

FURTHER OBSERVATIONS ON THE LIFE HISTORIES OF LITTORAL GASTROPODS IN NEW SOUTH WALES

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(Plate x)

[Read 29th September, 1965]

Synopsis

The spawn and early development are described for: (1) *Xenogalea labiata* (Perry) (Cassididae), in which several females appear to contribute capsules, each containing numerous small eggs, to a large common egg mass; (2) *Bedeva hanleyi* (Angas) (Muricidae), which lays dome-shaped capsules in which many eggs are consumed as nurse eggs and only a few embryos hatch as well developed crawling juveniles; (3) *Morula marginalba* (Blainville) (Thaididae), which lays bluntly rounded capsules containing numerous eggs hatching as planktotrophic veligers; (4) *Nassarius (Alectrion) particeps* (Hedley) (Nassariidae), which lays numerous stalked triangular capsules each containing a single egg developing to a crawling stage before hatching; (5) *Siphonaria denticulata* Quoy and Gaimard (Siphonariidae), which lays gelatinous egg strings containing numerous eggs hatching as planktotrophic veligers.

Each species is briefly discussed in relation to other species of its family, and a summary is given of development in N.S.W. littoral prosobranchs.

INTRODUCTION

A number of authors have recently described the spawn and early development of Australian littoral gastropods (H. Anderson, 1958; D. T. Anderson, 1959, 1960, 1961, 1962, 1965; MacIntyre, 1961; Murray, 1962a, 1962b, 1963, 1964). The present paper reports further observations on this subject for the mesogastropod *Xenogalea labiata* (Perry) (Cassididae), the neogastropods *Bedeva hanleyi* (Angas) (Muricidae), *Morula marginalba* (Blainville) (Thaididae) and *Nassarius particeps* (Hedley) (Nassariidae), and the pulmonate limpet *Siphonaria denticulata* Quoy and Gaimard (Siphonariidae). Of these species, the spawn and development of *X. labiata*, *M. marginalba* and *N. particeps* have not hitherto been described. The egg capsules of *B. hanleyi* were figured by Hedley (1916) and Roughley (1925) and the egg strings of *S. denticulata* by Dakin (1953; Plate 55), but development of the eggs of these species has not been investigated.

MATERIALS AND METHODS

Materials for the studies described in this paper have been gained from several sources. The egg mass of *X. labiata* was collected by Miss I. Bennett of the School of Biological Sciences, University of Sydney, from a sub-littoral rock face at Fairlight, N.S.W., in November, 1963. It was preserved shortly after collection, and observations have been made only on the egg mass itself and on the single developmental stage which it contains. The egg mass of *N. particeps* was also collected by Miss I. Bennett, at Long Reef, N.S.W., in October, 1962. This mass was maintained in aerated seawater in the laboratory and a number of observations made on the development of the embryos.

Capsules identified as those of *B. hanleyi* by comparison with the descriptions given by Hedley (1916) and Roughley (1925) were collected on numerous occasions during the winter months of 1962 and 1963 on the undersurfaces of loose rocks in tidal pools at Bradley's Head, on the north shore of Port Jackson. Their absence from this locality during the remainder of the year indicates

that the species is a winter breeder. These capsules were also maintained in aerated seawater in the laboratory, and observations made on the development of the embryos.

Morula marginalba was taken spawning on the underside of mid-littoral rocks at Long Reef, N.S.W., in January, 1963. The egg capsules were collected, maintained in aerated seawater in the laboratory and studied at intervals until the embryos hatched. Repeated searching at this and other localities where *Morula* is common has failed to provide further capsules, so that the general breeding habits are not yet clear. The ovaries of females, however, do not contain ripe eggs during the winter months.

Observations made at frequent intervals in the spring and summer of 1961/62 and 1962/63 at Harbord, N.S.W., and Long Reef, N.S.W., showed that *Siphonaria denticulata* breeds at least from September to March in these localities. Numerous egg masses were found attached to rock surfaces in the habitat of the adults, and animals were frequently seen in the act of spawning. Masses collected on various occasions were maintained in aerated seawater in the laboratory and studied at intervals until the embryos hatched.

Drawings of spawn, embryos and larvae investigated were made with the aid of a camera lucida. The photograph of Plate x was taken by the Department of Illustration, University of Sydney.

RESULTS

Xenogalea labiata

The spawn of *X. labiata* (Plate x) is a large, irregular, sponge-like mass consisting of several thousand egg capsules. The entire mass, when collected, had dimensions of about 30 cm., and observations made at the time of spawning suggest that it is the common product of several females spawning together. When fresh, the mass was pinkish-orange in colour, the colour being imparted by the eggs contained in the capsules.

The capsules themselves are colourless and translucent and are cemented together as shown in Figure 1. Each capsule is roughly rectangular in shape, about 2.5 mm. long and 1.5 mm. broad, with a thin irregular base plate attached to the capsules below it in the mass. The capsule contains a colourless albumen in which float several hundred eggs, each about 160 μ in diameter, filled with pale orange yolk. All the eggs in the capsule develop simultaneously, proceeding through a yolk-filled gastrula stage (Fig. 2). Development beyond this stage was not observed.

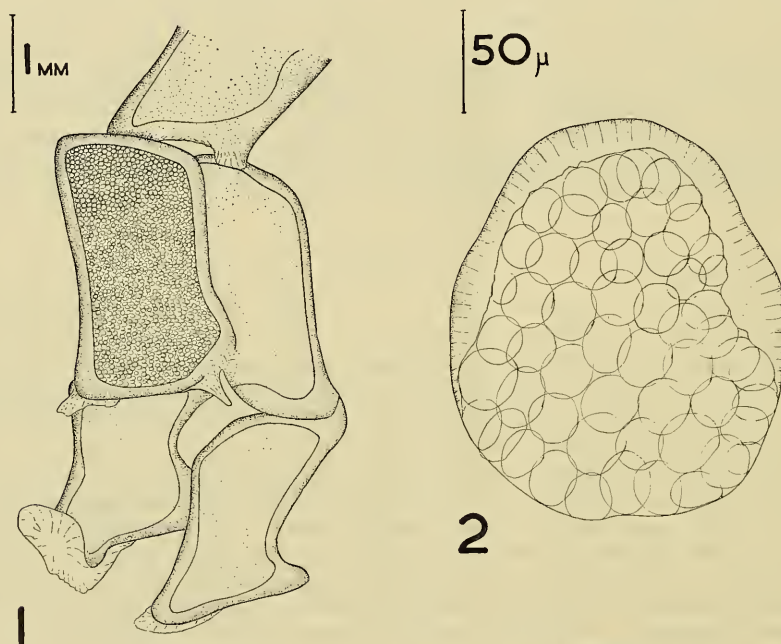
Bedevela hanleyi

The spawn of *B. hanleyi* consists of a group of about 10–20 separately attached, dome-shaped capsules, each about 3 mm. in diameter, whitish in colour and semi-transparent, with a transparent oval apical membrane (Fig. 3). Inside the capsule lie between 50 and 70 eggs, floating in a colourless albumen. A horny transparent base plate completes the capsule structure.

The eggs are opaque white, very yolky, and ovoid in shape, with a long diameter of 250 μ . Only about 15 eggs develop in each capsule, the remainder serving as nurse eggs for the developing embryos. A yolky early veliger stage, with an inconspicuous velum, simple colourless shell, small foot, and large, yolky visceral mass develops in about 4 days and begins to move slowly through the jelly in the capsule. Within a further 4 days, enlargement of the velum occurs, accompanied by elongation and ciliation of the foot and outgrowth of a convex, ciliated oral hood. The stomodaeum also becomes well developed, preliminary to the onset of the ingestion of nurse eggs. Further development during the next 7 days results in broadening of the velum and slight subdivision into 4 velar lobes, formation of black eyespots on either side of the oral hood, and the beginning of spiral coiling of the shell (Fig. 4). As the velar lobes

enlarge, each becomes wrapped around a nurse egg which rests against its concave posterior face. This, however, appears to be a simple consequence of the crowded conditions within the capsule and not a factor in nurse egg absorption.

Direct feeding on the nurse eggs now begins and is completed in about 5 days, during which the veligers retain a large active velum and glide rapidly through the albumen of the capsule. Some growth occurs during this phase, but the major part of the ingested yolk becomes stored in the visceral mass. Subsequent growth at the expense of the stored yolk proceeds at a slightly variable rate in different embryos in the capsule for a further 11 days. Gradual velar resorption is accompanied by elaboration of the head, foot and visceral mass and growth of the coiled shell, which becomes brown-pigmented (Fig. 5).



Figs 1-2. *Xenogalea labiata*. 1, egg capsules; 2, gastrula stage.

The fully developed juveniles, about $4\frac{1}{2}$ weeks old, escape in rapid succession from the capsule through an aperture formed by breakdown of the apical membrane. The newly hatched, crawling juvenile (Fig. 6) has a shell length of about $900\ \mu$.

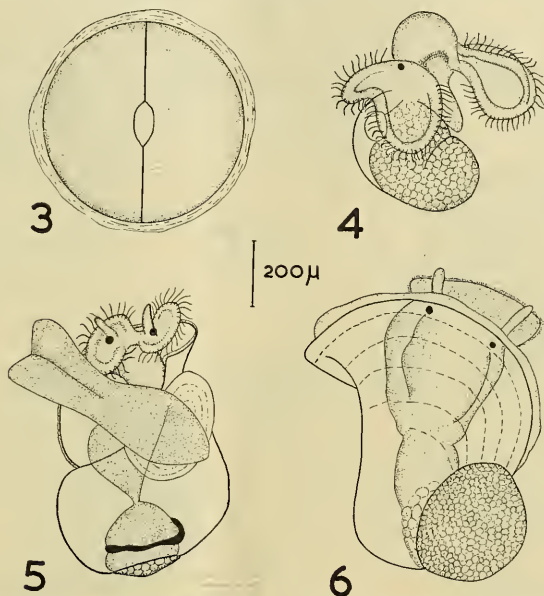
Morula marginalba

The spawn of *M. marginalba* consists of groups of about 20 low, rounded capsules. Each capsule (Fig. 7) has a tough, translucent wall, normally whitish in colour but sometimes tinged with purple, with a transparent thin oval area in the middle of one side through which hatching later occurs. The capsule is attached to the rock by an irregular, transparent, horny base plate and is filled with a colourless albumen in which float between 100 and 200 spherical, yellow, yolky eggs $220\ \mu$ in diameter.

The eggs in the capsule develop simultaneously, passing through a yolky trochophore stage to an early veliger stage (Fig. 8) within 2 days of oviposition. In the early veliger, the velum is still rudimentary, but a ciliated oral hood and stomodaeum are well developed, the foot rudiment is conspicuous and the yolky visceral mass is covered dorsally by a simple transparent shell.

During the next 3 days, the veliger becomes well developed (Fig. 9) and begins to move actively through the capsule albumen by means of its velar cilia. Torsion occurs and the shell enlarges and begins to develop a spiral form. The foot elongates, becomes ciliated, develops paired statocysts and secretes an operculum. The velar lobes expand and develop paired brown eyespots. The visceral mass remains yolky and undifferentiated, however, and no withdrawal of the head and foot into the shell is observed.

During the ensuing week, the veliger enlarges further and becomes highly active and much more differentiated (Fig. 10). The oral hood is reduced in size, but the velar lobes become larger and brown-pigmented around their margins. At the base of the right lobe, a tentacle grows out, tipped with a fan of stiff cilia. The foot also enlarges and becomes brown-pigmented on its ventral face. Further growth and coiling of the shell is accompanied by the



Figs 3-6. *Bedeva hanleyi*. 3, egg capsule; 4, 15-day veliger; 5, 25-day veliger; 6, newly hatched juvenile.

formation of numerous yellowish spots on the shell surface, together with the deposition of brown pigment at the umbo and around the margin (Fig. 11). The visceral mass develops a pulsating larval heart and a coiled gut in which the stomach is black-pigmented and contains yolk particles rotated by ciliary action. The yellowish yolk is now confined to the apex of the visceral mass.

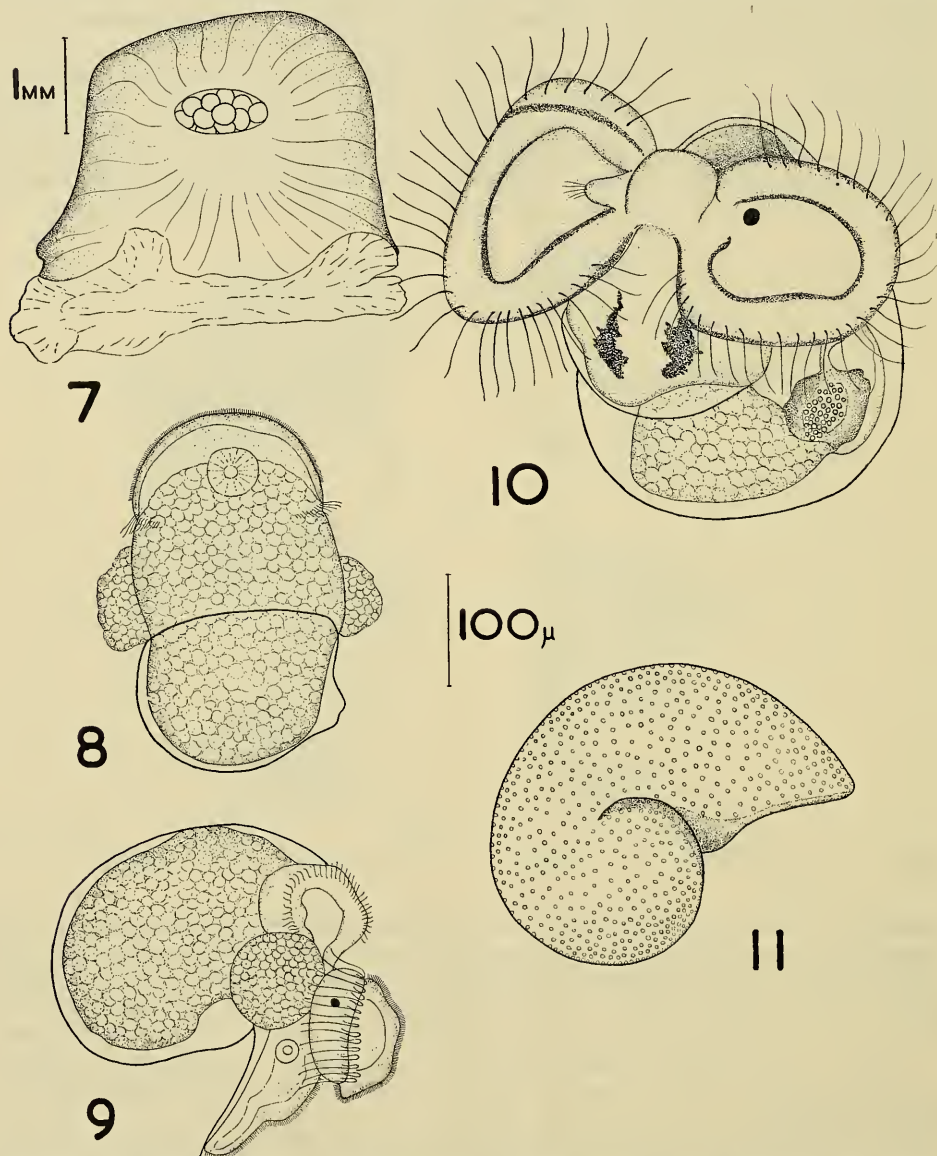
Due to the increased pigmentation of the developing veligers, egg capsules 12 or more days old are brown in colour, in contrast to the yellowish colour of fresher capsules.

Between 12 and 18 days after oviposition, little further change is observed in the veligers in the capsule, apart from a gradual reduction in the amount of yolk in the visceral mass. The veligers continue to swim actively in the capsule jelly, however, and at about 18 days the thin window in the side of the capsule breaks down and the veligers escape to a free swimming existence. Their development after hatching was not followed.

Nassarius particeps

The egg mass of *N. particeps* used in the present investigations was taken at the time of oviposition. Two females were associated with it, and both

proved to have numerous ripe oocytes in their ovaries. Whether both were contributing capsules to the egg mass could not be decided with certainty, but the extent of the mass suggested possible cooperative spawning. The mass consisted of several hundred small, stalked, triangular capsules attached by



Figs 7-11. *Morula marginalba*. 7, egg capsule ; 8, 2-day veliger ; 9, 5-day veliger ; 10, 12-day veliger ; 11, shell of 12-day veliger.

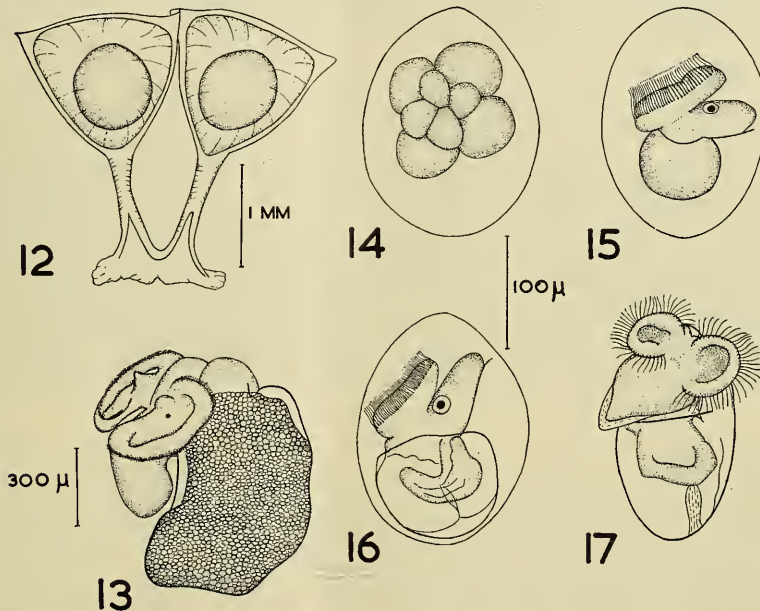
confluent base plates as a single layer directly to the under surface of a rock in the lower littoral, and covered an area of many square cms.

Each egg capsule of *N. particeps* (Fig. 12) is about 2.5 mm. in height colourless and translucent, and filled with a colourless albumen in which floats a single large, yellowish, spherical egg about 700 μ in diameter. In spite of the size of the egg, cleavage is total and the first two divisions are only slightly

unequal. Development proceeds through a highly modified veliger phase in which the velar lobes, although ciliated, remain relatively small and produce only slow rotation of the embryo inside the capsule. Development of the head, foot and shell are well advanced after 7 days (Fig. 13), although the large visceral mass is still yolk-filled and little differentiated. By 12 days, reduction of the velum is in progress and the yolk reserves are beginning to lessen. Development was not followed beyond this point but there seems little doubt that *N. particeps* hatches as a crawling juvenile, probably about 1 mm. in length.

Siphonaria denticulata

The egg mass of *S. denticulata* is an irregular, gelatinous, spiral coil about 5 cm. long, creamy-white in colour and firmly glued to the rock surface in the habitat of the adults. The jelly is colourless and the numerous closely-packed



Figs 12–13. *Nassarius particeps*. 12, egg capsule; 13, 7-day veliger.

Figs 14–17. *Siphonaria denticulata*. 14, embryo after 3rd cleavage, from animal pole; 15, 3-day veliger; 16, 5-day veliger; 17, newly hatched veliger.

eggs embedded in it are whitish and translucent. Each egg is about $100\ \mu$ in diameter and is enclosed in an ovoid, transparent egg capsule about $200\ \mu$ long and $160\ \mu$ broad.

The eggs cleave in a typical spiral manner, the first two divisions being equal, the third unequal (Fig. 14). Blastula and gastrula phases are passed through in 24 hours and a simple yolk trochophore is completed 48 hours after oviposition. During the third day of development, the operculate foot, bilobed velum and globular shell of an early veliger develop (Fig. 15). Growth and internal differentiation now set in and the veliger begins to rotate vigorously within its capsule. The ciliated gut becomes conspicuous as the yolk reserves are finally resorbed (Fig. 16) and hatching of the veligers as actively swimming planktotrophic larvae (Fig. 17) occurs on the sixth day after oviposition.

Hatched veligers fed on the diatom *Nannochloris* continued to swim and grow for a further 4 days, becoming more differentiated internally and developing a slight spiral twist to the shell. Laboratory culture beyond this stage was not achieved.

DISCUSSION

Xenogalea labiata

Very little is known of spawning in cassidid mesogastropods. The only two previous descriptions of egg capsules appear to be those of Erlanger (1893) for *Cassidaria echinophora* and Lo Bianco (1899) for *C. echinophora* and *Cassidaria sulcata*. These brief notes suggest that the egg mass of *X. labiata* is typical for the family, but it is not yet known whether the apparent cooperative spawning of *X. labiata* is a characteristic of cassidids.

Embryonic and larval development in the Cassididae remain to be described, but the number and dimensions of the eggs of *X. labiata* suggest that this species hatches as a pelagic planktotrophic veliger. In contrast, it appears from the work of Erlanger (1893) and Lo Bianco (1899) that the eggs of *Cassidaria echinophora* are larger (280 μ in diameter) and that only a few develop, the remainder serving as nurse eggs, to hatch at an advanced stage, probably as crawling juveniles.

Bedevea hanleyi

The present work confirms the descriptions given by Hedley (1916) and Roughley (1925) of the egg capsules of *B. hanleyi* and also shows that development includes feeding on nurse eggs and ends in hatching from the capsule as a crawling juvenile. Hatching at the crawling stage is characteristic of Muricidae (Anderson, 1960; MacKenzie, 1961; Murray, 1963, 1964) and, as pointed out by Thorson (1946), dome-shaped capsules of the type laid by *B. hanleyi* have been described for several species of *Trophon*, the genus to which *B. hanleyi* is alternatively referred. Feeding on nurse eggs has not previously been recorded in this genus, but is well known for other muricids (e.g. species of *Murex*, *Neptunea*, *Nucella*: Lebour, 1937; Ankel, 1937, 1938; Thorson, 1935, 1946; Natarajan, 1957; Golikov, 1961) and may yet be found in other species of *Trophon* or *Bedevea*.

Morula marginalba

Spawning and development in Thaididae have been described for a number of species of *Thais* (e.g. Burkenroad, 1931; Chari, 1950; Butler, 1953; Natarajan, 1957), all of which produce egg capsules of the general type exemplified by *M. marginalba*, though the shape of the capsule and the position of the hatching membrane vary in different species. Dakin (1953) has also figured massed capsules of the same general type for *Dicathais orbita*. Only one previous reference has been made to the egg mass of a species of *Morula*, however, that of Ostergaard (1950) for *M.* (= *Drupa*) *dumosa* and the gelatinous egg mass described is so aberrant for the family that it seems likely to be a misidentification.

The mode of development of the numerous encapsulated eggs in *M. marginalba*, and the form of the pelagic planktotrophic veligers at hatching, are closely similar to those of several species of *Thais* (e.g. *T. haemastoma*: Burkenroad, 1931; Franc, 1948; Butler, 1953; *T. bufo*: Natarajan, 1957; *T. javanica*: Natarajan, 1957; *T.* species B, *T.* species C: Natarajan, 1957). The genus *Thais*, however, also includes species with larger eggs which hatch at a later stage of development and are only briefly pelagic (e.g. *T. tissoti*: Natarajan, 1957) and species which develop directly to hatching as crawling juveniles (e.g. *T. emarginata*: Dehnel, 1955). It cannot be assumed, therefore, that the mode of development in *M. marginalba* is characteristic of all species of *Morula*.

Nassarius particeps

In several species of *Nassarius*, the females spawn bottle-shaped capsules containing numerous small eggs which hatch as pelagic planktotrophic veligers

(Lebour, 1937; Thorson, 1946; Natarajan, 1957; Scheltema, 1961, 1962). A similar mode of spawning and development is also described by Amio (1957) for *Tritia festivus*. In a number of Indo-Pacific nassariids, however, the spawn comprises numerous small triangular capsules with confluent base plates, each containing a single egg. It is to this group that *N. particeps* belongs. In *N. costata* and *N. thersites*, the capsules are stalkless, the eggs are relatively small (200 μ and 250 μ in diameter respectively), and hatching occurs as pelagic veligers which probably adopt a planktotrophic existence (Natarajan, 1957). In *N. liviscens*, the capsules have short stalks, the eggs are larger (320 μ in diameter), and development is more direct, with hatching occurring as a veliger in which the velum is relatively small and the visceral mass large and yolky. Development and metamorphosis to a crawling juvenile are completed in this species during a brief pelagic lecithotrophic phase (Amio, 1957). In *N. suturalis* the capsules have long stalks, the eggs are large (probably about 400 μ in diameter), and development appears to be direct, with hatching occurring as a crawling juvenile (Risbec, 1935). *N. particeps*, with its long-stalked capsules and very large eggs, shows the most extreme adaptation to direct development yet known for nassariids with this type of spawn.

Siphonaria denticulata

The egg mass and development of *S. denticulata*, hatching as a small planktotrophic veliger, are similar to those of several species of intertidal siphonariid limpet (Morton, 1955; Knox, 1955; Voss, 1959). In *Kerguelenella stewartiana* and *Siphonaria kurracheensis* the egg capsules contain a greater volume of albumen and the embryos hatch as crawling juveniles in a more typical pulmonate manner (Thorson, 1940; Knox, 1955), but *K. stewartiana* is a sub-Antarctic littoral species from Stewart Island and *S. kurracheensis* is a semiterrestrial species occurring in the Persian Gulf.

CONCLUSIONS

Studies of prosobranch reproduction in the northern hemisphere have shown that planktonic larvae are of common occurrence among temperate species (Thorson, 1946, 1950). Along the New South Wales coast, many more species need to be studied before any corresponding generalization can be made for the 52 species of littoral prosobranch listed by Dakin (1953) as common to this vicinity. At the same time, the species whose development has been recorded are now sufficient in number to warrant grouping into the developmental types distinguished by Thorson (1946, 1950), as follows:—

(a) Viviparous species—none yet described.

(b) Species with a non-pelagic development—5. *Bembicium melanostoma* (Littorinidae), *Glossaulax aulacoglossa* (Naticidae), *Cymatillesta spengleri* (Cymatidae), *Bedeve hanleyi* (Muricidae), *Nassarius particeps* (Nassariidae) (Anderson, 1959, this paper; H. Anderson, 1958; Murray 1962b, 1964).

(c) Species with a very short pelagic life (a few hours to a few days)—5. *Cellana tramoserica* (Patellidae), *Notoacmaea petterdi*, *Patelloida alticostata*, *Chiazacmaea flammea* (Acmaeidae), *Melanerita melanotragus* (Neritidae) (Anderson, 1962, 1965).

(d) Species with a long pelagic, planktotrophic veliger life—11. *Bembicium nanum*, *Bembicium auratum*, *Melaraphe unifasciata*, *Nodilittorina pyramidalis* (Littorinidae), *Velacumantus australis* (Potamididae), *Conuber conicum*, *Conuber strangei* (= *sordida*), *Conuber melastoma* (Naticidae), *Cypraea caput-serpentis* (Cypraeidae), *Xenogalea labiata* (Cassididae), *Morula marginalba* (Thaididae) (Anderson, 1961, 1962, this paper; MacIntyre, 1961; Murray, 1962b, 1964; Ostergaard, 1950).

Thus 11 out of 21 species whose developmental type is known almost certainly have a long planktonic larval life, a proportion which accords with

expectations based on northern hemisphere studies. Further investigation, however, may yet alter this picture, since of the remaining 31 common species, many are archaeogastropods, unlikely to have a long planktonic life, and several others belong to families for which non-plagic development is characteristic.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge my debt to Miss I. Bennett, who generously provided part of the material used in this study, to Dr. D. F. McMichael for advice on matters of taxonomy, and to Dr. G. Thorson for invaluable help in tracing relevant literature. The work was supported by a research grant from the University of Sydney.

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EXPLANATION OF PLATE X

The animal and part of the egg mass of *Xenogalea labiata*.