EGG CAPSULES OF PROSOBRANCH MOLLUSKS FROM SOUTH FLORIDA AND THE BAHAMAS AND NOTES ON SPAWNING IN THE LABORATORY[1]

CHARLES N. D'ASARO[2]

University of Miami, Rosenstiel School of Marine and Atmospheric Sciences

ABSTRACT

The egg masses and capsules are described and illustrated for 18 species of prosobranchs, including *Cerithium auricoma*, *C. literatum*, *Strombus gallus*, *Cypraea spurca acicularis*, *Murex florifer*, *M. pomum*, *Thais rustica*, *Cantharus tinctus*, *Leucozonia nassa*, *Fasciolaria tulipa*, *Pleuroploca gigantea*, *Vasum muricatum*, *Xancus angulatus*, *Oliva sayana*, *Mitra nodulosa*, *Prunum apicinum*, *Conus spurius atlanticus*, and *C. regius*. Data are presented on capsular dimensions, enumerations of the embryos and capsules, and the developmental pattern. The known range of the breeding season is given, as well as some information on methods for handling spawning adults in the laboratory.

INTRODUCTION

Gastropod mollusks, especially prosobranchs, are among the most conspicuous and easy to collect shallow-water marine organisms and have been a favorite subject of study for centuries. The egg capsules or oothecae of this group provide abundant, useful material for the experimental embryologists, as shown by the work of A. C. Clement, E. G. Conklin, T. H. Morgan, and others. Studies on reproduction and life histories have other implications as well. In most countries, a variety of gastropods are acceptable as food and are even reared for this purpose. Herbivorous marine species, like *Strombus gigas*, are ideal for rearing after metamorphosis because of their large size, rapid growth, limited motility, and habit of feeding on unexploited algal populations. The only obstacles encountered concern breeding habits and the rearing of planktonic larvae. Considerable success was achieved by Dr. Takeo Imai (personal communication) in the culture of abalone, including *Haliotis discus*, and by D'Asaro (1965) in rearing the early stages of the queen conch, *Strombus gigas*. A relatively complete understanding of the breeding habits and larval development is necessary to properly develop and improve a fishery to the point at which it becomes husbandry. Of the species whose egg masses are described here, only *Xancus angulatus* is used for human consumption with any regularity. However, data included here on the breeding habits of *Cerithium*, *Fasciolaria*, *Murex*, *Strombus*, and *Thais*

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[2] Present address: Faculty of Biology, University of West Florida, Pensacola, Florida 32504.

TABLE 1

A SUMMARY OF DATA ON THE SPAWN OF PROSOBRANCHS FROM SOUTH FLORIDA AND THE BAHAMAS
(dd, direct development; pv, planktotrophic veliger)

	Average No. capsules/ mass	Average No. eggs/ capsule, at hatching	Average No. eggs/ mass	Capsular dimensions H–W–T (mm)	Type of development
Cerithium auricoma	90,000 (1)	1	90,000	0.112 (diameter)	pv
Cerithium literatum	85,000	1	85,000	0.123 (diameter)	pv
Strombus gallus	80,000	1	80,000	0.170 (diameter)	pv
Cypraea spurca acicularis	215 (2)	1100	236,000	2.6–1.6–1.0	pv
Murex florifer	34 (1)	5	170	6.0–5.0–3.0	dd
Murex pomum	750	13	9700	7.5–6.0–2.5	dd
Thais rustica	38	400	15,000	6.5–1.3–1.0	pv
Cantharus (= *Pollia*) *tinctus*	14	8	112	3.0–4.0–3.3	dd
Leucozonia nassa	50	11	605	7.5–4.5–3.0	dd
Fasciolaria tulipa	71	14	1000	18.0–13.5–6.2	dd
Pleuroploca gigantea	125	54	6800	35.0–18.5–7.0	dd
Vasum muricatum	3 (1)	165	335	14.0–28.0–3.0	dd
Xancus angulatus	10 (1)	4	33	30.0–40.0–10.0	dd
Oliva sayana	1	24	24	0.550 (diameter)	pv
Mitra nodulosa	103	100	10,300	2.3–1.2–0.8	pv
Prunum apicinum	1	1	1	0.69–0.51–0.28	dd
Conus spurius atlanticus	65	59	3800	12.0–8.0–3.5	pv
Conus regius	37 (1)	—	—	16.5–11.5–3.0	pv

are definitely complementary, because many members of these genera are acceptable as food. Additional supplementary data on the numerous subtropical or tropical species are necessary because, as pointed out by Anderson (1960), most life-history studies on prosobranchs are concerned with north temperate species. This paper is intended to provide comparative information on breeding habits, the initiation of spawning in the laboratory, identification of egg capsules, and the type of development of species occurring in the subtropical or tropical habitats of south Florida and the western Bahamas.

METHODS

Unless otherwise noted, all adult animals were held in 60-liter aquaria with running sea water. Egg capsules were preserved in 10 per cent seawater formalin to maintain their shape. Separate specimens were placed in

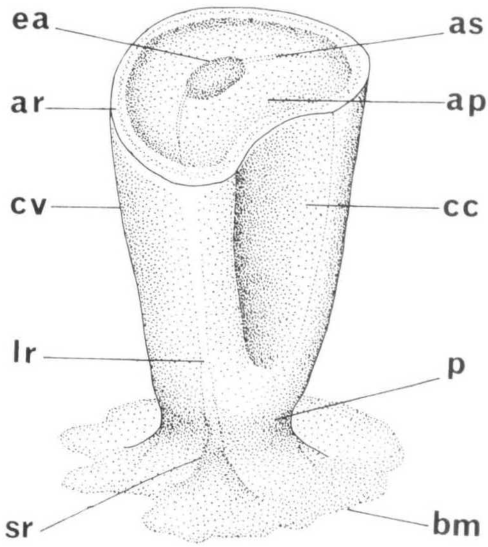

FIGURE 1. A generalized, vasiform egg capsule labelled to show the terminology employed. ap, apical plate; ar, apical ridge; as, apical suture; bm, basal membrane; cc, concave side; cv, convex side; ea, escape aperture; lr, lateral ridge; p, peduncle; sr, supporting rib.

70 per cent alcohol to prevent erosion of the protoconchs. Illustrations were prepared by the author and Miss Barbara Stolen from camera lucida drawings of fixed material. The photographs were taken by Mr. Robert Feigenbaum and Dr. Jerald Halpern.

Terminology used in the descriptions is based on the generalized egg capsule shown in Figure 1. The dimensions used are defined by the following criteria. Height is the distance from the apex to the basal membrane, width is the distance between the lateral edges at the widest point, and thickness extends from the convex side to the concave side at the widest point. Other measurements are defined in the text. The systematic arrangement is based on that used by Abbott (1954). A summary of the data is provided in Table 1.

Cerithium auricoma Schwengel

Fig. 2, A

Cerithium auricoma is a rare tropical species from coral reef habitats, in particular, patch reefs. Adult specimens were collected on Margot Fish Shoal, just east of Elliot Key, Florida. A female from this collection spawned shortly after capture in July 1965. Hard substrates were used for attachment of long rows of randomly coiled egg filaments.

Known cerithiid spawn, like that of *C. ferrugineum* (Lebour, 1945) or *C. morus* (Natarajan, 1958), has a filamentous construction closely resembling that of the spawn of *C. auricoma* and *C. literatum.* The opaque, white filaments of *C. auricoma* are composed of a rough limiting membrane surrounding a gelatinous matrix. The closely packed, round capsules, which have poorly defined walls and which contain a single embryo each, are embedded in the matrix (Fig. 2, A). Sand and detritus are sparsely attached to the limiting membrane. There is a narrow basal membrane running along one edge of the filament, which provides reinforcement and attaches the coils to each other and the substrate. The average dimensions of the filament are: diameter, 0.38 mm; and length, 1.5 m. There are about 60 capsules per mm of filament. The average diameter of the capsules is 0.112 mm. Approximately 90,000 embryos, a conservative estimate at best, were contained in the only available egg mass. Development is indirect, with a planktotrophic veliger stage.

Cerithium literatum Born

Fig. 2, B

This cerithiid is a very common tropical species which probably spawns throughout the year. Egg masses were collected from January through August 1965, on and under rocks at Soldier Key, Key Largo, and Pigeon Key, Florida. *Cerithium literatum* can be kept in spawning condition in the laboratory for periods of 10 months or more (January through October). Since this species is an herbivore, it must be supplied with a variety of fine filamentous algae and periphyton. Oviposition in the laboratory conveniently takes place on the glass walls of the aquaria. During the spawning process, the animals are often paired. There is no pattern in the gross coiling of the egg mass.

Spawn from *C. literatum* is typical of the cerithiids as a group. The transparent filaments are composed of a very resilient, external limiting membrane surrounding a thick, gelatinous matrix in which the ovate egg capsules are embedded (Fig. 2, B). One or more uneven, broken, fibrous ridges extend lengthwise on the membrane. Each transparent capsule is separated from the others and holds a single embryo. As the filament is extruded by the female, the foot is moved from side to side in uneven, one-millimeter arcs, folding the filament back and forth on itself, to form the structure visible to the unaided eye. The uneven loops may be partially or completely fused serially by a poorly defined, basal membrane. The average dimensions of the filament are: diameter, 0.46 mm; length, 1.3 m. Each capsule at its widest point has an average diameter of 0.133 mm. There are about 64 capsules per mm of filament. Due to the coiling, it is exceedingly difficult to measure accurately the total length. However, an estimate of 85,000 embryos in an average mass can be made. Development is indirect, with a planktotrophic veliger stage.

Strombus gallus Linné

Fig. 2, C

A pair of adult individuals of *S. gallus* were collected on the flats east of North Bimini, Bahamas, during November 1967. This pair was maintained by Mr. Robert Work in a fiber glass–lined, wooden tank (1.2 m × 1.2 m × 0.2 m) with running sea water and several centimeters of sand on the bottom. The sand was a mixture of calcium carbonate and silica, in contrast to the normal habitat, which is mostly carbonate. The adults were fed "Tetra Marin" flakes and a variety of marine algae and spermatophytes.

Copulation was first noted at the beginning of December 1967, and spawning began near the end of the month. The pair continued to breed until April 1968, producing 21 egg masses. Spawning occurred in the tank's corners or in the stream of water from the intake. Egg masses were either attached to the fiber-glass walls or deposited unattached on the sand.

Considerable variation in size and the arrangement of the egg filaments was noted. The smaller masses were only one third the size of the larger. One of average size (4 cm by 8 cm with an egg filament 3.8 m long) contained approximately 80,000 capsules. Filaments within the mass did not form a distinct pattern like those of *S. gigas* (D'Asaro, 1965); however, the larger masses as a whole were somewhat crescent-shaped.

Egg filaments from *S. gallus* are structurally similar to those of other strombids from the same habitat, for example *S. gigas*, *S. costatus*, and *S. raninus* (Robertson, 1959). Each filament is a brownish, opaque, tubular structure averaging 0.93 mm in width. The external limiting membrane, which has an outer rugose layer and an inner membranous layer, is covered with sand grains. The spherical egg capsules are held inside a coiled capsular tube, which is constricted between each unit (Fig. 2, C). The average diameter of the capsules is 0.17 mm. Development is indirect, with a long-term planktotrophic veliger stage.

Cypraea spurca acicularis Gmelin

Fig. 2, D

Adult specimens of this tropical subspecies are somewhat difficult to maintain for long intervals in the laboratory, because they require specific sessile invertebrates as food. Individuals collected from Bear Cut, Biscayne Bay, Florida, spawned shortly after being placed in aquaria in May 1964 and June 1965. In each case, the glass walls were used as a substrate.

A typical mass forms an irregular oval (2.2 cm × 1.6 cm, or smaller) and is several layers deep in the center. The closely packed layers and the smooth

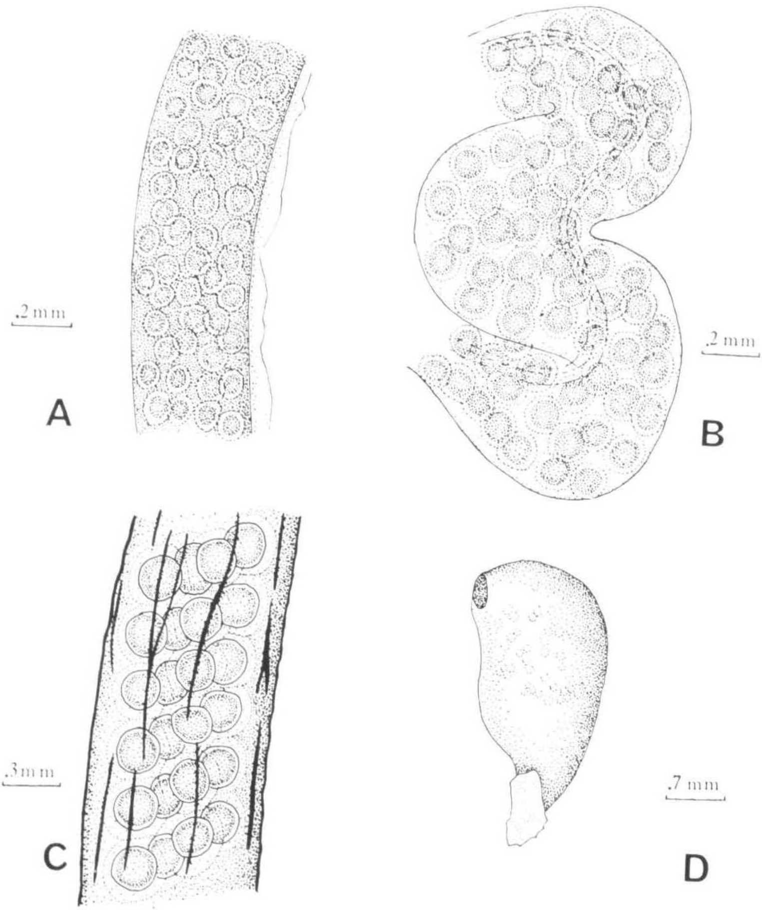

FIGURE 2. The egg filaments and capsules of prosobranchs: A, *Cerithium auricoma*, segment of the straight egg filament with the detritus removed; B, *C. literatum*, segment of the coiled filament; C, *Strombus gallus*, segment of the filament with the sand grains removed; D, *Cypraea spurca acicularis*, lateral view.

surface of the capsules give the mass a gelatinous appearance. After placing the capsules, the female broods until hatching begins by covering the cluster with her foot. The two masses examined contained approximately 140 and 290 capsules.

The oothecae are transparent structures of variable form, packed with white or pinkish embryos suspended in an albuminous fluid. There is a general capsular shape which the female apparently distorts at will during the formation of the egg mass. This type of capsule is crudely vasiform, with the hollow peduncle and the escape aperture placed laterally on opposite sides (Fig. 2, D). The basic pattern persists in 90 per cent of the oothecae. Basal membranes are often placed over the escape apertures of the lower layers; however, such obstructions apparently do not hinder hatching, because the whole envelope becomes soft and tears easily when the embryos are ready to escape. The average dimensions of the capsules are: height, 2.6 mm; width, 1.6 mm; and thickness, 1.0 mm. Individual oothecae contain from 800 to 1300 embryos, with an average of 1100. The total numbers of embryos in the two masses were estimated to be 154,000 and 319,000. A long-term planktotrophic veliger appears at hatching.

Descriptions of cypraeid spawn by Vayssière (1923) and Ostergaard (1950) and personal observations on *C. cervus* and *C. zebra* emphasize the existence of a generalized type of capsule in this genus. The basic differences among the known species include size, number of embryos, the relative position of the peduncle and escape aperture, and the presence or absence of a gelatinous matrix in which the capsules are embedded.

Murex florifer Reeve
Fig. 3, A, B

A specimen of *M. florifer*, collected at MacArthur Causeway, Miami, Florida, during June 1963, spawned immediately after being placed in an aquarium. The mass was attached to the glass and contained 34 capsules. Most capsules were placed with the convex side facing the direction in which the female was moving during oviposition. Rotation of the spawning animal around the periphery of the mass can confuse the pattern. Normally, the convex side of a capsule fits rather tightly between two capsules in the succeeding row.

The capsules are opaque white and vasiform, with a flat apical plate and convex and concave sides (Fig. 3, A, B). Usually, the concave side is considerably reduced in size. Laterally, the capsule is unribbed and rounded. Several supporting ribs, occurring at irregular intervals around the hollow peduncle, aid in anchoring the structure to the flat basal membrane. On the apical plate, a poorly defined ridge parallels the peripheral ridge (Fig. 3, B). The circular escape aperture, covered with a transparent membrane, is situated slightly off center. A suture bisects the membrane and extends to the edges of the apical plate. As noted by Fretter & Graham (1962), the suture reflects the bilobed structure of the oviduct. Random venation appears on all membranes, with the exception of the escape aperture. The average capsular dimensions are: height, 6.0 mm; width, 5.0 mm; thickness, 3.0 mm. The number of embryos in a sample of five, taken just prior to hatching,

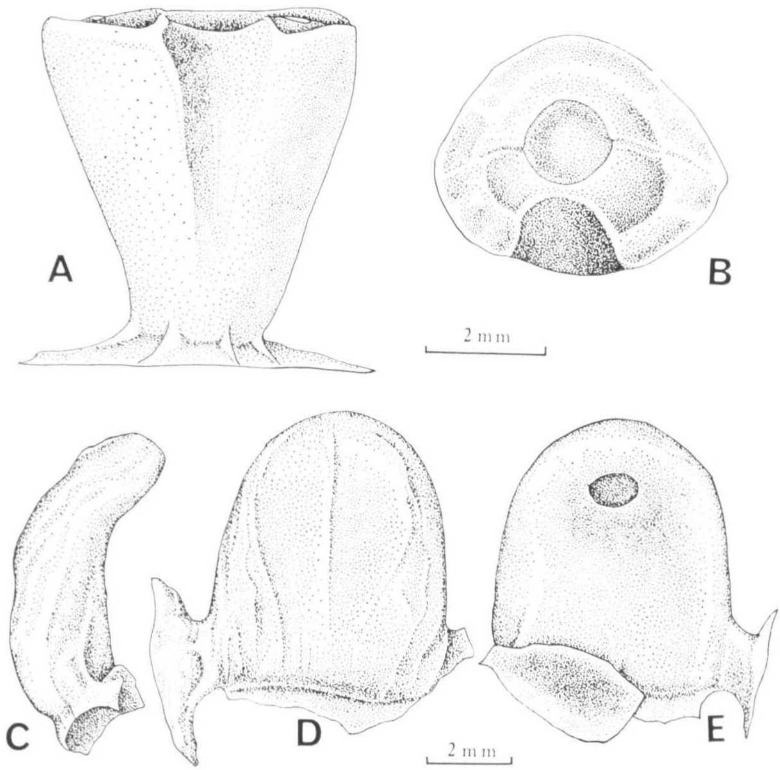

FIGURE 3. The egg capsules of prosobranchs: A, *Murex florifer*, concave side; B, *M. florifer*, apical plate; C, *M. pomum*, lateral view; D, *M. pomum*, concave side; E, *M. pomum*, convex side.

ranged from three to nine, with an average of five. Development is direct, and it is probable that nurse eggs are used for nutrition.

Because of their size and conspicuous appearance, the egg masses of *Murex* have been studied and illustrated by many authors. At least four distinct capsular shapes occur in the genus. A common type, produced by *M. florifer*, *M. affinis* (Risbec, 1932), and *M. virgineus* (Natarajan, 1958) for example, is a vasiform structure, with a flattened apex, attached to a basal membrane. A second type, with roughly a vasiform shape and a basal membrane but no flattened apical region, is typical of *M. turbinatus* (Thorson, 1940). The third type, known from *M. senegalensis* (Knudsen, 1950) and *M. pomum*, was described as tongue-shaped and curved. This one is usually found in masses in which each capsule is connected to two or more of its

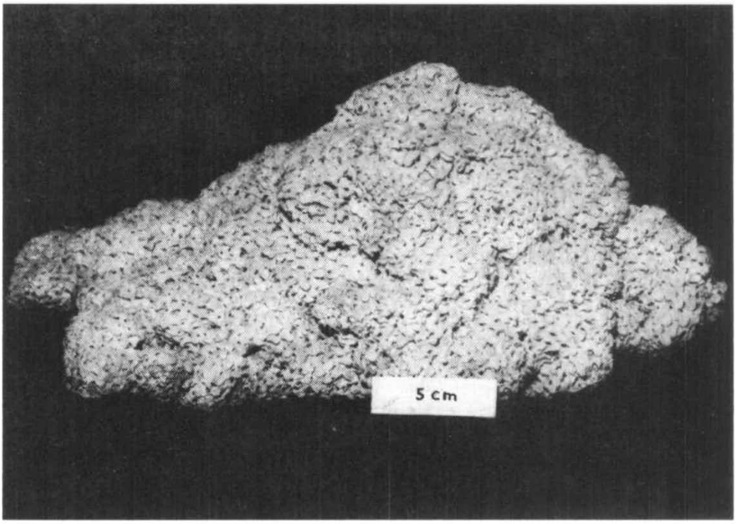

FIGURE 4. A communal egg mass of *Murex pomum* containing the spawn of over 30 individuals.

neighbors, with the whole arranged in an amorphous mound. The fourth type is a more rounded or spherical capsule, typical of *M. recurvirostrus* (Owre, 1949) from south Florida, which is found in rounded, lattice-like masses. Of the four types, the first and second mentioned are similar and are probably from related species. The same appears to be true of the third and fourth.

Murex pomum Gmelin
Figs. 3, C, D, E; 4

Spawn from this species was collected from Biscayne Bay, Florida, from March through May 1965. Individuals kept in the laboratory deposit eggs during the same period of the year; however, the egg masses are somewhat smaller. In the field, oviposition begins on a solid object such as a bivalve shell, rock, or clump of *Thalassia*, and continues to build upon the first layer of capsules. Within a cluster, most capsules in each layer are oriented in the same direction. A mass may contain from 240 to 1800 capsules, with an average of 750. The most interesting characteristic of the breeding habits is the tendency to produce communal egg masses. In areas with dense populations, a spawning individual attracts others and apparently induces ripe animals to commence oviposition. The process is similar to that occurring in *M. trunculus* (Dulzetto, 1946) and *M. incarnatus* (Gohar & Eisawy, 1967). Communal structures contain spawn from two to more than one hundred individuals. The largest structures are about 50 cm in diameter and 20 cm high. They are shaped into an irregular mass surrounded by a wide base (Fig. 4). In many cases, when spawning females are attracted to a certain point, they deposit many smaller clusters around a much larger, central mass. Females continue to add to each communal structure for several days.

The yellowish-white, opaque capsules are tongue-shaped with a rounded apex and have convex and concave sides (Fig. 3, C, D). Each concave side is marked by irregular longitudinal ridges, usually in a pattern of one central and two laterals, both extending over the apex. Minor intermediate or interconnecting ridges occur on the rounded surfaces. The escape aperture appears as a large, round, slightly transparent membrane on the convex side (Fig. 3, E). Minor interconnecting ridges occur on this surface also. The basal membrane is almost always attached at two separated points to other capsules, even on the side of the mass in contact with the substrate. There is only a slight similarity between the preceding description and Tryon's (1882) figure of the egg mass. The average dimensions of the capsules are: height, 7.5 mm; width, 6.0 mm; thickness, 2.5 mm. Nurse eggs are present. The number of embryos per capsule at hatching varies from 11 to 18, with an average of 13. Development is direct.

Thais rustica Lamarck
Fig. 5, A, B

This moderately common, tropical species can be maintained in aquaria in breeding condition on a diet of barnacles and littoral bivalves like *Crassostrea*. The spawning habits are almost identical to those of *T. haemastoma* (D'Asaro, 1966), a species which shares the same habitat. Egg masses were obtained in the laboratory from February through April 1965, from specimens collected at Norris Cut, Virginia Key, Florida. The breeding season probably is much longer. *Thais rustica* selected either carbonate or wooden substrates for oviposition. Like many other thaidids, communal spawning by this species is common, even interspecifically with *T. haemastoma*. The number of capsules per mass was low, ranging from 10 to 45, with an average of 38. The pattern of orientation, like that of *T. haemastoma*, places concavities against convexities.

Thais rustica has characteristic vasiform oothecae with colorless, transparent membranes, concave and convex sides, a flattened apex, and a reduced, solid peduncle (Fig. 5, A). Lateral ridges outline the concave side. A low, transparent apical ridge surrounds the crescent-shaped apical plate and is fused with the laterals. The escape aperture is located to one side (Fig. 5, B). The average capsular dimensions are: height, 6.5 mm; width, 1.3 mm; thickness, 1.0 mm. In comparison with those of *T. haemastoma*, the capsules of *T. rustica* are narrower and have sharper ridges. The con-

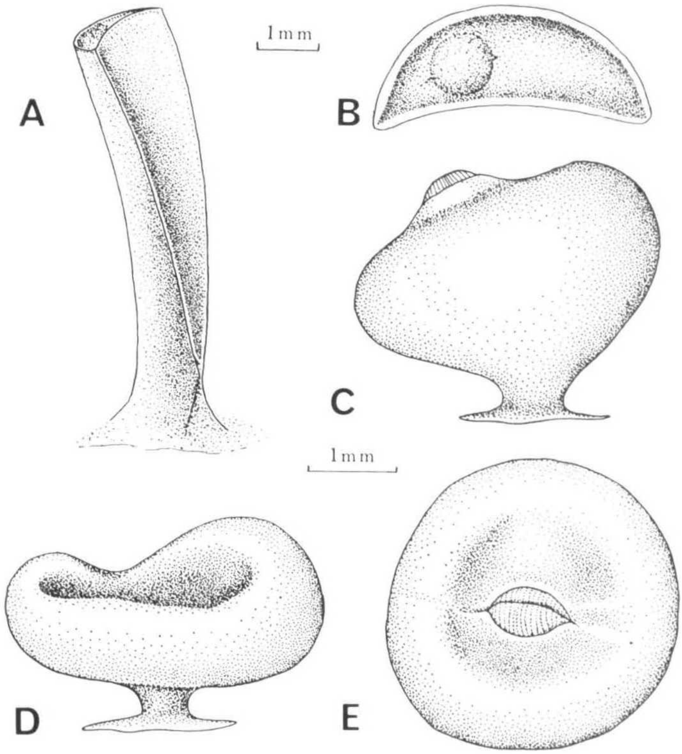

FIGURE 5. The egg capsules of prosobranchs: A, *Thais rustica*, lateral view; B, *T. rustica*, apical plate; C, *Cantharus tinctus*, lateral view of a typical capsule; D, *C. tinctus*, lateral view of a depressed capsule; E, *C. tinctus*, apical view.

tents of the capsules vary from 220 to 650 embryos, with an average of about 400. The number of embryos per mass ranges from 4000 to 17,000, with an average of 15,000. This species has a long-term planktotrophic veliger stage.

Cantharus (= *Pollia*) *tinctus* Conrad
Fig. 5, C, D, E

This neogastropod can be kept in the laboratory for long periods, if provided with rocks covered with barnacles, oyster spat, and assorted small bivalves. Adults from Norris Cut, Virginia Key, Florida, spawned between May and July 1965. A question can be raised concerning the origin of the spawn, since the aquaria also contained several *Pisania pusio*. It is probable that the egg capsules of both species are very similar; however, specimens identical to the described material were found in a habitat where *P. pusio* never occurs. Egg masses contain from 5 to 20 capsules randomly placed and occasionally arranged in two layers. Mollusk shells—especially the nacreous interior of freshly killed, but clean, bivalves or gastropods—located in dark, secluded areas, are the preferred substrate.

Lebour's (1945) description of the capsules of *Pollia tincta* from Bermuda matches the specimens from Biscayne Bay. The body of the opaque, yellowish-white, vasiform capsule ranges in shape from spherical to discoidal or even cup-shaped with the apical escape aperture raised (Fig. 5, C, D). The aperture has a transverse suture and distinctive venation (Fig. 5, E). In most cases, the flat sides of the solid peduncle are parallel to the transverse suture. No fusion of the basal membranes occurs. The average capsular dimensions are: height (perpendicular to the transverse suture), 3.0 mm; width (parallel to the transverse suture), 4.0 mm; thickness, 3.3 mm. Counts of hatching young range from 3 to 16, with an average of 8. Development is direct, with the aid of 100 to 150 nurse eggs per capsule.

Leucozonia nassa Gmelin
Fig. 6, A, B, C

Egg masses were found in shallow water under rocks around Key Biscayne and Virginia Key, Florida, from June through August 1966. *Leucozonia nassa* is also easy to maintain in the laboratory on a diet of bivalves—in particular, *Chione cancellata*. Females spawn readily when abundant food is available, attaching their capsules in very uneven masses on any hard substrate in a secluded place. Occasionally, the units are arranged serially. Communal spawning occurs, and each female spawns several times in a season.

The slightly opaque, yellowish-brown, vasiform capsules have a convex side and a flattened side (Fig. 6, A, B). Both sides may be somewhat depressed. Weak lateral ridges extend from the solid peduncle to the edge of the apical plate. Another ridge surrounds the apical region (Fig. 6, C). There is a centrally located, circular or oval escape aperture covered with a transparent membrane. A suture extends from the junction between the lateral ridge and the apical ridge, through the apertural membrane to the opposite junctional point. Minute striations parallel to the apical plate mark the sides. The average dimensions of the capsules are: height, 7.5 mm; width, 4.5 mm; thickness, 3.0 mm. The number of embryos in an egg capsule just prior to hatching ranges from 5 to 12, with an average of 11. Typical masses contain 10 to 60 capsules; therefore, production per spawning varies from 110 to 660 viable embryos. Total egg production is higher because nurse eggs are present. Development is direct.

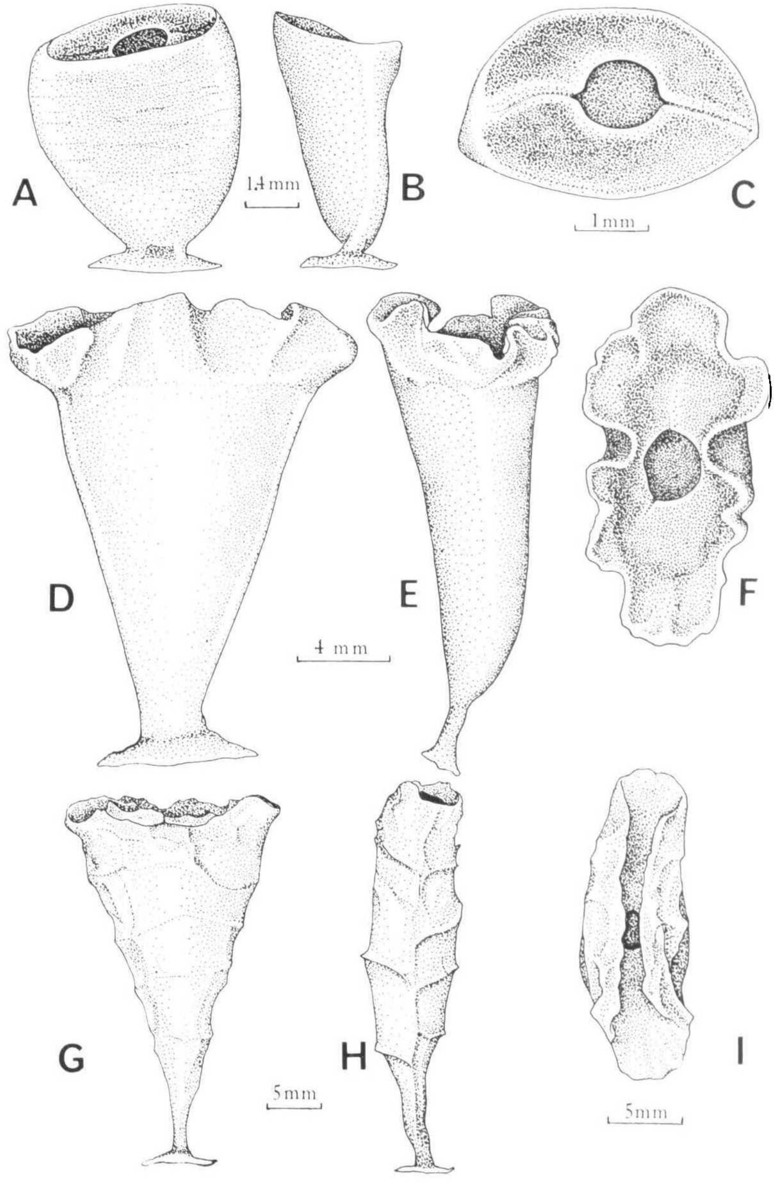

FIGURE 6. The egg capsules of prosobranchs: A, *Leucozonia nassa*, flattened side; B, *L. nassa*, lateral view; C, *L. nassa*, apical plate; D, *Fasciolaria tulipa*, concave side; E, *F. tulipa*, lateral view; F, *F. tulipa*, apical plate; G, *Pleuroploca gigantea*, convex side; H, *P. gigantea*, lateral view; I, *P. gigantea*, apical plate.

Fasciolaria tulipa Linné
Fig. 6, D, E, F

Egg masses of this well-known warm temperate and tropical species are common in Biscayne Bay, Florida. Specimens were collected from January through August 1965, and were most abundant in April. Any hard substrate, such as a small stone, shell, or blade of *Thalassia*, may be used for oviposition. Spawning was not observed in the laboratory. The number of capsules per unit ranges from 20 to 115, with an average of 71.

The spawn of *Fasciolaria tulipa* was described or illustrated by Lund (1834), Tryon (1882), Glaser (1905), and others. Comparative data on the spawn of *F. lignaria* (Bacci, 1947) and *F. audouini* (Gohar & Eisawy, 1967) are available also. Oothecae of those species are similar in shape, differing mainly in the structure of the apical plate and the apical ridge. The opaque, white, vasiform capsules of *F. tulipa* have smooth convex sides and a concave apical region (Fig. 6, D, E). Laterally, a weak ridge extends from the basal membrane across the solid peduncle to the undulated apical ridge (Fig. 6, F). An internal suture extends across the concave apical plate from the junction of the lateral ridge, through the opaque escape aperture, to the opposite junction. The peduncles are attached to the basal plates which are fused into a continuous band. The average dimensions of the capsules are: height, 18.0 mm; width, 13.5 mm; thickness, 6.2 mm. Nurse eggs are present. About 14 embryos hatch from each capsule. Development is direct.

Pleuroploca gigantea Kiener
Fig. 6, G, H, I

This relatively common species is temperate or tropical in distribution. Its large egg masses are usually seen on sandy or muddy substrates. Due to the great size of the animals (specimens 40 cm in siphonal length are not uncommon), they are difficult to keep in the laboratory; but egg masses are easily collected in the field from March through May. Specimens were obtained in 1965 and 1967 from Biscayne Bay, Florida. The capsules are usually attached randomly to a central point, forming a ball-shaped mass which may roll freely over the bottom. Large masses exceed 15 cm in diameter. The number of oothecae per unit ranges from 35 to 140. Johnson (1929) recorded egg masses containing 400 capsules.

The opaque, vasiform capsules are flattened or slightly convex and have a concave apical region. Four or more ridges running parallel to the apical plate cross the sides (Fig. 6, G, H). Additional ridges branch randomly just below the undulated apical margin in an area that tends to fold toward the apex (Fig. 6, I). Lateral ridges run from the apex to the peduncle. An internal suture extends from one lateral ridge across the concave apical plate, through the opaque escape aperture and terminates on the opposite lateral ridge. The solid peduncles are attached to a fused basal membrane which extends beltlike through the center of the mass. The average dimensions of the capsules are: height, 35.0 mm; width, 18.5 mm; thickness, 7.0 mm. Between 44 and 61 embryos, with an average of 54, will hatch from each capsule. Additional nurse eggs are present. Development is direct.

Vasum muricatum Born
Fig. 7, A, B

Although the author maintained specimens of *V. muricatum* for a year in the laboratory, using various bivalves as food, spawning did not occur. A single egg mass was found in May 1962, at Soldier Key, Florida. No adult was in the immediate vicinity; however, a survey of the larger species inhabiting the area and the known egg masses of these species and other xancids suggests that *V. muricatum* is the most probable producer. A limestone substrate was used for oviposition. The mass consisted of three capsules arranged successively and somewhat unevenly.

When seen from either the convex or concave side, each slightly opaque capsule is roughly the shape of an obtuse chevron with rounded corners (Fig. 7, A). Lateral ridges with sharp edges extend from the apex to the basal membrane. Each capsule is attached to the substrate along the obtuse side by a poorly formed and somewhat diffuse basal membrane. The escape aperture is covered by a thin, unmarked membrane and extends along the upper edge of the concave side (Fig. 7, A, B). Faint internal striations, running from the apex to the basal membrane, mark both curved surfaces. The average dimensions of the three capsules are: height, 14.0 mm; width, 28.0 mm; thickness, 3.0 mm. Unfortunately, the individuals in two of the capsules had already hatched. The third capsule still contained an albuminous fluid and 165 embryos. Development appears to be direct. Since the capsules hold few embryos in relation to the total volume, it is probable that nurse eggs of some sort are involved in larval nutrition.

Xancus angulatus Solander
Figs. 7, C, D, E; 8

A single egg mass was collected at Turtle Rocks, South Bimini, Bahamas, in July 1967. One end of the mass was attached to a piece of organic debris. Ten capsules with a total length of 10 cm were included (Fig. 8).

The spawn of *Xancus* is typically complex and massive, and diverges greatly from the generalized neogastropod structures figured earlier. Previous reports on the egg masses of *X. pyrum* (Chidambaram & Unny, 1947) and *X. rapa* (Natarajan, 1958) demonstrate the complexity of the oothecae in this genus. Each opaque, circular petaloid structure is attached to a com-

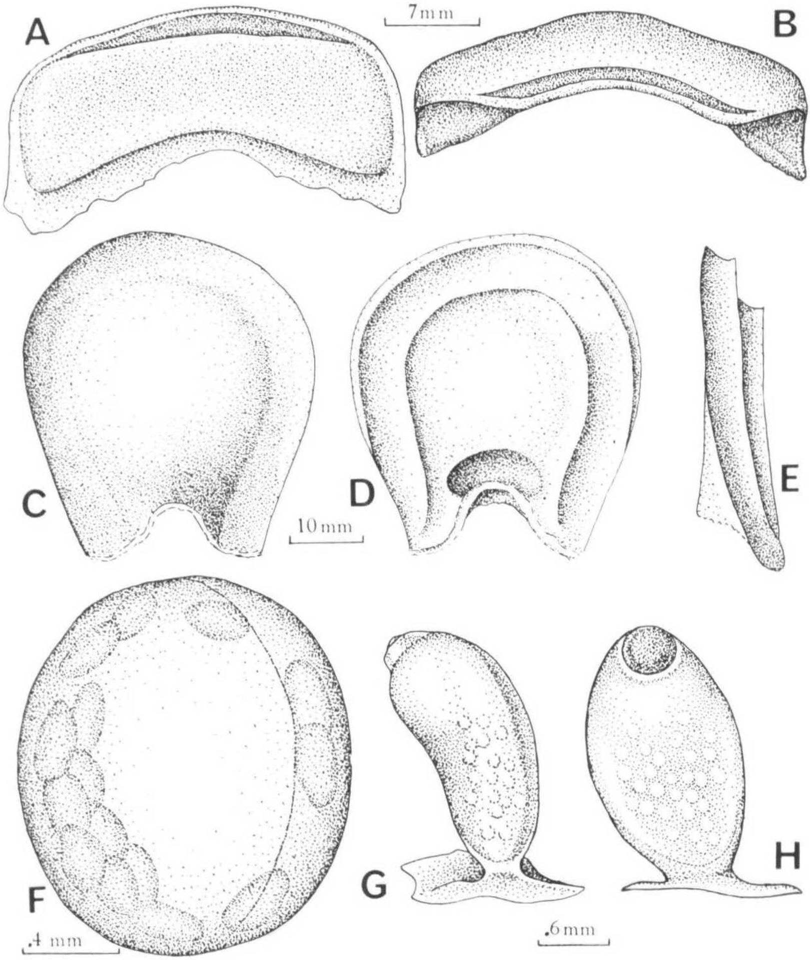

FIGURE 7. The egg capsules of prosobranchs: A, *Vasum muricatum*, concave side; B, *V. muricatum*, apex; C, *Xancus angulatus*, upper surface of a detached capsule; D, *X. angulatus*, lower surface of a detached capsule; E, *X. angulatus*, lateral view of a detached capsule; F, *Oliva sayana*, spherical, unattached capsule; G, *Mitra nodulosa*, lateral view; H, *M. nodulosa*, concave side.

mon basal membrane which is fused into a rigid stalk (Fig. 8). At the point of attachment, the stalk is modified to wrap over or around a hard substrate. Each petal has an upper convex and a lower concave surface (Fig. 7, C, D). The margin is flattened or pushed in slightly, and its upper and lower surfaces each have a sharp ridge extending around the petal to the stalk on both sides. At the stalk, the marginal ridges are turned downward where they meet the medial ridge of the lower concave surface (Fig. 7, D, E). The medial ridge fits tightly behind the upper marginal ridge of the next petal in series, to form a compact mass. A flaw in the thin membrane behind the medial ridge marks the point at which hatching will take place. The dimensions of the capsule are: height (between the stalk and the outer lip of the petal), 3.0 cm; width (between the lateral edges), 4.0 cm; thickness (between the upper marginal ridge and the medial ridge), 1.0 cm. A rapid, serial decrease in size occurs in the last three basal capsules. The number of embryos in the capsules varies from 2 to 5, with a total of 33 for the egg mass. The basal capsule was unopened and empty. Development is direct. Embryos with 3 to 5 whorls on the protoconch were found in the capsules, feeding on an albuminous fluid.

Oliva sayana Ravenel
Fig. 7, F

Adults of this south-temperate species were collected at Marco Island, Florida, and maintained in a noncirculating aquarium for one year by Mrs. M. E. Crovo. The adults prey upon small mollusks and will accept a variety of fresh animal tissue. Spawning was noted in July 1967. Spherical egg capsules are released unattached on the sand. Each female appears capable of producing several hundred oothecae.

Details of spawning and a description of the egg capsules of *O. sayana* were given by Olsson & Crovo (1968); therefore, a brief outline will suffice here. Each transparent, roughly spherical egg capsule initially contains a large amount of albumen, which forces the white embryos against the walls (Fig. 7, F). There is a distinct semicircular suture in the membrane, which marks the site of the escape aperture. The average diameter of the capsules is 1.6 mm. Counts of the embryos range from 14 to 48, with an average of 24. This species has a long-term planktotrophic veliger.

Mitra nodulosa Gmelin
Fig. 7, G, H

Adult specimens of *M. nodulosa*, collected at Peanut Island, Lake Worth, Florida, have been maintained in aquaria with running sea water by Mr. Robert Work of the Rosenstiel School of Marine and Atmospheric Sciences. These animals spawned during July 1965. Copulation was observed several days prior to spawning. Hard substrates were used for oviposition. Several egg masses were produced with the number of units per mass ranging from 50 to 155. Unfortunately, no record was made of the pattern in the mass.

The general outline of the capsule is more or less typical of the mitrids

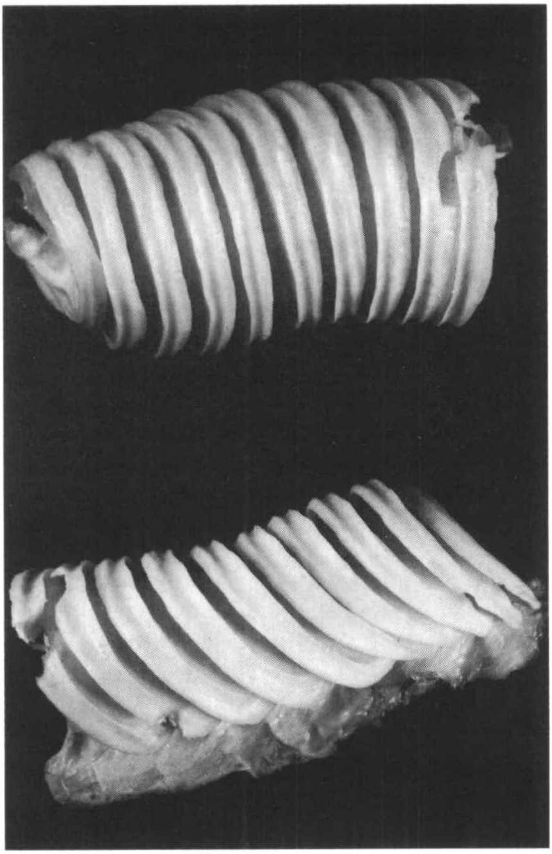

FIGURE 8. Fused egg mass of *Xancus angulatus*, length, 10 cm: top, frontal view; bottom, lateral view.

described by Ostergaard (1950). Each transparent, compressed, vasiform structure has concave and convex sides and a rounded apex (Fig. 7, G, H). All edges are rounded, and the peduncle is solid. When seen from the convex side, the outline of the structure above the peduncle is ellipsiodal. The apical region and the escape aperture are decurved from the vertical, while the escape-aperture plug is raised slightly. The walls of the capsule are smooth, with the only marks being internal flaws around the plug or in the peduncle. Capsular dimensions are as follows: height, 2.3 mm; width, 1.2 mm; thickness, 0.8 mm. Counts of the embryos in five capsules range from 90 to 120, with an average of about 100. At this average, the total number of embryos per egg mass varies from 5000 to 15,500. No data on development are available; but judging from the small size of the embryos, the large number per unit and the degree of development, it is probable that this species has a planktonic stage.

Prunum apicinum Menke
Fig. 9, A, B

Egg capsules from *P. apicinum* were collected on sand or mud flats surrounding Key Biscayne and Virginia Key, Florida, from June through August 1966. The spawning season probably includes most of the spring and summer months.

Marginellids like *P. apicinum* are easy to handle in aquaria, since they are nonselective carnivores and scavengers. Tissue from bivalves or crustaceans is excellent food and can be used to maintain spawning animals. The use of live bivalves, such as *Chione cancellata* or *Codakia orbicularis*, prevents fouling of the water and provides food in relation to demand. As with many neogastropods, oviposition occurs when food is abundant. Since development is direct, *P. apicinum* can be reared through many generations in either running sea water or a closed system.

Hard substrates, including the shells of other prosobranchs and bivalves, are selected for oviposition. There is no evidence of communal spawning. Egg capsules are attached individually to the substrate and rarely occur in groups. When a female deposits several capsules on the same shell or in close proximity on the walls of the aquarium, there is no pattern in the arrangement.

Individual capsules are pustulate structures, oblong or ovate at the base, have no ornamentation, and are situated on a basal membrane that extends beyond the capsular walls (Fig. 9, A, B). The walls are transparent; however, the enclosed albuminous fluids and the embryo impart a whitish tint. Occasionally, sutures occur at either end of the long axis. The basal membrane normally reflects the pattern of the substrate. For example, the sculpture of a bivalve's shell may be superimposed on the membrane. The average dimensions of the pustulate capsules are: length, 0.69 mm; width, 0.51 mm; height, 0.28 mm. Only one embryo occurs in each capsule. At hatching, the pustulate structure breaks away from the basal membrane. Knudsen (1950) noted that two types of marginellid capsules occur: stalked and pustulate. *Prunum apicinum* is most similar to his descriptions of *Persicula persicula* and *Marginella eveleighi*.

Conus spurius atlanticus Clench
Fig. 9, C, D, E

Mature specimens will spawn in the laboratory, but in most cases, only immediately after collection. In one instance, the author was able to obtain

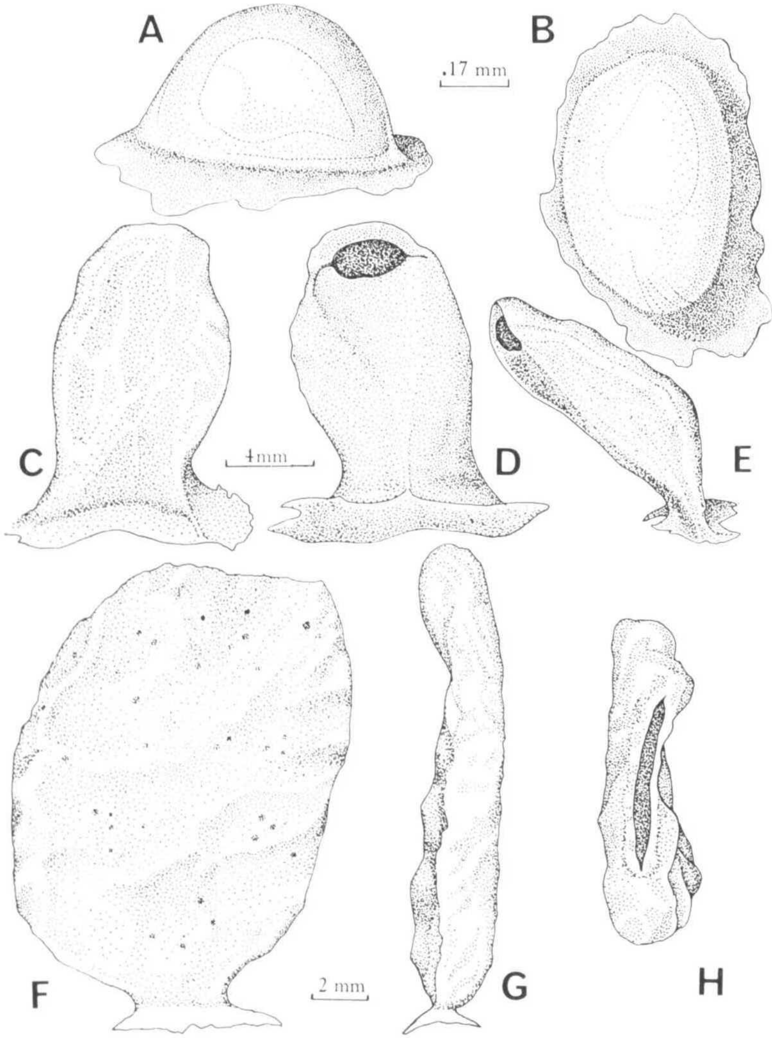

FIGURE 9. The egg capsules of prosobranchs: A, *Prunum apicinum*, lateral view; B, *P. apicinum*, apical view; C, *Conus spurius atlanticus*, upper, wrinkled side; D, *C. spurius atlanticus*, lower, smooth side; E, *C. spurius atlanticus*, lateral view; F, *C. regius*, flattened side; G, *C. regius*, lateral view; H, *C. regius*, apical plate.

spawn after two months by keeping several individuals in aquaria with running sea water and about 10 cm of sediment collected from the natural habitat. Hard substrates above the sediment are used for oviposition. In the laboratory, specimens collected from Biscayne Bay, Florida, produced egg masses containing from 3 to 87 capsules between May and August 1964. Additional material was collected in the field as early as April.

The capsules are arranged in a definite pattern. Each is attached to the substrate by a basal membrane until a layer is formed, with the majority of the escape apertures facing one direction. Additional capsules are added atop the original ones. The basal membranes of the second layer adhere to the upper surface of one or more earlier units. Three or four layers may be added in this manner, with most units oriented in the same direction.

Each flattened, tongue-shaped, opaque-white capsule has a wrinkled upper and an almost smooth lower side (Fig. 9, C, D). The wrinkles on the upper side extend randomly from the base toward the apex. The apical region is continuous with the lower side. A transparent membrane covers the entire apical region, which is tilted toward the lower side and functions as an escape aperture (Fig. 9, D). Laterally on both sides, a thin, poorly defined ridge extends from the basal membrane to the apex. Characteristically, all capsules are sharply decurved from the vertical at the peduncle (Fig. 9, E). The average dimensions of the structures are: height, 12.0 mm; width, 8.0 mm; thickness, 3.5 mm. Counts of the embryos in five capsules ranged from 54 to 67, with an average of 59. The total number of embryos per egg mass spawned in the laboratory ranged from 170 to 5100. Development by this species is indicative of the formation of a planktotrophic veliger stage.

The spawn of *C. spurius atlanticus* is typical of the conids examined by Kohn (1961a, 1961b) from the Indopacific. The habit of attaching capsules in layers, using the initial group as a foundation, was noted in *C. textile* and *C. pennaceus*. The latter also has sharply decurved capsules.

Conus regius Gmelin
Fig. 9, F, G, H

The author was unable to induce this species to spawn in the laboratory, but it was observed spawning on large coral fragments at Long Reef, Florida, just east of Elliott Key, during January and February 1965. Unfortunately, these specimens were lost. The only material available, which can be referred to this species, is a mass of 37 capsules collected in August 1967 at Long Reef. Several individuals were in the immediate vicinity when the capsules were collected, and there was a large population in the area. The size of the capsules and the mass as a whole suggest either *C. regius* or *C. ranunculus*. Since the latter is extremely uncommon in the area, this egg mass is assigned to *C. regius*. Some arrangement of the capsules does occur, in that rows of closely spaced capsules usually are mixed with randomly deposited ones. In each linear group, the basal membranes are fused.

The flattened, roughly rectangular, opaque-white capsules are wrinkled unevenly on all sides (Fig. 9, F, G). The solid peduncle is displaced laterally. Typically, the narrow side closest to the peduncle is straighter than the opposite or curved side. An escape aperture closed by a transparent membrane covers the entire apical region (Fig. 9, H). Many round or elliptic flaws mark, but do not penetrate, the capsular walls. It was not possible to count the embryos, since hatching had begun. There is a planktotrophic veliger stage. The average dimensions of the capsules are: height, 16.5 mm; width, 11.5 mm; thickness, 3.0 mm.

Discussion

Breeding Habits.—Communal spawning occurs in certain muricids, fasciolarids, thaidids, and conids. Several factors are involved in the process. Initially, a mature female, responding for the most part to thermal stimuli (Thorson, 1946), locates an acceptable substrate, and oviposition begins. As stated by Hancock (1959) and Kohn (1961b), the subsequent aggregation of mature individuals appears to be a chemotactic response. Although both sexes respond, the females are usually more numerous. The chemical factor responsible may be a metabolite excreted by the eggs and early embryos. D'Asaro (1966) noted that the thaidids no longer spawn on a communal mass after the embryos have reached a certain point in development. The attracting metabolite is not entirely specific, since it will stimulate related species which spawn in a communal area. Congregation at a central point can be significant for several reasons. Although copulation may take place weeks before spawning, in many neogastropods there is always a percentage of females without viable sperm in their receptacles. Aggregations of both sexes allow these individuals to find a mate. The sheer bulk of the communal egg masses of species like *Murex pomum* insures survival. Prosobranch egg masses are preyed upon by other prosobranchs, as well as crustaceans and certain fishes. The formation of a large, layered mass actually produces a physical barrier to many predators, which easily penetrate the outer layers but are unable to proceed farther, due to the resistance of the tough, spongy mass. Communal egg masses of *M. pomum* or *M. recurvirostris* are often found with evidence of extensive predation on the outer layers and no damage to the protected interior.

Brood protection by the parent is a widespread phenomenon within certain groups of the Prosobranchia. The female normally covers the egg mass with her foot, resists displacement, and may actively attack a predator. She will return to the mass when removed and placed nearby. Certain sedentary prosobranchs like *Calyptraea* (Knudsen, 1950), *Capulus* (Ankel, 1936), *Crepidula* (Coe, 1949), and *Crucibulum* (Thorson, 1940), which protect their capsules, simply as a result of their sedentary habits, by holding the spawn under the mantle or the foot, should not be confused with the aggressive brooders. *Cypraea spurca* is an excellent example of a long-term brooder that is not otherwise sedentary in habit, but which does remain with its capsules until hatching takes place. Protection was well documented in this genus by Ostergaard (1950) for *C. isabella* and *C. helvola*. Ostergaard noted that both species use the radula for defense during brooding. Lebour (1932), who found that another cypraeacean, *Simnia patula*, is a brooder, believed that protection of the capsules is a characteristic of the group. However, there are exceptions. Nonbrooding cypraeaceans include *Trivia monacha* (Lebour, 1933), *Jenneria pustulata* (D'Asaro, 1969), and many ovulids (personal observations). Tonnaceans are also known to be aggressive brooders. *Bursa corrugata* (D'Asaro, in press) protects its egg masses by producing a cup-shaped structure only as wide as the aperture and then covering the mass with its foot. When disturbed, the female presses against the capsules and attacks the predator with her radula. When removed from the capsules and placed near by, the parent will, in most cases, return to her previous position. Other examples of brooding tonnaceans include *Lotorium spengleri* (Hedley, 1904), *Fusitriton oregonensis* (Howard, 1962), and many species of *Cymatium* (personal observations).

Spawning in the Laboratory.—Most mature prosobranchs will spawn when they are held in aquaria of sufficient size and provided with abundant food and assorted substrates. The temperature must be in the range at which oviposition normally occurs. Spawning during the breeding season can be controlled by regulating the amount of available food. Starving ripe animals for periods up to one month prevents final maturation of the gonads and may precipitate partial absorption. A sudden abundance of food permits complete maturation and spawning. The time interval before oviposition begins varies considerably among species. In some cases, it may be as short as six days. This method has been used successfully with tonnaceans, muricaceans, and buccinaceans.

Since the material examined was obtained for the most part from spawn produced in the laboratory, it is important to note any structural variations between it and spawn collected in the field. Where comparable samples were available, two rather minor variations did occur. First, egg masses produced in the laboratory tend to contain smaller numbers of capsules. When abundant food is available, the differences are considerably reduced. Second, in many species, the shape of the mass as a whole reflects the contours of the substrate. Animals spawning in aquaria tend to congregate on the glass walls and produce beltlike, flattened masses, which, in the field, would have a more uneven appearance.

Variations in the Structure of the Capsules.—Intrageneric differences in the shape of oothecae are slight in most cases. A large percentage of variants are produced by the characteristic molding and hardening processes. When capsules of this type are examined closely, the generic characters are usually discernible, as exemplified by *Cypraea spurca* and *Mitra nodulosa.* In a few cases, the intrageneric differences are so great that one could speculate that it is a reflection of the widespread tendency within the Prosobranchia to evolve caenogenetic characters. Fretter & Graham (1962) gave *Littorina* as an example in which diverse spawn or breeding habits occur; but in this genus, all capsules can be recognized as variations of the littorinid type. A better example from a structural point of view already has been presented for *Murex florifer* and *M. pomum.* In this genus, several distinct types occur, each having a range of variations. Oothecae with adaptive modifications also occur. The minute, unattached, spherical capsules of *Oliva sayana,* which are quite similar to the pustulate, attached structures of *Olivella* (Edwards, 1968), a related genus, are a good example. Both groups are normally found in areas with shifting sand which can cover capsules attached to stationary objects. Unattached oothecae are not affected, because they move with the turbulent water and may even become a part of the plankton, like the littorinid capsules described by Lebour (1937). The unattached or planktonic capsules insure dispersal and remove the eggs from a somewhat adverse habitat, the shifting sands of *Oliva's* environment or the physical extremes of the intertidal zone.

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Sumario

Cápsulas Ovígeras de Prosobranquios del Sur de la Florida y las Bahamas y Notas sobre su Desove en el Laroratorio

Se describen e ilustran dos masas de huevos y las cápsulas de 18 especies de prosobranquios incluyendo: *Cerithium auricoma*, *C. literatum*, *Strombus*

gallus, Cypraea spurca acicularis, Murex florifer, M. pomum, Thais rustica, Cantharus tinctus, Leucozonia nassa, Fasciolaria tulipa, Pleuroploca gigantea, Vasum muricatum, Xancus angulatus, Oliva sayana, Mitra nodulosa, Prunum apicinum, Conus spurius atlanticus y *C. regius.* Se presentan datos sobre las dimensiones de las cápsulas, la enumeración de embriones y cápsulas y el patrón de desarrollo. Se da la duración conocida de la época de reproducción, así como alguna información sobre métodos para manipular en el laboratio adultos en etapa de desove.

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