EGG CAPSULES AND DEVELOPMENT OF FUSUS TUBERCULATUS CHEMNITZ

By

A.M. Eisawy, Ph. D.

Institute of Oceanography and Fisheries. Academy of Scientific Research and Technology, Cairo, A.R.E.

and

A.E. Sorial, M. Sc.,

Institute of Oceanography and Fisheries, Alexandria, A.R.E.

SUMMARY

Fusus tuberculatus lays its brick-red eggs in adherent, transparent, colourless, flattened vase-shaped capsules. Each capsule contains an average of about 250 eggs (180 to 200 μ), of which only 3% develop into embryos and the rest are nurse cells. The first two cleavages are nearly equal. The development proceeds slowly, the gastrula is reached after 6 days and the free swimming larva hatches after 30 to 50 days of spawning. The veliger is provided with a four-lobed velum (the two posterior ones are longer than the anterior), a very powerful foot differentiating into a cylindrical propodium and flat metapodium with a protruding large operculum, and a dark brown fusiform elongated shell of about two whorls (1.5 mms. long and 1 mm. wide). The planktonic life is short, and the creeping young is reached after two days of swimming. The new growth of the shall consists of parallel undulating ridges, and a complete new whorl is formed after 25 days of creeping.

INTRODUCTION AND HISTORICAL

The study of development of *Fusus* (Family Fasciolaridae) is of trifold functions : Firstly to elucidate life history of some Prosobranchs from the Red Sea as in the programme of our Institute. Secondly, it adds to our previous knowledge of the well identified Prosobranch larvae that from an important part of the temporary plankton which is used as food for most of the economical pelagic fishes. Thirdly, *Fusus* is an edible mollusc as well as a predator on some other economic molluscs.

Generally the species of family Fasciolaridae have transparent or semitransparent egg capsules of different shapes. These capsules are fixed side by side on a common base. The spawn and development of few species were described.

In genus Fasciolaria, the egg capsule which was described by Esper (1930) under the name *Tubularia angulosa* was found to be similar to those of *Fasiolaria trapizium* figured by Homell (1922) from the Indian Ocean.

A spawn of *Fas. tulipa* was described by Lund (1834) and it was formerly attributed to *Vesicaria marina* by Sloane (1707) (After Lamy 1928). The egg capsules and development of this species were described by MacMurrich (1887) and Osborn (1886 and 1904). Glaser (1905) studied the cannibalism and excretory organs of the larvae

Lo Bianco (1899) mentioned that the egg capsules of the Mediterranean species *Fas. lignaria* are transparent, flower-shaped and contain small violaceous-red eggs. They were also described by Bacci (1947).

Charles (1929) described the egg capusles of *Fas. gigantae* from Florida.

The egg capsules of*Pleuroploca* (= *Fasc*) *trapozium audouini* were described by Arakawa (1960), Habe (1960), and Amio (1963) from Japan.

The first studied species of genus *Fasciolaria* from the Red Sea was *Fasc. audouini* (Gohar and Eisawy 1967). They described and figured the spawn, larval development and metamorphosis and mentioned that the animal lays separate adherent funnel-shaped capsules with long stalks.

Among genus *Fusus*, Bobretzky described in greater detail the early embryology and the formation of blastula and gastrula of a gastroped which was supposed to be *Fusus* species (?) (After Dakin, 1912, p. 94). Portamann (1955) described the metamorphosis of a *Fusus* species.

Habe (1960) studied the spawn of *F. ferrugineus* and *F. nigrirostratus* from Japan.

Amio (1963) described the egg capsules and larvae of *F. perplexus* and summarized the spawns of other Japanese species in his study on comparative embryology of marine gastropods. He mentioned that the egg-capsules of these species are of the sessile type.

HABITAT, MATERIAL AND METHODS

This species is common at Al-Ghardaqa, and usually lives in the intertidal zone coral flats and between coral weeds normally on sandy bottom. Sometimes it is found in deeper water at depths which may reach down to 3 meters or more. During the breeding season,, the animal comes out to shallower water where they may be exposed to air at low tide. It crawls by its sticky food as in other species of the family.

It is carnivorous, but less than *Fas. audouini,* attacking small economic shells as *Trochus dentatus, Pinctada radiata, Circe arabica, Mytilus variabilis* and others. It differs from *Purpura* and other species of Muricidae in the way that it does not bore the shell before eating the prey, but, as in *Fasc. audouini,* it introduces its proboscis into the opening of the shell and sucks the juice of its victem. The animal itself is attacked by other carivorous prosobranchs such as *Murex incarnatus.*

Its flesh is edible and is used also as fish bait, and its shell is used for making ornamental objects. The empty shell was observed as shelters for the hermit crab *Coenobita* species.

The egg capsules of this species are separate with a common basal membrane covering the substratum. They are laid in groups near one another in the rearing aquarium. It was observed that the egg capsules are eaten by the brittle stars in the sea and by xanthid crab (*Chlorodiella nigra*) in the laboratory.

The specimens were collected from the intertidal zone of the area round the Marine Biological Station at Al-Ghardaqa on the north western coast of the Red Sea. They were kept in vivaria where they live in good condition for long time. Observation of the adult at the sea was carried out by the aid of diving equipment. Description and Illustration of egg capsules and the developmental stages were made from living material. Microscopic drawings were made from narcotized and fixed stages with the aid of a camera lucida. Preservation and narcotization of developmental stages were done by the same method described in other Prosobranch species (Gonar & Eisawy 1963 & 1967, Eisawy & Sorial 1970).

SPAWNING AND EGG CAPSULES

The spawning season of *F. tuberculatus* extends from February till the end of May, at a water temperature ranging between 22° and 27°C. In this season several individuals appear in shallow water near the Station for pairing and deposition of egg capsules. The egg capsules are laid in shallow crevices on a solid substratum of rocks, empty shells or pieces of dead corals. In all cases the capsules are fixed at the lower surface of the substratum far away from direct sunlight. In indoor cement aquarium, this species lays its egg capsules shortly after mating on the walls near the water surface or on rocks which were formerly kept in the aquarium.

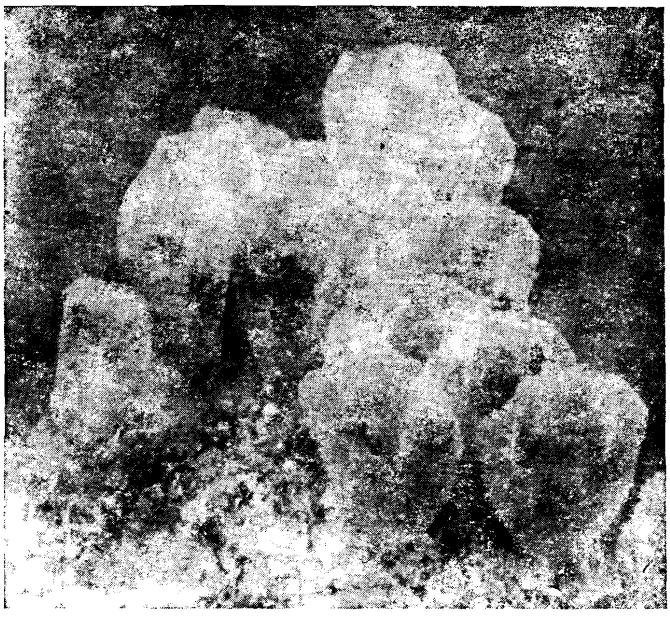
The egg-laying process usually starts in the morning and ends in the afternoon, but in very few cases the animals start by night and continue during the day. The animal takes about 30 minutes to produce one capsule.

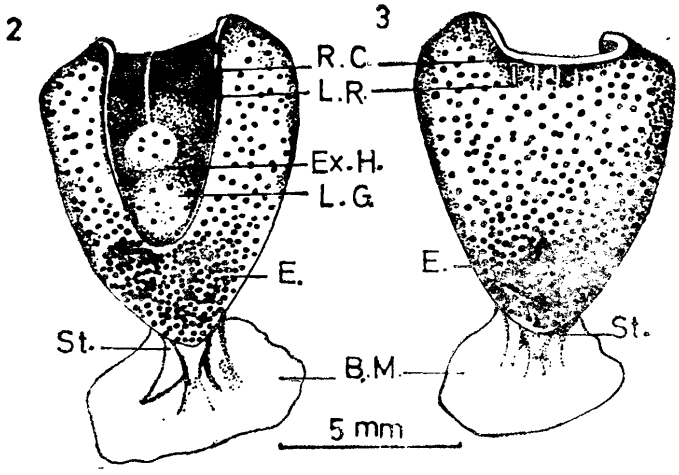
The animal spawns twice in the breeding season. At each time the single individual deposits a group which consists of 10—18 capsules. This species is also gregarious in its spawning, as in other species of Fasciolaridae, Thiadidae and Muricidae and others. Groups of about 120 capsules were observed in the spawning area, and these might be laid by several individuals.

The egg capsules (Fig. 1), which are laid by a single individual are separate, arranged in a group standing upright, side by side and have confluent bases which form a continuous common basal membrane with their walls never touching.

The egg capsule (Figs. 2 & 3) is leathery nearly transparent, colourless and flattened vase-shaped. Its size, as in many prosobranchs, varies accordnig to that of the parent animal. It measures about 11 mms. long and 7 mms. in greatest breadth. At one broad side of the capsule, there is a longitudinal median goove which extends from the top till a little below the middle of the capsule. This groove is about 6 mms. long and 3 mms. in the greatest breadth. It is deeper at the top, becoming shallower on going downwards and is surrounded from the top by a small raised collar which

extends on the sides. In the middle of this groove there is a circular transparent exit hole (about 1.5 mms. in diameter) and a longitudinal low ridge which extends from the top till the exit hole. The second broad side is convex with some small low ridges extending shortly from top downwards for a distance of about 0.5 to 1 mm. The egg capsule is attached to the substratum by a slightly broad base through a short 4—branched stalk (about 1.5 — 2 mms. long).





The eggs are suspended in transparent mucus which fills nearly the whole cavity of the capsule. This mucus fluid coagulates to an albumin-like substance on coming in contact with sea water. The number of contained eggs in a single capsule is about 750 eggs (average of 10 capsules of different sizes).

The undevelopd egg (Fig. 4) is brick-red in colour, spherical in shape, coarsly granulated, and measures about 180 μ to 200 μ in diameter. Not all eggs of the capsule develop into larvae, but only few of them are true ova while the remainder are yolk spherical or nurse cells. It is impossible to differentiate between these two types of eggs when they are freshly deposited because of their great similarity in shape and diameter. The distinction between them is manifested at the time of the first cleavage. The true egg divides into two nearly equal blastomeres, while the nurse cell gives successive small buds which separate and are then ingulfed by the embryos. Actually the nature of these nurse cells or yolk spherules are obscure. Some authors considered them as unfertilized eggs, others suggested that as segmentation takes place in both this may be either due to an actual difference in the laid egg or fertilization takes place by different kinds of spermatozoa. Portmann (1925 & 1930) suggested that, in *Purpura,* they are the result of fertilization by apryne spermatozoa.

DEVELOPMENT

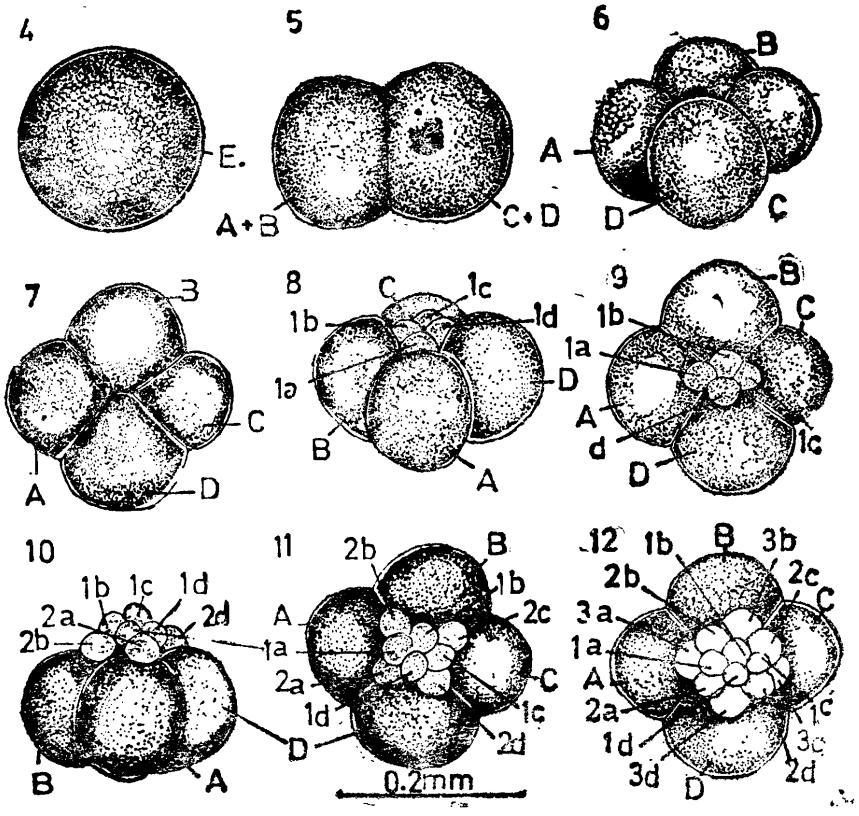
The development of *F. tuberculatus* proceeds rather slowly and depends mainly on the water temperature during the breeding season. The higher the temperature the shorter the embryonic life and vice versa. At the beginning of the season (February) when the water temperature is about 22°C (average) it lasts 45 to 50 days; and extends 30 days only at a temperature average of about 27°C (end of April).

As mentioned above, not all eggs develop into embryos but most of them are used as food by the growing stages. Only 5 to 25 veligers (average of 20 capsules is 22 larvae) hatch out from a single capsule, and thus about 3% of eggs form embryos.

The following description and the corresponding figures are for egg capsules laid at the third of February and hatched out at 23rd of March 1967.

After spawning, the egg passes through a resting stage of 3 to 5 days without cleavage resembling those of *Fas. audouini* (Gohar and Eisawy 1967). Also segementation does not begin in all eggs at the same time, and this results in the presence of different developmental stages in the capsule. This phenomenon is accompanied with difference in the ingulfing power of nurse cells and the result is the appearance of different sizes in embryos of the same capsule. Accordingly the hatched larvae differ in size as well as in growth, and they vary between the normal veligers and the creaping young which are described below.

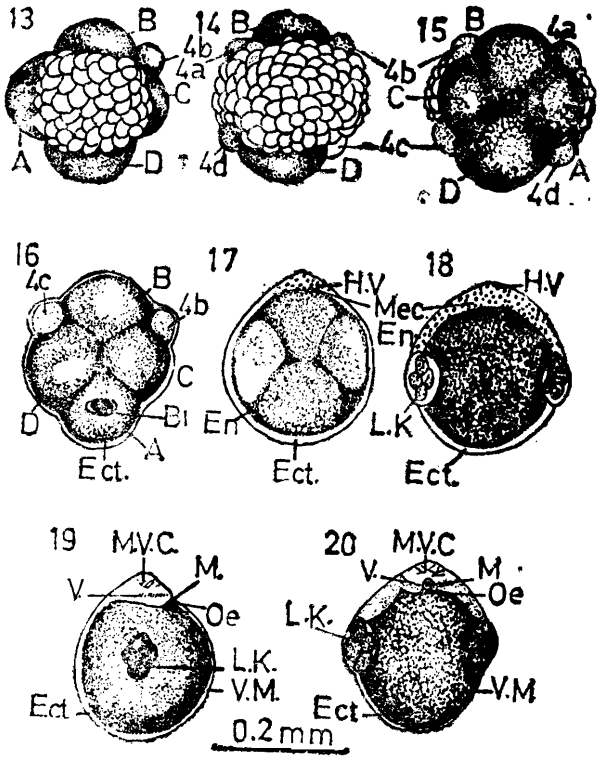
The first cleavage in real eggs, gives rise to two nearly equal blastomeres (Fig. 5). The second cleavage which occurs after three hours is perpendicular to the first and a stage with 4 cells is obtained' in which the cell 'D' is slightly larger than the other 'A', 'B' and 'C' (Figs. 6 & 7).



The third cleavage (first quartette) is attained after another three hours by cutting off 4 small micromeres in a dextral position to the lower 4 larger macromeres (Figs 8 & 9). The second quartette follows the first after another 6 hours and another 4 small micromeres (slightly larger than those of the first) are cut off sinistrally (Figs. 10 & 11). The third quartette is dextral and a stage with 12 micromeres and 4 macromeres is obtained (Fig. 12). After 18 hours from the beginning of segmentation, the micromeres of the first three quartettes divide sucessively forming a small heap of cells at the animal pole of the embryo. At the same time the fourth quartette proceeds gradually beginning with 4 b, followed by 4 d, 4 c and lastly 4 a (Figs. 13 to 15). The comparatively larger micromeres of the fourth quartette are dextral in position and are slightly located outside between the macromeres. The micomeres divide rapidly and grow over the macromeres forming a thin transparent layer which represents the primordium of the ectoderm. When the micromeres of the fourth quartette and the macromeres are nearly surrounded by the ectoderm, the blastula stage is formed, with a blastopore at the vegetative pole (Fig. 16). The boundaries between the fourth quartette and the macromeres gradually disappear. When they arrange themselves in such a manner to form the endoderm and the mesoderm the gastrula is obtained (Fig. 17). This stage is completely formed after two days from the beginning of segementation (i.e. five days from spawning). It is nearly cirular and measures about 263 μ in diameter. At the next day of gastrulation, two pairs of circular transparent larval kidneys are formed on each side of the embrgo Fig. 18) and the boundaries between the macromeres completely disappear forming a central visceral mass.

The embryo takes a rest of about two days without formation of other organs except slight elongation of its body and formation of anterior head vesicle.

The further formed organs are the circular mouth which leads to a very short oesophagus and two lateral bands of cilia which are the primordium of the velar lobes at sides of the mit-velar cone (Figs. 19 & 20). This stage is about 260 μ long and possesses slightly enlarged larval kidneys and starts to show rotation inside the egg capsule.



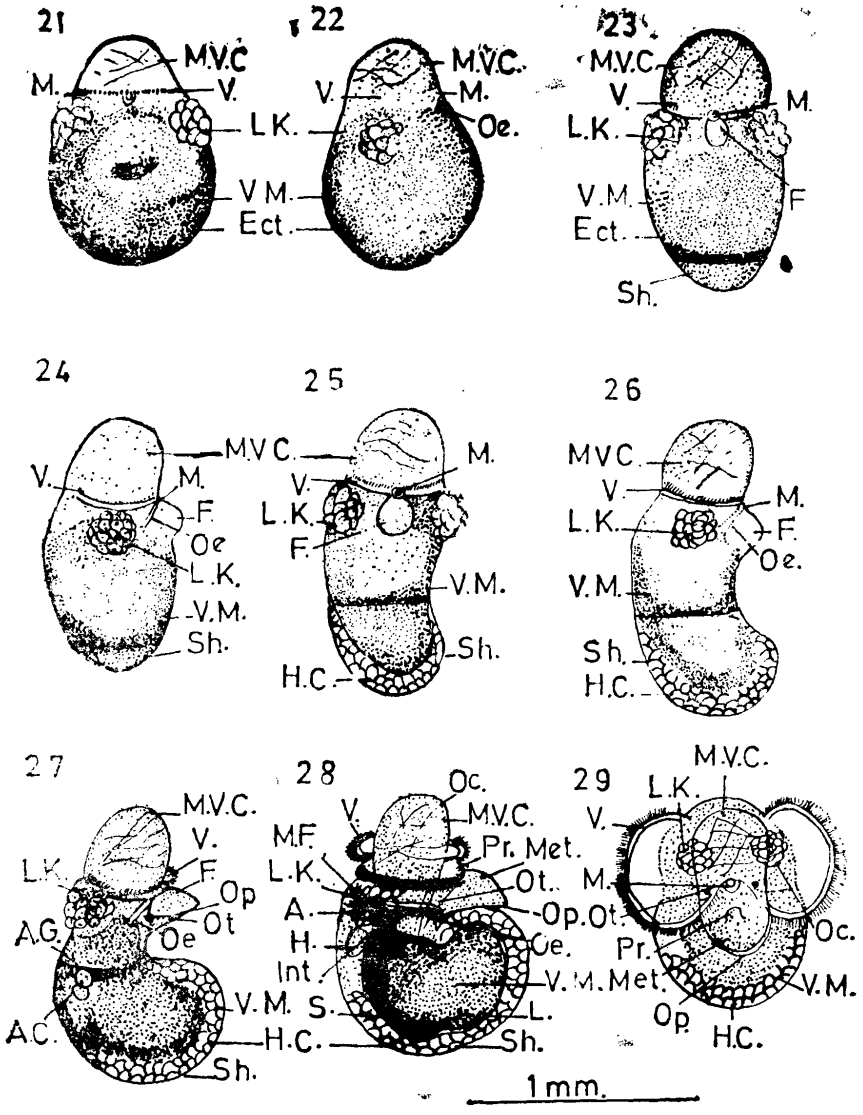
After the former stage the organogensis of the embryo stops for a period of about one week. During this period the embryo starts to feed vigorously on the nurse cells which disintegrate into very small pieces which are swallowed and stored in the visceral mass. At the end of this period when all nurse cells are ingulfed the embryo which is about 15 days old is accordingly very large in size, measuring about 955 μ in length (Figs. 21 & 22). All previously formed organs increase in size and the larval kidneys divide into numerous transparent bulbs which are situated on the sides of the embryo just below the velum.

After 17 days from spawning, an elongated embryo which measures about 1.078 mms. long is formed (Figs. 23 & 24). The embryo aquires newly developed organs in addition to the enlargement of the previously formed ones. The foot develops as on oval protrusion just below the mouth, and the primordium of the shell is formed as a transparent basal disc-like structure. The two velar lobes elongate and slightly protrude out of the body. The rotatory movement of the embryo is faster. The larval kidneys are divided and this leads to great increase in number of the small bulbs.

The development proceeds further and the embryo of 20 days old, measures about 1.232 mms. long and 462 μ in greatest breadth (Figs. 25 & 26). This stage is characteristic in shape, being longer but narrower, as a result of the special development of its sheli. All other organs enlarge in size, especially the shell, velar lobes and foot, as well as the increasing number of the larval kidneys. The shell is about 416 μ in length 460 μ in breadth, comparatively narrow, slightly curved and surrounds the lower part of the body. The important feature of this stage is the transformation of the lower part of the visceral mass into transparent hexagonal cells.

After 24 days from spawning, these embryo grow rapidly especially in breadth due to the characteristic development of the shell (Fcg. 27). The length of the embryo is about 1.160 mms. while the breadth becomes about 690 μ. The anal gland, anal cells, two symmetrical otocysts (on the base of the foot) and a small transparent operculum are newly developed. The other organs increase in size, especially the foot. the hexagonal cells and the velar lobes are protruded more from the body with long cilia. The shell is now about one whorl and measures about 450 μ in length and 690 μ brood. Its dorsal side is more developed than the ventral one this results in broadening of the embryo and shortening of its length.

After 28 days from spawning an advanced stage is reached (Figs. 28 & 29). Several new organs are developed as well as the enlargement of the previously formed ones. Two eye spots on the sides of the mit-velar cone, a circular mantle fold protruding from the shell, single chambered heart, anus and short intestine are newly formed. The velum surrounds completely the slightly reducd mit-velar cone, and each lobe is oval with longcilia and measures about 462 long. The foot is about 308 μ long and is differentiated into a small contractile upper propodium and a lower oval metapodium below which is protruded a thin transparent operculum. The visceral mass begins to show tendency towards differentiation into its components and the hexagonal cells which are apparently nutritive are slightly reduced due to the consumption of the embryo. The shell twists a little and is slightly more than one whorl, measuring about 847 μ long and 790 μ in breadth.



The 30 days old embryo, is characterised by the development of two small tentacles on the sides of the slightly reduced mit-velar cone (Figs. 30 & 31). The velum with its cilia enlarges in size and each lobe is about 539 μ long. The foot and its operculum are larger, and the former is about 369 μ long. The visceral mass is differentiated into two hepatic lobes (not completely divided), and a

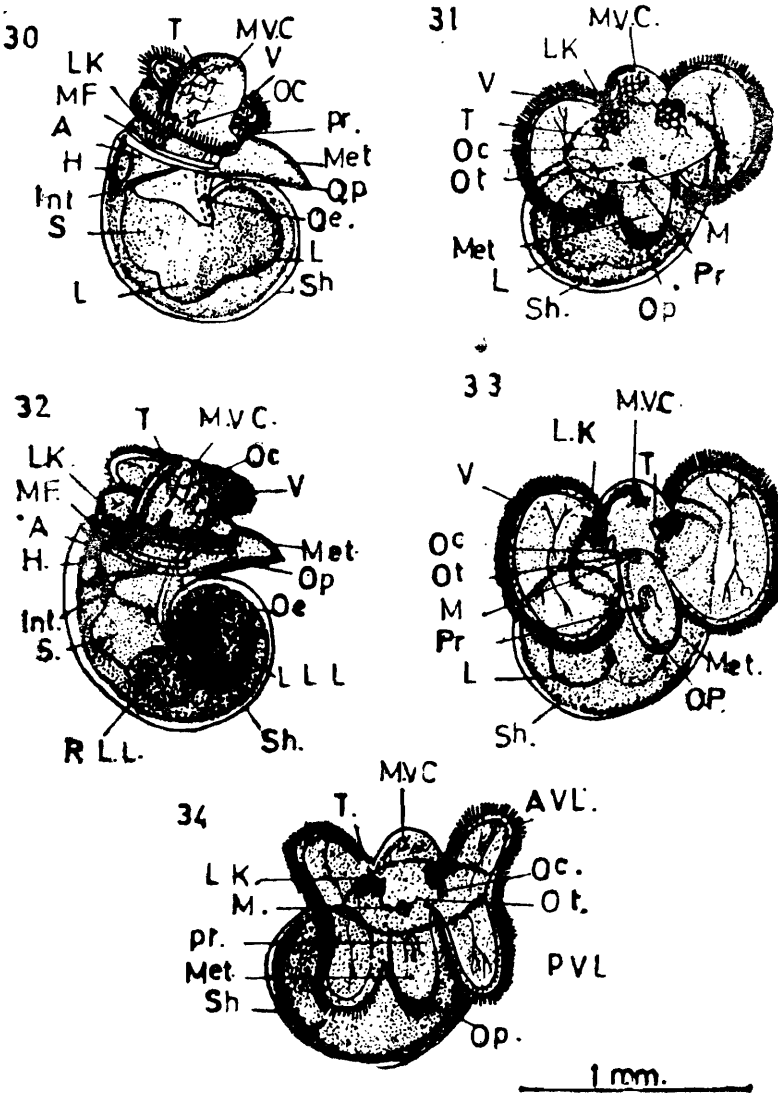
large stomach. This is accompanied by elongation of the oesophagus and intestine, and slight reduction of the hexagonal cells. The larval kidneys are reduced in size and reduced in number, and are slightly shifted towards the dorsal side of the embryo just below the velum. The shell starts to be coloured with faint brownish tint and measures about 955 μ in length and 847 μ in greatest breadth.

In the 32 days old, embryo the liver differentiated into two asymmetrical lobes (Fig. 32&33). The velum is greatly elongated, and each lobe is about 646·8 μ. The foot with its propodium, metapodium and operculum enlarges and measures about 447 μ long. The mantle fold becomes thick and ornamented with irregularly scattered black patches, especially on its dorsal side. The mit-velar cone and the larval kidneys are more reduced and the hexagonal cells are nearly absorbed. The shell acquires a dark brown colour which tends to hide the internal organs, and is about 1.047 mms. long and 803 μ in greatest breadth.

In an embryo of 34 days each velar lobe is secondarily divided into two unequal lobes, the anterior one is about 310 μ long divided into two unequal lobes the anterior one is about 310M long and the posterior is about 415 μ long (Fig. 34). The mit-velar cone and larval kindeys are more reduced in size. All other organs increase in size, especially the foot which is about 462 μ long and now possesses black pigments regularly scattered at its border.

The shell is of about 1.25 whorls and measures about 1.093 mms. long and 893 μ in the greatest breadth. It acquires the brownish colour which hides completely the internal organs.

Development proceeds qcickly and the embryo of 36 days is characterized by the great reduction of the mit-velar cone and larval kidneys (Fig. 35). The four lobes of the velum are elongate, the anterior lobes are about 400 μ long while the posterior measure 600 μ long. The foot becomes larger and more contractile, with more distinct black pigments on its border, and measures about 630 μ long. The shell is now about one & half whorls, and is about 1.2 mms. long and 900 μ in greatest breadth.



In a stage 40 days old, the mit-velar cone and the larval kidneys are completely absorbed (Fig. 36). All other organs enlarge in size, especially the velum whose anterior lobes measure 700 μ long and the posterior are 960 μ long. The contractile foot is about 800 μ long boardered with more concentrated black pigments. The mantle fold becomes more thick and the black patches are more condensed at its right side. Two rows of gills develop at the inner surface of the dorsal side of the mantle fold. The shell is slightly more than one and half whorls and measures 1.4 mms. long and 960 μ in the greatest breadth.

The embryo remains inside the capsule for another 10 days before hatching. During this period it moves as a small veliger showing advancing growth in all organs in all organs except the velum which shows its maximum length on the 47th day (Fig. 37). In this stage, the anterior lobes of the velum are about 1 mm. long while the posterior ones measure about 1.1 mms. long and because of their great length they are usually twisted round the shell. The foot becomes more contractile, powerfull, with protruding large operculum, measuring about 820 μ long and is used for short instantes in creeping.

From the last stage, the embryos move slowly near the exit hole of the capsule, and their organs increase in size, except the velum which is gradually absorbed till hatching of the normal veligers.

HATCHING AND METAMORPHOSIS OF VELIGER

As mentioned above, devlopment does not proceed equally in all embryos of the same capsule. Most of the larvae hatch out as normal swimming veligers but few of them emerge in advanced stages which may reach up to the crawling young. Also the embryonic period varies according to the water temperature and ranges between 30 and 50 days.

In the present description, commonly hatching of the new veligers takes place after 50 days of spawning (Fig. 38). It is slightly active swimmer, moving just below the water surface and is more attracted towards the brighter area of the rearing basin. It possesses a 4-lobed velum which is slightly more reduced than that of the previously described embryonic stage, and this means that it will spend a short planktonic life. The anterior velar lobes measure about 800 μ long while the posterior ones are about 920 μ long. The veliger is provided with two violet eye-spots which are situated at the swollen bases of two long tentacles. The mantle fold is thick, slightly reflected from the opening of the shell, ornamented with black patches which are more concentrated at the right side, and carries two rows of small gills at its inner dorsal side. The circular mouth is situated below and between the posterior velar

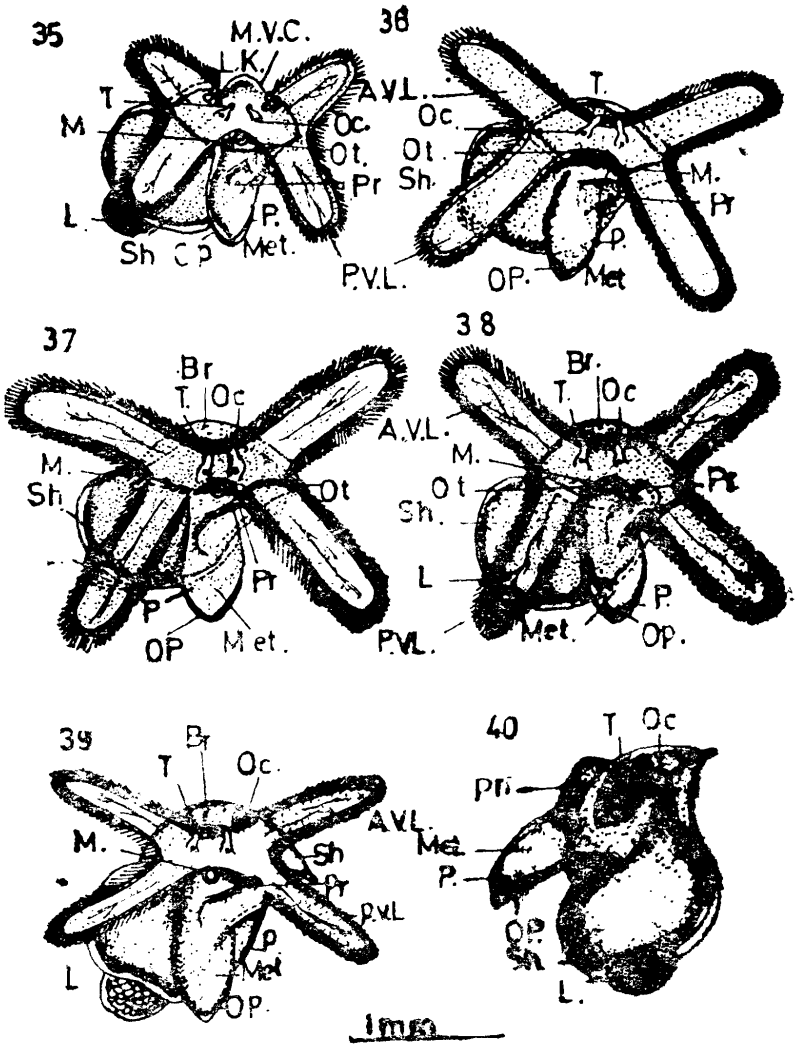
lobes and leads to a long oesophagus. The visceral mass does not appear through the brown shell, but from the previous description of the embryonic stages, it is differentiated into its normal components with left lobe filling the whorls of the shell. The foot is large (about 890 μ long), powerfull, capable of contraction, and consists of an upper cylindrical propodium and a lower flat elongated metapodium to which a transparent slightly protruding operculum is attached. It possesses black pigments which are irregularly scattered on its surface and more concentrated at its border. The veliger is provided with dark brown fusiform elongate shell (Fig. 41), which consists of two whorls and measures about 1.48 mms. in lenght and 1 mm in the greatest width.

The veliger larva remains for another one or two days in the planktonic life, showing further growth in all organs except the velum. and then transforms to the creeping young. In few cases the creeping young hatch out directly from the egg capsules.

After one day from swimming, the veliger (Fig. 39) has a further reduced velum whose anterior lebes are about 700 μ and posterior ones are 800 μ long. Its foot grows more, especially the propodium, and the metapodium is about 900 μ long. The larva swims for short instances, and spends longer periods at the bottom of the aquarium creeping with its foot. The new growth of the shell (Fig. 42) is nearly transparent, consisting of longitudinal lines and is about 115 μ wide.

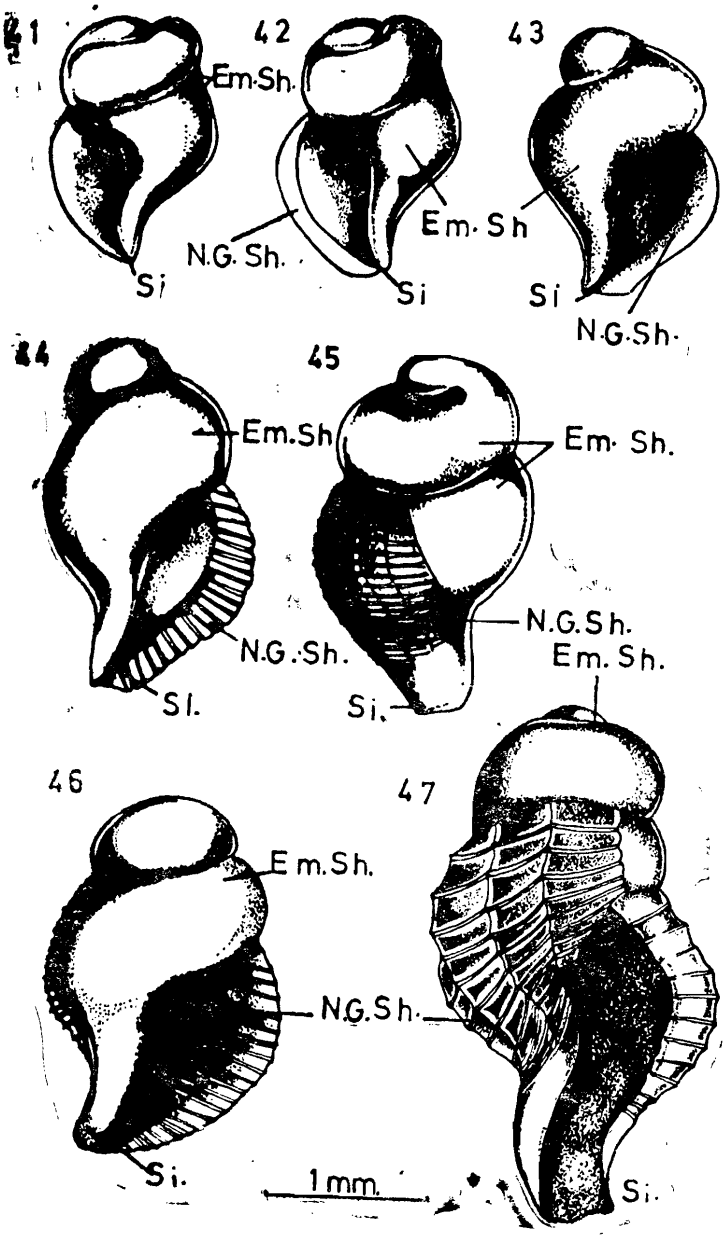
After another day, the velum is completely resorbed and the creeping young is attained. (Fig. 40). The foot is powerful, large (about 1 mm. long) and contracts quickly inside the shell whose opening is closed with thick oval operculum. The shell (Fig. 43) is dark brown in colour, a little more than two whorls and is about 1-7 mms. long by 1.06 mms. in greatest width. The new growth is still striated longitudinally, pale brown in colour and measures about 180 μ to 230 μ in width.

The growth of the young proceeds gradually with the enlargement of its organs. On the third day of creeping, the new growth of the shell is characterised by the formation of parallel transverse whitish ridges which are more raised near the body whorl. In a young stage about 5 days old, the shell (Fig. 44) is about 2.045 mms. long by 1.235 mms. in the greatest width, and the new



growth is about 285 μ wide. After that stage the new growth growth is about 285M. in width. After that stage the wew growth of the shell and its transverse ridges grow more but are undulated longitudinally. In a young of about 2.14 mms. long by 1.33 mms. in greatest width ; the new growth is about ¼ of a whorl and measures about 477 μ in width. After another 4 days, the new growth is about ½ a whorl and the whole shell measures about 2.19 mms. long and 1.428 mms. in greatest width (Fig. 46): The first whorl of undulating new growth of shell is reached after about

25 days of creeping (Fig. 47.) The lines between the raised transverse whitish ridges and the embryonic shell as well as the outer area of the column of the body whorl are dark brown in colour. The shell which is now 3 whorls, measures 3.01 mms. long by 1.67 mms. in the greatest width.



LIST OF ABBREVIATIONS

A. = Anus
A.C. = Anal cell
A.G. = Anal gland
A.V.L. = Anterior velar lobe
Bl. = Blastopore
B.M. = Basal membrane
Br. = Rudiment of gills
E. = Egg
E.C. = Egg capsule
Ect. = Ectoderm
Em.Sh. = Embryonic shell
Ex.H. = Exit hole
F. = Foot
H. = Heart
H. C. = Hexagonal cells
Int. = Intestine
L. = Liver
L.G. = Longitudinal groove
L.K. = Larval kidney
L.R. = Longitudinal ridge
M. = Mouth
Met. = Metapodium
M.F. = Mantle fold
M.V.C. = Mid-velar cone.
N.G.Sh = New growth of shell
Oc. = Ocellus
Oe. = Oesophagus
Op. = Operculum
Ot. = Otocyst
P. = Pigment
Pr. = Propodium
R.C. = Raised coller
S. = Stomach
Sh. = Shell
Si. = Siphon
St. = Stalk
T. = Tentacle
V. = Velum
V.M. = Visceral mass

DISCUSSION

The adherent egg capsules of *Fusus tuberculatus* are nearly similar to those of other species of family Fasciolaridae (*Fusus perplexus, F. ferrigineus, F. nigrirostratus* and other species of *Fusus, Fasciolaria lignaria, Fasc. tulipa, Fasc. gigantea, Pleuroplaca* (= *Fasc.*) trapizium and *Fasc. audouini* of the Red Sea), but differ in general shape and some specific structures. All these species lay their eggs in separate transparent or semitransparent capsules with a common basal membrane. In our species, the capsule has a short stalk, and thus differs from both the sessile ones of the Japanese *Fusus* species and the long stalked ones of other *Fasciolaria* species. The studied species agrees also with the other species of the family in the fact that the majority of the eggs in a capsule serve as food for the growing embryos. The number of nurse cells differs from one species to another and accordingly the number of growing embryos are variable. In our species about 3% develop into embryos, while in *F. perplexus* about 8%, in *Fasc. audouini* about 15 %, and in *Fasc. tulipa* less than 0.3 % do so. Thorson (1950). who has great experience of Prosobranch development from different parts of the wrold, mentioned that the number of nurse cells varied according to the geographical distribution of the same species. These nurse cells are either swallowed completely as in *Fasc. tulipa,* or are first cruched into small granules before ingulfing as in our species and *Fasc. audouini.* The early embryology of *F. tubereculatus* is nearly similar to that of *Fusus* species (?) described by Borbretzky (after Dakin 1912), where the first two cleavages result in the formation of four nearly equal blastomeres. These cleavages differ from those of *Fasc. audouini* : where highly unequal blastomeres are obtaine-d. During the development of *F. tuberculatus,* organogenesis of the embryo stops for a certain period until all nurse cells are completely ingulfed, but in *Fasc. audouini* the development proceeds while the embryo is feeding. In our species, the larvae hatch out in the mojority as free swimming veligers with slightly absorbed 4-lobed velum, some as swim-crawl stages, and few as crawling young. Thus they are nearly similar to those of *Fasc. audouini* of the Red Sea, and differs from those of *F. perplexus* which hatch in the crawling young.

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