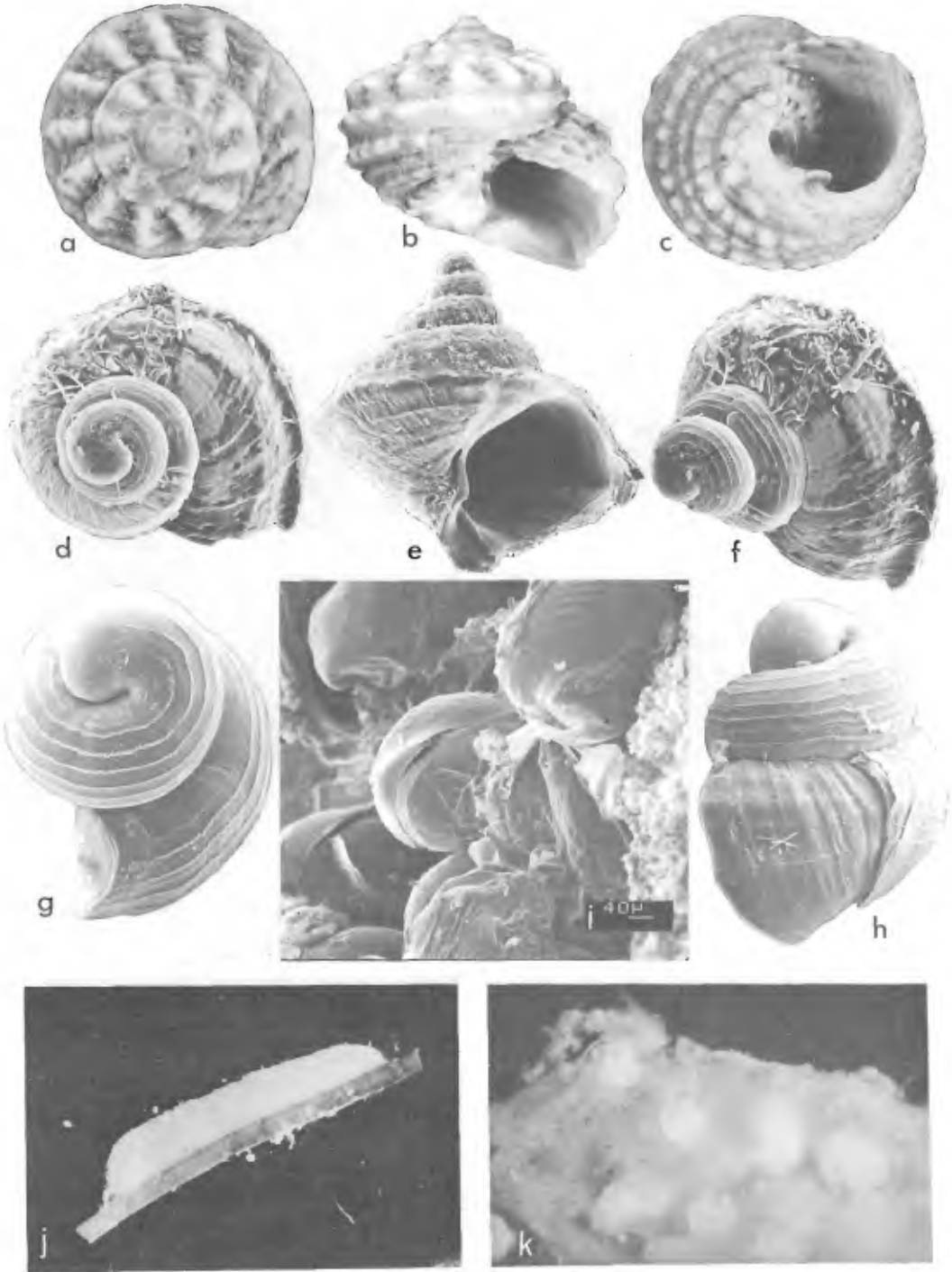
In addition to the above work, the anatomy of *Modulus tectum* (Gmelin, 1791) was studied at Suva, Fiji for comparison with that of *Modulus modulus*, but this work was only at a superficial level.

All measurements are relative to average sized snails (see Table 1).

#### ANATOMY

*Shell* (Fig. 1a–c).—The shell is top-shaped, umbilicate, wider than high, and consists of 5–6 strongly convex, angulate whorls of which the body whorl is disproportionately large.

FIG. 1. Shells, spawn mass and embryos of *Modulus modulus*; **a–c**, Apical, apertural and basal views of adult shell with typical sculpture; **d–f**, Apical, apertural and side view of young shell. Note sharp transition between sculpture of embryonic shell and that of teleoconch (1.5 mm wide); **g**, Newly hatched snail showing distinctive sculpture (0.5 mm long); **h**, Five day old snail showing sharp transition in sculpture between embryonic shell and new growth area of outer lip (0.8 mm long); **i**, Portion of spawn mass critical point dried and fractured to show hyaline capsule surrounding each embryo. Embryonic shell sculpture is visible beneath surface of each capsule; **j**, Typical spawn mass attached to grass blade (9 mm long); **k**, Portion of spawn mass with surface debris removed to display encapsulated embryos.



The spire is low and turbinate. The suture is slightly irregular and moderately impressed. The periphery of each whorl has a prominent spiral cord that forms a keel. Three to four weaker spiral cords are above the peripheral cord. Apical to the peripheral cord each whorl is sculptured with 12–13 axial ribs that form low, blunt nodules where they cross the spiral cords. The body whorl descends just before the aperture in adults and has 4–5 spiral cords on its base sculptured with numerous tiny nodules that are aligned to form weak axial riblets. In juvenile shells the body whorl is extremely angulate and keeled (Fig. 1d–f). The aperture is ovate and the columella deeply concave and terminated with a deep notch or chink that forms a tooth-like lamella. This notch accommodates the pallial tentacles of the inhalant siphon. The outer lip is moderately thin and strongly crenulate, each scallop fitting a pallial tentacle. The inner surface of the outer lip is reinforced with 5–6 spiral ridges. The umbilicus is small but deep and in adults is slightly covered by the columellar fold. The protoconch consists of two whorls that are convex but not angulate, and sculptured with 5–6 thin, spiral lirae except for the smooth nuclear tip. Basic shell color is a dirty white but is normally hidden by the periostracum and algal epiphytes. Brownish purple splotches occur on the spiral chords and adjacent to the suture of the body whorl. The columella is tinged with purple and the columellar notch has a purple spot. Average shell dimensions of the Link Port population were 8.31 mm in length and 9.24 mm in width (see Table 1). The operculum is thin, corneous, circular and multispiral with a central nucleus. It fits snugly into the aperture of the shell when the animal is retracted. The periostracum is thin, and tan.

*Animal: external features* (Fig. 2).—The base color of the head, neck and foot regions

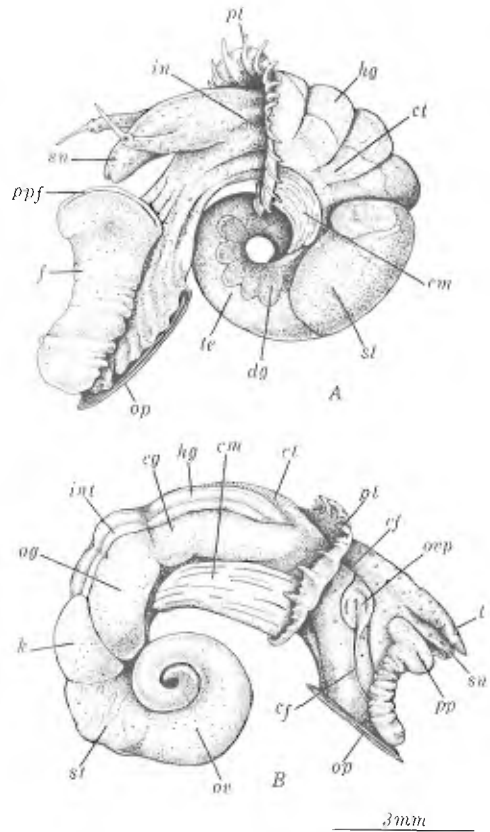


FIG. 2. A, *Modulus modulus*, male removed from shell and viewed from left side. B, Female removed from shell and seen from right side. ag, albumen gland; cf, ciliated furrow; cg, capsule gland; cm, columellar muscle; ct, ctenidium; dg, digestive gland; f, foot; hg, hypobranchial gland; in, inhalant siphon; int, intestine; k, kidney; mt, mantle tentacle; op, operculum; ov, ovary; ovp, ovipositor; pp, propodium; ppf, propodial furrow; pt, pallial tentacle; sn, snout; st, stomach; t, tentacle; te, testis.

TABLE 1. Analysis of shell dimensions (measurements in mm).

Statistic	No.	%	Length			Width		
			$\bar{x}$	Sd	Range	$\bar{x}$	Sd	Range
All shells	61	100	8.31	0.63	6.3–10.1	9.24	0.66	7.7–10.6
Males	27	44.26	8.24	0.78	6.3–10.1	9.09	0.67	7.7–10.6
Females	32	52.46	8.40	0.47	7.5–9.5	9.94	0.64	9.2–10.5
Parasitized	2	3.27	—	—	—	—	—	—

No., number of snails

Sd, standard deviation

$\bar{x}$ , mean

is pinkish-cream with dusky green and chalky white blotches, spotted with tiny red flecks. The white blotches are composed of fine white dots. Some yellow pigment occurs on the proximal portion of the dorsal surface of the neck and body. The base of the foot is more lightly pigmented. The overall appearance is a light green or mossy green color, as described by Abbott (1944: 3).

When fully extended the foot is slightly smaller than the diameter of the shell. The foot is shield-shaped and begins with a crescent-like propodium that has a deep glandular furrow (Fig. 2A, *ppf*) set off anteriorly with a pigmented band of alternating green and white bars and posteriorly with a thin, lightly pigmented area. This furrow is formed by an invagination of numerous, highly vacuolated, glandular cells. Although the muscles of the sole produce monotaxic retrograde waves, the animal moves by jerk-like contractions of the columellar muscle.

The head has a short, rounded, dorso-ventrally flattened snout with a bilobed tip bearing a longitudinal slit leading to the mouth (Fig. 1A, *sn*). The dorsal surface of the snout is dark brownish-green and the tip is bordered with alternating white and green blotches and randomly placed red dots. The ventral surface is pinkish. The snout can be extended considerably when the animal is seeking to right itself but is normally held in a retracted state, even while feeding.

The head has two thin tentacles (Fig. 1B, *t*), about 3 mm in length, in an average-sized animal. The tentacles and head are covered with tiny prominent white pustules. The proximal two thirds of each tentacle is thicker than the tip. When crawling, the tentacles are placed at 45 degrees to the snout and the thin tips are placed on the substratum where they probably serve a sensory function. The eyes are placed on the tentacles where they narrow, about two thirds the way from the base. Eyes are black and surrounded by a narrow circle of deep yellow pigment. There is a dark horizontal green band of pigment adjacent to each eye. Animals respond quickly to a shadow or sudden movement.

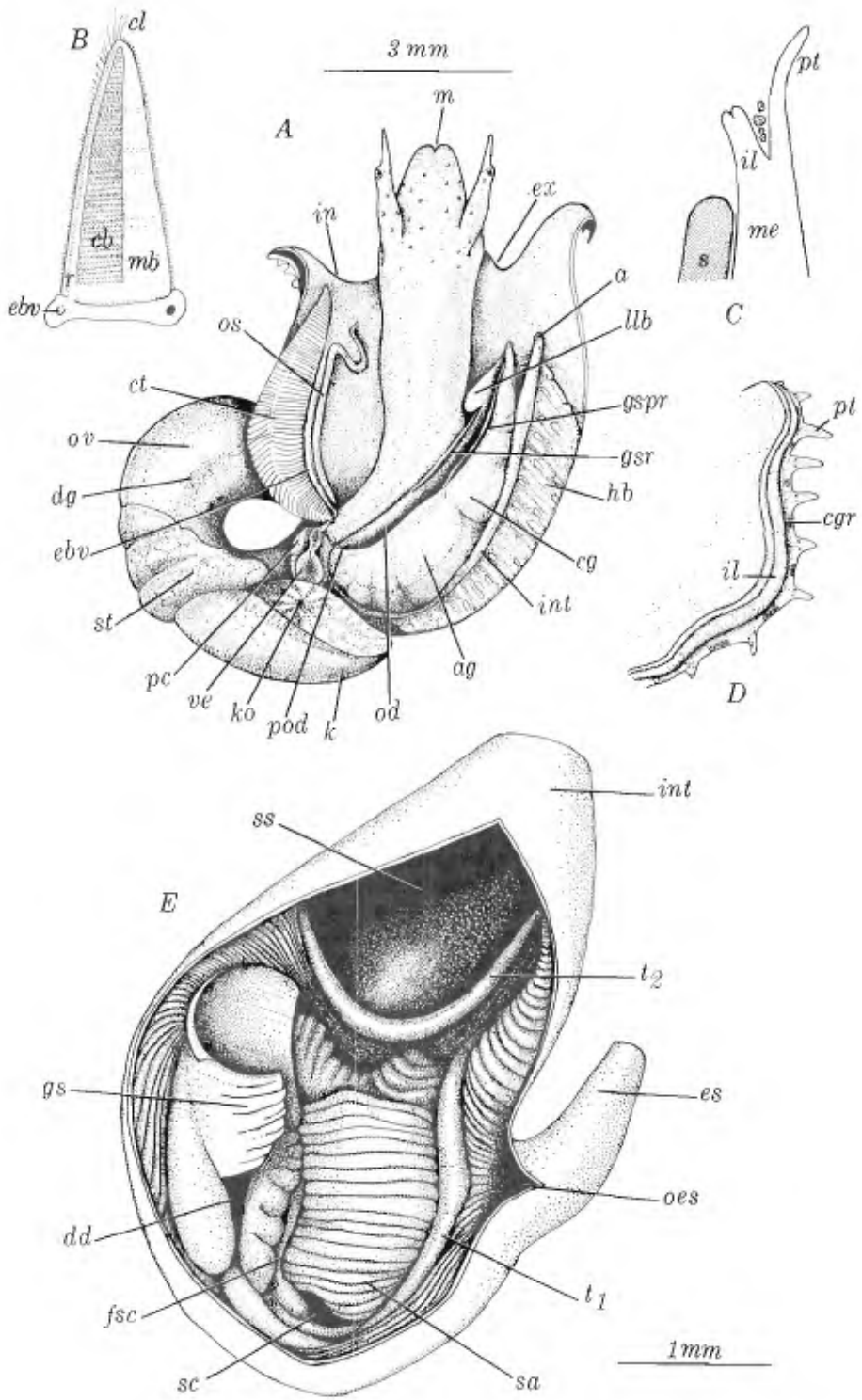
The dorsal half of the mantle edge is scalloped and fringed with about 20 thick, white pallial tentacles (Fig. 3D), each having two tiny pink dots on its medial ventral surface. Between each pallial tentacle is a dark green blotch. The mantle edge, as seen in cross section, is trilobed (Fig. 3C). There is a deep ciliated furrow between the lobes. This furrow

prevents foreign matter from getting between the shell and mantle by collecting debris which is then moved down the right side of the mantle edge and expelled by the exhalant siphon. The outer lobe, adjacent to the shell, is transparent, microscopically scalloped and has a slight groove at its tip. The inner edge bears the pallial tentacles and is brightly pigmented. The inhalant and exhalant siphonal portions of the mantle edge are thicker and slightly curved but have no distinguishing morphological characteristics. The ventral half of the mantle edge lacks the lobes and is smooth.

A ciliated furrow (Fig. 2B, *cf*) extends from the exhalant siphonal area down the right side of the foot. It carries fecal pellets and debris entwined in mucus away from the mantle cavity to the bottom of the right side of the foot where they move back under the unattached edge of the operculum and are cast off. The ciliated strip is not readily seen without the application of carmine particles. Marcus & Marcus (1964: 500) described a similar ciliated tract in *Cerithium atratum* (Born, 1778) and I have noted its presence in other cerithiid species. In females, this ciliated strip is a groove that also functions in transporting egg capsules from the distal pallial oviduct to the ovipositor (Fig. 2B, *ovp*) with which it is intimately associated. The ovipositor is a bulbous, swollen area that comprises a thickly furrowed flap under which lies a glandular area of vacuolated cells. It is located midway along the ciliated groove on the right side of the foot and has a distinctive darker color and unusual swollen appearance in ripe females. I did not observe the use of this organ during spawning; consequently, its exact function is unknown. Sections of the organ reveal numerous glandular cells and vesicular elements. Presumably, the ovipositor adds the outer jelly coat that surrounds the egg capsules formed in the pallial oviduct and assists in both the formation of the outer surface and attachment of a completed spawn mass.

Mean length of animals removed from their shells is about 9 mm in their natural coiled state and about 15 mm uncoiled. These mean values are the standards against which other anatomical measurements in this paper should be compared.

The mantle, as seen in snails extracted from shells, is bright orange and green. The portion covering the pallial gonoducts is whitish while that over the intestine and hypobranchial gland is brilliant green. The mantle



covering the ctenidium and osphradium is orange. The mantle cavity is 5–6 mm deep and is broadest at its distal end where the edge flairs up and backwards. The exhalant siphon is marked on the mantle surface by a prominent, rounded ridge that is thick, muscular and curved in a semicircle down towards the medial right part of the mantle edge.

The columellar muscle (Fig. 2B, *cm*) is broad and quite large (2.5 mm long; 3 mm wide) in relation to the animal. It is tightly attached for one complete whorl to the inner columella of the shell about one-half whorl's distance from the aperture. The columellar muscle is located at the ventral surface of the snail just behind and on the ventral mantle edge where it extends diagonally backwards in relation to the antero-posterior orientation of the mantle cavity. This muscle is powerful in *Modulus* and is used by the animal to retract into the shell and to produce quick jerky movements and violent twisting behavior that will be described in more detail later in this paper.

The whorls of the animal comprising the stomach, gonads and digestive gland taper off sharply and curl beneath the columellar muscle. The stomach (Figs. 2A,B, *st*) occupies about 1.5 whorls and is colored white, brown and green. The remaining two and a half to three whorls comprise the digestive gland and gonad. The digestive gland (Fig. 2A, *dg*) is chocolate brown and is almost entirely overlain by the gonad in ripe animals. The ovary (Fig. 2B, *ov*) is white and extends over the digestive gland in a branching network. The testis (Fig. 2A, *te*) is yellow-orange and covers most of the digestive gland. Since males are aphyllid, the pigmentation of the testis is an easy way to sex ripe individuals. Animals parasitized by trematodes frequently have their gonadal and lower alimentary

tracts filled with rediae, cercariae and sporocysts and have pinkish-colored gonads.

**Mantle cavity and associated organs** (Fig. 3).—At the lower left side of the mantle cavity is the brown-pigmented osphradium (Fig. 3A, *os*), a thin, ridge-like structure that is triangular in cross section and about 5 mm long and 0.35 mm wide. The osphradium begins at the proximal end of the mantle cavity and extends forward, adjacent to the ctenidium for about two-thirds of its length. As the osphradium nears the inhalant siphon it sharply turns to form an "S" shape and tapers to an end about 0.25 mm from the mantle edge. It is separated from the ctenidium by an orange-russet pigmented strip about 0.20 mm wide. Sections of the osphradium show a highly ciliated surface and numerous, darkly staining cells. At its base is a thick osphradial nerve that has connections with the left mantle nerve.

The ctenidium (Fig. 3A, *ct*) is relatively large, about 6 mm in length and 1.5 mm in width. It extends the length of the mantle cavity and comprises about 125 long finger-shaped, flattened filaments. Each filament is 1.5 mm long and 0.45 mm wide at its attached base and tapers toward the tip. Individual filaments are strengthened on the right side (edge) by an internal rod (Fig. 3B, *r*). A ciliated longitudinal band (Fig. 3B, *cb*) is on each side of the flattened surface of a filament, adjacent to the rod. The narrow edges of each filament are lined with cilia and exceptionally lengthy cilia are on the filament tip (Fig. 3B, *cl*). Thin transverse bands of muscles (Fig. 3B, *mb*) allow each filament to respond to the stimulus of a probe by quickly retracting and bending.

The hypobranchial gland (Fig. 3A, *hb*) lies to the right and next to the ctenidium. It is about 4.0 mm long and 1.0 mm wide and highly conspicuous because of its swollen, glandular state and bright russet-green color.

FIG. 3. Anatomical features of *Modulus modiolus*. A, Animal removed from shell and mantle cavity opened mid-dorsally. The kidney has been pulled back to expose the kidney opening and heart. B, Individual ctenidial filament. C, Cross section through mantle edge showing trilobed condition and ciliated groove containing debris. D, Dorsal view of mantle edge displaying ciliated groove and inner lobe. E, Stomach opened by dorsal longitudinal cut. Crystalline style has been removed. a, anus; ag, albumen gland; cb, ciliated band; cg, capsular gland; cgr, ciliated groove; cl, long cilia; ct, ctenidium; dg, digestive gland duct; dg, digestive gland; ebv, efferent branchial vessel; es, esophagus; ex, exhalant siphon; fsc, fold emerging from spiral caecum; gs, gastric shield; gspr, groove leading to spermatophore receptacle; gsr, groove leading to seminal receptacle; hb, hypobranchial gland; il, outer lobe of mantle edge; in, inhalant siphon; int, intestine; k, kidney; ko, kidney opening; lb, baffle of lateral lamina; m, mouth; mb, muscle band; me, mantle edge; od, pallial oviduct groove; oes, opening from esophagus to stomach; os, osphradium; ov, ovary; pc, pericardial sac; pod, proximal portion of pallial oviduct; pt, pallial tentacle; r, internal strengthening rod; s, shell; sa, sorting area; sc, reduced spiral caecum; ss, style sac; st, stomach; t<sub>1</sub>, typhlosole 1; t<sub>2</sub>, typhlosole 2; ve, ventricle.

Tapering at both ends, it begins at the proximal end of the mantle cavity and rapidly widens, extending longitudinally and ending behind the anus. The hypobranchial gland lies close to and slightly overlaps the intestine. It is covered externally with numerous tiny papillae and has a transversely ridged surface that is russet colored. Oval and goblet-shaped areas appear within the gland when viewed from the surface. If a snail is violently disturbed or if the hypobranchial gland is stimulated with a probe, it exudes copious strands of tiny, globular, mucus-like bodies. These are shot out in salvos from small openings in the surface of the gland until the mantle cavity is nearly filled with them. The exudate is rapidly moved by cilia and expelled by the exhalant siphon. The animal will continue to exude globular particles whenever stimulated until the gland is spent. The exudate is probably used defensively by the snail when under attack. The composition and nature of the exudate is unknown. I have not seen this phenomenon in other cerithiacean snails. Sections of the hypobranchial gland show numerous columnar, vesicular and darkly stained glandular cells at its surface. Beneath these are vesicle-like chambers that appear to store the hypobranchial exudate. No ducts leading from these chambers to the surface of the gland were seen.

The intestine (Fig. 3A, *int*) is 0.25 mm wide and usually dark colored due to many small, transversely oriented, ovoid fecal pellets that fill it. The pallial epithelium overlying the intestine is covered with tiny papillae that extend over it from the adjacent hypobranchial gland. The anus, borne on a large papilla, is about 2.5 mm from the mantle edge (Fig. 3A, *a*).

The pallial gonoducts are open in both males and females and males are aphyllic. The open condition of the gonoducts is best visualized as a slit tube that runs the length of the mantle cavity, consisting of inner and outer laminae. The male pallial gonoduct (Fig. 8A, *C*) is a thin-walled, glandular, open tube while the pallial oviduct of females (Fig. 8B) is a larger, white glandular organ comprising laminae with complex inner chambers and tiny ducts. The functional aspects of both male and female pallial gonoducts are discussed in detail later in this paper, in the section on the reproductive system.

At the proximal end of the mantle cavity lies the anterior wall of the pericardial sac (Fig. 3A, *pc*) and to its right is the kidney which has

a typical slit-like opening on its ventral surface (Fig. 3A, *ko*).

*Alimentary system* (Figs. 3A, 4, 5).—This system is typically mesogastropodan and is somewhat like that described by Fretter & Graham (1962: 25–32) for *Littorina*. The mouth lies at the tip of the snout but is usually recessed between the two lobes that comprise the snout apex. At the anterior end of the buccal cavity and inserted in its lateral walls are a pair of chitinous jaws (Fig. 4, *j*) composed of tiny rhomboidal plates. Dissection of the buccal apparatus reveals two large radular retractor muscles that arise from the walls of the anterior body cavity and insert on the postmedian surface of the buccal mass (Fig. 4, *lrm*, *rrm*).

The buccal mass (Fig. 4, *bm*) is about 1.65 mm long and 1.24 mm wide. The radular ribbon is 2.25 mm long and 0.35 mm wide, comprises about 68 rows of teeth, and is one-fourth the length of the shell (see Table 2). It is typically taenioglossate (2+1+1+1+2) and has a rounded, quadrate-shaped rachidian tooth (Fig. 5). The basal plate of the rachidian is smooth and has a long central projection and convex lateral sides. It is similar to that of *Cerithium* species and lacks the basal cusps that are seen on potamidid species such as *Batillaria*. The top of the rachidian tooth is markedly convex and has a cutting edge comprised of a large, pointed central denticle that is flanked on each side with 2–3 smaller pointed denticles that diminish in size laterally. The lateral tooth of the radula is trapezoidal in shape, and has a long lateral extension that curves down at its insertion point in the radular membrane. On the basal plate of the lateral tooth there is a long, blunt longitudinal extension. The top of the lateral tooth is straight and serrated with a small inner cusp, a second larger cusp and 3–4 smaller ones. The inner and outer marginal teeth are long, spatulate and serrated at their tips with 5–6 closely set, blunt denticles. The two marginal teeth are virtually identical, and thus differ from those of *Cerithium* species, which have distinguishable outer and inner marginal teeth. The radular sac begins ventral to the esophagus and coils in a spiral to the right. There are no esophageal pouches. A large spade-shaped esophageal valve is present.

The paired salivary glands (Fig. 4, *lsg*, *rsg*) are loosely compacted lobes, lying behind the buccal mass above and beside the anterior esophagus. The left is four-lobed, and twice as large as the right, and extends through the



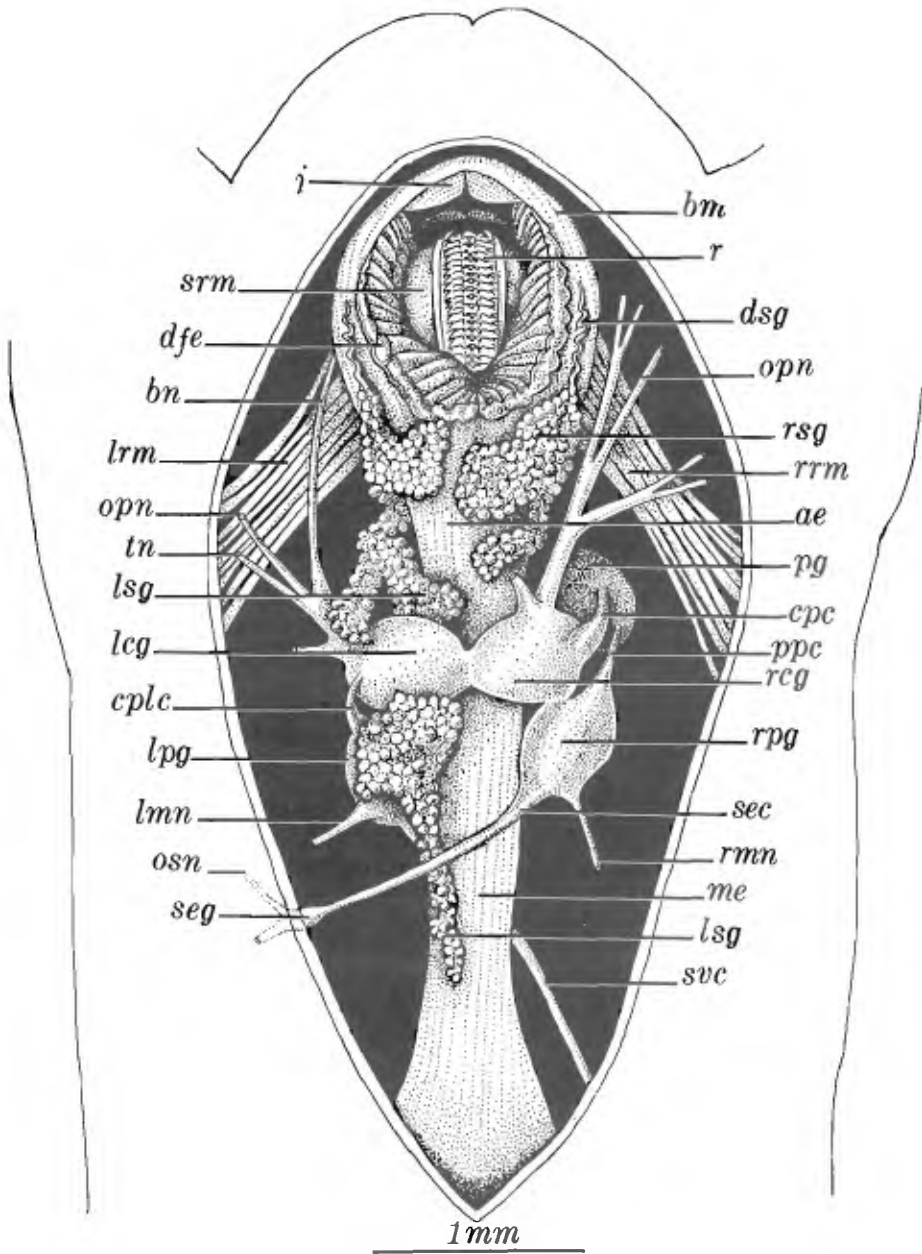


FIG. 4. Dissection of the head of *Modulus modulus* opened by a dorsal longitudinal cut exposing anterior alimentary tract. *ae*, anterior esophagus; *bm*, buccal mass; *bn*, buccal nerve; *cpc*, cerebral-pedal connective; *cplc*, cerebral-pleural connective; *dfe*, dorsal fold of esophagus; *dsg*, duct of right salivary gland; *j*, jaw; *lsg*, left salivary gland; *lmn*, left mantle nerve; *lpg*, left pleural ganglion; *lrm*, left radular retractor muscle; *lsg*, left salivary gland; *me*, mid-esophagus; *opn*, optic nerve; *osn*, osphradial nerve; *pg*, right pedal ganglion; *ppc*, pleural-pedal connective; *r*, radula; *rcg*, right cerebral ganglion; *rmn*, right mantle nerve; *rpg*, right pleural ganglion; *rrm*, right radular retractor muscle; *rsg*, right salivary gland; *sec*, supraesophageal connective; *seg*, supraesophageal ganglion; *svc*, subvisceral connective; *tn*, tentacle nerve.

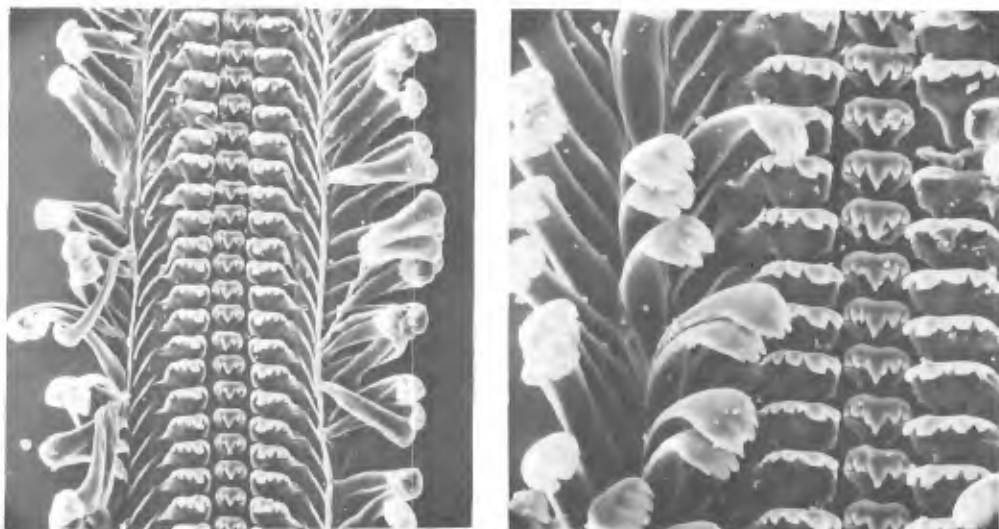


FIG. 5. Radula of *Modulus modulus*. Left, general view of radular ribbon; right, half row showing cusp arrangement on rachidian, lateral and marginal teeth. Rachidian tooth length = 0.06 mm.

TABLE 2. Statistical summary of radular and shell measurements.

Statistic	No.	$\bar{x}$	Sd	Range
Shell length	8	8.75	0.37	8.1– 9.2
Shell width	8	9.75	0.49	9.1–10.2
Radula length	8	2.21	0.17	2.0– 2.5
Rows of teeth	8	68.8	2.60	66 –73

No., number of snails  
Sd, standard deviation  
 $\bar{x}$ , mean

nerve ring a short way down the mid-esophagus. The right gland is three lobed, and lies wholly in front of the nerve ring. The ducts arise in front of the cerebral ganglia, and enter the buccal cavity at each side (Fig. 4, *dsg*).

The anterior esophagus has a pronounced dorsal food groove, and twists, due to torsion, at the cerebral ganglia; but the dorsal folds do not extend back ventrally as in *Littorina*. The dark-pigmented mid-esophagus can be seen through the dorsal body wall. It is enlarged into a well developed esophageal gland comprising numerous deep folds and diverticula, giving it a loosely compacted flocculent structure that easily falls apart under dissection. Beginning behind the nerve ring, it tapers rapidly, like the mid-esophagus itself towards the rear of the mantle region. The posterior esophagus is also dark-pigmented, and has 4–6 longitudinal ridges. It opens into the stomach shortly behind the mantle cavity.

The stomach (Fig. 3E) is about 4 mm long, occupies about two-thirds of a whorl, and is typically cerithioid in layout. Topographically, it is not unlike that depicted for *Turritella* by Graham (1938). It has a short, wide style sac and a well-formed crystalline style. If the stomach is opened by a dorsal longitudinal cut, the esophagus is seen to enter at its right anterior end. An opening to the digestive gland (Fig. 3E, *dd*) and what appears to be a much reduced spiral caecum (Fig. 3E, *sc*) are both near the esophageal opening. A broad sorting area (Fig. 3E, *sa*) is in the ventral portion of the stomach. A thick cuticular gastric shield (Fig. 3E, *gs*) lies to the left, directly across from the anterior opening of the intestine and style sac. The crystalline style is present in all freshly collected specimens and is a short, transparent dumb-bell shaped rod about 2.8 mm in length. The style sac (Fig. 3E, *ss*) from which it emerges, although joined to the intestine, is a separate structure with a blind end. The major typhlosole (Fig. 3E, *t<sub>1</sub>*) emerges from the intestinal groove and curves around to the spiral caecum. A small minor typhlosole (Fig. 3E, *t<sub>2</sub>*) runs from the sorting area into the intestine.

The intestine leaves the stomach at the left anterior end of the style sac region and coils back over the style sac before turning anteriorly where it enters the mantle cavity. The portion of the intestine that exits from the stomach has a large dorsal typhlosole that is

gradually lost as the intestine nears the mantle cavity where it has a smooth interior. It becomes ridged and more glandular in the mantle skirt.

**Reproductive system** (Fig. 8).—Open pallial gonoducts in both sexes, the lack of a penis in males and the formation of spermatophores by males are fundamental features of the reproductive system in *Modulus modulus*. The basic groundplan of the pallial gonoducts in *Modulus* is the same as in other cerithiaceans such as *Cerithium*, *Bittium*, *Rhinoclavis* and *Batillaria* but differs in the placement and arrangement of internal ducts and seminal receptacles in the laminae of the gonoduct. The pallial gonoduct is best visualized as a tube-like duct, extending from the proximal end of the mantle cavity to the mantle edge, and slit open along its longitudinal axis. In both sexes the pallial gonoduct comprises lateral (right) and medial (left) laminae that are fused dorsally to each other and to the lateral mantle wall. The ventral margins of the laminae are free and open to the mantle cavity. In *Modulus* both laminae have internal ducts and pouches used for the reception, transmission and storage of spermatophores and spermatozoa.

**Male reproductive tract** (Fig. 8).—In males the laminae of the gonoducts are white, thin-walled structures (Fig. 8). The medial (left) lamina is membranous and semi-opaque and its inner surface has numerous, transversely oriented ridges. Near the axis of attachment there are wider, denser and less numerous ridges. The lateral (right) lamina (Fig. 8A, *ll*) is fused along its axis to the mantle and partially on its left side to the epidermis of the visceral hump. It is opaque and thick and its inner surface has thick convoluted ridges. The male pallial gonoduct is slightly closed at its proximal end due to the medial lamina folding over the posterior portion of the lateral lamina (Fig. 8A, *pmg*). This creates a closed pouch filled with numerous glandular axial ridges. This area of the gonoduct is probably the prostate gland (Fig. 8C, *pg*). Distal to the closed portion of the gonoduct is a thicker longitudinal glandular ridge and several wide axial glandular folds that stain darkly with Methylene Blue. Adjacent to these folds are numerous smaller axial folds. This glandular area of the inner surface of the lateral lamina extends to the distal end of the gonoduct and is probably the spermatophore organ. Its exact mode of functioning is unknown. I have not seen a developing or a completed spermatophore in the

male gonoduct nor the method of transfer to the female, but it probably occurs via siphonal currents as I have described in *Cerithium muscarum* (Houbriek, 1973). In the aquarium I saw some spermatophores pass out the exhalant siphon of a male and fall to the bottom.

The bright orange testis lies on the outer dorsal surface of the digestive gland. The seminiferous tubules empty into a branching network of microscopic ducts that lead to about 10 vasa efferentia. These empty into the vas deferens that lies on the inside of the visceral coil and appears as a white duct that in ripe males is packed with eupyrene and apyrene sperm.

SEM preparations of spermatozoa reveal that a eupyrene spermatozoon (Fig. 6, *f*) is about 36  $\mu\text{m}$  in length, has a pointed acrosome, a short, cylindrical, thick head and constricted neck region, and a long midpiece about one-fifth the length of the spermatozoon. A long narrow flagellum follows the midpiece. Eupyrene spermatozoa taken from the vas deferens are attached by their acrosomes in small clusters.

Apyrene spermatozoa (Fig. 6a, *g*) are larger, about 48  $\mu\text{m}$  in length, bear six flagella, have a spiral configuration, and very long pointed heads almost one-half the length of a sperm. It is not clear if there is a midpiece; consequently, this long head region may consist of head and midpiece. Although no counts were made, there appears to be an equal number of both kinds of sperms, tangled together by the numerous flagella into dense masses. Thus the apyrene spermatozoa may serve to bind the mass together with their flagella. Apyrene sperm move in a slow sinuous manner while eupyrene sperm are fast moving.

The spermatophores of *Modulus* are immobile, thinly walled, acellular structures of 1–3 mm length. Fresh spermatophores are white, shiny, crescent-shaped and swollen with spermatozoa. One end is round and pointed and the other more flattened and bifurcate (Figs. 6, 7a–b). A prominent keel extends axially along one side of the spermatophore (Fig. 6a). The pointed end (Fig. 7c), when lodged in the female gonoduct, lies closest to its proximal end. If pressure is applied to a fresh spermatophore, sperm emerge from the lower branch of the bifurcated end, where there appears to be a tube-like exit (Fig. 7b). Equal numbers of eupyrene and apyrene spermatozoa are contained in the spermatophore.

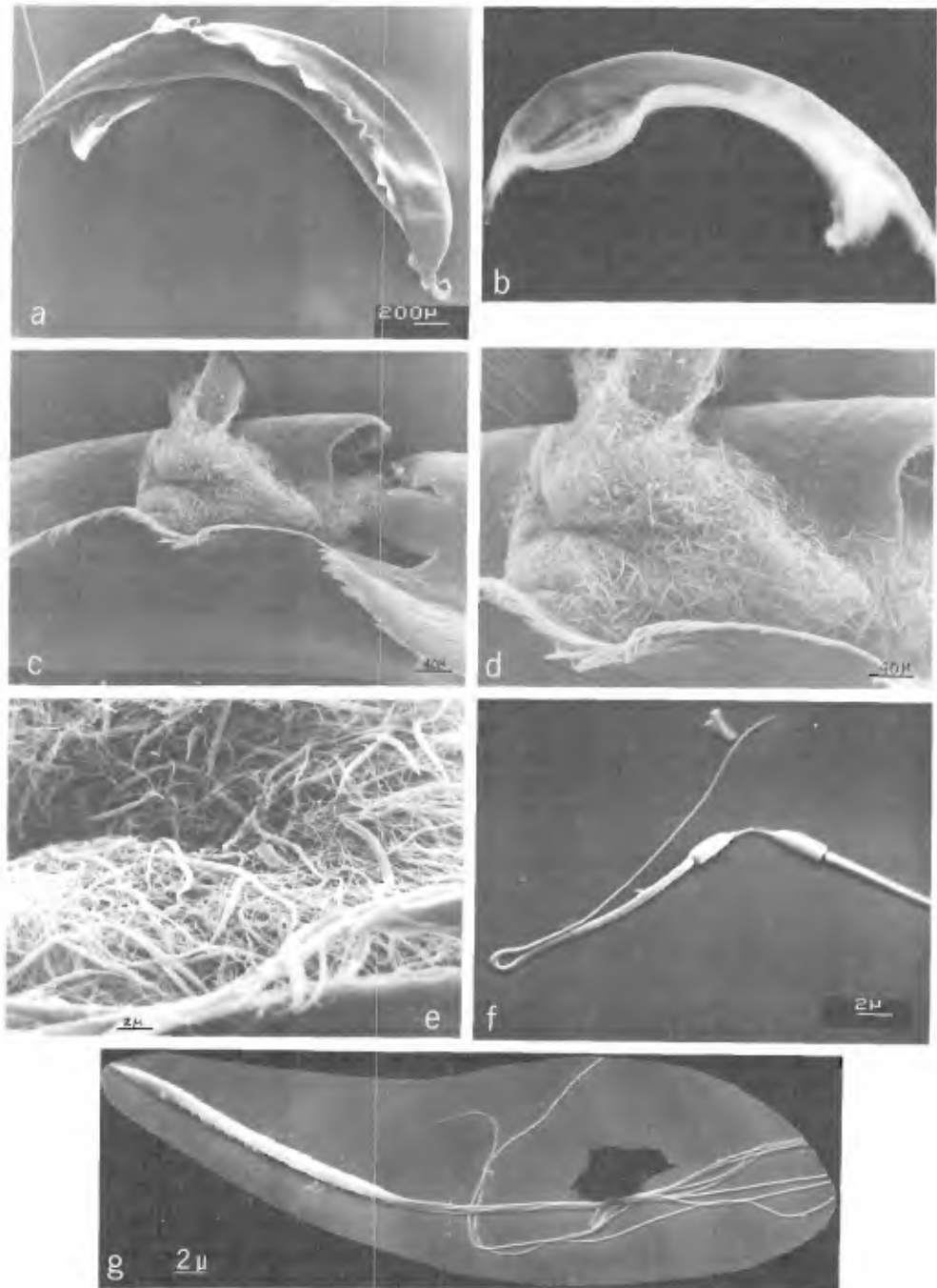


FIG. 6. Spermatophore and sperm of *Modulus modulus*. SEM micrographs; **a**, Spermatophore, critical point dried and partially collapsed. Note distinctive axial keel; **b**, Spent spermatophore, freshly extracted from spermatophore receptacle, showing remaining sperm at bifurcate end; **c-e**, Details of torn portion of critical point dried spermatophore (as seen in Fig. 6a) showing densely packed sperm; **f**, Eupyrene sperm attached by acrosomes and showing long mid portion; **g**, Apyrene sperm demonstrating multiflagellate condition and spiral configuration of mid head piece.

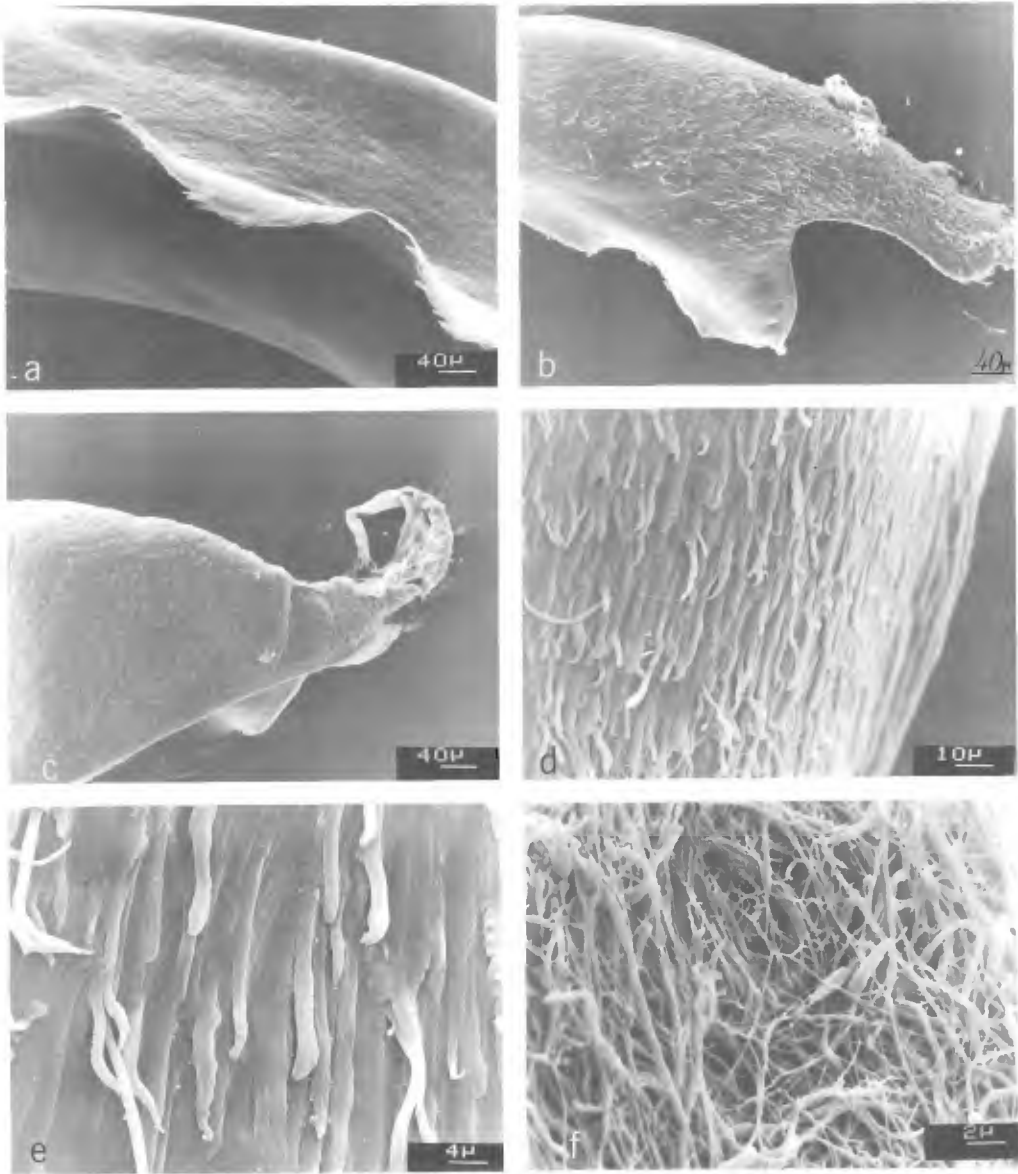


FIG. 7. Spermatophore of *Modulus modulus* showing details of keel (a), bifurcate end (b), round pointed end (c), and acellular fibrous matrix comprising surface structure (d-e); f, Eupyrene and apyrene sperm extracted from seminal receptacle of female.

SEM preparations of critical point dried spermatophores reveal a complex surface structure (Fig. 7a-e). Spermatophores are composed of long, axially oriented string-like fibers embedded in a matrix (Fig. 7d-e). At the pointed end the fibrous matrix is closely bound together and the external surface is relatively smooth. In the bifurcate part, the

ends of individual fibers are free, creating a shaggy appearance (Fig. 7b). The edge of the keel is serrated due to free fiber ends that point away from the pointed tip. SEM pictures of a fractured spermatophore wall show that it is about  $5\ \mu\text{m}$  thick and composed of three layers: an outer fibrous layer, a thick middle layer filled with spongy-looking globules of

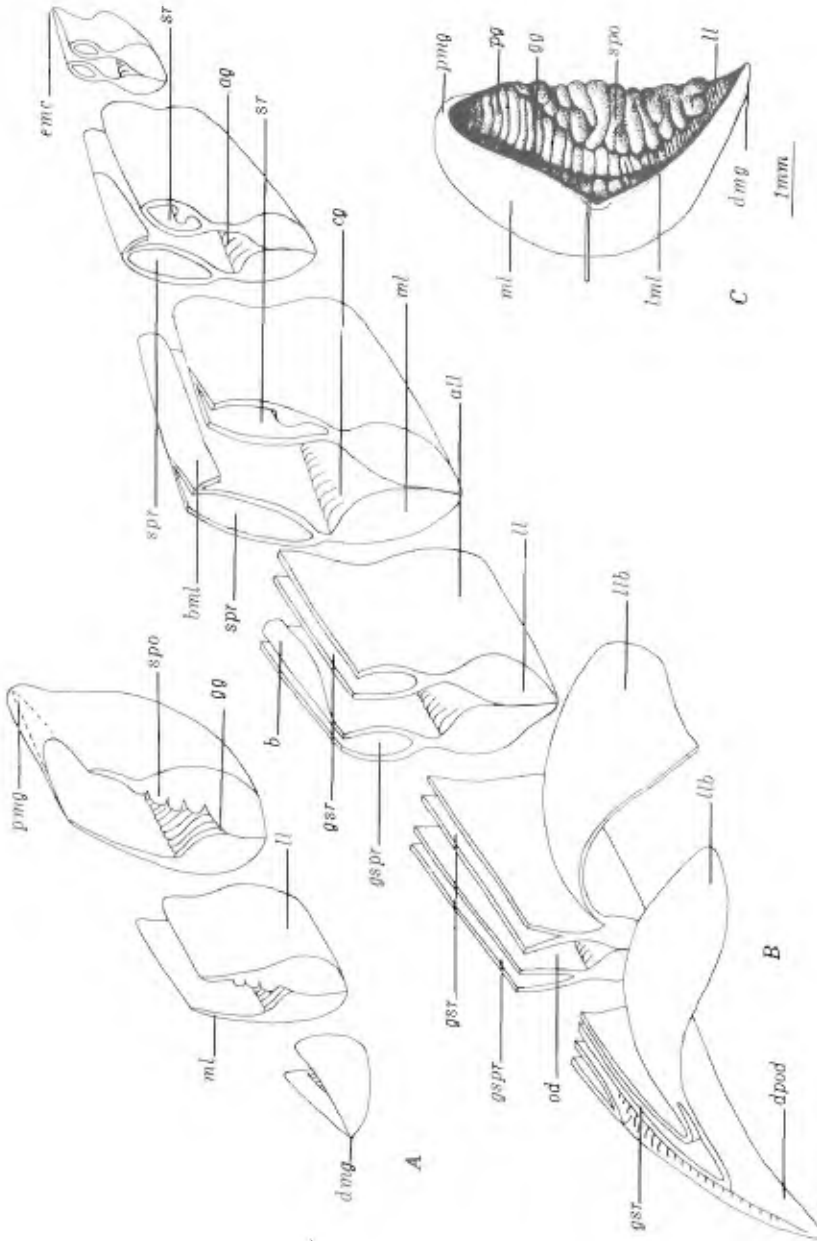


FIG. 8. Pallial gonoducts of *Modiolus modiolus*. A, Schematic representation of male pallial gonoduct viewed from left with columnellar muscle removed (compare with C). B, Schematic representation of female pallial oviduct viewed from left with columnellar muscle removed. C, Male pallial gonoduct with medial lamina pulled back exposing glandular interior (compare with A). *ag*, albumen gland; *all*, attached surface of lateral lamina; *bml*, baffle of medial lamina; *cg*, capsule gland; *dmg*, distal part of male pallial gonoduct; *dpod*, distal portion of female pallial oviduct; *emc*, end of mantle cavity; *gspr*, gonoduct groove; *gspr*, groove leading to spermatophore receptacle; *gsr*, groove leading to seminal receptacle; *ll*, lateral lamina; *llb*, baffle of lateral lamina; *ml*, lip of medial lamina; *od*, oviduct, main passage; *pg*, prostate gland; *pmg*, proximal part of male gonoduct; *spo*, spermatophore organ; *spr*, spermatophore receptacle; *sr*, seminal receptacle.

unknown composition, and a thin inner fibrous layer.

*Female reproductive tract* (Figs. 3, 8).—The pallial oviduct is an opaque, cream-colored organ about 5.5 mm long and differs from the male gonoduct by its larger size and longer, swollen laminae. The bases of the laminae stain darkly in sections and are highly glandular. The medial (left) lamina (Fig. 8B, *ml*) has a thick lower portion composed of transversely oriented glandular folds adjacent to the line of axial fusion to the mantle. There is a constriction in the medial lamina, about half-way to its outer edge, separating the lower swollen, glandular part from the upper, more membranous part. An open slit in the upper portion of the lamina begins at the distal end and becomes a ciliated gutter (Fig. 8B, *gspr*). The highly ciliated gutter gets deeper and becomes a large, closed, internally ciliated tube-like pouch occupying the proximal third of the medial lamina. Both the ciliated gutter and pouch comprise the spermatophore receptacle (Fig. 8B, *spr*) which is probably homologous to the "bursa copulatrix" or sperm-collecting pouch in *Cerithium* and *Rhinoclavis* (Houbrick, 1974a; 1978). Sections show that the inner walls of the receptacle consist of columnar epithelial cells with darker staining glandular cells.

Spermatophores are drawn by ciliary currents into the mantle and enter the spermatophore receptacle pointed end first. An individual spermatophore fills the entire length of the spermatophore receptacle, its bifurcated end sticking out at the distal end. Both the serrated edge of the spermatophore keel and the minute free fibrous ends of its surface help to anchor it in the receptacle. An individual spermatophore receptacle normally holds one spermatophore but occasionally two may be found.

Sperm emerge from the lower, bifurcate end of the spermatophore and move into another ciliated groove formed by a fold arising from a baffle on the middle part of the free edge of the medial lamina. This forms a long, deep, highly ciliated slit with an open edge facing and slightly overhanging the free edge of the lateral lamina. Sperm leaving the spermatophore are probably transferred by this ciliated groove to the ciliated gutter (Fig. 8B, *gsr*) of the lateral lamina leading to the seminal receptacle in the upper portion of the lateral lamina (Fig. 8B, *sr*). Spermatophores slowly dissolve within the spermatophore receptacle and may be recovered in various stages of disintegration.

The lateral lamina (Fig. 8B) has the same layout as the medial lamina: i.e., a thick glandular, attached axial base separated from the upper membranous, free part of the lamina by an axial constriction. The upper membranous part of the lateral lamina also has the same groundplan as the membranous part of the medial lamina, but is mostly fused to the columellar muscle. Not far from the distal end of the lateral lamina, an open slit develops into a long ciliated gutter (Fig. 8B, *gsr*), that proximally becomes a closed pouch. This pouch is the seminal receptacle (Fig. 8B, *sr*) and is distended with sperm during the reproductive season, when its inner walls are glandular and villous.

The morphology of the gutter and seminal receptacle of the upper lateral lamina is complicated by an involution and doubling back of the upper lateral, membranous wall of the ciliated gutter. This involution in the wall of the gutter assumes the form of a large flap of tissue (Fig. 8B), covering the top of the open slit and gutter at the upper part of the distal third of the gonoduct. The flap probably serves as a baffle which may prevent spermatophores from entering the seminal receptacle instead of the spermatophore receptacle. It may also guide released sperm into the seminal receptacle.

The thick, lower, inner portions of both laminae form the albumen gland and the capsule gland. The albumen gland (Fig. 8B, *ag*) is located in the proximal part of the axial base of the oviduct. The capsule gland (Fig. 8B, *cg*) is a loosely compacted darkly staining area located in the middle portion of the lateral lamina.

The pale green ovary consists of numerous, tiny, compact lobes. A thin-walled ovarian duct, about 0.4 mm wide, extends from the ovary and runs forward along the ventral side of the viscera where it passes under part of the kidney and lies adjacent to the intestine and pericardial cavity before entering the mantle cavity. Oocytes from the ovarian duct are about 0.15 mm in diameter.

*Nervous system* (Fig. 4).—The nervous system is similar to that of *Cerithium* and *Rhinoclavis* and is typically cerithioid. It is not as highly condensed as in other mesogastropods such as the rissoaceans. If one uses the "RPG" ratio of Davis et al. (1976: 263) (length of the pleurosupraesophageal connective divided by the sum of the lengths of the right pleural ganglion) to determine the state of condensation, a mean value of 0.59 is obtained which is a little above an intermediate

TABLE 3. The RPG ratio for *Modulus modulus*. This ratio is the length of the pleuro-esophageal connective divided by the sum of the lengths of the supra-esophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion.

No.	$\bar{x}$	Sd	Range
7	0.59	5.21	0.54-0.70

No., number of snails  
Sd, standard deviation  
 $\bar{x}$ , mean

value (Table 3). As Davis pointed out, the higher the value the "looser" and more primitive is the nervous system. Distinctive characters are the lightly pigmented cerebral, pleural and pedal ganglia which are covered with tiny dots of tan color. The origin of the tentacular nerve is also lightly pigmented and is slightly swollen. The cerebral ganglia are moderately fused to the pleural ganglia and have virtually no connectives (Fig. 4, *rcg*, *rpg*, *lpg*, *lpg*). The cerebral-pedal connective is also short, about 0.25 mm long. The pedal ganglia are large, about 0.50 mm in length and deeply embedded in the muscle of the foot. The cerebral ganglia are of equal size (0.50 mm) and joined by a very short commissure. The pleural ganglia are slightly smaller, each about 0.40 mm long. A schematic representation of the ganglia and their relationship to other organs of the head are shown in Fig. 4.

*Circulatory and excretory systems.*—There is nothing particularly distinctive about either of these systems in *Modulus*. Both kidney and heart are typically monotocardian and not unlike those of *Littorina*, described in detail by Fretter & Graham (1962: 34-35). It is noteworthy that the anterior aorta is very wide as it passes over the mid-esophagus.

## REPRODUCTIVE BIOLOGY

The percentages of males and of females and statistics relevant to their shell measurements are presented in Table 1. Females are more numerous than males. Gametes have been described in detail in the sections on the reproductive tract. Most reproductive activity takes place from late winter through spring (February through May).

*Pairing.*—Males become ripe in mid-winter and produce spermatophores from January through May. Females begin spawning in the spring. In May, pairing of males and females

is frequent. The male's foot is attached to the female's shell so that the two edges of their mantle cavities are adjacent. Spermatophores leave the mantle cavity of males by the exhalant siphon and presumably enter the female's mantle cavity via her inhalant siphon because males lack a penis or other organ of intromission. Not all spermatophores are successfully introduced: some drop to the bottom of the aquarium. The same phenomenon was seen in *Cerithium muscarum* (Houbrick, 1973) and may be due to artificial lab conditions. Spermatophores in the female's mantle cavity are moved by ciliary currents over the head-foot into the open ciliated gutter and spermatophore receptacle in the medial lamina of the pallial oviduct. The flap on the distal part of the lateral lamina and the second ciliated gutter of the medial lamina overhanging the lateral lamina probably prevent premature entry of the spermatophore into the seminal receptacle.

*Spawn.*—Deposition of spawn was first seen in May, although spawning may have occurred in March and April when I was away from the study site. Spawn is deposited on grassy blades of marine angiosperms, such as *Halodule*, in worm-like gelatinous tubes about 14.10 mm in length, and 2.13 mm in width (Fig. 1j-k). Each spawn mass contains an average of 121 eggs. Within the gelatinous tubes fertilized eggs are enclosed in hyaline capsules of 0.50 mm diameter, each capsule containing a single egg, 0.15 mm in diameter (Fig. 1i, k). Although a few eggs contain teratological embryos, there are no nurse eggs. Table 4 presents more statistics about egg masses.

Individual spawn masses are cylindrical except for a narrow, flattened surface at the point of attachment to a grass blade. They are axially attached to grass blades (Fig. 1j) but occasionally curve or have a spiral configuration. The tough parchment-like outer wall of a spawn mass is frequently covered with fine sand grains and detrital particles, making it

TABLE 4. Statistical summary of spawn mass dimensions and of embryos per spawn mass.

Statistic (n = 8)	$\bar{x}$	Sd	Range
Length (mm)	14.1	5.05	9.3- 24.2
Width (mm)	2.13	0.26	1.8- 2.5
No. of embryos	121	43.33	70 -169

$\bar{x}$ , mean  
Sd, standard deviation



somewhat opaque. Internally, a spawn mass is viscous and comprises a matrix of spiral, gelatinous strands that contain tear-shaped, jelly-filled compartments each of which holds an egg capsule. In cross section, the entire spawn mass appears to be two gelatinous strands thick. There is no internal cavity evident.

Spawn masses are deposited in vast numbers in the grass beds at Link Port. There is an average of 360 spawn masses, comprising 43,560 embryos, per square meter of grass bed.

*Development.*—Only a brief descriptive account of the developmental process is presented below because a more detailed study was beyond the scope of this research.

Development of *Modulus modulus* is direct. Each spawn mass contains capsules with embryos in various stages of development. That portion of the spawn first deposited by the female has more advanced embryos than the latter part, which may contain capsules having embryos in early cleavage stages. Thus, within a single spawn mass one may find fertilized eggs, early cleavage stages, blastula and gastrula stages and early veliger embryos, progressively arranged from one end to the other. Fertilized eggs and early cleavage stages are the same pale green color as eggs that emerge from the oviduct. Freshly laid spawn may be easily identified by the pale green embryos whereas older spawn masses lack this color. Embryos become light tan when they attain the mid-veliger stage.

To study development, newly deposited spawn masses, laid on the evening of May 9, 1978 were placed in petri dishes with sea water and the growth of embryos from the first portion of each spawn mass was monitored until they hatched from their capsules.

Early cleavage stages are about one-fourth the diameter of the egg capsule. As embryos develop into blastulas and gastrulas they become larger and continue to grow throughout the veliger and hatching stages until the embryonic shell occupies the entire capsule (Fig. 1j). Capsule diameter remains constant throughout all developmental stages.

Cleavage is rapid; the 8-cell stage was attained within 3 hours after deposition. Blastula and gastrula stages were attained on May 10 and May 11. By May 12, a shell gland and prototroch were present, indicating the beginning of the veliger stage. On May 15 early veliger stage embryos with cap-like protoconchs, ornamented with the beginnings of a

distinctive spiral sculpture, were present. A large, yolky digestive "anlage" was also present as well as the early pedal structure. Although early velar lobes were present, no stomodaeum was seen. Embryos at this stage begin to spin within their capsules. On May 16 the start of the second whorl of the protoconch was noted and two large, darkly pigmented statocysts appeared at the base of the head-foot region. By May 17, velar lobes were well-developed, tiny black eyespots, small cephalic tentacles and a stomodaeum appeared, and spinning of embryos was more rapid. On May 18 the foot was better defined and the protoconch comprised two whorls. No operculum was seen. The pale green color, so indicative of earlier embryonic stages, began to fade and was completely gone by May 19 when embryos were a light tan color. Spinning of embryonic veligers, due to ciliary beat of the velum and foot, was more rapid but sharp jerky movements began and sometimes individuals would periodically stop and resume spinning in a reverse direction. On May 19 the foot was further enlarged and an operculum was present. The larval heart could be seen pulsating within the mantle cavity. The external morphology of embryos remained the same for the next five days, but internal development was obscured by their opaque color. By May 24 the late veliger stage was attained and embryos almost filled their capsules. Statocysts were no longer visible, cephalic tentacles were large and the eyes enlarged. Embryos frequently stopped spinning as they probed the capsule wall. Velar lobes began to disappear, and the embryos began to look like tiny snails. Hatching of juveniles began on May 27 and continued through June 2 until the spawn mass was empty. Five other monitored spawn masses underwent similar development within the same time.

Incubation of embryos lasts from 18–24 days. In general the Link Port population takes about 2.5 to 3.5 weeks to undergo direct development.

*Hatching.*—Young snails escape as the capsule wall splits and breaks apart due to pressure from the foot and snout of the encapsulated snail. Young snails do not leave the interior of the spawn by any definite route or exit but escape randomly. As they emerge from their capsules they crawl about the interstices of the spawn mass which becomes more viscous and begins to slowly disintegrate. After hatching, young snails graze on

detritus of the outer wall of the spawn mass and gradually move off onto grass blades. In May, thousands of juvenile snails, from 0.5–1.8 mm in diameter were observed in the grass beds (Fig. 1g–h). Although obviously of different size classes due to different hatching times and the long spawning period, these young snails may be considered to form one large group of young. Newly hatched snails quickly twist and turn as they explore the environment. Young snails each have large black eyes, a typical radula and a long tactile propodium that bears a heavily ciliated groove along its anterior margin.

*Growth.*—New growth of the protoconch occurs rapidly. Within a few days, a change in sculpture separates the embryonic shell from the new shell growth (Fig. 1h). This is marked by axial shell sculpture that lacks the spiral elements of the protoconch. The aperture becomes angulate and flaring due to the appearance of the median keel that is so indicative of adult shells.

By mid June young snails have added a much larger whorl sculptured with spiral cords and a prominent median keel and have shells that range from 1.3–2 mm in diameter. The outer lip is sharply angulate and the distinctive columellar notch of adults is present (Fig. 1d–f).

Observations were not made during the mid-summer months, but in September young *Modulus* were abundant in the grass beds. No living adults were found but numerous adult shells occupied by hermit crabs were seen. Adolescent *Modulus*, 2–5 mm in size, were covered with thick filamentous green algae and were difficult to detect in the grass beds. Shells were thick and had typical adult sculpture except for their outer lips which were thin due to recent growth. Animals had adult pigmentation and the internal anatomy appeared normal except for the incipient pallial gonoducts. The ctenidium was slightly smaller and comprised only 80 filaments. The pleuro-esophageal connective was slightly longer than in adults; consequently, the RPG ratio of adolescent snails is higher, about 0.70. This indicates a looser concentration of the nerve ring. The ganglia probably become more condensed as they grow larger.

By December, snails have nearly reached adult size and males are ripe. Females become ripe in January. The pallial oviducts are developed but ovaries are just beginning to ripen. By spring (late February–early March) *Modulus* is reproductively mature and the

shell has reached its maximum size. Adults appear to die after spawning, when many empty adult shells may be found.

A summary of these data and other observations indicate that the Link Port population of *Modulus modiolus* has a life cycle of one year. Although the spawning period is long and results in various cohorts of young, these overlap to form one large group that develops during spring and grows quickly throughout the year, reaching maturity in late winter–early spring, when spawning occurs. Developmental stages occur throughout the spring with the subsequent emergence of the new progeny and death of adults.

These conclusions are supported by examination of large monthly samples of benthic animals taken from other sites in the Indian River during the Indian River Study conducted by the Harbor Branch Consortium in 1973–1974 (see Young et al., 1974). Growth stages of *Modulus* from these samples fit the general pattern given above. It thus appears that populations of *Modulus* from other areas of the Indian River estuary have a similar life cycle that lasts about one year.

## ECOLOGY

*Modulus modiolus* is one of the more common prosobranchs associated with marine grassbeds in Florida and the Caribbean. As an abundant primary consumer it is an important factor in the trophic structure of this ecotope. It is thus surprising that so little was known about its anatomy and ecology.

*General observations.*—A thorough study of the autecology of *Modulus* was not attempted; nevertheless, some ecological observations made during this study will provide information for future workers.

The study site consisted of dense stands of *Halodule wrightii* Ascherson, and two other less common angiosperm grasses, *Syringodium filiformis* Knetz and *Thalassia testudinum* König & Sims, all covered with dense epiphytic growth which traps detritus. The entire site is rich with detritus, and the water is frequently turbid with suspended particulate matter. The salinity in this habitat, normally 33‰, undergoes considerable variation sometimes within a short period of time due to heavy rainfall.

*Modulus* occurs on the grass blades and occasionally on the substratum. The population studied lives at a depth of about one

TABLE 5. Epiphytic algae growing on shells of *Modulus modulus* (\* = dominant).

Phaeophyta	* <i>Sphacelaria furcigera</i> Kützing
Cyanophyta	<i>Microcoleus lyngbyaceus</i> (Kützing) Crouan <i>Callothrix crustacea</i> Thuret
Rhodophyta	<i>Goniotrichum alsidii</i> (Zanardini) Howe
Chlorophyta	<i>Enteromorpha linguleta</i> J. Agardh <i>Cladophora</i> sp.

meter and is never exposed, even at extreme low tides.

Shells of living *Modulus* are normally densely covered with algal epiphytes. A list of these is given in Table 5. The dominant epiphyte is *Sphacelaria furcigera* Kützing. It is noteworthy that this alga does not grow on the sea grasses whereas all of the other epiphytes on *Modulus* occur also on the grasses.

Living *Modulus* snails frequently have an unidentified colonial hydroid growing on the bases and peripheries of their shells. The slipper shell, *Crepidula fornicata* (Linnaeus) may also occur on the base of the shell and barnacles occasionally are found on the shell top.

Empty shells are common and are frequently utilized by the hermit crab *Pagurus bonairensis* Schmitt and the sipunculid *Phascolion cryptus* Hendrix.

**Food and feeding.**—*Modulus modulus* is an active browser that engulfs microphytic algae and detrital particles. Like other microphagous, style-bearing mesogastropods it feeds more or less constantly. Mook (1977: 136) presented evidence that the grazing action of *Modulus* may retard the accumulation of fouling organisms by dislodging their newly settled larvae. *Modulus* thus aids in keeping the surfaces of seagrass blades clear and available as a substratum for microphytic algae.

Stomach contents of freshly-collected specimens contained sand grains, occasional foraminifer tests, numerous diatoms, algae, detrital particles, and fragments of larger filamentous macro-algae. The bulk of the algal contents comprises diatoms and of these, the dominant species is *Melosira moniliformis*, a relatively large diatom. An analysis and identification of stomach contents is presented in Table 6. Fecal pellet analysis shows that detrital particles, sand,

complete diatoms, and diatom fragments pass through the gut. The most common unbroken diatoms in fecal pellets were *Nitzschia* and *Navicula* species. The evidence of stomach, gut and fecal pellet contents leaves no doubt that *Modulus* ingests primarily diatoms. Analysis of the dominant diatoms suggests that larger diatoms are preferred to smaller ones. Although ingested food is not necessarily what is digested by the snail, it is probable that diatoms are the chief source of energy. Gut contents of very young *Modulus* had no appreciable diatom content. This indicates that the young are feeding on different plant food.

**Associations and predators.**—The most common prosobranchs co-existing with *Modulus modulus* on seagrasses are *Cerithium muscarum* Say and *Bittium varium* (Pfeiffer), both cerithiaceans and also style-bearing, algal-detritus feeders. Several other common snails found on the seagrass are the carnivores *Mitrella lunata* (Say) and *Haminoea elegans* (Gray).

The blue crab, *Callinectes sapidus* Rathbun was the only predator observed feeding on *Modulus* and many shells with chipped apertures point to heavy crab predation. Very few drilled shells of *Modulus* were found, suggesting that predation by naticid snails is insignificant. This is not surprising because *Modulus* is generally found on the grass blades and not as frequently on the substrate. Large rays were frequently seen in the grass beds and these along with other fish such as the sheepshead, *Archosargus probatocephalus* Walbaum, are suspected as chief predators. The numerous young snails observed in the spring are thin-shelled and small and are probably eaten by a variety of predators.

**Behavior.**—*Modulus* is a slow-crawling grazer and does not demonstrate a wide variety of behavior. It moves with retrograde, monotaxic muscular waves and sudden jerky motions. Although its normal habitat is on the blades of seagrass it will move down onto the substratum when weather conditions cause estuary waters to be rough.

When irritated or attacked, *Modulus* strongly twists itself, turning its shell back and forth with the columellar muscle, as if to dislodge a predator. If the irritation continues, the hypobranchial gland exudes a mass of sticky particles that probably discourages predators. The animal will then withdraw completely into its shell, about 5 mm beyond the edge of the

TABLE 6. Analysis of algal stomach contents of *Modulus modulus*.

Taxon	Mean size (M)		Form	Jan.	Feb.	May
	Diameter	Height				
Class BACILLARIOPHYCEAE						
Order Centrales						
Suborder COSCINODISCINEAE						
Family MELOSIRACEAE						
<i>Melosira moniliformis</i> O. F. Müller	24.4	26.9	chains	*	+	-
<i>Melosira sulcata</i> Ehrenberg	19.5	17.1	chains	-	+	-
Order PENNALES						
Suborder ARAPHIDINEAE						
Family FRAGILARIACEA						
<i>Synedra</i> sp. (fragments only)	16.1		chains	+	+	-
<i>Striatella unipunctata</i> Agardh (fragments only)	56.1	68.3	chains	-	+	*
<i>Rhabdonema</i> sp.	9.8	44.0	chains	+	-	-
Suborder BIRAPHIDINEAE						
Family NITZSCHICEAE						
<i>Nitzschia</i> sp.	5.2	61	solitary	-	+	+
Family NAVICULACEA						
<i>Mastogloia crucicula</i> (Grunow) Cleve	14.22	10	solitary	+	-	-
<i>Mastogloia</i> sp.	11.5		solitary	+	-	-
<i>Navicula</i> sp.	25.3		solitary	-	-	+
Family SURIRELLANCEAE						
<i>Camplyodiscus</i> sp.	95		solitary	-	-	+

\*Dominant species

+Present

-Absent

outer lip, until the operculum snugly fills the aperture.

*Modulus* reacts violently with the same twisting movements when it is exposed to secretions given off by other wounded *Modulus* snails, and will move rapidly away. This behavior has been documented in other marine and freshwater snails by Snyder (1967; 1971).

## DISCUSSION

A consideration of the interrelationships of higher taxa is contingent upon the amount and quality of comparative data available. Many familial definitions are based only on shell characters and there are few comprehensive anatomical studies upon which to rely. I have used the anatomical data I found available for cerithiaceans, although this was

frequently incomplete and/or contradictory. Thus my conclusions, while based on anatomical evidence, are tentative and partially speculative.

On the basis of anatomy, I believe that the Modulidae should be regarded as a distinct family within the Cerithiacea. On balance, *Modulus* species share more anatomical characters in common with members of this superfamily than with any other group. They appear to be closest to the Cerithiidae and Potamididae. My reasons for these conclusions are developed in the following discussion.

*Phylogenetic relationships.*—*Modulus* species differ conchologically from other cerithiaceans by their turbinata shape and umbilical notch. The family is a small one (one genus and about 6 species) in comparison with other cerithiacean families such as the Cerithiidae, Potamididae, Dialidae, Turritel-

laidae and Vermetidae, all comprising numerous genera and species.

Risbec (1927: 17) believed that the family Modulidae was intermediate between the Cerithiidae and Strombidae and cited a number of characters that he said were shared with each group. His remark that both cerithiid and *Modulus* species have short anterior siphons is incorrect: two genera of cerithiids, e.g. *Rhinoclavis* and *Pseudovertagus*, are characterized by long siphonal canals (Houbrick, 1978). Risbec (1927) also erroneously reported that *Modulus* and the cerithiids lacked salivary glands. As I have demonstrated in this paper and others (Houbrick, 1974a, 1978) both *Modulus* and all cerithiids heretofore studied have salivary glands. Bright (1958: 135) has reported salivary glands in a potamidid, *Cerithidea*, and I have observed them in *Batillaria*. I do not agree with Risbec's (1927) opinion that *Modulus* has close affinities with the Strombidae. While his observation that the anterior position of the eyes on the tentacles of *Modulus* is shared with the strombs is correct, his citation of a crystalline style as a unique shared character is incorrect because a style is characteristic of most algal-detrital feeders in the Mesogastropoda. He was apparently unaware that many cerithiaceans have styles. Risbec's (1927) citation of an osphradium with indistinct lamellae as a shared character between the Modulidae and Strombidae is accurate, but among the Cerithiinae, the Potamididae also have a similar osphradium (personal observation). The similarity of the radula between *Modulus* and *Strombus* species is superficial: any similarity is probably due to convergence of generalized taenioglossate radulae adapted for feeding on epiphytic algae and detritus. The reproductive tract of *Modulus* is very different from that of *Strombus*. The open condition of the pallial gonoducts in both sexes and a lack of a penis in males are conservative cerithiacean characters not seen in the Strombidae.

Although comparison may be made between the sudden jerk-like motions of a crawling *Modulus* and those of *Strombus*, the movement of the former is more like that of other cerithiids, only more pronounced, and is in no way similar to the jumping motions of *Strombus*.

Aside from the turbate shape of the shell, *Modulus* also has some distinctive anatomical features. Among these are short, stout pallial tentacles that reach extreme development in *M. tectum*. Pallial tentacles are also

present in cerithiid genera such as *Cerithium*, *Rhinoclavis*, *Pseudovertagus*, *Clypeomorus* and *Bittium*, but in relation to the animals' body they are never of the same size as are those of *Modulus*. Another distinctive feature of the external anatomy is the forward position of the eyes on the tentacles. In the Cerithiidae, Potamididae, Turritellidae and Vermetidae, the eyes are located at the bases of the cephalic tentacles. Although the Strombidae are similar to the Modulidae in regard to eye placement, this does not necessarily indicate close relationship, as noted before.

An unusual feature of the mantle cavity in *Modulus modiolus* is the large and highly glandular hypobranchial gland. The ability of this gland to exude salvos of sticky mucoid particles and discharge them via the exhalant siphon is, to my knowledge, unrecorded for other cerithiaceans. I assume that this behavior, coupled with quick twisting movements of the body, is a deterrent to predators. Although the hypobranchial gland of *M. tectum* is not exactly the same, the identical twisting behavior was noted. Another noteworthy feature of the mantle cavity of *Modulus* is the sinuously twisted distal portion of the osphradium that ends near the entrance of the inhalant siphon. The osphradium is a ridge-shaped structure much like the osphradium seen in the members of the Potamididae, while in species of the Cerithiidae, it is bipectinate.

The placement of the salivary glands and their ducts anterior to the cerebral commissure is a noteworthy feature of *Modulus*. The salivary ducts do not appear to pass through the nerve ring, but sections show that they begin very close to it. Although this arrangement is unlike that of many monotocardians, it is shared by the cerithiid genera *Cerithium*, *Rhinoclavis*, *Pseudovertagus* and *Clypeomorus* (personal observation) and has been described by Davis et al. (1976: 276) in members of the rissoacean families Assimineidae, Truncatellidae, Bithyniidae and Hydrobiidae. In *Modulus*, the passage of a portion of the left salivary gland through the nerve ring and partially behind the cerebral commissure, shows that the Modulidae stand in an intermediate position among the Mesogastropoda in regard to this trait. Some *Cerithium* species also have a similar arrangement of the left salivary gland. Bright (1958: 134) found that the salivary glands and ducts of the potamidid, *Cerithidea californica* (Haldeman, 1840) were located behind the nerve ring next to the "crop" (esophageal gland). He noted that the

left gland was the largest and that the salivary ducts were highly convoluted and partially embedded in the connective tissue of the "preesophagus" (anterior esophagus). It is not clear from his statement that the ducts pass through the nerve ring but his figure indicates this is the case. Thus, while most mesogastropods have their salivary glands located behind the cerebral commissure they lie anteriorly in some rissoaceans and have an intermediate position in the Modulidae and in many Cerithiidae. This supports Davis' (1976: 276) position that location of salivary glands and their ducts is a poor character to differentiate mesogastropods from stenoglossan neogastropods.

The combination of a well-developed esophageal gland and a crystalline style in *Modulus*, although thought to be unusual in mesogastropods (Fretter & Graham, 1962: 220), is a common condition shared with cerithiids I have examined in the genera *Cerithium*, *Rhinoclavis*, *Pseudovertagus* and *Clypeomorus*. Sections of this large gland in *Modulus* clearly show numerous and deep glandular lateral outpouchings arising from the mid-esophagus, leaving no doubt about its function.

The nervous system of *Modulus* differs from that of *Cerithium* or *Rhinoclavis* in lacking a large siphonal ganglion, but this may be due to the short siphon of *Modulus*. It is interesting to compare the RPG ratio of *Modulus* with that of other marine mesogastropods. Davis et al. (1976: 267) presented a table of RPG ratios which compared selected hydrobiid, rissoid and littorinid taxa. As mentioned previously, the higher the value of the RPG ratio the less concentrated are the ganglia of the nerve ring and presumably the more prim-

itive the nervous system. In Table 7, I compare the ratios of selected cerithiaceous taxa. The mean value for *Modulus* is the same as in *Cerithium*, 0.59, but both of these taxa have lower values than the potamidid, *Batillaria minima*, which has a value of 0.77, closer to the littorinid value.

*Modulus* has one of the more complex pallial oviduct systems found in the Cerithiacea. The open pallial gonoducts of some Cerithiacea have been surveyed by Johansson (1953; 1956), Fretter (1951), Fretter & Graham (1962: 625) and Houbrick (1971; 1974a, 1977, 1978). Although all of the species studied have a basic groundplan of open pallial gonoducts, those of *Bittium* and *Cerithiopsis* are very complex in organization. However, the allocation of *Cerithiopsis* within the Cerithiacea is uncertain. The layout of the pallial gonoducts of *Modulus* are even more complex and unusual. While one can interpret the pallial gonoducts of the Cerithiacea from a functional viewpoint, it is difficult to relate these open systems to each other in a comparative systematic manner. As Johansson (1953: 8) pointed out, pallial gonoducts sometimes differ considerably, even in closely related species. This has been seen in several rissoaceans (Johansson, 1953) and I have found many differences in the arrangement of the sperm gutter, bursa copulatrix and seminal receptacle in different species of *Cerithium*, *Clypeomorus* and *Rhinoclavis*. Too little is known of the arrangement of the gonoducts in other members of the Cerithiacea to discuss their comparative anatomy satisfactorily; moreover, the epithelial origin of pallial gonoducts renders any homologies suspect. Thus, any attempt to decide what is a primitive or derived state would be premature and purely speculative. Nevertheless the unique groundplan of the pallial gonoducts of *Modulus* clearly separates the Modulidae from other cerithiaceous families and is a reliable discriminating character.

I have observed spermatophores in other cerithiid members of the genera *Cerithium*, *Rhinoclavis*, and *Gourmya* and suspect that this method of sperm transfer is characteristic of the group. Spermatophores have also been described by Dazo (1965) in the freshwater cerithiaceous *Goniobasis*. The spermatophore of *Modulus* has a more complex surface structure and shape than those I have seen in the cerithiid species. The general physiognomy of the sperm of *Modulus* and in particular the elongate midpiece of the eupyrene

TABLE 7. The RPG ratio for selected cerithiid, modulid and potamidid taxa. (This ratio is the length of the pleuro-esophageal connective divided by the sum of the lengths of the supraesophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion).

Taxon	RPG
Cerithiacea	
Cerithiidae	
<i>Cerithium lutosum</i> Menke	0.59
<i>Cerithium atratum</i> (Born)	0.59
Modulidae	
<i>Modulus modulus</i> (Linnaeus)	0.59
Potamididae	
<i>Batillaria minima</i> (Gmelin)	0.77

spermatozoon, are comparable to those described for other cerithiids, e.g. *Cerithium* (Tuzet, 1930; Houbrick, 1973), *Bittium* and *Cerithiopsis* (Fretter & Graham, 1962).

*Interspecific comparisons.*—Aside from the observations presented in this paper and those recorded on the anatomy of *Modulus tectum* by Risbec (1927) (cited as *Modulus candidus* Petit), nothing is known of the anatomy or ecology of other *Modulus* species. I was able to study *Modulus tectum* in Fiji and offer the following observations for comparison with *M. modulus*. *Modulus tectum* differs from *M. modulus* by living on hard substrates in coral reef habitats. It is a much larger snail and not abundant. *Modulus tectum* clamps tightly on dead coral rubble when disturbed and is dislodged with difficulty. It has a transparent operculum through which may be seen the foot, brightly colored with large orange spots and irregular white blotches on a black pigmented background. These bright colors and the eye-like spots may startle predators who are able to remove snails from the rocks. Males are smaller than females and both sexes have highly colored soft parts. The snout is dark brown and spotted with white while the tentacles are reddish and papillate. The eyes are located near the distal ends of each tentacle, as in *M. modulus*. The foot is reddish brown and covered with whitish blotches and small brown dots. A large propodial furrow is present. The foot is much broader than in *M. modulus* and serves to keep the animal tightly clamped to the substrate. The mantle edge has long pinnate or multi-branched papillae in contrast to the simpler mantle papillae of *M. modulus*. The hypobranchial gland is smaller than that of *M. modulus*. When irritated, *M. tectum* does not emit salvos of sticky mucoid particles as does *M. modulus*. *Modulus tectum*, however, makes the same violent twists as *M. modulus* when irritated, but the former also clamps down on the substratum to discourage predators.

The thick, open pallial oviduct of *Modulus tectum* is highly glandular and the outer lamina is internally more convoluted with glandular folds than that of *M. modulus*. The male pallial gonoduct has a large yellow glandular area located on the inner lamina adjacent to the columellar muscle. This may be homologous to the structure seen in *M. modulus* and is probably a spermatophore-forming organ. Females of *M. tectum* have a large ovipositor on the mid right side of the foot that is identical

to that I have described in *M. modulus*. Within the buccal cavity of *M. tectum*, lying anterior to the nerve ring, are paired salivary glands with ducts that empty into the anterior esophagus. The radula is very much like that of *M. modulus*. Behind the nerve ring the esophagus rapidly widens and a large, wide, chocolate-colored esophageal gland is present.

The large black kidney is covered with a network of fine white branch-like blood vessels. The testis is light green and a large vas efferens runs from the testis to the pallial gonoduct along the inside of the whorls. In females the ovary is dark green and filled with large green ova that suggest direct development may take place. Green ova were also seen in *M. modulus*.

*Reproductive biology.*—Spawn masses of *Modulus modulus* are deposited at Link Port at the same time as those of *Cerithium muscarum*. Both species are abundant on seagrasses, undergo direct development, and their spawn is somewhat similar. Thus, spawn masses of both species may be confused and future workers should be alerted to this fact. They can be easily separated with careful examination. The spawn of *Modulus* is deposited along the axis of a seagrass blade as a cylindrical tube with smooth outer walls and resembles a caterpillar, whereas that of *Cerithium muscarum* is a more irregular, disk-like mass with a lumpy outer surface. I have figured the spawn of *Cerithium muscarum* elsewhere (Houbrick, 1973: 880; 1974a: 78). The embryos and young snails of the two species are also different. *Cerithium* embryos do not have the pale green color of *Modulus* embryos during their earlier stages of development. The embryonic shells and protoconchs of newly hatched *Cerithium muscarum* are characterized by the purple color of the outer lip and umbilical region. The aperture is oval while in *Modulus* it is more angulate. Finally, the embryonic shell and protoconch of *Cerithium muscarum* lack the spiral striae so characteristic of *Modulus*.

The reproductive mode of the Link Port population of *Modulus modulus* is direct. It is interesting to note that Lebour (1945: 470–471), in Bermuda, and Bandel (1976: 258) in Santa Marta, Colombia, each observed indirect development in *Modulus modulus*. These observations are contrary to what I have seen and present a discrepancy for which there are several possible explanations: 1) Both Lebour (1945) and Bandel (1976) were mistaken about the identity of their specimens; 2) What

has been called *Modulus modulus* in the stenohaline environments of Bermuda and the Caribbean is a separate species; 3) *Modulus modulus* has two developmental modes.

The first explanation is unlikely because *Modulus carchedonius*, which has planktonic larvae, has not been recorded from Bermuda and Bandel (1976) described the spawn of both species of *Modulus* at Santa Marta.

The second explanation, while possible, does not seem to be likely. Although considerable variation in shell sculpture occurs between populations of *Modulus modulus*, there are intergrades between the various morphs indicating that there is but a single species. Abbott (1944: 4) believed that these differences were within the normal range of variation and regarded them as one species. I have examined the extensive collections at the National Museum of Natural History and concur with him. I have examined the anatomy and radulae of the Caribbean forms and find no differences.

I believe that the third explanation is the most probable, and that *Modulus modulus* has a reproductive strategy comprising two developmental modes, direct and indirect. These modes are correlated with euryhaline and stenohaline environments, respectively. The utilization of direct development by estuarine populations such as those at Link Port may provide better protection against sudden changes in salinity or exposure and thus enhance the maintenance and survival of the embryos. Although not a common phenomenon, there are seven documented cases of a single species having both direct and indirect developmental modes. These have been reviewed by Robertson (1974: 227). Intraspecific variation of developmental modes has also been recorded among other invertebrates such as echinoderms and polychaetes.

*Modulus carchedonius* is the only other species for which eggs and larvae have been described. This species has free-swimming planktonic larvae. The spawn masses of this species differ from those of *M. modulus* by having an inner cavity formed by the outer walls of the egg mass. The spawn masses of *M. carchedonius* contain many more embryos (7,000) that hatch in 5–6 days as free swimming veligers (Bandel, 1976: 259–260, fig. 12, a, b).

The populations of *Modulus modulus* that Lebour (1945) and Bandel (1976) observed had smaller and more numerous eggs, and a

short incubation period of 5–7 days prior to hatching, typical of indirect development. In these populations the egg capsules dissolved and the veligers swam into the hollow center of the spawn mass and then to the outside. Spawn masses of the Link Port population did not have hollow centers. The longer developmental time of the Link Port population is similar to those I have observed in *Cerithium lutosum* and *C. muscarum*, euryhaline species which also have direct development (Houbrick, 1973, 1974b).

The developmental mode of *Modulus modulus* is much like those of *Cerithium muscarum* Say and *Cerithium lutosum* Menke (Houbrick, 1973). The veliger stage of *Modulus modulus* was reached in five days, about the same rate observed in *C. muscarum*, and the total incubation period of the former (2–3 weeks) is likewise similar to those of the *Cerithium* species cited above. *Cerithium muscarum* shares many of the reproductive and developmental patterns seen in *Modulus modulus* such as open pallial gonoducts, spermatophores, dimorphic sperm, spawn masses and direct development. Moreover, both species are abundant and occur together in the same habitat. This is probably explained by a common reproductive anatomy imposed by similar phyletic origin as well as convergence due to similar ecology.

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