# THE SPAWNING AND DEVELOPMENT
# OF *TROCHUS (TECTUS) DENTATUS* FORSKAL

By

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## INTRODUCTION AND HISTORICAL

The Trochidae of the Red Sea have been fairly thoroughly treated by systematists but only the egg-masses and development of *Trochus erythraeus* Brocchi were studied (Gohar and Eisawy 1963). *Trochus (Tectus) dentatus* Forskal is the largest and most important member of the family in the Red Sea. The meat is valued as food and the shell is utilized for botton manufacture, and is therefore of commercial importance.

Several authors studied the spawning and development of different species of Trochidae in other regions of the world. From them the following can be mentioned : Grant 1827, Jeffreys 1865, Salensky 1872, Haeckel 1875, Robert 1898, 1901 and 1902, Boutan 1899, Lamy 1928, Moorhouse 1932, Thorson 1935, 1940 and 1946, Gersch 1936, Lebour 1936 and 1937, Gaillard 1952 and 1963, Ducros 1957, Habe 1960, Vinogradova 1960, Kojima 1961 and 1962 and others. They worked on the following species : *Trochus* sp., *Tr. obeliscus*, *Tr. niloticus*, *Tr. turbinatus*, *Tr. varius*; *Gibbula magus*, *G. albida*, *G. divericata*, *G. cineraria*, *G. pennanti*, *G. tumida*, *G. umbilicalis* = *Tr. obliquatus*; *Monodonta lineata*; *Margrites helicinus*, *Mar. cinerea*; *Calliostoma papillosum* = *Tr. granulatus*, *Cal. zizyphinum* = *Tr. conuloides*; *Cantharidus striatus*, *Can. exasperatus*, *Can. cleondi* = *Tr. milligranus* = *Cal. miliare*, *Can. montagui*, *Can. japonicus*, *Can. callichroa jessoensis*; *Skenea surpuloides* and other species.

These species can be divided, according to the type of their spawns into two groups. The first group includes : the deep-sea type of *Tr. varius*, *Tr. obeliscus*, *Tr. erythraeus*, *Mar. helicinus*, *Cal. zizyphium*, *Cal. papillosum*, *Can. striatus*, *Can. exasperatus*, *Can. japonicus*, *Can. callichroa jessoensis*, *G. tumida* and other species. The eggs which are laid in an accumulated mass, are usually large ranging between 140-300 μ (except in *Tr. erythraeus* about 75 μ across), and the developmental period is mostly long (72-180 hours). In all species, except the deep-sea variety of *Tr. varius* and *Tr. erythraeus*, the veliger stage is passed within the egg-case and the young hatched in the crawling stage. The second group includes : the coastal form of *Tr. varius*, *Tr. niloticus*, *Gibbula magus*, *G. cineraria*, *G. umbilicus*, *G. pennanti*, *Monodonta lineata* and other species. In this group, the eggs are shed singly into the surrounding water and are usually small (105-250 μ). The developmental period is comparatively short (about 20 hours) and the larvae come out as free swimming veligers.

## HABITAT, MATERIAL AND METHODS

*Trochus dentatus* (Fig. 1) lives in shallow waters of coral reefs round Al-Ghardaqa in the Red Sea, as well as along rocks and coral patches in Suez Bay. It is usually abundant on edges of reefs and islands that are open to direct action of dominant winds, prefering the weather side where there is very little silt and mud, but abundant food and maximum aeration. On the edges of islands it moves up and down with the movement of the tide but keeping mostly near the bottom. Sometimes it comes out above the water surface where it may remain a long time. The animal is herbivorous, scraping the algae from the rocks and boulders by its strong and rasping radula.
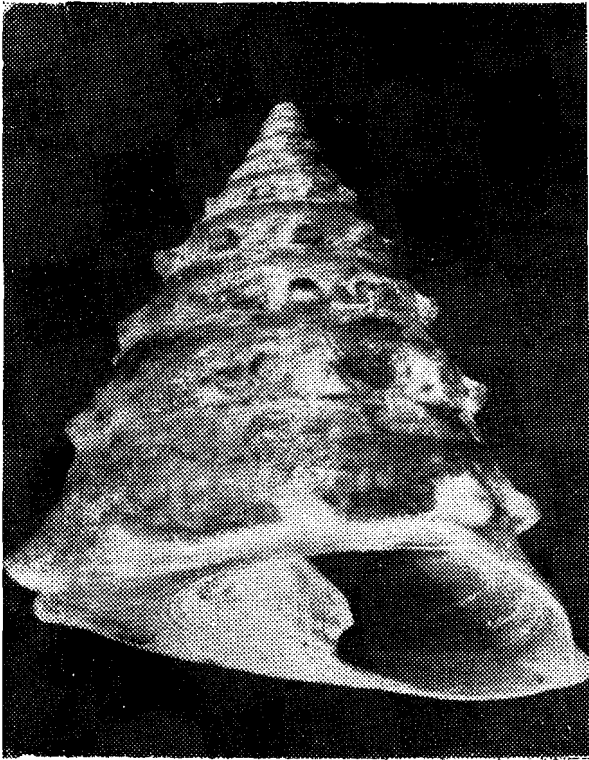
Fig. :

1.—Cleaned shell of *Trochus dentatus.*

The materials were gathered by swimming and wading in shallow water and collected by hand. The specimens were cleaned carefully by a brush and four to six animals were kept in glass bottles of about 50 litres capacity. Filtered running sea-water was used, where the draining water was filtered with very fine plankton net. Fresh algae were added daily for feeding of the animals.

It was succeeded in promoting spawning by stimulation produced by alternating warm and usual sea water (as in Fig. 2). The temperature of normal sea water ranged from 24° to 30°C during the breeding season, while that of warmer water was usually about 5° to 8°C higher.

The eggs, which were laid free in the water, were kept in the laboratory in glass aquaria till the larvae hatched out. The newly hatched veligers were kept in separate glass aquaria and were daily pipetted, washed and then placed into a fresh supply of sea-water which had been filtered through cotton woll. The sea water was aerated by a copious supply of air bubbles from an aerating system.

Description and illustrations were made from living material. Microscopic drawings were done from narcotized and fixed stages, with the aid of a camera lucida.
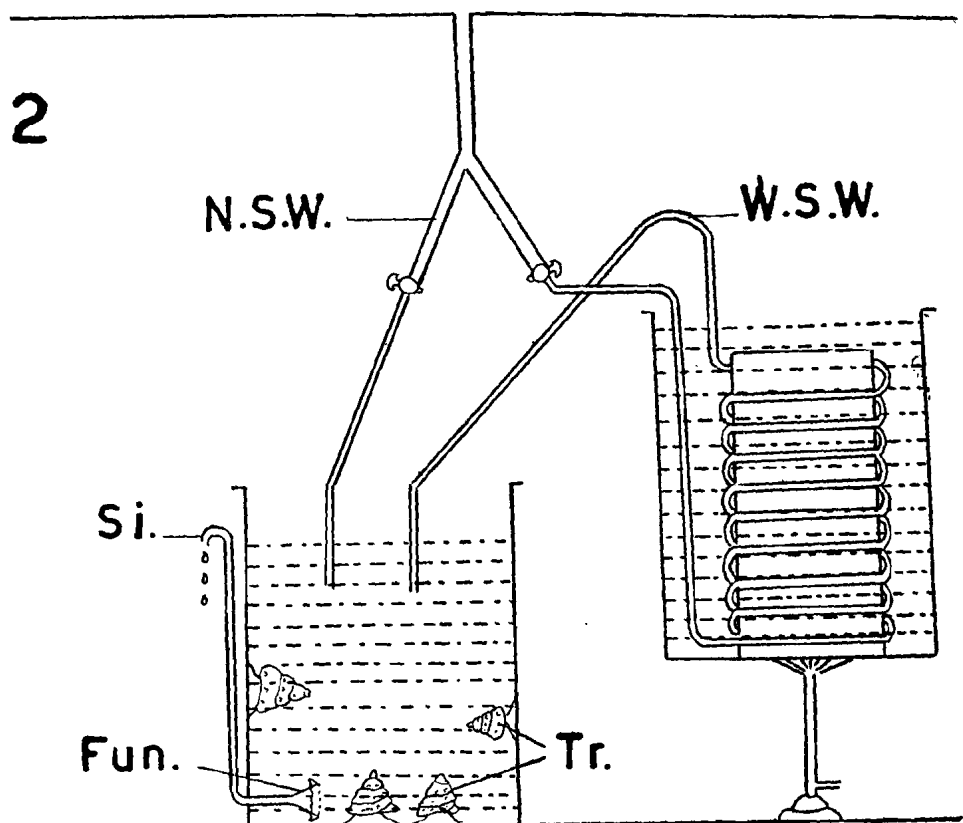
FIG. :

2.—An apparatus for promoting spawning by stimulation produced by alternating normal and warm sea water.

## SPAWNING AND EGGS

Sexes of *Trochus dentatus* are separate, without external sexual differences but internally the gonads, which are situated within the apex of the shell of mature or nearly mature specimens, are white or creamy in males and light blueish green in females.

The spawning season extends from April to July, at a water temperature ranging between 20° and 30°C (optimum temperature 27° to 28°C). Isolated numerous eggs are deposited in the surrounding sea water, usually at the morning. The eggs are contaminated with transparent mucus, floating in the sea water for short time and soon settled down on the bottom, floating again at stirring of the water (similar to eggs of *Trochus niloticus* Moorhouse 1932). The egg (Fig. 3) is nearly spherical, 200 to 225 μ in diameter and is surrounded by a thin

large vitelline membrane varying in size from 260 to 480 μ mostly about 400 μ, in diameter. Sometimes the latter is oval and measuring about 450 to 510 μ, in long axis and 400 to 460 μ, in short axis. The yolk globules are either greenish or blueish, and are concentrated at the vegitative pole of the egg, and become sparsely dispersed towards the animal pole where sometimes a small clear area may be seen.

## DEVELOPMFNT

The development of this species proceeds very rapidly, taking only three to four hours from the time of spawning to hatching, at a temperature average of 27.5°C.

Shortly after spawning, two polar bodies are extruded at the animal pole of the egg. The first cleavage starts 5 to 10 minutes after oviposition, giving rise normally to two nearly equal blastomeres which are attached usually along a comparatively long area (Figs. 4 and 5) and rarely along a narrow area in between (Fig. 6). In abnormal cases two unequal cells are noticed (Figs. 7-9). At the two cell stage the green or blue yolk globules become clearly condensed at the vegitative side.

The second division, in normal and nearly equal cells, is perpendicular to the plane of the first, resulting in the formation of four nearly equal blastomeres (Figs. 10 and 11) of which one cell D is slightly larger than the others. Mostly there is no cavity at the centre, but the embryos arising from stages of Fig. 6 have a comparatively large cavity (Fig. 12). In these normal stages the two cells divide mostly simulteneously, but in some cases the cell of A + B divides first (Fig. 13). The second division in abnormal and unequal cells gives a very large D cell and other three cells as buds on its side (Fibs. 14 and 15).

Later, the first quartette is formed where four smaller dextral micromeres at the animal pole of normal embryos (Figs. 16-18). The difference in size between the micromeres and macromeres is not very great. In abnormal stages, this division gives the stages of Figs. 19 and 20. By the lapse of few minutes, the macromeres of normal embryos divide again, this time the spindles of cleavage are inclined in a laeotropic direction. The second quartette is markedly larger than the first. Before its complete formation, the micromeres of the first one start dividing (Fig. 21), getting at the end of this quartette an embryo (Figs. 22 to 24) with 16 cells (8 small micromeres from the first quartette, 4 larger micromeres from the second quartette and 4 largest macromeres).

The third quartette, formed by the next and dextral division, starts with 3a cell (Fig. 25). The micromeres of that quartette are smaller than those of the second one. Also before the complete formation of the third quartette the micromeres of the second one and the original micromeres of the first one divide giving rise at the end to an embryo (Fig. 26) with 28 cells (12 small micromeres from the first quartette, 8 larger micromeres from the second, 4 small micromeres from the third and 4 largest macromeres).

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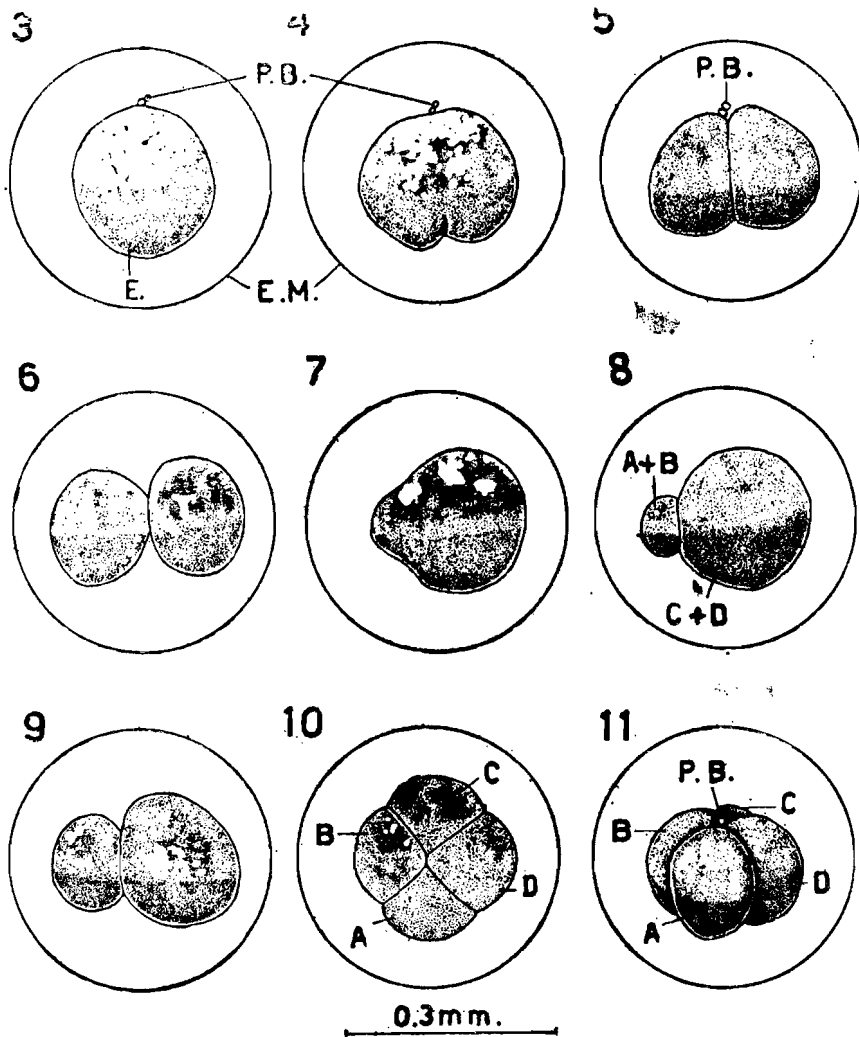
Fig. :

3.—Undeveloped egg surrounded by its large egg-membrane.

4.—Start of first normal division in the egg.

5.—& 6.—Embryo in the two equal blastomere stage.

7.—Start of first abnormal division in the egg.

8.—& 9.—Embryo in the two unequal blastomere stage.

10.—& 11.—Top and lateral views of embryo in 4 equal compact cell stage.
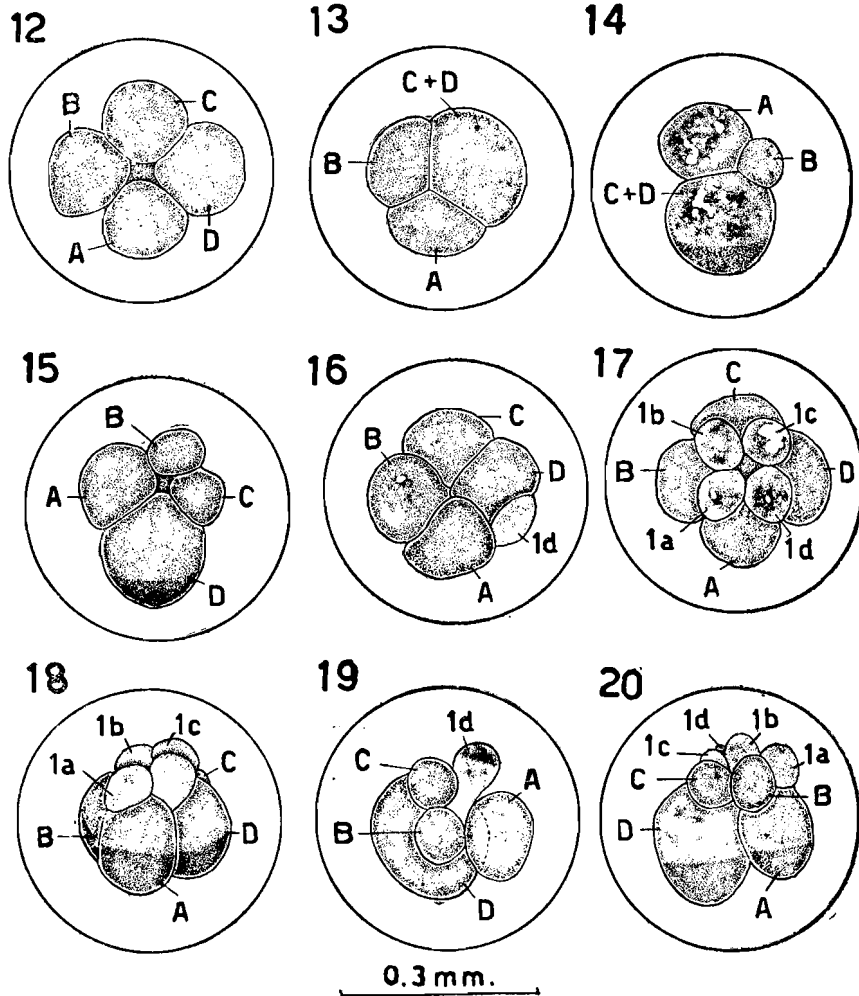
0.3 mm.

Fig. :

12.—Top view of embryo in the four equal separated cell stage.

13.— Top view of embryo in the three blastomere stage.

14.— Top view of embryo in the three abnormal blastomere stage.

15.— Top view of embryo in the four abnormal blastomere stage.

16.— Top view of embryo with the first quartette just beginning.

17.— & 18.—Top and lateral views of normal embryo in the 8 cell stage.

19.—Top view of abnormal embryo with first quartette just beginning.

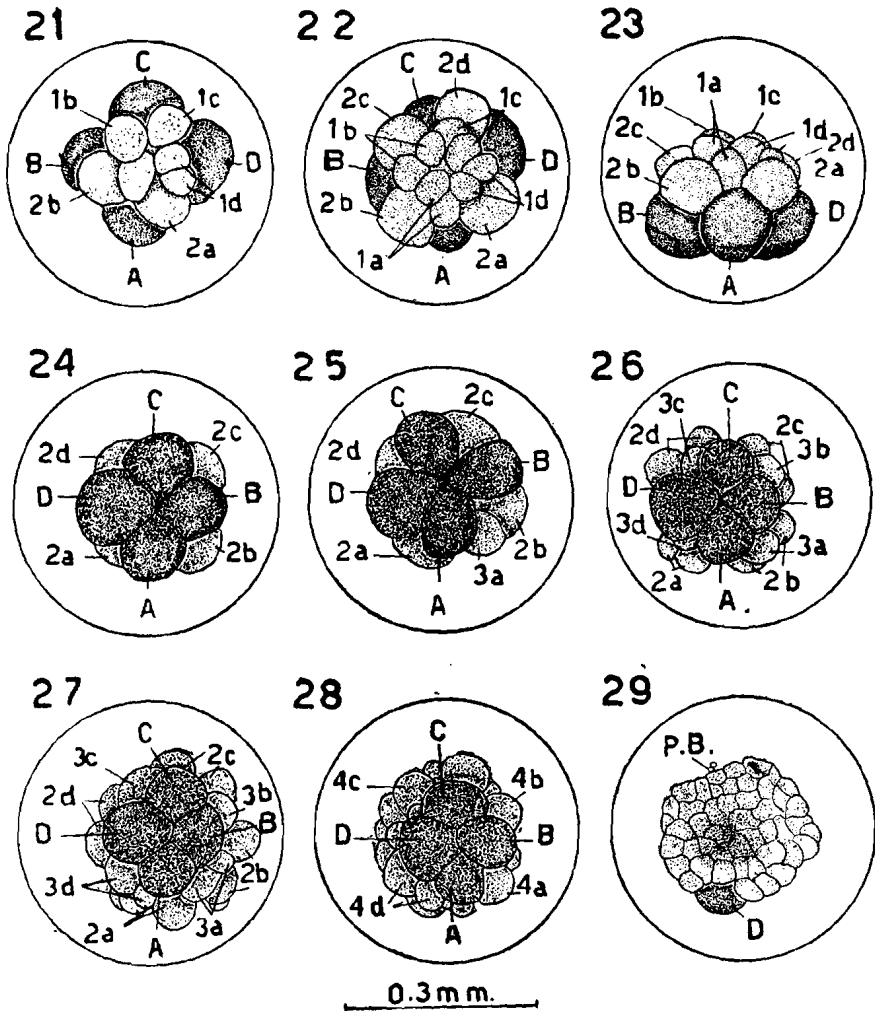20.—Lateral view of abnormal embryo in the 8 blastomere stage.

Fig. :

21.—Top view of embryo during the formation of the second quartette.

22 & 23.—Top and lateral views of embryo with completely formed second quartette and division of micromeres of the first one.

24.—Embryo with completely formed second quartette, seen from the vegitative pole.

25.—Embryo starting the third quartette, seen from vegitative pole.

26.—Embryo with completely formed third quartette, seen from the vegitative pole.

28.—Embryo with divided micromeres of the third quartette, seen from the vegitative pole.

28.—Embryo with completely formed fourth quartette, from the vegitative pole.

29.—Blastula stage, seen from lateral side.

Before the begining of the fourth quartette, the micromeres of the third one divide into unequal cells (Fig. 27). The cells of the fourth quartette are also dextral and are larger than those of the third one (Fig. 28). In this stage two sister 4d are formed. Meanwhile the first three quartettes continue division and proliferation and the morula stage is reached 30 to 40 minutes after oviposition. This stage consists usually of distinct rounded cells, but sometimes compact angular cells are present.

In the abnormal stage of figure 20 the following quartettes could not be exactly noticed, but only a group of cells could be seen on the animal pole of the largest cell D.

The rapid multiplication of the micromeres of the first three quartettes results in surrounding the macromeres which at the same time invaginate together with the cells of the fourth quartette inwards (Fig. 29), and a blastopore is left (Fig. 30). Thus the gastrulation takes place by both epiboly and emboly, and is reached one hour after spawning.

Just after the closure of the blastopore, a ciliated circle, which is the velar rudiment is formed around a convex apical area (Fig. 31), and a slow rotatory movement is aquired, usually from the right side to the left. Later the cilia of the velum elongate, the embryo is now very active, rotating rapidly. The two anal cells and the anal gland appear on the right side of the visceral mass. A trochophore stage, which grows slightly in size attaining its long axis antero-posteriorly is now established (Fig. 32).

## HATCHING AND METAMORPHOSIS OF THE LARVA

Differing from all previously described species of Trochidae, the newly hatched larva of *Trochus dentatus* is in the trochophore stage. This stage which is reached three to four hours after oviposition, is an elongated ball, about 270 to 300 μ long and about 200 μ wide. The primordium of the velum and the anal gland and cells are only formed (Fig. 33). It swims near the bottom, rotating from right side to the left, then it moves toward the water surface with the velum upwards.

The first formed organs are the mouth and a small lobe which is the primordium of the foot, at the ventral side (Fig. 34). Sometimes this stage is passed within the egg-case before hatching.

Three hours after hatching, the primordium of the shell is formed as a small dish-like structure at the base of the larva (Fig. 35), and its progressive development is accompanied by the formation of a thin cup-shaped shell enclosing the posterior part of the larva (Fig. 36). In the latter stage the foot primordium projects vertically as semicircular extension. In a slightly advanced stage (five hours old, Fig. 37) the velum projects from the body surface with the elongation of its cilia, the shell which is decorated with small white lines and dots, encloses most of the visceral mass, and the foot increases in size becoming triangular and twisting towards the right side of the larva. One hour later, the larva (Figs. 38 and 39) increases in size with the shell enclosing all the visceral mass which begins to differentiate into distinct parts. In this stage the anterior part of the larva is now completely twisted towards the right side of the shell.
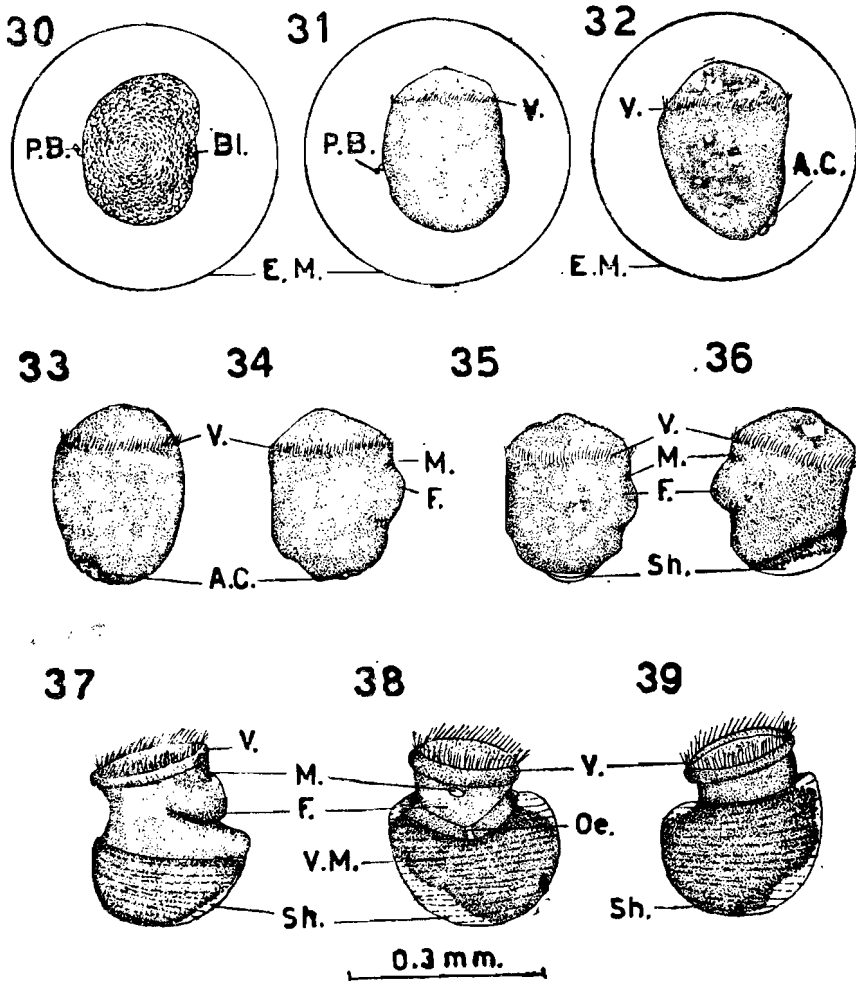
Fɪɢ. :

30.—Gastrula stage, seen from lateral side.

31 & 32.—Right views of trochophore stages within the egg-case..

33.—Newly hatched trochophore stage.

34.—Right view of advanced trochophore stage with foot and mouth newly formed.

35.—Right view of a three hours old trochophore stage.

36.—Right view of a three and half hours old trochophore stage.

37.—Right view of a five hours old trochophore stage.

38 & 39.—Right and left views of a 6 hours old trochophore stage.

In a more advanced swimming larva (about 8 hours old, Fig. 40), the shell is now about one complete whorl, the visceral mass is differentiated into the stomach and the two asymmetrical liver lobes, and the operculum appears as a small protrusion below the foot. From this stage, the larva can not swim all the time near the water surface, but swims for a while then settles down to the bottom, rotating round itself, then swims again and so on.

In a later stage (about 20 hours old, Figs. 41 and 42), the larva which swims and rotates near the bottom of the rearing basins, attains all the particulars of a typical veliger larva. In this stage, the shell is slightly larger than one whorl and twists dextrally; the velum is notched at the middle line anterior to the mouth; the alimentary canal is differentiated into the mouth, oesophagus, stomach, two asymmetrical liver lobes, intestine and anus; and the larval kidneys, the two symmetrical otocysts (one on each side of the foot), the two ocelli and the mantle fold are formed. Also in this stage, the foot is differentiated into propodium and metapodium, and the oval operculum is larger than the foot.

The veliger larva moves near the bottom for about 2 to 3 days during which it is gradualy metamorphosing to the crawling stage. In a 45 hours old larva (after hatching, Figs. 43 and 44), the velum is slightly absorbed and decreased in size; the foot, especially the propodium, increases in size, and the heart is formed. This stage moves by the combined action of the foot and the velum. In a later stage (three days after hatching, Figs. 45 and 46) the velum is greatly reduced with the cilia completely absorbed, the foot increases in size with a contractile powerful large propodium, and the tentacles are formed with the ocellei on their bases. The shell becomes slightly larger and opaque in colour due to the secretion of more fine white dots. This stage crawls by the foot only.

The small young stage (Figs. 47 & 48) is reached after about four days from hatching. In this stage the velum is completely absorbed, and the foot is larger and powerful. The shell is about 1¼ whorls, opaque in colour with few yellowish brown dots, and measures about 350 μ long and 250 μ wide.

## DISCUSSION

As mentioned before, the previously described species of the family Trochidae can be divided, according to the type of their spawns, into two groups. It is clear that *Trochus dentatus* belongs to the second group in which the eggs are shed singly in the surrounding water. The developmental period, which is about 3-4 hours, is shorter than that of any species of this group. It differs also in another main point, that the hatched larva is not in the veliger stage, but in the trochophore type. This phenomenon, as well as the hatching of swimming veliger stages in the other Red Sea species *Trochus erythraeus* (Gohar and Eisawy 1963) which belongs to the first group, emphasises and agrees with the view of Thorson (1940, p. 230) that "the prosobranchs, in correspondance with the food conditions for the Veliger-larvae in different seas, vary their mode of reproduction from totally non-pelagic development in the Arctic, the Antarctic and the deep-sea to the superpelagic Echinospira type in the surface of tropical Oceans". The cleavage of the eggs in our species agrees with the general rule in all species of the family.
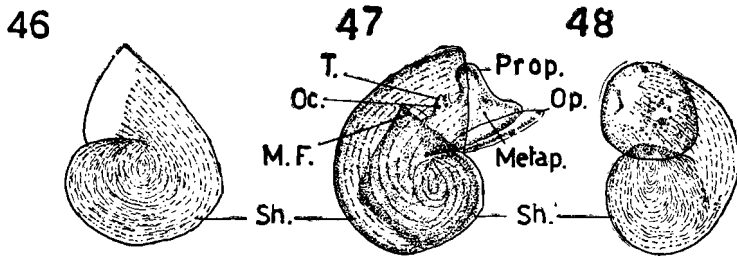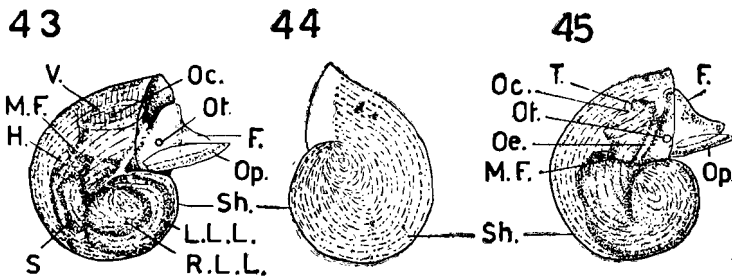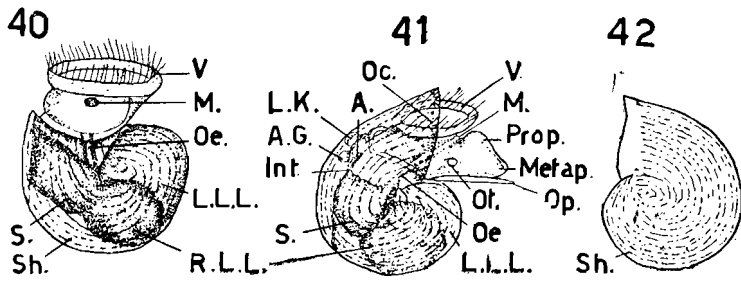
.—Right view of an 8 hours old trochophore stage, assuming the veliger shape.

.—Right view of a typical veliger larva (20 hours after hatching).

.—Shell of same from left side.

.—Right view of a 45 hours old larva.

.—Shell of same from left side.

.—Right view of a just crawling stage (3 days after hatching).

.—Shell of same from left side.

.—Right view of a young crawling stage (4 days after hatching).

.—Ventro-lateral view of shell of same.

## SUMMARY

*Trochus dentatus* lays numerous isolated eggs (200 to 225 μ in diameter), which float in the water and soon settle down. The breeding season extends from April to July. The development proceeds very rapidly and the free swimming trochophore larvae hatch 3-4 hours after oviposition. The typical veliger larva is reached after about 20 hours from hatching. Metamorphosis proceeds also very rapidly and the small crawling young stage is reached after three to four days from spawning.

## KEY TO LETTERING OF FIGURES

A. : Anus ; A.C. : Anal cell ; A G. :Anal gland ; Bl. :Blastopore ; E. : Egg ; E.M. : Egg-membrane F. : Foot ; Fun. : Funnel ; H. : Heart ; Int. : Intestine ; L.K. : Larval kidney ; L.L.L Left liver lobe ; M. : Mouth ; M.F. :Mantle fold ; Metap. : Metapodium ; N.S.W.: Normal sea water ; Oo. Ocellus (Eye - spot) ; Oe. : Oesophagus ; Op. : Operculum ; Ot. : Otocyst ; P.B. : Polar body ; Prop. : Propodium ; R.L.L.: Right liver lobe ; S. : Stomach ; Sh. : Shell ; Si. : Siphon ; T. : Tentacle ; Tr. : Trochus ; V. : Velum ; V.M. Visceral mass ; W.S.W. : Warm sea water ; A, B, C and D : first four blastomeres or macromeres ; 1a, 2a, 3a, 4a, 1b . . . . 4d : micromeres of the four quartettes.

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