

ON THE HABITAT AND HABITS OF *TROCHUS NILOTICUS* LINN. IN THE ANDAMAN SEAS.

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(Plate I.)

Trochus niloticus Linn., one of the largest species among the Trochidae, has a fairly wide distribution in the Indo-Pacific seas. Its range extends from Ceylon, Mergui and the Andamans and Nicobars to Samoa in a west to east direction, and from the coasts of Queensland and Western Australia through New Caledonia, Philippine and Fiji islands to Lu Chu islands in Japan in a south to north direction.¹ It probably also occurs in the Laccadive islands in the Arabian sea but the shells found there have not been identified as *T. niloticus*.²

Before proceeding to describe the habits of *T. niloticus* it is important to consider whether amongst the large populations of *Trochus* in the Andaman waters there are not forms, varieties, and species resembling *Trochus niloticus* in form, shape, colouration, and sculpture of the shell. On the same beds with *T. niloticus* occur commonly *T. pyramis* Born (= *T. obeliscus* Gmelin) and *T. maculatus* Linn. which are easily distinguished from *T. niloticus* by the general outline, colour and sculpture of the shell. There are, however, certain forms of shells amongst *T. niloticus* differing slightly in their outline, convexity of the base and whorls of the shell, thickness, disposition of the last whorl in relation to the penultimate and other whorls, colour, pattern, and sculpture. In the very large series of full-grown *T. niloticus* shells from various localities in the Andamans and Nicobars which I have been able to examine, there were two common types of shell (pl. I, figs. 11 and 12) (1) the broad, short-spined shell with the outlines of the last whorl curved and its periphery thickened, and with convex base, and (2) the regularly conical, long-spined shell with the outlines of the whorls more or less straight and its base flat. A third and rather uncommon type (pl. I, fig. 13) resembling the second in general facies but with a distinct broad, somewhat convex ridge along the periphery of the base of the last whorl seems also to occur, but only one example of this type was found in several thousands of shells examined. Also among young shells with a diameter upto 5 centimetres the first two types of shell occur, but with a number of intermediate forms which grade imperceptibly one into the other; and in very young shells below 3 cms. in diameter the outlines of the whorls are masked by the peripheral hollow spinous processes on the suture. The regularly conical straight-sided type seems, however, to prevail amongst the very young shells. That the differentiation in shell-outlines was not a manifestation of sex differences was ascertained by examining the gonads of a large number of adult shells of the two types. The proportions of the two types of

¹ Hedley (1917).

² Ramaswami Ayyangar (1922).

shells in large samples of collections from various localities differed widely, sometimes one type predominating over the other in numbers. von Martens (1867) was of the opinion that types 1 and 2 were distinct species, namely, *T niloticus* Linn. and *T maximus* Koch, and that the Indian Ocean was the common home of both the species. While the latter statement inclined Pilsbry (1889) to agree with von Martens, the very slight differences in shell-form or sculpture led him to express the opinion that *T maximus* was an arrested and primitive form of *T. niloticus* resembling an immature specimen of the latter in its "conic form, flat lirated base and sculptured spire", but retaining these characters in the adult stage. The differences in the environment,¹ and the changes in shell-form as a result of growth would seem to account for the occurrence of the various types of shell. Moorhouse (1933) found that in the Low Isles on the Queensland coast, retarded growth in shells of *T niloticus* was characterised by "an extremely thick shell which is correspondingly heavier than a shell of the same diameter taken from an area of normal growth, as, for instance, from the outer surf-beaten zone of the reef", and by "a curved base, for all shell found on the outer edge of the reef are flat-based". In the course of my observations on growth of *T niloticus* in the Andamans over a period of about three years, I had the opportunity to observe the changes in the form of the shell of a certain number of marked shells. These changes were usually associated with the exaggeration of the curvature of the sides of the last two or three whorls and of the base of the shell brought about, presumably, by the increased deposition of shell-substance in the region of the growing parts of the last whorl. In shells above 10 cms. in diameter these changes are more marked than in those of smaller dimensions.² It would appear that changes in shell-form may partly represent changes due to senescence (*vide infra*, p. 69). The proportion of the height of the shell to the maximum diameter seems also to undergo a change with the growth of the shell. In random samples of shells above 7 cms. in diameter collected from the same locality, it was observed that the difference between the height and the maximum diameter showed a tendency to increase with the size of the shell. Russell (1909) showed for *Patella vulgata* that changes in the ratios of dimensions of the shell during growth were merely "the expression of the laws of growth, and not due to natural selection". It, therefore, seems probable that in the Andaman waters, at any rate, the various forms of *Trochus niloticus* represent either plastic phases of this species or changes in shape and outline of the shell due to differences in the rate of growth at various ages.

Although *Trochus niloticus* has been commercially exploited for over 35 years, very little is known of its habitat and habits. It lives amidst coral reefs and under rocky ledges covered with growths of green and brown algae from between tide-marks to depths upto 12 fathoms.³ In

¹ The Japanese divers who are licensed to fish *Trochus* in the Andaman seas have informed me that flat-based shells are more common in the Nicobar Islands than in the Andaman Islands.

² Moorhouse (1932) observed that in Low Isles only shells above 8 cms. in diameter had their last whorl expanded.

³ See Watson (1886) where *T. niloticus* is reported to have been dredged in 12 fathoms off Levuka, Fiji.

the Andaman sea it is most abundant on the reefs in the inshore waters, not more than half to one mile from the rocky or sandy shore of most of the islands comprising the Andaman and Nicobar groups. The depth of the sea-floor in the reef area round the islands is usually between 1 to 5 fathoms, but rarely exceeds 7 fathoms. The Japanese Fishery Companies of Singapore which have been licensed to fish *Trochus* shells in the Andamans and Nicobars since 1929 employ Japanese naked divers for the purpose who are brought over to the Andamans every year in their own motor boats. The divers, with their simple but efficient hand-made water-goggles well-adjusted to their nose-bridge and eyes by elastic rubber-tubing secured to the outer ends of the goggles, swim at the surface looking down on the sea-floor, and as soon as a shell or group of shells has been sighted, dive down and bring them up.¹ Where the bottom is covered with large masses of Madreporarian coral with overhanging ledges which cast deep shadows and render the finding of shells from the surface of the sea rather difficult, the divers swim near the bottom passing in and out amongst the meandering narrow corridors and lanes at the bottom, examining the crevices and the under-surface of ledges for specimens of *Trochus*.

At the commencement of the *Trochus*-fishery in October 1929 when the beds were virgin ground, it was comparatively easy to pick up shells in very shallow water. The results of the Fishery at the end of 3 months showed that approximately 500 tons of shells had been gathered from what, presumably, were overstocked shell-beds. After 3 seasons of fishing, the shell-populations in the shallower regions between 3 to 5 fathoms were so greatly diminished in numbers that the Japanese had to extend their operations to the fishing grounds at depths of 7 fathoms. It appears that naked diving would be impossible at depths exceeding 7 fathoms, and the Japanese were soon driven to the necessity of applying for licenses for the use of diving apparatus. Actually, however, no diving apparatus was employed, presumably because of the difficulty of securing the services of special divers at Singapore for the purpose. The Japanese assert that there is still an abundant shell-population in depths beyond 7 fathoms, from which apparently the shallower regions are replenished from time to time. However, continued fishing for *Trochus* since 1929 has reduced quantities of shell fished from 500 tons to less than 40 tons in a fishing season, although the period of fishing has been doubled. There is no doubt that the shell-population has suffered considerable depletion, as may be seen from the fact that the rate of collection per diver per hour has fallen from over 20 in 1933 to 2—3 in 1935.

Moorhouse's (1932, p. 147) observation that despite a tendency for zoning of the animals in the Low Isles there was a frequent mixing of forms of various sizes does not appear to be quite in accord with mine in the vicinity of Port Blair. The young forms below 5 cms. in diameter appear to be rather scarce in depths between 2 and 7 fathoms² as the

¹ For a more detailed account of the Japanese Fishing methods, boats, equipment etc., see Setna (1932).

² It is quite possible that the young forms occur in greater abundance at depths beyond 7 fathoms and creep gradually into shallower waters, but no evidence of such occurrence in the Andamans has been obtained.

Japanese divers in the Andamans testify, but amongst the coral shingle and under coral slabs between spring tides they are usually found at all times of the year. The type of locality in which they commonly occur is shown in fig. 1, pl. I, of the present note and in fig. 1, pl. xiv (Rao, 1936). The older forms above 5 cms. generally occur below the low-water mark of spring and neap tides.

Moorhouse (1932) also observed that *T. niloticus* was gregarious in the Low Isles of the Great Barrier Reef, as many as 15 individuals having been taken from one slab or boulder of coral on several occasions. My observations on the reefs round the Andaman and Nicobar groups of islands with the help of a water-glass, while the Japanese divers were working in those areas, showed that the individuals of the shell population on the reefs were greatly scattered, and that in consequence the divers were unable to obtain more than 2 or 3, or at the most, 5 shells at a time from a chosen spot on the reef. This may have been due to the fact that the shell-beds were, at the time of my investigation, more or less depleted of their normal stock of shells by heavy and continuous fishing. On one occasion, however, in October 1932, looking for shells in a small bay south of the South Corbyn's Cove, Port Blair, 36 specimens ranging from 5.0 cms. to 12.5 cms. in diameter were picked up either singly or in twos and threes in an area 10 yards square. Some of them were attached to the under surface of rocks, others to coral shingle, while a few were crawling on coarse coral sand in crevices under stones. A few were found on wet ground some distance below the high-water mark. The lowest tide on this day was 0.2 feet at 4.42 P.M. and the highest 6.5 feet at 10.38 A.M. (I. S. T.). The congregation of such a large number of individuals in a small area between tide-marks is no doubt exceptional, and may have resulted from the action of strong currents or some adverse weather conditions. But in comparison with other species of Gastropods such as *Nerita polita*, *N. albicella*, *N. chameleo*, *Acmaea saccharina* var *stellaris*, and *Littorina scabra* which are found in large numbers in the Andaman and Nicobar Islands on rocks between tide-marks, *Trochus niloticus* cannot be said to be really gregarious. On several occasions when marked shells were on purpose massed together round boulders under which there were adequate shelter and abundant food in the form of growths of algae, the individuals were found to have scattered within a fortnight to considerable distances from their original shelter. The tendency to wander about seems to be a feature of this species which, therefore, does not admit of its being classed among the strictly gregarious species of Gastropods.

Trochus niloticus does not seem to thrive under artificial conditions of the laboratory. Attempts to keep the animals alive in glass aquaria in which sea water was constantly kept circulated after renewal everyday proved a complete failure.¹ The longest period for which a specimen was kept alive in the aquarium was 5 days, during 3 out of which the animal was in a semi-comatose condition; but usually individuals did not survive the conditions in laboratory aquaria after 48 hours,

¹ Small reservoirs on a higher level than the aquaria were constantly filled with fresh sea-water which was led through rubber tubing into the aquaria. There were no facilities at Port Blair for a higher grade of aeration than mere renewal of sea-water,

some dying even within 24 hours. The very high degree of aeration which is maintained on the reefs is extremely difficult to imitate under the artificial conditions of the laboratory.¹ During the first three or four hours of immersion in aquaria *T. niloticus* crawls about on the small stones and shingle placed at the bottom, but in a partially expanded state in which the head and tentacles of the animal are barely visible (pl. I, fig. 2). The mouth is, however, closely applied to the surface of the stone on which it crawls in the act of browsing on the algae and the vegetable and mineral debris which constitute its food. After this period, the feeding activities of the animal cease altogether, but the foot and the columellar muscles continue to expand and contract giving the shell a partial rotary motion with the columellar muscles as the fulcrum. The epipodial lobe which in conjunction with the mantle forms the siphon for the intake of the respiratory current is observed to be mobile. After 6-8 hours in the aquarium, the animal is overcome by a state of torpor which is maintained unless disturbed. The renewed activity following any disturbance is, however, for a very short period, and the animal falls into a comatose condition again. During the first few hours of activity the animal feeds and defaecates constantly, leaving pellets of faecal matter $\frac{1}{2}$ to 1 inch long in its trail. Later, it stops feeding but continues to throw out faecal pellets a little longer. Finally it withdraws itself into the shell, but with the movements of the epipodial siphon continued until the animal is actually in a comatose state. The animals seem to survive suspension in the sea for several hours or days even though they are crowded in a net bag and deprived of food.² They are also able to survive dessication for a little over 48 hours. On several occasions it was found convenient to transport live animals from distant beds to Port Blair by carrying them in a dry state. When exposed to the sun and wind on the open deck of the Japanese fishing boats, the live animals do not withdraw themselves into the shell and remain inactive, but protrude the whole or part of the foot gradually and withdraw it with such suddenness and force as to eject jets of sea-water from within the shell to a distance of 3 to 5 feet. This movement of the animal goes on at short intervals until the water contained in the whorls of the shell and in the tissues is dried up when the animal becomes inactive and finally dies. Some of the animals which had ceased their movements two days after their removal from the reefs were revived on immersion in the sea, and observed to grow.

It is difficult to observe the details of movements of the animals in their natural haunts between tide-marks. The quick succession of waves which dash against the coral boulders renders continuous observation impossible. At depths of about one or two fathoms the animals can be observed with the help of a water-glass³ from a small boat

¹ Stephenson (p. 491, 1923-25), Moorhouse (p. 147, 1932), and Weymouth (p. 9, 1923) have observed that in the case of *Haliotis tuberculata*, *Trochus niloticus*, and *Tivela stultorum* respectively ordinary laboratory conditions in aquaria are unsuitable for keeping them alive in captivity.

² Some animals have been observed to browse on the algae growing on the shells of other animals confined in the bag.

³ A pyramidal trumpet-shaped wooden structure with plate-glass fixed to the broader side acting as the window.

anchored at the place of observation, but the details of their movements except when they are crawling on the vertical sides of a coral mass are obscured. Sometimes an individual may be seen crawling on a rock projecting above the surface of the water and bathed by the spray from the waves.

Although *T niloticus* is extremely slow in its movements, it moves about a great deal in search of food and shelter. In exposed positions between tide-marks it is rarely found, but is common in holes and crevices amidst or under rocks and coral masses where algae grow in abundance. In the course of observations on growth of marked individuals (Rao, 1936) considerable difficulty was experienced in recovering them every month from the reefs, as with every ebb and flow of the tides they seemed to crawl slowly backwards and forwards. The younger individuals below 5 cms. in diameter are far more active, and move about a great deal more than the older ones above this size. Except in places protected against strong currents and waves by natural barriers provided by large masses of coral rock or by artificial piers, the recovery of the smaller animals was extremely difficult, and instances of marked shells recovered after an interval of 3 or 4 months were not uncommon. These observations show that *T niloticus* wanders about a great deal, assisted by tides in search of food and shelter. It seems, however, improbable that it travels long stretches of the sea-bottom, particularly those between two distant islands, devoid of continuous reefs. In the Andaman and Nicobar Islands, subject to the rough weather of the south-west and the north-east monsoons, the species is found along the east and west coasts of these islands, but where the coasts are protected from the effects of the monsoons by large inlets of the sea and hills in the path of the monsoons the species is rather rare. The islands of the Nicobar group which receive a heavier rainfall than those of the Andaman group have a relatively denser population of *T niloticus*. Even after six continuous years of fishing the Nicobars are still the more prolific area than the Andamans, and have yielded a bigger tonnage of shells. As has been observed by Moorhouse (1932, pp. 146-147) in the Low Isles, the species avoids sandy and muddy places along the coasts.

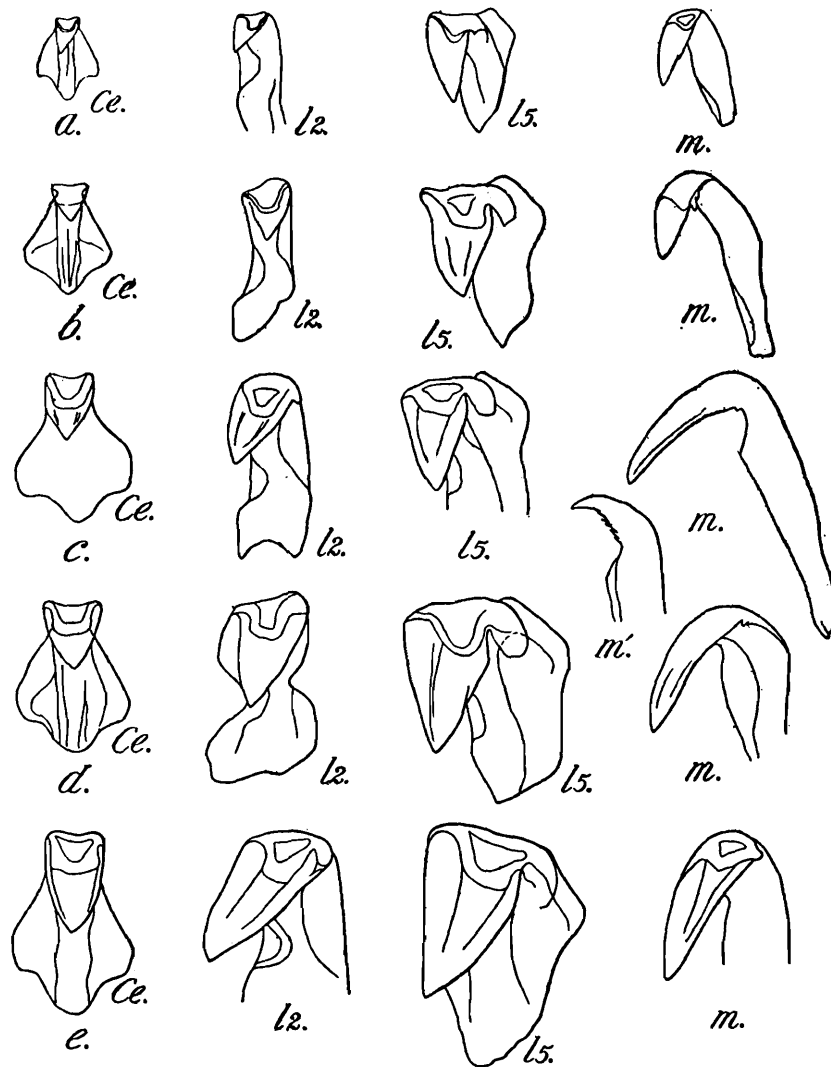
The difficulties of observing the habits of this animal both in its natural haunts and when kept in captivity in aquaria have been explained above. On one occasion (8-1-35) while searching for examples of small size on a wide stretch of coral shingle in Murdakhari Bay, Port Blair (pl. I, fig. 1) a specimen was found crawling slowly on a branch of coral covered with growths of algae, and on observing with a magnifying lens was found to be feeding. The contractions and movements of the foot are extremely slow and suggest those seen in slow-motion films.¹ The respiratory siphon, which is partially closed while in water, seems to open out when the animal is removed from water so that the pallial cavity is in communication with the outside atmosphere. The proboscis-like part of the head which is mobile is extended slowly downwards over the front part of the foot to the surface on which the animal

¹ Robert, A. (1903) described the undulatory movements of the integument of the foot in *Trochus*.

crawls until the aperture of the mouth is closely applied to it. Moorhouse's observation that a small, very short, and non-retractile muzzle is present is not in accord with mine. Then the parts surrounding the aperture are presumably depressed to form a shallow cup in which a partial vacuum may be formed. The contractions of the integument round the aperture and the adjoining parts suggest the formation of a partial vacuum. All the particles of sand and disintegrated coral, and the minute growths of algae on the branch of coral are presumably sucked into the buccal cavity. At the same time the radular teeth appear to assist in rooting out the algal filaments from their attachment. At brief intervals the proboscis-like part of the head is removed from the surface of the coral on which the animal crawls, and on the slightest disturbance in its vicinity, is withdrawn into the shell, followed by the foot, the two sides of which fold along the median line. Examination of the gut contents of a large number of individuals of *Trochus niloticus* from various localities shows that brown and green algae, chiefly the minute species, form part of its food. As the animal feeds by scraping the rocks and coral masses on which it lives, the contents of the gut include a large proportion of inorganic and organic debris, and a variety of organisms which live amidst the algal vegetation. Thus, in the course of the examination of the gut-contents, remains of small Crustacea such as Copepods, Ostracods and Isopods, tests of Foraminifera and Radiolaria, spicules of Sponges and Alcyonaria, fragments of Hydroid colonies, small Polychaete worms, Nematodes, small Molluscs (soft parts as well as shells), Pycnogonids, Insect-larvae (Chironomidae) and demersal eggs of fish have been found in addition to bunches or fragments of leaf-like or filamentous algae including young and immature forms of *Ulva*, *Polysiphonia*, *Chaetomorpha*, *Turbinaria*, *Hypnea*, *Lyngbia*, *Neomeris*, etc.¹ The commonest alga found in the gut of *T. niloticus* was a *Hypnea* sp., pink in colour. According to Yonges's (1928) classification of the feeding mechanisms in the Invertebrates, *T. niloticus* should belong to his section B of group II in which the feeding mechanism is intended for scraping and dealing with large particles or masses, but judging from the contents of the gut, *T. niloticus*, which seems to swallow large quantities of bottom deposits also, may therefore be included in his section A as well. In the rectal portion of the hind-gut, in addition to the inorganic debris in the faecal matter algae in a more or less undigested state are also found. The anterior loop of the rectum contains a soft muddy mass including a few algal filaments and inorganic matter, while the posterior loop contains a somewhat friable mass of debris consisting of large grains of sand and other inorganic material, bunches of undigested algae, and the hard remains of Foraminifera, Sponges, Hydroids, Crustacea, and Mollusca. This fact coupled with that of the absence of food material in the oesophageal part of the fore-gut seems to indicate that the passage of the food through the entire gut is fairly rapid and that digestion is only partial. In some specimens dissected soon after capture the stomach

¹ I have to thank my friend, Prof. M. O. P. Iyengar, Director of the University, Botanical Laboratory, Madras, for the identification of the algae.

was found to be empty, while the loops of the hind-gut were full of partially digested matter. The weight of the stomach-contents including the algae and the inorganic and organic debris is very small in proportion to the weight of the entire animal excluding the shell. In fresh specimens of *Trochus niloticus* examined, the weight of the algae alone (separated from the debris) was 6-10 per cent. of the weight of the stomach contents while the organic and inorganic debris constituted over 90 per cent. of the total weight. The weight of the entire animal (including a large quantity of sea-water in the tissues and amongst the internal organs) was 32 times the weight of the contents of the stomach, while that of the shell (usually varying from 3 to 14 ounces) was 2.25 times



TEXT-FIG. 1.—Radular teeth of individuals of *Trochus niloticus* with shell-diameter not exceeding 5.0 cms. (The entire teeth have not been drawn in all cases owing to the high magnification).

a. 1.74 cms. ; b. 2.32 cms. ; c. 3.27 cms. ; d. 4.30 cms. ; e. 5.00 cms.

ce. central ; l_2 . second lateral ; l_5 . fifth lateral ; m. marginal ; m^1 . marginal slightly tilted to a side.

the weight of the animal. It would appear that *T niloticus* extracts its nourishment mainly from the bottom deposits consisting of organic and inorganic material but supplements it with nutriment derived

from an inconsiderable proportion of vegetable matter.¹ This species may therefore be classed as a "selective deposit-feeder".² Although species of *Trochus* are known to be herbivorous and selective deposit-feeders, they occasionally seem to adopt carnivorous habits. Robert (1903, p. 10) recorded that in an aquarium at Roscoff in which *Trochus conuloides* and two specimens of *Palmipes membranaceus* L. Agassiz (slightly injured by the fishing gear) were kept, the former had attacked and devoured the latter in about two days.

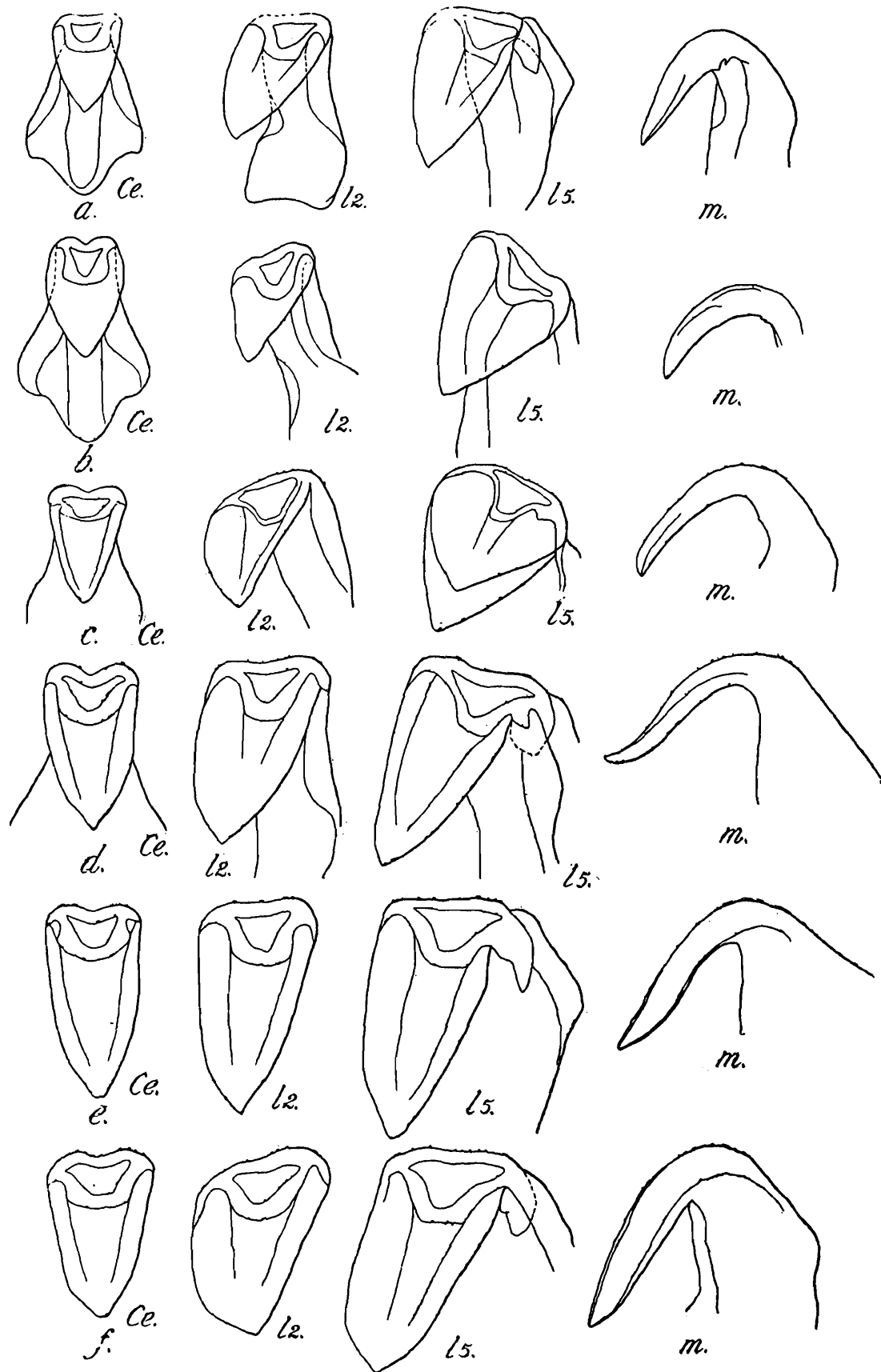
The nature of the food of *Trochus niloticus* and the manner of feeding involve a considerable wear and tear of the radular teeth, and the very long radular sac and ribbon seem to meet the constant need for replacing the worn out teeth. The features of the radular teeth of *T. niloticus* are figured by Troschel (1879), but his figures seem to represent those of a much worn series. The marginals, however, seem to be from a different row in that the main cusp and the denticulations are fairly sharp and well-defined. In the series of camera lucida drawings of radular teeth (text-figs. 1 and 2) (central, 2nd and 5th laterals, and the marginal) from approximately the middle region of the ribbon of individuals with shell of diameter 1.74 cms. to 11.14 cms., the features of the radula are shown. The proportions in dimension between the cusps and the basal part remain the same except for slight individual variations. In older individuals there is a tendency for the cusps of the central to become blunt, and for the reduction in the number of small cusps on the marginals. The radular sac is bifid in its terminal portion as in *T. lineatus* (Da costa), *T. magus* (Linn.) and the other species of the sub-genus *Gibbula*, and the radular teeth resemble in structure those of *T. lineatus* (*vide* Randles, 1905), the first marginal not being different in size and structure from the rest of the marginals.

It is a well-known fact that the sexes are separate in *Trochus niloticus*, but no feature in the external form of the shell or in the visible soft parts of the animal when extended gives a clue to the sex of an individual. The differences in the curvature of the whorls and the basal part and in the thickness of the shell met with in the three types of shell-form mentioned above (p. 47) led me to examine the gonads of several individuals belonging to the three types, but no correlation between sex and type of shell was found to exist, that is to say, all three types of shell had male and female elements, thereby establishing that the sex of a given individual cannot be determined at a glance by examining its external features. Moorhouse (1932, p. 146) found no difference in shell-form in the two sexes. Amirthalingam (1932, pp. 72-73) claimed, however, that the outlines of the cavities inside the shell of over 7 cms. diameter as revealed by longitudinal sections "passing through the extreme end of the suture of the outer lip to the bodywhorl and the columella" showed significant differences in the two sexes. In the

¹ Several specimens of *Turbo marmoratus* from the Andamans showed that their feeding habits were similar to those of *Trochus niloticus*,

² Hunt (1925) in the course of his study of the food of the bottom fauna of the Plymouth Fishing grounds found that *Turritella communis* and *Aporrhais pes-pelicanis* (among the various Gastropods present) had roughly sorted bottom material in their stomach.

determination of the sex of a shell at a glance his claim, if confirmed, will have little practical application. No accessory organs indicative



TEXT-FIG. 2.—Radular teeth of individuals of *Trochus niloticus* with shell-diameter above 6.0 cms. and below 12.0 cms. (The entire teeth have not been drawn in all cases owing to the high magnification).

a. 6.79 cms. ; b. 7.29 cms. ; c. 8.72 cms. ; d. 9.69 cms. ; e. 10.12 cms. ; f. 11.14 cms.
 ce. central ; l_2 . second lateral ; l_5 . fifth lateral ; m. marginal.

of sex are present in the animal, but when the latter is extracted from the shell, or the spire of the shell is broken exposing the visceral coil, the colour of the gonads in sexually mature individuals, which is dark-green in the female, white or cream in the male, helps in the identification of sex. In immature individuals the portion of the visceral coil representing the gonad is of a more or less uniform gray colour which renders identification of sex difficult, but examination under the microscope of the contents of the gonad either in fresh smears or in sections usually reveals spermatozoa or oocytes in various stages of development. In examples with a shell diameter of less than 3 cms. in which the gonads are still in an undifferentiated state even microscopic examination may often fail to reveal the sex (see text-fig. 6, p. 63). Moorhouse (1932, p. 153) in stating that "in no case were sperm and eggs found together" apparently expected to find sex-change in *T. niloticus*, at any rate, in moderately young *Trochus*. From an examination of a large number of microtome sections of the gonads of both sexes of all ages, I consider that no sex-change is probable, although as Moorhouse suggests the matter requires further examination. A practicable method of examining the sex-products at different stages of the growth of individuals without causing material injury to the animal may help to solve the question of sex-change in *T. niloticus*. At a point three or four whorls below the apex of the shell a tiny hole was made on a few shells with the help of a drill, and the sex-products drawn into a hypodermic syringe through a small puncture in the integument of the gonad were examined on a slide. The specimens thus punctured were returned to the sea, but were recovered dead after a few weeks. A second attempt to examine sex-products by this method resulted again in the death of the animals under observation. A satisfactory method of closing hermetically the puncture in the shell after a sample of the sex-products has been drawn would perhaps eliminate the chance of death of the animals. In the course of the examination of the gonads of several hundred examples of *T. niloticus*, there was no single instance in which sex could not be determined in microtome sections of the gonad of examples with a shell-diameter exceeding 3 cms., and no case of hermaphroditism comparable to that of *Patella vulgata* (see Orton, 1928, pp. 853-857) was observed in *Trochus niloticus*. Even in the former species instances of hermaphroditism appear to be the exception rather than the rule.

Samples of *T. niloticus* having a shell-diameter above 5 cms. from various localities in the Andamans from which smears of the gonads were examined microscopically showed that those having a shell-diameter under 7.0 cms. were usually immature, and that the sexes, were present in almost equal numbers. Shells having a diameter of 7.0 cms. and above were therefore considered adult. The records of the frequency distribution of shells of various adult size- or age-groups of both sexes from various localities in the Andamans lend support to the view that the proportions of males and females are about equal. For the purpose of the investigation of sex-ratio in *T. niloticus*, the records of sizes and sexes of shells collected from two separate groups of islands in the Andamans were selected for study. Dr. K. C. K. E. Raja

to whom I am indebted for the statistical treatment of the records, has kindly furnished the following note :—

Ritchie's Archipelago.

A sample of 806 shells of *T niloticus* was obtained. Of these 309 were picked up at random and were examined for sex giving the following frequency distributions :—

Age. (Size in centimetres.)	Frequency.	
	Male.	Female.
7— 7.99	42	40
8— 8.99	64	57
9— 9.99	25	30
10—10.99	14	16
11—11.99	10	11
	155	154

Taking these two samples of 155 and 154 shells as random samples,

$$\chi^2 = 1.086$$

$N=4$, P lies between 0.8 and 0.9.

Hence there is no reason to assume that the numbers of males and females at each size- or age-group are different from each other.

The same problem may be approached from another point of view. We have a larger sample of 806 shells and the assumption that the sexes are equally represented may be tested by comparing the actuals for males and females given above with the expected numbers at each age period, if the totals of 155 and 154 are distributed in the proportions given by the sample of 806.

Age. (Size in centimetres.)	Male.		Female.	
	Observed.	Expected.	Observed.	Expected.
7— 7.99	42	39.61	40	39.36
8— 8.99	64	70.58	57	70.12
9— 9.99	25	25.77	30	25.60
10—10.99	14	13.46	16	13.37
11—11.99	10	5.58	11	5.55

Males.— $\chi^2=4.303$, $N=4$, P lies between 0.5 and 0.3.

Females.— $\chi^2=9.091$, $N=4$, P lies between 0.1 and 0.05.

Hence, in both cases, no significant difference between the expected and observed distributions has been made out.

Cinque, Passage, Sister, Brother and Little Andaman Islands.

In the case of these islands a larger sample of 2,031 shells was available. From this sample a smaller sample of 363 was taken at random

and an examination for the sexes was carried out. The distributions are given below :—

Age.	Male.	Female.
7— 7.99	17	21
8— 8.99	36	30
9— 9.99	33	40
10—10.99	30	41
11—11.99	30	27
12 and over	25	33
	171	192

For the sake of comparability of these figures with those for Ritchie's Archipelago, we leave out the last group (12 and over). A comparison between these two distributions shows that there is no significant difference.

$\chi^2=2.952$, $N=4$, P lies between 0.7 and 0.5.

Further, a comparison between the observed and expected frequencies on the proportions given at each age by the large sample of 2,031 also brings out that there is no significant difference in the case of both sexes.

Males.— $\chi^2=1.596$, $N=4$, P lies between 0.9 and 0.8.

Females.— $\chi^2=10.076$, $N=4$, P lies between 0.05 and 0.02.

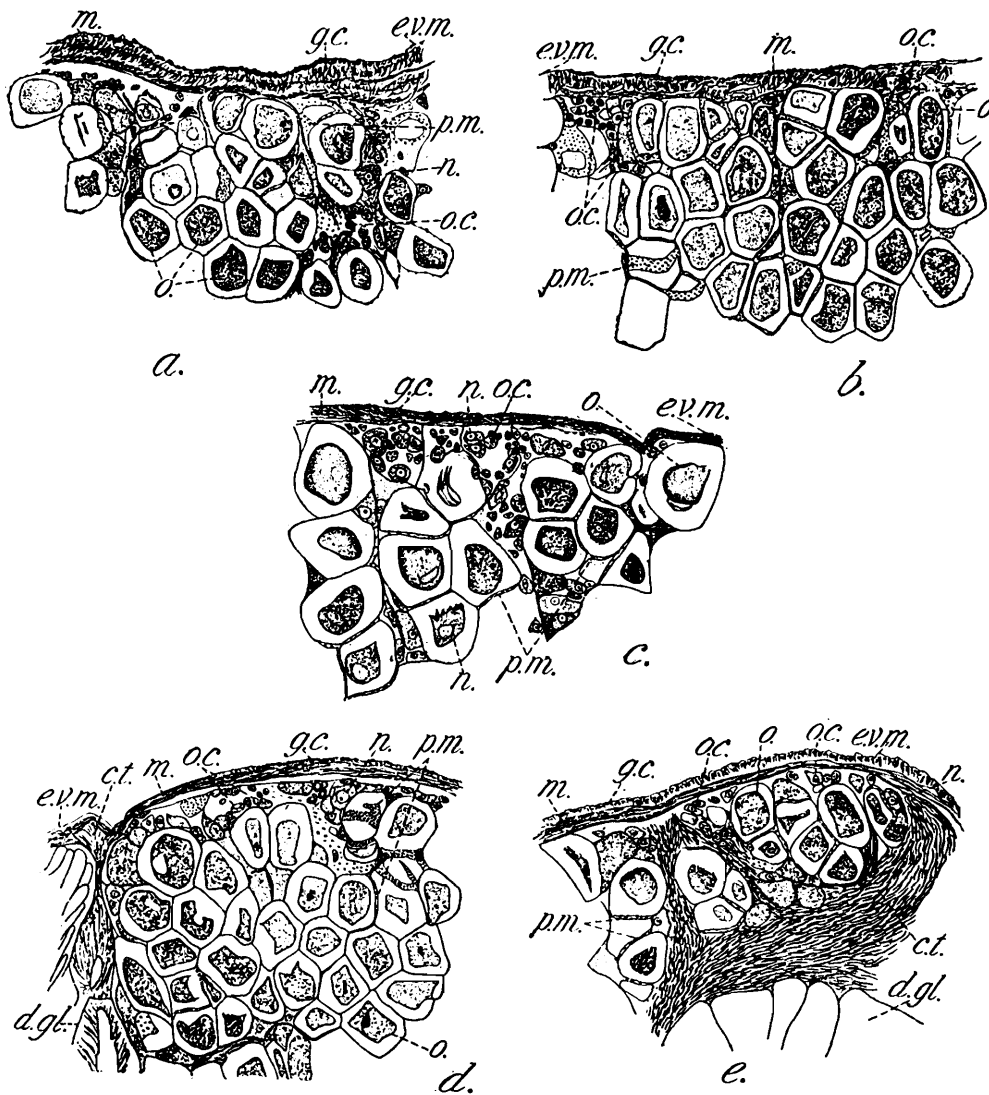
The last result suggests that the difference between the two distributions is just emerging into significance. Taking all the tests into consideration it may be said that males and females appear to be present in about equal numbers at the respective ages. It may be remembered that we have confined ourselves to the ages represented by the sizes from 7—7.99 to 11—11.99. At the later age groups the divergence between the sexes seems to be significant.

In the two samples the bulk of the shells fell into these groups. In both, shells below 7.0 cms. do not come into consideration, as the sex elements are immature at this stage. Above 11.99 cms., there were in the first sample only 0.25 per cent. shells and in the second only 9.80 per cent. The samples represent almost complete collections of the shells in two separate areas and they may be taken to be representative samples of the adult population of *T. niloticus* of these islands. On the information afforded by these samples the inference is that, within the age groups indicated, males and females may be present in about equal numbers.

The conclusions of Moorhouse in regard to the sex-ratio of *T. niloticus* in the Low Isles are thus corroborated by my own observations in the Andamans.

The correlation between age and size in *Trochus niloticus* as indicated by the maximum diameter of the shell has been referred to in a previous paper (Rao, 1936). The determination of the criterion for maturity in both sexes, and of the minimum size or youngest age at which such maturity is reached must precede that of the breeding period. After examining the smears of the sex elements of a large series of examples of all ages from different localities, it was decided that the presence of active

spermatozoa in the male and the size of ova with a diameter between 0.20 and 0.25 mm. (excluding the pitted gelatinous outer cover-



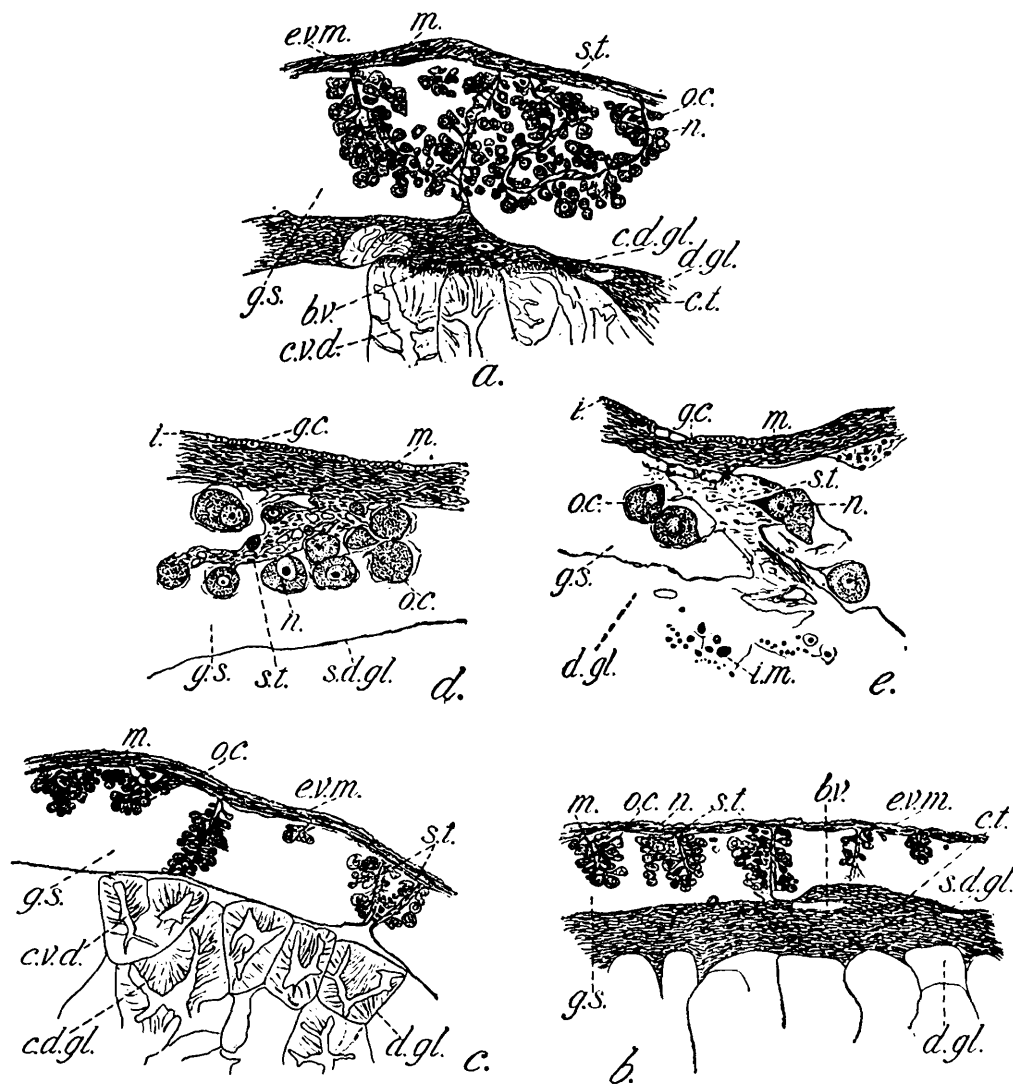
TEXT-FIG. 3.—Vertical longitudinal sections of ovary from specimens of *Trochus niloticus* (collected in various months) with shell-diameter ranging between 9.0 cms. and 12.5 cms.

a. 12.25 cms. (March); b. 11.72 cms. (January); c. 10.38 cms. (November); d. 9.93 cms. (November); e. 9.02 cms. (January). (Drawn under low power and eye-piece $\times 10$).

bv. blood-vessel; c. d. gl. cells of the digestive gland; c. i. cellular inclusions tinted blue by Mallory's stain; c. t. connective tissue; c. v. d. cavity of the tubule of the digestive gland; d. gl. digestive gland; d. p. dark pigment; e. v. m. epithelium of visceral mass; g. c. globular or cubical mucus cells of the integument; g. s. coelomic space between the gonadial layer of the epithelium of the visceral mass and the digestive gland; i. integument; i. m. irregular masses in cells of the digestive gland which take a deep blue tint in Mallory's stain; m. muscles of the integument; n. nucleus of oocytes; o. ova fully developed; o. c. oocytes; o. g. spherical inclusions (with granules) which stain olive-brown or olive-green in Mallory's stain; p. m. pitted membrane; s. d. gl. gonadial surface of the digestive gland; s. t. branching trabeculae of the coelomic epithelium (lying between the integument and the connective tissue of the digestive gland) with developing oocytes; t. d. gl. tubules of the digestive gland; t. s. transparent spherical inclusions with olive-yellow granules.

ing) in the female should be the criteria for sexual maturity. In the latter sex the presence of developing oocytes with a diameter ranging from 0.05 to 0.20 mm. rendered the determination of sexual maturity somewhat difficult. It was, however, found later that the development of a pitted membrane round the ova roughly coincided with their maturity, and that in sexually mature females of all sizes there was always

a varying number of oocytes also. For the purposes of a rough and ready method of determining the state of maturity of females smears in which a majority of the number of ova had a diameter exceeding 0.20 mm. were taken as samples representing mature females, and those in which the majority of ova had diameter above 0.05 mm. and below 0.20 mm. were treated as samples representing immature females.



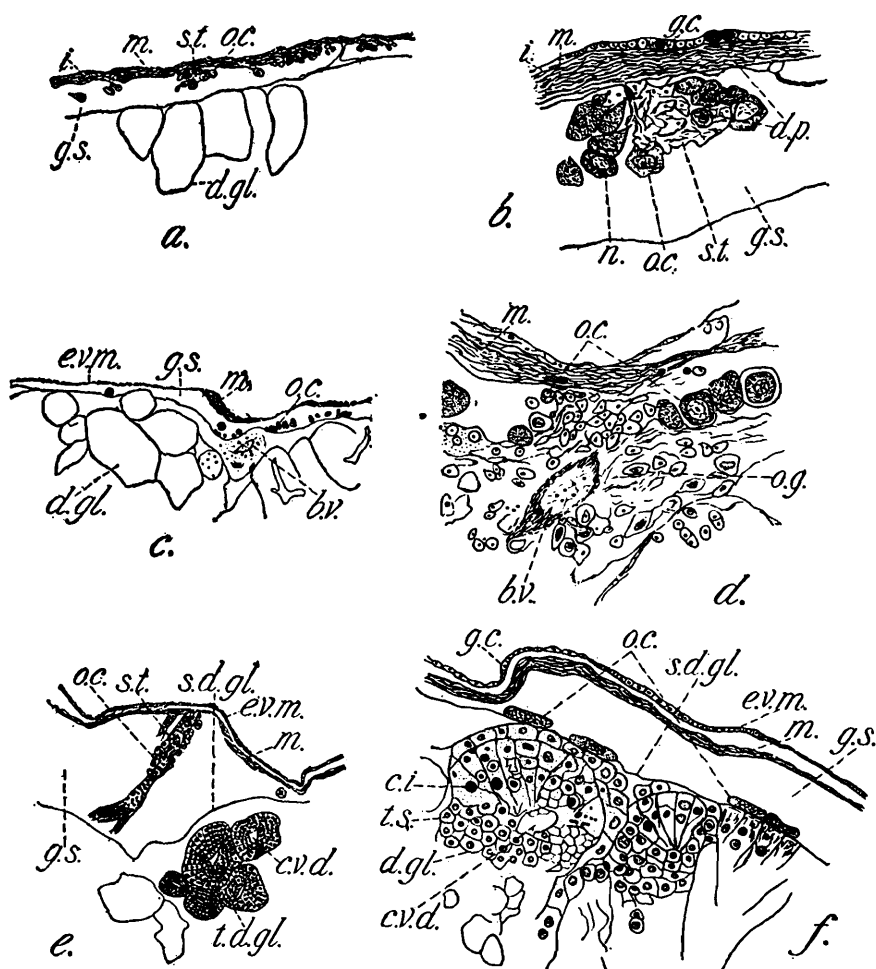
TEXT-FIG. 4.—Vertical longitudinal sections of ovary from specimens of *Trochus niloticus* (collected in various months) with shell-diameter ranging between 6.0 cms. and 8.5 cms.

a. 8.11 cms. (February); b. 7.25 cms. (January); c. 6.87 cms. (February); d. and e. (from different regions of the section) 6.52 cms. (February).

a. to c. drawn under low-power and eye-piece $\times 10$, d. & e. drawn under high power and eye-piece $\times 10$. For explanation of lettering see under Text-fig. 3, p. 60.

In Table I (see p. 75) the number of individuals with ova and/or oocytes of the three categories of dimensions, and the total number of shells from each locality examined are shown at the bottom. The percentage frequency of individuals of each size or age-group under each of the three categories of ova-size is shown in the vertical columns of the table. A careful scrutiny of this table would show that in all the localities, 95—100 per cent. of the individuals with a shell-diameter above 10.00 cms. have a majority of fully mature ova, while over 50—90 per cent. of the individuals with a shell-diameter of 9—9.99 cms. have a majority of mature ova. In the individuals of the age-groups with a diameter below 9 cms. the percentage frequency of individuals with mature ova

is reduced to an average of about 33. The examination of the condition of the gonads in a large series of females of all age or size-groups as revealed by microtome sections also brings out the fact that individuals with the shell-diameter below 9.0 cms. have as a rule the gonad in the form of an arborescent racemose gland (Text-fig. 4) while those with the shell-diameter above 9.0 cms. have a relatively large majority of mature ova covered with a pitted gelatinous membrane and arranged in the form of a honey-comb (Text-fig. 3). The proliferation of oocytes on the branching trabeculae of the coelomic epithelium which lie between the integument and the connective tissue of the digestive gland seems to be an invariable feature of the gonads in individuals with a shell-diameter exceeding 9.0 cms. The text-figures (3 to 6) illustrate clearly what has



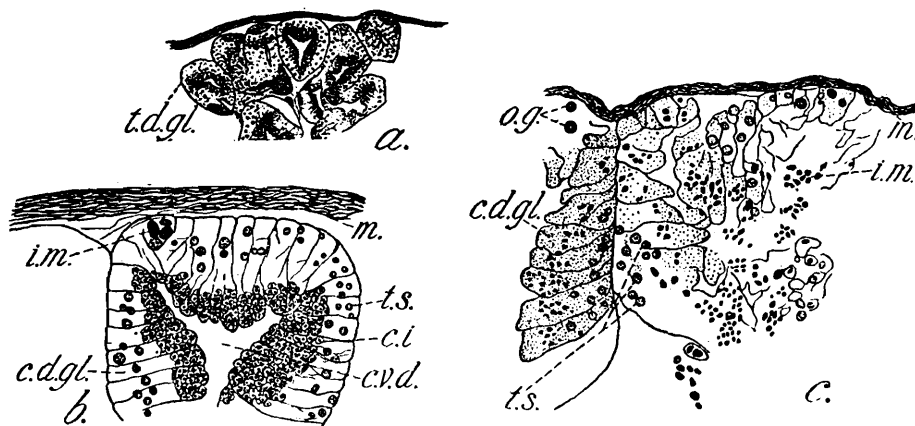
TEXT-FIG. 5.—Vertical longitudinal sections of ovary from specimens of *Trochus niloticus* (collected in various months) with shell-diameter ranging between 3.5 cms. and 5.7 cms.

a. 5.70 cms. (December); drawn under low power and eye-piece $\times 10$; b. same as a. but with the portion of the section marked s. t. and o. c. enlarged and drawn under high power; c. 4.47 cms. (December) drawn under low power and eye-piece $\times 10$; d. same as c. but with the portion of the section marked m., o. c., and b. v. enlarged and drawn under high power; e. 3.55 cms. (January) drawn under low power and eye-piece $\times 10$; f. same as e but from a different portion of the section and drawn under high power.

For explanation of lettering see under Text-fig. 3, p. 60.

been said above. The inference that in the Andaman waters the female of *Trochus niloticus* becomes sexually mature when it has attained a shell-diameter of 9.0 cms., which as stated in my previous paper (Rao, 1936, p. 482) will be in its third year of life, seems to be justified.

Although no detailed observations on the maturity of the male of *T niloticus* were made, it was found that individuals with a shell-diameter of 6—7 cms. had generally mature or active sperms in their gonad. The age at maturity of *Trochus niloticus* does not appear to be uniform in all the regions in which the species has been studied. Montague (1915) concluded from his observations in New Caledonia that individuals of *T niloticus* with shell-diameter above 8.5 cms. (about 3 years old) were mature, while Moorhouse (1932, pp. 154-155) basing his observations on *Trochus niloticus* of the Low Isles came to the conclusion that they were mature in their second year of life when the shell-diameter was generally between 5.00—6.25 cms. Moorhouse found that a few female specimens between 4.40 and 5.00 cms. in shell-diameter were also sexually mature. The range of shell-size for sexual maturity among males was according to him between 5.61 and 7.22 cms. in diameter. The results of my observations are more in accord with those of Montague. Whether the differences in the age at maturity in the three areas have anything to do with the differences in the environmental conditions such as temperature, food, salinity, etc., cannot be stated without further observations¹. Orton (1922, pp. 351-353) gives several instances of the attainment of sexual maturity at a very early age under suitable temperature conditions, and points out that size or age at maturity will depend on the duration of growth and breeding, and that in favourable breeding conditions development of the gonads at an early stage of growth takes precedence over mere increase in size. The comparatively early attainment of maturity by *T niloticus* in the Low Isles is presumably to be attributed to favourable temperature or other conditions which in the case of New Caledonia and the Andamans seem to be lacking, or as Moor-



TEXT-FIG. 6.—Vertical transverse sections of the digestive gland of specimens of *Trochus niloticus* (collected in July) with shell-diameter ranging between 2.5 cms. and 3.5 cms. The sections indicate no trace of the ovary in the space between the integument and the digestive gland.

a 3.17 cms. (drawn under low power and eye-piece $\times 10$); *b*, a portion of the same section drawn under high power. *c*. 2.73 cms. (drawn under high power and eye-piece $\times 10$).

For explanation of lettering see under Text-fig. 3, p. 60.

house himself surmised, the occurrence of maturity in small-sized shells may indicate a retardation in the growth of the shell.

¹ The recent works of Newcombe (1936), and of Newcombe and Kessler (1936), on the relationship of growth and environment in the clam, *Mya arenaria* Linn. deal with these questions in some detail.

The rate of growth at different ages has been dealt with in a previous paper (Rao, *loc. cit.*). Despite the fact that shell-growth is very irregular even in the individuals of a given size-category, there is a definite falling off in the rate of growth as the shell increases in size. Moorhouse speaks of "a definite slackening off in the amount of shell deposited by the animals during the colder months", and of a period of "rest from shell-building" which he terms the "time of hibernating", but in the Andamans I have not been able to obtain any evidence to show that *T niloticus* has a slack season for growth of shell or a definite period of aestivation when the animal does not feed or move about. Amirthalingam's (1932, p. 98) observations on the growth of *T niloticus* at Port Blair led him to the conclusion that it "grows during the monsoon and 'winter' months, that is, July to March", a statement which seems to imply that the remaining part of the year from April to June constitutes a season of slow or no growth.

The determination of the breeding period or periods of *T niloticus* in the Andamans presented considerable difficulties. The main criterion for breeding is the discharge of eggs and spermatozoa at about the same time, and the fertilisation of the former leading to development. Observations in the field and in the laboratory of several hundreds of adult sizes of *T niloticus* during the years 1932 to 1935 failed to reveal any male or female in the act of discharging its sex-products. Artificial fertilisation experiments with the ripe sex-products obtained from individuals having a shell-diameter of 10.0 cms. during the months September to July proved a failure.¹ The mature state of the sex-products of the adults throughout the year seemed to show that at any time of the year individuals bearing ripe sex elements were not altogether absent. Amongst them were those with gonads full of ova or spermatozoa as well as individuals (with flabby gonads) which may be considered to have recently shed their sex-products in part. A second method of approach to the problem of the breeding season adopted was the periodical examination of the plankton of the inshore waters round about Port Blair and other localities to discover the occurrence of any advanced veligers with shell resembling the types common to Trochidae. Several forms allied to the Cerithidae, Rissoidae, Turbinidae, Neritidae, etc., were found in the plankton during the warmer months of the year, and it was thought that the occurrence of advanced larvae of Trochidae would give a clue to the breeding period. Unfortunately, none of the Trochoid forms was obtained during the months December to April when the weather conditions were suitable for the collection of plankton.

If breeding in *T niloticus* were confined to a short season in the year one would expect to find the shell-populations distributed in several sharp well-defined categories of sizes. Supposing that the breeding season was spread over a period of 2—3 months only commencing in April, and a random sample of the population in a given area measured, say in March of the following year, one would find only shells with a diameter

¹ The looseness of the ova in the gonads which washed freely when a jet of water was directed on it, and the presence of ova in the passages connecting the gonad with the kidney were taken as the criteria for judging the readiness of specimens to breed. The impurity of the sea-water in the shore area around Port Blair which had to be used for the experiment was probably responsible for the failure of artificial fertilisation,

of about 5 cms. in the first year of growth, of 8 cms. in the second year of growth, of 10 cms. in the third year of growth and so on exhibiting gaps in size between the various groups, but none amongst the size-ranges of 1—4 cms.¹ In fact, however, the data of shell-collection of *T. niloticus* round about Port Blair for a period of 4 years ending in July 1935 show no well-defined gaps in the distribution of shells amongst the various categories of sizes (see Table II, pp. 76-79). The absence of small-size shells of diameter upto 1.99 cms. in the years 1931-34 has no significance. Because of their cryptic habits and small-size, and the dull colour of the shell which so well harmonizes with that of its surroundings, the small shells may have been overlooked.² The intensive fishing for *Trochus* shells by the Japanese during the years 1929 and 1930, may have also been partly responsible for the scarcity of both the small and the very large shells with a diameter range of 1-3 cms. and 12-14 cms. respectively. A glance at Tables II and III (pp. 76-79 and p. 80) would seem to emphasise the point that intensive collection has made inroads on the large-sized shells as the frequency distribution of shells of various sizes in the four years 1931-35 shows. The mode of frequency seems to move gradually from 7.0 and 8.0 cms. categories in 1931-32 to 3.0 and 4.0 cms. categories in 1934-35.

Of the three types of evidence available for determining the breeding period, that provided by the larvae is negative. The mature and gravid condition of the gonads in adult individuals throughout the year leads one to the conclusion that breeding is not noticeably interrupted, while the samples of shells, collected throughout the twelve months of the four years in the same locality, which include shells of all ages amply support the conclusion that breeding is continuous (see Tables II and IV, pp. 76-79 and p. 81).

In the Low Isles, Moorhouse (1932, p. 154) observed that the spawning period was of some five months' duration at least, commencing in March, and that eggs were liberated not in great clouds but in small quantities at a time. He thought however that the egg-laying was protracted over a period longer than five months. In New Caledonia Montague (*loc. cit.*) found in the month of December several specimens (9 cms. in diameter) distended with eggs ready for deposition. In the Andamans, Amirthalingam (1932, p. 31) inferred that spawning would probably begin in April, presumably from the fact that females with spent gonads were observed from that month onwards, but did not mention whether he had seen any individuals actually spawning. If spawning is continuous over only a short period, one may expect to find a majority of individuals with spent gonads during that period. Actually, however, examples with full and spent gonads were obtained during the warm as well as the cold months of the year. These terms 'warm' and 'cold' have relatively less significance in the latitudes in which the Andamans

¹ The results of the rate of growth studies embodied in another paper (Rao & Raja, 1936) have been used to estimate the age-groups.

² It is also possible that the younger forms inhabit the deeper parts of the sea from which a few stray into the shallower parts and the intertidal region. Hedley (1917, p. 70) stated that the youngest stages of *T. niloticus* are passed in deep water on the reefs. Gopala Aiyar (1935) found that specimens of the Echinoid *Salmacis bicolor* of small size (3.4 cms. in diameter) were singularly absent amongst hundreds of large forms obtained from the Madras Harbour, and suggested that the young forms may probably be confined to the deeper parts, creeping up only after attaining maturity.

are situated where the annual range of the average monthly temperature of the surface-water does not exceed 2° C.¹ The influence of temperature on breeding is discussed below. It may be pointed, however, that in the Andamans there is no definite evidence to show that spawning is confined to any well-marked season, although spawning has probably a tendency to be more intensive in the warm months from February to May, than during the monsoon months June to November.

The temperature observations on the east coast of Ross I. were taken at various hours of the day from 6 A.M. to 6 P.M. in knee-deep water between the rocks constantly washed by the waves. The highest and lowest temperatures recorded during these nine months were 32.0° C. in May and 25.9° C. in December respectively, while (the daily average) high temperatures prevailed during the months of May and October. The average temperature for April would presumably be higher than that of May, but owing to other work no observations could be taken at Port Blair during the dry and warmer months of February, March, and April (see Table V, p. 82).

Amirthalingam in his note to *Nature* (p. 98, 1932) stated that *Trochus niloticus* "has a minimum temperature above which alone it would spawn" basing his conclusion presumably on the fact that individuals with spent gonads were found from the month of April onwards, and on the results of Sewell's temperature observations (*loc. cit.*) in the Andaman sea which indicate a double oscillation in temperature in the course of a year. He also stated that the observation that *T. niloticus* starts spawning in April when the first rise of temperature takes place emphasised "the idea that the marine invertebrates in tropical waters do not breed haphazardly but with a similar regularity to that observed in temperate waters" My observations in the Andamans for about 3 years do not establish any definite correlation between breeding in *T. niloticus* and the observed high temperature epochs of the Andaman sea, and the analogy of the correlation between these two phenomena in the temperate seas may not hold good in the tropics.² Recently Whedon (1936) studying the spawning habits of *Mytilus californianus* Conrad in the vicinity of San Francisco with reference to temperature doubted that the changes in temperature which occur in that region were severe enough to influence spawning. He found the sex products developing in the warmer months when food was most abundant, and the mussels spawning in the cooler months, while on the contrary *Mytilus edulis* of the Atlantic coast of America was observed to develop sex products in the coldest months and to spawn with the onset of warmer conditions. In the same manner the warmer periods during March and April and again in October in the Andamans may stimulate the activity of sex-glands in *T. niloticus* leading to a comparatively intensive spell of spawning at their end, or during the cooler months following the warm periods.

¹ The average daily range of temperature at Port Blair as given by Sewell (1927, pp. 104-118) seems to be much higher than the one given here. My observations at Port Blair during 1933 show that the difference in maximum and minimum temperatures attained in the course of the day is no more than 2° C.

² Adult specimens of *T. niloticus* kept in samples of sea-water the temperature of which was raised by artificial heat up to 35° to 40° C. did not show any signs of spawning, although active movements of the animal were observed.

Orton (1922) has shown that in marine animals of temperate regions sexual activity is induced under normal biological conditions by the stimulus of temperature, and that in the temperate regions the breeding temperature which is a physiological constant for each species of marine animal may be the minimum or the maximum attained in that particular locality. In regard to the tropics where constant or nearly constant temperature conditions prevail, he has stated that "there is apparently good evidence that breeding in marine animals is continuous, but a thorough investigation of this problem is desirable". The main problems in regard to the breeding of tropical marine animals may be stated in the form of a questionnaire: (1) does the small range of variation in the temperature of tropical seas admit of considering temperature as the main stimulus for breeding, (2) if the answer to this question is in the affirmative, do the maxima and minima of temperatures attained in various localities act as physiological constants in the breeding of marine animals, (3) do factors other than temperature have any correlation with breeding, and if so, to what extent. In the present state of our knowledge of the breeding of tropical marine animals the answers to the questionnaire would presumably be incomplete. Observations in the different regions of the tropical seas seem to have led to divergent conclusions. A short review of the opinions held in regard to the general question of the epoch and frequency of breeding in the tropical seas may not be out of place here. Mortensen (1921), while admitting that temperature has an important bearing on development which proceeds at a conspicuously quicker rate at the higher temperature of the tropics than in the colder regions, did not agree with the view that all tropical marine animals breed continuously throughout the year. From his experience of some species of tropical Echinoderms he could only concede that they have more than one breeding season in the year. He was able to confirm Orton's statement that "where biological conditions do not vary much marine animals will breed continuously" but "would only object to making this a general rule; this it is certainly not, especially not in the tropics", by which Mortensen apparently meant that biological conditions do vary in the tropics and that therefore breeding cannot be continuous. Anne Stephenson (1934), as a result of her observations on the breeding of various marine Invertebrates such as Coelenterates, Echinoderms, Molluscs, and Crustaceans in the Great Barrier Reef in 1928-29, came to the conclusion that the breeding was by no means confined to any one part of the year, but occurred every month, in winter as well as in summer. She believed, however, that although spawning was going on all the year round, a majority of the species investigated "would be found spawning either exclusively or most actively in the warmer months". She also thought that "the actual breeding season of any one species would probably fluctuate considerably from one year to another, in the same place, not to mention its varying from one district to another". She observed four main types of breeding in the Great Barrier Reef, (1) a single breeding period not lasting the whole year round, (2) continuous breeding throughout the year but more active in one part of the year than during the remainder, (3) discontinuous breeding occurring in relation to lunar phases during a longer or shorter portion of the year, (4) two spawning periods

in the year with a quiescent phase between them. Moore (1934) observed considerable variation in the breeding periods of *Echinus esculentus* even in localities separated only by a few miles and at different depths. Gopala Aiyar (1931) found the Polychaete worm *Marphysa* breeding in Madras from January to September and again in December. The same author (1935) collected sexually ripe individuals of the Echinoid *Salmacis bicolor* in the Madras Harbour throughout the year at temperatures varying from 24° C. to 30° C., and found (1935) *Acentrogobius neilli* (Day) breeding at all times in the Adyar backwaters, Madras, at temperatures varying from 24°·4 C. to 29°·65 C., but with an intensive breeding period during the monsoon in October and November.¹ Subramaniam (1935) observed the brackishwater hermit-crab, *Clibanarius olivaceus* (Henderson) at the mouth of the Adyar River, Madras, breeding throughout the year but with a well-marked intensive period from September to March. Whedon (1936) found *Mytilus californianus* Conrad in the region of San Francisco spawning at all times of the year, but with a maximum period of spawning beginning early in October, followed by two other periods of lesser degree in January and February, and in May and June. This short review of recent work on breeding in tropical marine animals in relation to temperature changes seems to indicate that the evidence in support of the view that tropical marine animals breed continuously tends to gather weight. It does not seem to be clear, however, what, under the uniform biological conditions of tropical seas, constitute the stimulus for inducing marine animals to spawn. Whedon (*loc. cit.*) has "shown that spawning occurs at all times of the year, apparently irrespective of temperature or other external stimuli", and the observations of Anne Stephenson (*loc. cit.*) and Moore (*loc. cit.*) seem to lend support to that author's findings.

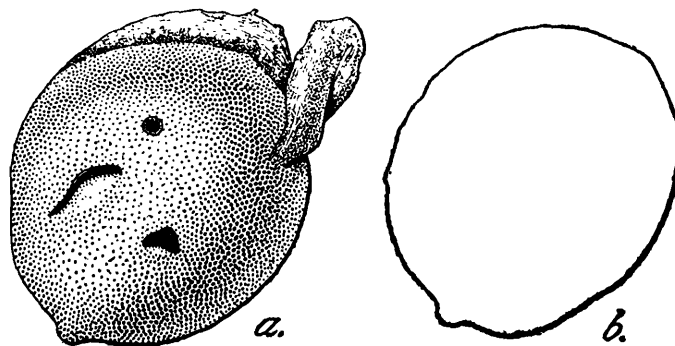
In regard to the factors which influence breeding in *T. niloticus* the observations of Montague (*loc. cit.*), Moorhouse (1932) and Amirthalingam (*loc. cit.*), and those recorded in the present paper tend to show that the physiological constant which induces spawning is not merely temperature or latitude or food. The optimum condition for spawning in a given region would probably be a combination of several factors which may include one or more of those mentioned. Without a detailed investigation of the physiology of *T. niloticus* it would be difficult to determine the factor or combination of factors which induces sexual activity throughout the year. On the whole the question of sexual maturity and spawning in individual species of tropical marine animals in relation to the physical and biological conditions at different latitudes cannot be settled satisfactorily without further knowledge of the habits of marine animals from various regions of the tropical seas.

The longevity of *Trochus niloticus* in the Andamans has been dealt with (Rao, *loc. cit.*) in another paper. Individuals with shell-diameter up to 15 cms. have occasionally been taken in collections from various islands of the Andaman and Nicobar groups. Under normal conditions an individual may live for well over 10 years attaining a diameter of

¹ In the Andamans I have observed the Blennioid fish *Andamia heteroptera* Bleeker on the rocks between tide-marks in the vicinity of Port Blair with fully developed eggs from September to the beginning of May, and young ones 1-2 cms. long practically throughout the year.

over 12 cms., but specimens with shell-diameter exceeding 14 cms. may be 12 years old.¹ Death in *T niloticus* due to old age is very little known. Certain characters of the shell (in examples with diameter exceeding 11 cms.) observed in the course of the investigation seem to suggest their association with senility. The tendency of the upper margin of the last whorl to be discrete from the suture or the previous whorl, the irregularity of the oblique lines of growth on the last whorl, the thickening of the shell, and the tendency to the formation of blisters on the nacreous surface of the mouth of the shell are some of the features commonly observed in shells above 11—12 cms. in diameter and may be associated with the senile changes in this species. There may be other features of senility exhibited by the internal organs such as the digestive and the nervous systems,² but these have not been investigated.

The sheltered positions on the reefs in which *T niloticus* occurs probably protect the species to some extent from predatory enemies, such as sharks, rays, Gymnodontid fishes, etc. In the more exposed parts of the reefs, however, the extremely thick and hard shell of the species seems to be of doubtful utility in protecting the species from the attacks of such enemies mentioned above, for fragments of shells of *Trochus* and *Turbo* have been found amongst the gut contents of these fish.³ The thin and weak operculum seems to provide inadequate protection against the attacks of large crabs which with the help of their powerful chelipeds seem to tear the soft parts of *Trochus* in the expanded state. On one occasion a large crab on the reef near South Point, Port Blair, was seen helping itself to morsels of the flesh of *T niloticus* under a stone when the animal was in a partial state of expansion. The snail was found to be dead, but it was difficult to say whether the crab was merely feeding on the carcass of an individual, or had caused the death of the animal



TEXT-FIG. 7.—Calcareous concretion from the apex of the visceral coil of *Trochus niloticus* from Sister Is., Andamans (24.ii.1933).

a. In the investing membrane which is produced into a short twisted stalk at one end., *b.* The concretion removed from its investment.

prior to feeding on the flesh of its victim. A species of Gastropod (Purpurinae-Muricidae) was also found feeding similarly on the soft

¹ Hedley (p. 70, 1917) stated that according to native tradition in Fiji, *T. niloticus* lives for 4 years.

² For a detailed study of senility among Gastropods the works of Burnett Smith (1905), of I. and M. Szabó (1934) and of I. Szabó (1935) may be consulted with advantage.

³ Moorhouse (1932, p. 148) recorded that sting-rays, hermitcrabs (*Dardanus megistos*) and whelks were responsible for the destruction of live *Trochus niloticus* on the Low Isles.

parts of *T niloticus* kept under a rock covered by the tide and examined 24 hours later. The incidence of mortality, due to diseased conditions, or to attacks by crabs, fish, molluscs, etc., as revealed by the number of empty shells or of those occupied by hermit-crabs in samples of shell collections made by divers in the course of a day, appears to be negligible *i.e.*, less than 3 per cent.

The surface of the whorls of the shell is covered by growths of various brown and green algae, by growths of animal colonies such as Sponges, Hydroids, Polyzoa, small Madreporarian corals, barnacles, molluscs, etc. The smaller shells below 7 cms. in diameter are usually free from these growths on the whorls, but the larger ones, particularly those above 10 cms. in diameter, are invariably covered with plants and animal colonies. These presumably afford the animal some degree of protection from predatory enemies. Amongst the animals causing damage to the shell were observed the following: the bivalve molluscs *Lithophaga (Lithopaga) nasuta* (Philippi), *L. (L.) laevigata* (Quoy & Gaimard),¹ *Parapholas quadrizonata* Spengler, and *Rocellaria* sp. often boring into the nacreous layer of the shell; Gastropods like the Lepetellid *Saptadanta nasika* Prashad & Rao, the Patellid *Patella (Patellidea) tara* Prashad & Rao,² the Vermetid *Vermetus (Spirogyphus) andamanicus* Prashad & Rao³ which cause some damage to the periostracal and nacreous layers of the shell by excavating deep impressions of the outline of their respective shells; and the boring Sponge *Cliona* sp. which destroys the periostracal layer.⁴ Irritation caused by sand-grains or other foreign particles on the mantle inside the shell usually leads to the formation of rounded or irregular nodules of mother-of-pearl on the nacreous layer inside the mouth of the shell. In an adult shell from Sister I., Andamans, an oval mass of calcium carbonate (pl. I, fig. 17) about the size of a small pea was found in a small sac of mantle tissue (text fig. 7a.) in the top-whorls of the spire.⁵ This may also have been due to the irritation set up initially by a foreign particle, but resulting in the deposition of a calcareous amorphous mass instead of nacreous substance.

No internal parasites causing damage to the soft parts have been found in *T niloticus*, but the Copepod, *Panaietis camerata* Stebbing, found living generally in the buccal cavity and oesophagus of the living *T niloticus* appears to be a commensal rather than a parasite. No discernible damage has, at any rate, been done to the host by this Copepod. This species, known previously from a unique example (♀) taken from the pallial cavity of an unknown Gastropod from the Louisiade Archipelago off the south eastern coast of New Guinea, has been fully described

¹ Winckworth (1933) described *Acanthochitona penetrans* found living in the holes made by these two species of *Lithophaga*.

² *Rec. Ind. Mus.*, XXXVI, pp. 1-4, pl. i (1934).

³ *Rec. Ind. Mus.* XXXV, pp. 409-412, pl. x (1933).

⁴ A species of *Petrosia* Vosmaer found filling up the cavity in the apex of the spire above the white mass of amorphous calcareous deposit in certain specimens of *T. niloticus* does not appear to be harmful to its host, but it is difficult to understand how the sponge could have gained access to the interior of the apical part of the shell which was entire and without cracks or holes on the outside.

⁵ My friend, Dr. M. S. Krishnan of the Geological Survey, whom I have to thank for examining the mass, reported that its composition was almost pure calcium carbonate (Aragonite).

from several examples by Monod (1934), and is invariably found in the living state in the buccal cavity or oesophagus of *Trochus niloticus* of all ages known in the Andamans. This Copepod has recently been recorded by Yamaguti (1936) from the mouth cavity of *Turbo (Batillus) cornutus* Solander from the Sea of Japan. A closely allied *P. haliotis* Yamaguti from the Pacific Coast was found in the mouth cavity of *Haliotis (Sulculus) gigantea* Gmelin.

In conclusion I wish to take this opportunity to express my indebtedness to Dr. Bani Prasad for much encouragement in my investigations, to the authorities of the Andaman administration for the grant of laboratory and transport facilities on land and sea respectively, and to the representatives of the Japanese Fishery Companies of Singapore stationed at Port Blair, who rendered the most valuable assistance in my field-work by taking me in their motor-boats to nearly all the *Trochus* shell-beds in the Andaman and Nicobar groups of islands and permitting me to examine their collections of shells. To Mr. K. S. Misra, Laboratory Assistant at Port Blair, my best thanks are due for diligent and willing assistance rendered throughout the period of my investigations.

SUMMARY.

1. The geographical distribution of *Trochus niloticus* is indicated.
2. The two common types of shell of *T. niloticus* which occur throughout the Andamans and Nicobars do not represent two distinct species as was supposed by some authors, but only plastic phases of *T. niloticus* or changes due to differences in the rate of growth at various ages.
3. *T. niloticus* occurs commonly on the reefs and boulders between tide-marks and at depths ranging from 2—7 fathoms on the weather side within $\frac{1}{2}$ to 1 mile from the shores of the islands of the Andaman and Nicobar groups. The younger shells up to 5 cms. in diameter are found at all times of the year amongst coral shingle and under coral slabs between tide-marks, but are rather scarce where the adult shells are found. There is no evidence at present to show that they are more abundant at depths greater than 7 fathoms from where they crawl up to the shallower parts on reaching maturity.
4. *T. niloticus* is not a gregarious species in the strict sense of the term. It is not massed in large numbers like the members of the families, the Neritidae and Littorinidae, which are well-represented on the rocks and boulders between tide-marks of the Andaman islands.
5. The species does not thrive under the artificial conditions of Laboratory aquaria. The behaviour of animals under these conditions is described. The animal is able to survive dessication for 48 hours.
6. Within the limits of the reefs surrounding the islands, *T. niloticus* wanders a great deal in search of food and shelter.

- 7 The feeding habits of *T niloticus* are described. It is shown that the species lives chiefly on bottom deposits and on fresh algal vegetation. The features of the radular teeth of animals of various ages are described.
8. No certain method of determining the sex of the shell without breaking it open or damaging it is known. The sexes are separate and are distinguished by the colour of the gonads, green in the adult female, white or cream in the adult male. The young male or female can only be distinguished by examining smears of the gonad under the microscope, or by microscopic examination of microtome sections. Hermaphroditism and sex-change have not been observed, and are considered improbable of occurrence.
9. The two sexes occur in about equal numbers in the adult age-groups with shell-diameter between 7.0 and 11.99 cms. This fact is supported by statistical evidence.
10. In the Andamans and Nicobars, sexual maturity is reached in the female when the shell has attained a diameter of 9.0 cms., and in the male when the shell has a diameter of 6.0—7.0 cms.
11. No evidence of a slack season for growth in shell or of a period of aestivation for *T niloticus* in the Andamans has been obtained.
12. The mature condition of the gonads and the readiness for spawning which has been observed in adults of *T niloticus* throughout the year, and the occurrence, during the twelve months of the year, of shells of all ages indicate that breeding is continuous with perhaps an intensive spell of breeding during or immediately after the warm seasons.
13. The opinions held in regard to the problems of the stimulus for spawning, and of the period and frequency of breeding in tropical marine animals are reviewed. The inadequacy of any one environmental factor alone to stimulate sexual activity is pointed out. It is suggested that a more detailed investigation of the physiology of tropical marine animals would provide satisfactory solutions to these problems.
14. The age of *T niloticus* in the Andamans is shown to exceed 10 years. Certain features in the shell suggestive of senility are described.
15. The incidence of mortality due to diseases or old age is indicated to be low. Animals associated with the shell or the soft parts of *T niloticus* and causing in some instances damage to the shell are described.

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TABLE I.

Table showing the percentage frequency of individuals with ova of three different dimensions.

Age or size-group (Diameter in cms.).	RITCHIE'S ARCHI-PELAGO.			CINQUE, SISTER, BROTHER, PASSAGE AND LITTLE ANDAMAN ISLANDS.			INTERVIEW I. AND OTHER ISLANDS OF THE WEST COAST OF ANDAMAN ISLANDS.			PORT BLAIR AND ENVIRONS.		
	PERCENTAGE FREQUENCY OF INDIVIDUALS WITH OVA			PERCENTAGE FREQUENCY OF INDIVIDUALS WITH OVA			PERCENTAGE FREQUENCY OF INDIVIDUALS WITH OVA			PERCENTAGE FREQUENCY OF INDIVIDUALS WITH OVA		
	below 0.05 mm.	between 0.05 and 0.20 mm.	above 0.20 mm.	below 0.05 mm.	between 0.05 and 0.20 mm.	above 0.20 mm.	below 0.05 mm.	between 0.05 and 0.20 mm.	above 0.20 mm.	below 0.05 mm.	between 0.05 and 0.20 mm.	above 0.20 mm.
6—6.99	100.0
7—7.99	41	59	..	85.7	14.30	..	80	..	20.00	66.6	..	33.3
8—8.99	19	46	35	60.0	23.30	16.70	18	32.00	50.00	..	66.6	33.3
9—9.99	10	13	77	7.5	40.00	52.50	..	16.42	83.58	11.2	..	88.8
10—10.99	100	..	4.88	95.12	100.00	100.0
11—11.99	100	100.00	..	1.25	98.75	100.0
12—12.99	100.00	100.00
13—13.99	100.00
Total No. of shells examined	148			192			340			55		
No. of shells in each group	29	51	68	41	28	123	13	28	299	11	6	38

TABLE II.

No. of shells collected at Port Blair in each month of the year 1931-32.

Age-group (Maximum diameter of shell in centimetres).	May.	June.	July.	August.	September.	October.	November.	December.	January.	February.	March.	April.	Total No. of shells for the year.	Percentage.
1— 1.99		
2— 2.99	..		2	2	0.29
3— 3.99		1	2	3	0.44
4— 4.99			1	4	10	2	4	2	23	3.36
5— 5.99	3	2	18	5		3	7	2	3	4	47	6.86
6— 6.99	..		6	6	37	33	9	5	7	2	4	1	110	16.06
7— 7.99			6	7	29	39	16	4	4	8	6	2	121	17.66
8— 8.99			4	9	25	27	10	6	10	12	14	10	127	18.54
9— 9.99		..	4	8	19	15	5	6	7	4	9	12	89	12.99
10—10.99			2	11	17	8	4	6	3	4	19	6	80	11.68
11—11.99			..	3	6	10	1	4	5	1	23	2	55	8.03
12—12.99	2	2	..	3	5	2	..	11	..	25	3.65
13—13.99				3	..	3	0.44
Total No. for each month	27	48	155	137	48	43	57	35	96	39	685	100.00

TABLE II—contd.

No. of shells collected at Port Blair in each month of the year 1932-33.

Age-group (Maximum diameter of shell in centimetres).	May.	June.	July.	August.	September.	October.	November.	December.	January.	February.	March.	April.	Total No. of shells for the year.	Percentage.
1— 1.99			
2— 2.99			1	1	1	..	3	1.0
3— 3.99			2	2	1	5	1	1	12	4.7
4— 4.99			1	1	1	3	10	3	2		21	8.2
5— 5.99	1	1	..	5	8	1	..		2	3	8		29	11.4
6— 6.99	1	4	..	4	14	16	1	2	1	6	2	..	51	20.0
7— 7.99	1	3		6	19	19	2	2		2	1		55	21.6
8— 8.99	1	1	1	1	5	19	..		1	..	2	..	31	12.2
9— 9.99		1				6	3	1	2	1			14	5.5
10—10.99		3	2	3	..	5	1			..	14	5.5
11—11.99		3		5		5		1	2			..	16	6.3
12—12.99	..	1	1	1	..	6	9	3.5
13—13.99		
Total No. for each month	4	17	4	25	49	80	8	14	21	16	16	1	255	99.9

1937.]

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TABLE II—contd.

No. of shells collected at Port Blair in each month of the year 1933-34.

Age-group (Maximum diameter of shell in centimetres).	May.	June.	July.	August.	September.	October.	November.	December.	January.	February.	March.	April.	Total No. of shells for the year.	Percentage.
1— 1.99
2— 2.99	5	1	3	6	1	1	17	7.26
3— 3.99	2	5	8	4	3	2	1	1	3	4	1	..	34	14.53
4— 4.99	4	10	4	..	1	..	1	10	..	1	31	13.25
5— 5.99	1	7	..	5	6	2	2	2	..	2	27	11.54
6— 6.99	..	4	..	7	6	4	3	1	..	4	..	1	30	12.82
7— 7.99	..	1	..	7	1	2	5	5	..	6	..	3	30	12.82
8— 8.99	3	1	5	10	..	5	..	3	27	11.54
9— 9.99	..	3	1	1	5	2	..	2	..	3	17	7.26
10—10.99	2	2	..	1	2	..	4	11	4.70
11—11.99	1	4	1	6	2.56
12—12.99	1	1	2	4	1.71
13—13.99
Total No. for each month	7	30	19	31	24	18	25	19	7	36	1	17	234	99.99

TABLE II—concl'd.

No. of shells collected at Port Blair in each month of the year, 1934-35.

Age-group (Maximum diameter of shell in centimetres).	May.	June.	July.	August.	September.	October.	November.	December.	January.	February.	March.	April.	Total No. of shells for the year.	Percentage.
1— 1.99					2		1			3	0.62
2— 2.99 .		1	4	8	5	10	9	5	6	4	9	..	61	12.55
3— 3.99	8		4	4	17	16	23	5	24	11	34	11	157	32.30
4— 4.99 .	11	4	14	3	7	5	9	1	7	4	4	4	73	15.02
5— 5.99 . .	5	5	5	4	7	6		2	2		2	3	41	8.44
6— 6.99	5	6	4	7	1	3	2		2	1	1	32	6.58
7— 7.99 .		..	5	4	3	2	2		4	6			26	5.35
8— 8.99 .	..	6	5	3	1			5	3	5	1		29	5.97
9— 9.99 .	1	8	2	9	1	1	1	11	2	2	..	1	39	8.03
10—10.99 .	..	1	1	1	1		2	7	1		1		15	3.09
11—11.99	1	1	1		3	1			..	7	1.44
12—12.99					1			1	0.20
13—13.99					2			2	0.41
Total No. for each month .	26	31	46	40	51	42	50	41	50	37	52	20	486	100.00

TABLE III.

Table showing the percentage frequency of shells of the various age-groups collected in the four years, 1931-35 at Port Blair.

Age-groups.	1—1.99.	2—2.99.	3—3.99.	4—4.99.	5—5.99.	6—6.99.	7—7.99.	8—8.99.	9—9.99.	10—10.99.	11—11.99.	12—12.99.	13—13.99.
1931-32	..	0.29	0.44	3.36	6.86	16.06	17.66	18.54	12.99	11.68	8.03	3.65	0.44
1932-33	..	1.00	4.70	8.20	11.40	20.00	21.60	12.20	5.50	5.50	6.30	3.50	..
1933-34 .	..	7.26	14.53	13.25	11.54	12.82	12.82	11.54	7.26	4.70	2.56	1.71	..
1934-35 . .	0.62	12.55	32.30	15.02	8.44	6.58	5.35	5.97	8.03	3.09	1.44	0.20	0.41

TABLE IV.

Table showing the occurrence of shells of *T. niloticus* at Port Blair of various age-groups in the twelve months of the year.

Months.	Age-groups.												
	1	2	3	4	5	6	7	8	9	10	11	12	13
May	—	×	×	×	×	×	×	×	×	—	×	—	—
June	—	×	×	×	×	×	×	×	×	×	×	×	—
July	—	×	×	×	×	×	×	×	×	×	×	×	—
August	—	×	×	×	×	×	×	×	×	×	×	×	—
September	×	×	×	×	×	×	×	×	×	×	×	×	—
October	—	×	×	×	×	×	×	×	×	×	×	×	—
November	×	×	×	×	×	×	×	×	×	×	×	×	—
December	—	×	×	×	×	×	×	×	×	×	×	×	—
January	—	×	×	×	×	×	×	×	×	×	×	×	—
February	—	×	×	×	×	×	×	×	×	×	×	×	—
March	—	×	×	×	×	×	×	×	×	×	×	×	—
April	—	×	×	×	×	×	×	×	×	×	×	—	—

× = indicates occurrence.

TABLE V

*Daily average surface-water temperature of the inshore region on Ross I.
in degrees centigrade.*

Months.	Forenoon.	Afternoon.	Difference in average.
1933—			
May	28·8	29·5	0·7
June . . .	28·1	28·1	0·0
July . . .	27·7	28·5	0·8
August . .	28·7	29·2	0·5
September	27·9	28·0	0·1
October .	28·5	30·4	1·9
November	28·4	29·3	0·9
December .	27·5	28·2	0·7
1934—			
January .	27·4	28·5	1·1