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DEVELOPMENT AND LIFE HISTORY OF A NUDIBRANCHIATE GASTROPOD *CUTHONA ADYARENSIS* RAO*

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INTRODUCTION

A GENERAL account of the habits, habitat and structure of *Cuthona adyarensis*, an aeolidiform nudibranchiate Gastropod of the Family Tergipididae occurring in the Adyar estuary was given in an earlier paper by the author (Rao, 1952). The present paper deals with descriptions of the gross structure of the early developmental stages of the embryos, the larvae and all further stages through which the free-swimming larvae of *Cuthona adyarensis* pass to attain the characteristics of the adult for an adaptation to a creeping mode of life. A very adequate information is available on the early development up to the formation of veligers in both the cladohepatic and holohepatic Nudibranchs from the works of Grant (1827), Alder & Hancock (1855), Reid (1846), Keferstein and Ehlers (1861), Casteel (1904), Rasmussen (1944 & 1951), Thorson (1946) and Rao & Alagarswamy (1960), but the changes which the larvae undergo to reach the adult condition are not fully understood. However, among the earlier workers Nordman (1846) in *Tergipes edwardsii* and Schultze (1849) in *Tergipes lacinulatus* and very recently Thomson (1958) in *Adalaria proxima* and Gohar and Abul-Ela (1959) in *Discodoris erythraeensis* had observed some post-larval developmental stages of Nudibranchs. The paucity of information on the subject is due to the reason that under laboratory conditions the larvae soon after hatching perish in enormous numbers in spite of the best care and attention and even a few that survive show no signs of further development. In the following account the methods adopted in obtaining successfully a complete series of developmental stages in *C. adyarensis* are described.

MATERIAL AND METHODS OF STUDY

Full grown adults of *C. adyarensis* which measured about 12 mm. in length were obtained when they were found creeping on the floating algal masses of *Hypnaea* from the estuary of the Adyar river from March to August in 1948. When they were taken along with the algae and placed in the laboratory finger bowls holding dilute sea water they thrived well feeding upon the hydroids of the genera *Bimeria* and *Laomedea* which were found often on the algae and deposited strings of spawn after copulating at fairly frequent intervals. The finger bowls were wrapped in moist cotton gauze and placed in shallow enamelled trays holding ordinary tap water to a depth of about three-fourths of an inch, as a result of which the water contained in them remained at a temparature of 22°C to 24° C which was nearly 2 to 4°C below the room temperature. At the beginning water from the original habitat alone was

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used for keeping the animals or the spawn alive for observations, but subsequently sea water diluted with ordinary tap water to lower the salinity was found to be equally efficient. The salinity of water in the Adyar estuary ranged during the five month period from 20‰ to 38.47‰. The animals were found in fairly large numbers mostly during periods when the salinity was fair to moderately low between 20‰ to 28‰. Sea water after diluting to bring down the salinity to about 24‰ was tried and found suitable and this medium was continued thereafter during the period of observations. The finger bowls were cleaned and the water was changed twice a day at 10 a.m. and at 5 p.m. Freshly deposited spawn was periodically removed to separate finger bowls.

For tracing the early development, bits of spawn were mounted in cavity slides in the medium of dilute sea water, covered with a cover-slip and examined either under the low or high magnification of the microscope. Rotating embryos and larvae were narcotised for camera lucida sketches by letting in a drop of 2% magnesium sulphate solution to each of the mounted preparations. Where the embryos were slightly opaque they were fixed in 1% glacial acetic acid and cleared in dilute glycerine.

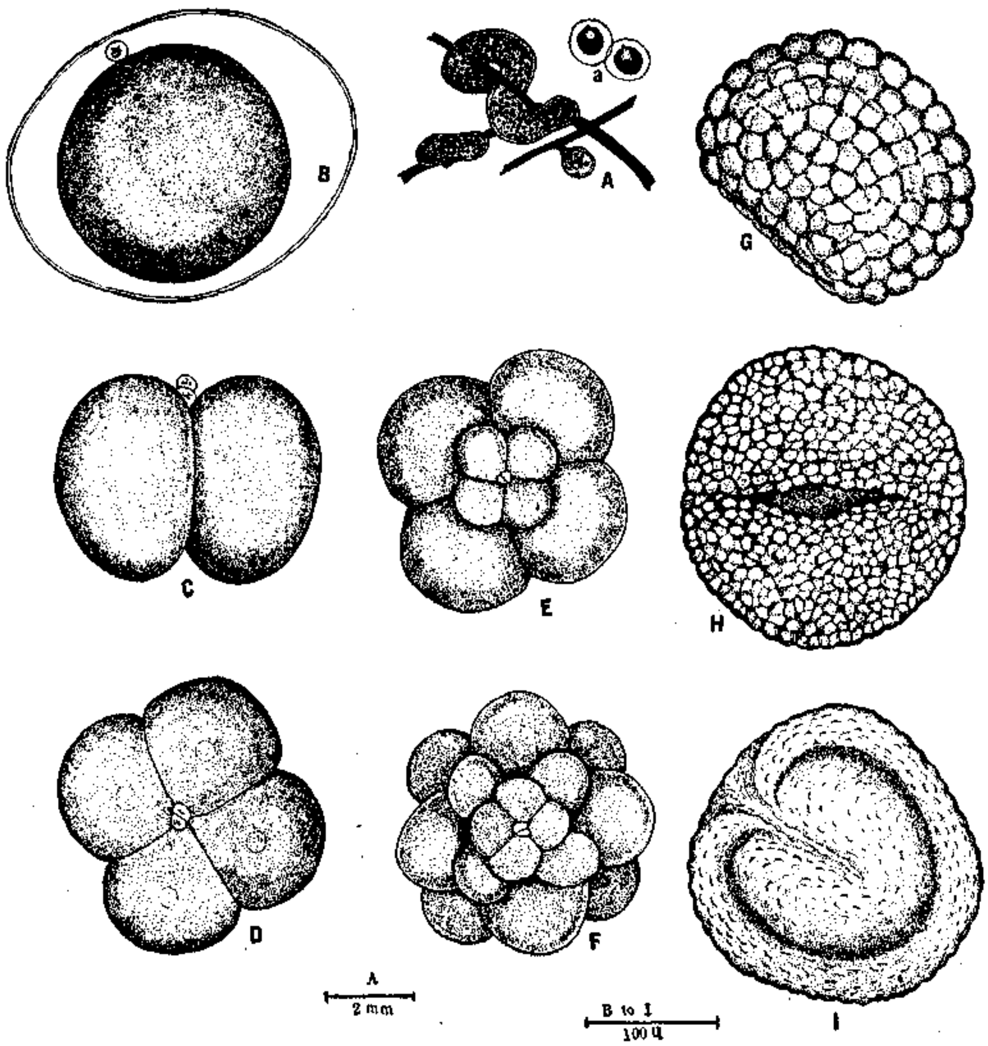
When the eggs had hatched, the contents of the entire finger bowls were examined under a binocular microscope, the larvae were then picked one by one by means of a pipette with a narrow drawn out nozzle and transferred to a separate finger bowl with freshly diluted sea water. The process which gave useful results, although very tedious, was repeated daily even after the creeping post-larval forms had made their appearance. The problem of feeding the post-larval stages of nudibranchs has been a difficult one as in the absence of the right type of food they soon perish. As it was noticed that the adults of the species take to minced brackish water anemones viz., *Phytocoetes* and *Boloceractis* under laboratory conditions, a few particles of the material was dropped once a day into the finger bowls and the post-larvae were observed to feed on them and grow well. All the creeping stages were narcotised in the same manner as the larval forms for microscopic observations.

Early Development upto the Formation of Veliger

Spawn.—The organs of reproduction, the act of copulation and the deposition of spawn have been described in a previous paper (Rao, 1952). The spawn is in the form of colourless mucous strings of varying length from a few to about 10 mm. or slightly more and of a diameter of 0.8 to 0.9 mm., with closely packed minute fertilised yellowish white eggs which lie encased in membranous capsules. The sticky mucous secretion as it extrudes out with the eggs through the female genital aperture hardens on exposure serving to fix the spawn either to the weed or to any other suitable material where it is deposited. Smaller masses of spawn are usually found attached by means of short mucous stalks (Text Fig. 1, A). Spawning in an individual starts half an hour to one hour after copulation and is continued several times at short intervals of a few hours each even without their coming together for a second time. Very young forms isolated when they were still immature and reared carefully under laboratory conditions grew to maturity and deposited spawn without pairing. As the adults are hermaphrodite with fully ripe sperms and eggs occurring simultaneously and as the placement of the male reproductive organs allows passage of the spermatozoa to the oviducal region, there is scope for self-fertilization of the eggs in an individual member (*vide* reproductive organs in *C. adyarensis*, Rao, 1952, p. 235).

Eggs in freshly deposited spawn.—The eggs in the spawn are semi-transparent, yellowish, spherical in outline and heavily yolk laden each measuring about 180 μ

in diameter. External to the yolk globules which are evenly distributed in the cytoplasm, there is an extremely delicate vitalline membrane. The egg is surrounded by a transparent albuminous fluid and enclosed in a double walled membranous capsule, which at first appears oval measuring about 270 μ by 220 μ. At the time of oviposition no polar bodies are usually present but nearly half an hour thereafter one polar body is extruded and it comes to lie on top of the egg (Text Fig. 1, B).



TEXT FIG. 1, A. Strings of spawn of *Cuthona adyarensis* deposited on weed ; (*a*) two of the eggs from the spawn viewed under low magnification ; B. freshly deposited egg after the extrusion of the first polar body ; C. two-cell stage ; D. four-cell stage ; E. eight-cell stage ; F. sixteen-cell stage ; G. side view of gastrula ; H. lower view of gastrula showing blastopore ; I. side view of gastrula showing the formation of the archenteric space.

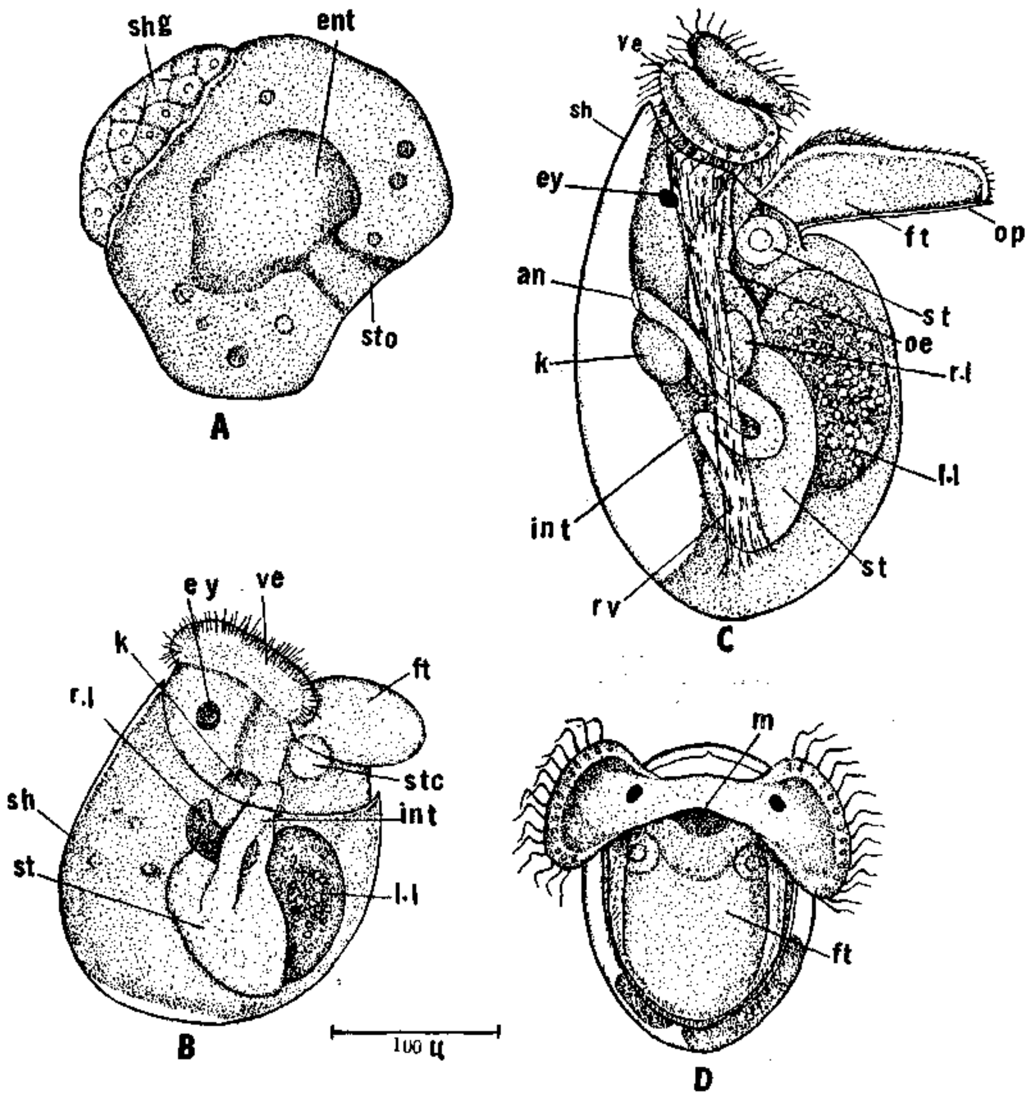
Early cleavages.—The extrusion of the first polar body is followed by the appearance of a second one, which is a little smaller and lies close to the former during the period when the egg undergoes division. About two hours after the deposition of the spawn the first cleavage which has a spiral trend divides the egg vertically into two equal halves. They are spherical to begin with but subsequently become a little elongated as they lie pressed to each other along the plane of the cleavage (Text Fig. 1, C). An hour later a second vertical cleavage which is laeotropic in character as in all molluscs appears at right angles to the first, dividing the egg into four cells (Text Fig. 1, D). About four hours after oviposition, a third horizontal cleavage appears resulting in four small micromeres lying on top of four large megameres (Text Fig. 1, E) and this stage is quickly followed by one showing sixteen cells (Text Fig. 1, F). While these cleavages are in progress, the capsule enclosing the egg assumes a rounded form instead of its being oval as at the time before the commencement of the division.

Gostrulation.—Subsequent divisions take place in quick succession leading at the end of eighteen hours to the formation of a mass of cells and at the end of twenty-four hours to an inverted cup-like gastrula by a process of invagination (Text Fig. 1, G). The gastrula, to begin with, has a height of about 170 μ and a diameter of 226 μ. The blastopore, which is a wide opening lies at the centre of the broad base (Text Fig. 1, H). Very soon the gastrula undergoes slight elongation, its height now being more or less equal to the diameter at the base with the apical region a little pointed. Next the archenteric space appears and the blastopore closes (Text Fig. 1, I).

Early veliger. A pit-like depression is formed at the region where the blastopore has closed giving rise to the stomodaeum which subsequently establishes communication with the enteron. Rudiments of the velar lobes and the foot make their appearance in the embryo dorsal and ventral in position to the stomodaeum respectively. In a shallow depression at the aboral region the shell gland appears and gradually spreads over the surrounding region like a cap. This stage in the developing embryo is attained in 28 to 30 hours after the deposition of the spawn (Text Fig. 2, A). About two hours after this stage the embryo begins to rotate within the capsule by means of cilia developed in the anterior region along the borders of the developing foot and the velar lobes.

In about forty-eight hours (Text Fig. 2, B) the formation of the shell (*sh.*) has progressed well, the velar lobes and the foot are better developed and the embryo rotates faster than in the previous stage. All other larval structures viz., a pair of dark pigmented eyes (*ey.*), a pair of clear statocysts (*stc.*), and oesophagus (*oe.*), stomach (*st.*), intestine (*int.*) and the right and the left liver lobes (*r.l.* & *l.l.*) have all appeared as in the corresponding early veliger stage of an ascoglossan Opisthobranch, *Stiliger gopalai*, described in detail by Rao (1937).

Veliger larva.—In seventy-two to eighty hours a veliger is fully formed (Fig. 2, C) with an elongate, inflated or 'egg-shaped' shell, a type characteristic of the members of the Nudibranch families, Flabellinidae and Tergipididae as contrasted with the 'cup-shaped' and 'spiral' types presented by the Duvacelidae and Polyceridae respectively (Thorson 1946). The veligers are not liberated free till the end of the fourth day, when the enveloping membranes of the capsules give way and the larvae wriggle out one by one into the surrounding water. The just hatched out larva is 370μ by 195μ. The shell is colourless and transparent with a smooth texture and a small aperture. The soft body is very slightly translucent and fairly bulky filling the major part of the lumen of the shell. The liver lobes are massive, the left lobe (*l.l.*) being very much larger than the right (*r.l.*) and the velum (*ve.*), though well developed, is small in proportion to the general build of the larva. The sub-velum is poorly developed. Ventral in position to the velar lobes is the foot, beneath which lies the operculum. The mouth opening, (*m.*) leads into the oesophagus (*oe.*) followed by a spacious stomach (*st.*) with which communicates a coiled intestine (*int.*) and is



TEXT FIG. 2, A. Embryo of *Cuthona adyarensis*, *ent.* enteron, *shg.* shell gland, *sto.* sto modaeum; B. side view of the early veliger, *ey.* eye, *ft.* foot, *int.* intestine, *k.* excretory organ, *l.l.* & *r.l.* left and right liver lobes, *sh.* shell, *stc.* statocyst, *ve.* velum ; C. side view of the fully formed veliger just liberated from the capsule, *an.* anus, *oe.* oesophagus, *op.* operculum, *r.v.* retractor muscle of the velum, and the rest of labelling as in B ; D. larva in swimming position viewed from above, *ft.* foot, *m.* mouth.

continued by a short rectum opening out into the mantle space by the anus situated dorso-laterally to the velar lobe on the right side. Close to the anus is a well developed greenish yellow vesicular excretory organ (*k.*). The liver lobes are greenish and laden with granular reserve material. The sense organs are presented by a pair of dark pigmented eyes each mounted on a small elevation dorsally behind the corresponding velar lobe and a pair of deep seated clear statocysts (*stc.*) each with a single otolith at about the root of the foot. The retractor muscle of the velum (*r.v.*) and those of the foot are present as in other Opisthobranch veligers (Rao, 1937, Casteel 1904 and Rasmussen, 1951). All the larvae are liberated free from a string of spawn by the end of the fifth day or the beginning of the sixth day and they swim about in water for a very short period, varying from a few to about twenty-four hours at the end of which they settle down and creep at the bottom.

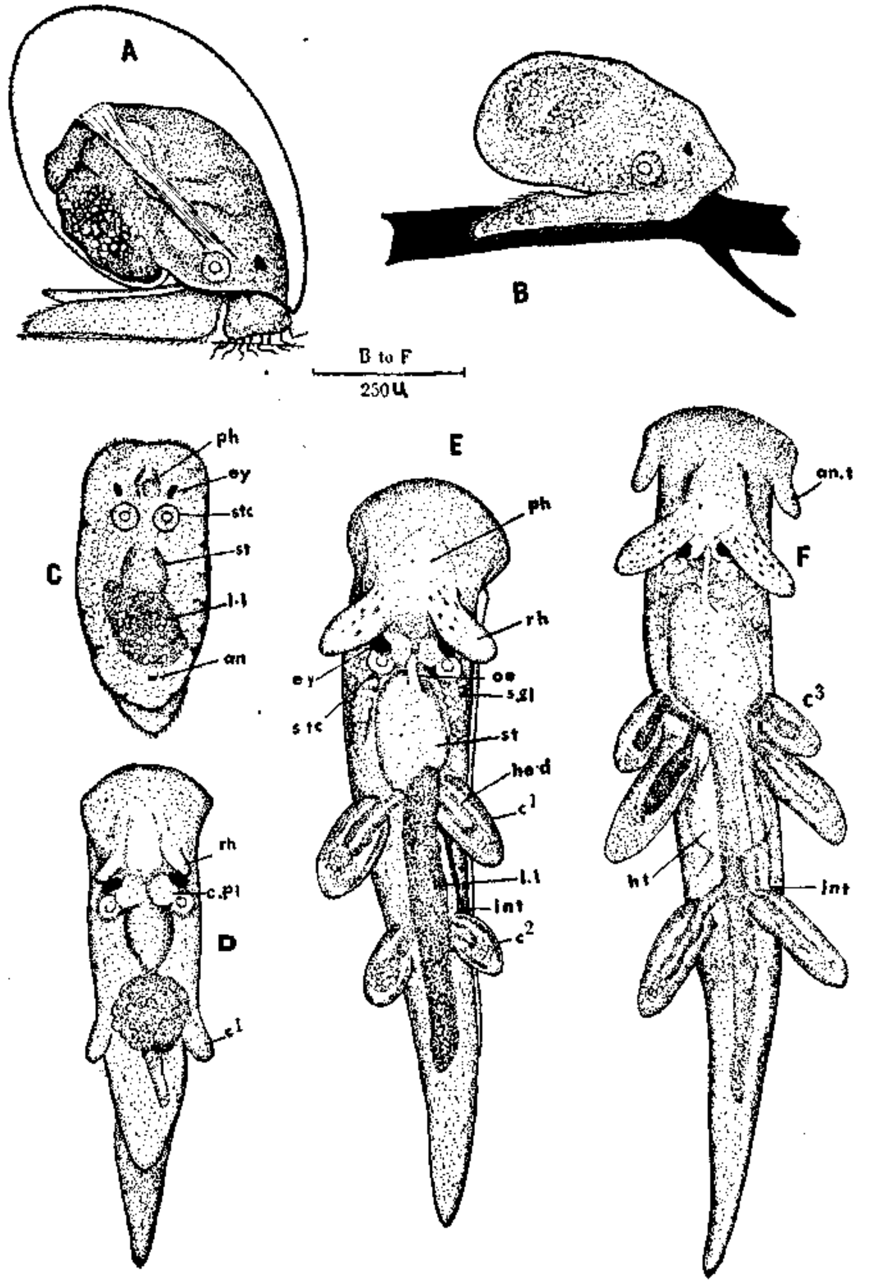
Post-Larval Development Leading to Juvenile Stages

Earliest creeping phase.—During the brief free swimming existence, the larva frequently touches the bottom or settles on the weed and begins to take to creeping as shown in Text Fig. 3, A. Within a few hours thereafter, the velum is gradually reduced, the now ventral surface of the foot which had been its upper surface in the erstwhile free swimming phase has expanded to provide the sole to creep with and the shell which had helped for floating in water having become a hindrance to its new mode of life is discarded as the soft body wriggles out of it. The operculum is dropped more or less at the same time as the shell.

The earliest creeping phase in the development of *C. adyarensis* is a minute clumsy looking yellowish elongate or oval form 500μ long and 225μ broad. The anterior region is roundish with only a faint indication of the much reduced velar lobes. A small plumpy visceral mass lies over the flattened foot. Within the visceral mass are a pair of dark pigmented eyes, a pair of clear statocysts and an alimentary tract with a prominent pharyngeal bulb, an enlarged stomach and a large greenish bilobed liver mass. The mouth opening is anterior and median and the anal opening dorso-median and a little anterior to the posterior extremity of the body. The pharyngeal bulb reveals the rudiments of the jaws and the radula. The tentacles and the cerata are absent and the form is found to move rather slowly (Text Fig. 3, B & C).

Post-larva with rudiments of rhinophores.—In about twenty-four hours after discarding the shell the postlarva presents an elongated appearance. The anterior extremity of the head region is rounded in its dorsal profile and it gradually slopes down a little backwards to reach the foot which is slightly rounded in front but tapering into a tail behind to a little distance beyond the posterior extremity of the dorsum. Two tiny blunt bud-like outgrowths which mark the beginnings of the rhinophores, corresponding roughly to about the middle region of the pharyngeal bulb make their appearance. Another pair of outgrowths also appear a laterally and slightly behind the middle region of the dorsum and these represent the first pair of cerata. In the region of the eyes and close behind them the cerebro-pleural ganglia appear through the transparent skin covering them. The anus is not exactly along the median line but slightly to its right. The post-larvae at this stage are translucent and almost colourless but for the dark pigmented eyes and they measure 818μ by 255μ (Text Fig. 3, D). They were observed to move very rapidly and to feed on fresh hydroids or on tiny particles of the flesh of brackish water anemones.

Post-larva with two pairs of cerata and ramifications of hepatic diverticula.—At the end of the next twenty-four hours the post-larva has reached a stage as presented in Text Fig. 3, E. It has an elongate form 123μ by 270μ with its anterior region slightly



TEXT FIG. 3, A. View of larva in creeping position before discarding the shell; B. post-larva immediately after dropping the shell and absorption of the velum, as viewed creeping on a weed; C. dorsal view of the earliest creeping stage, *an.* anus, *ey.* eye, *l.l.* liver lobes, *ph.* pharyngeal bulb, *st.* stomach and *stc.* statocyst; D. post-larva with primordia of rhinophores and cerata of the first pair, c^1, cerata, *c.pl.g.* cerebro-pleural ganglia, *rh.* rhinophores; E. post-larva with two pairs of cerata and ramifications of hepatic diverticula, c^1 & c^2. cerata of the first and the second pairs, *ey.* eye, *he.d.* hepatic diverticula, *int.* intestine, *l.l.* left liver lobe, *oe.* oesophagus, *ph.* pharyngeal bulb, *rh.* rhinophore, *s.gl.* salivary gland, *st.* stomach, *stc.* statocyst; F. post-larva with anterior tentacles and heart. c^3. cerata of the third pair.

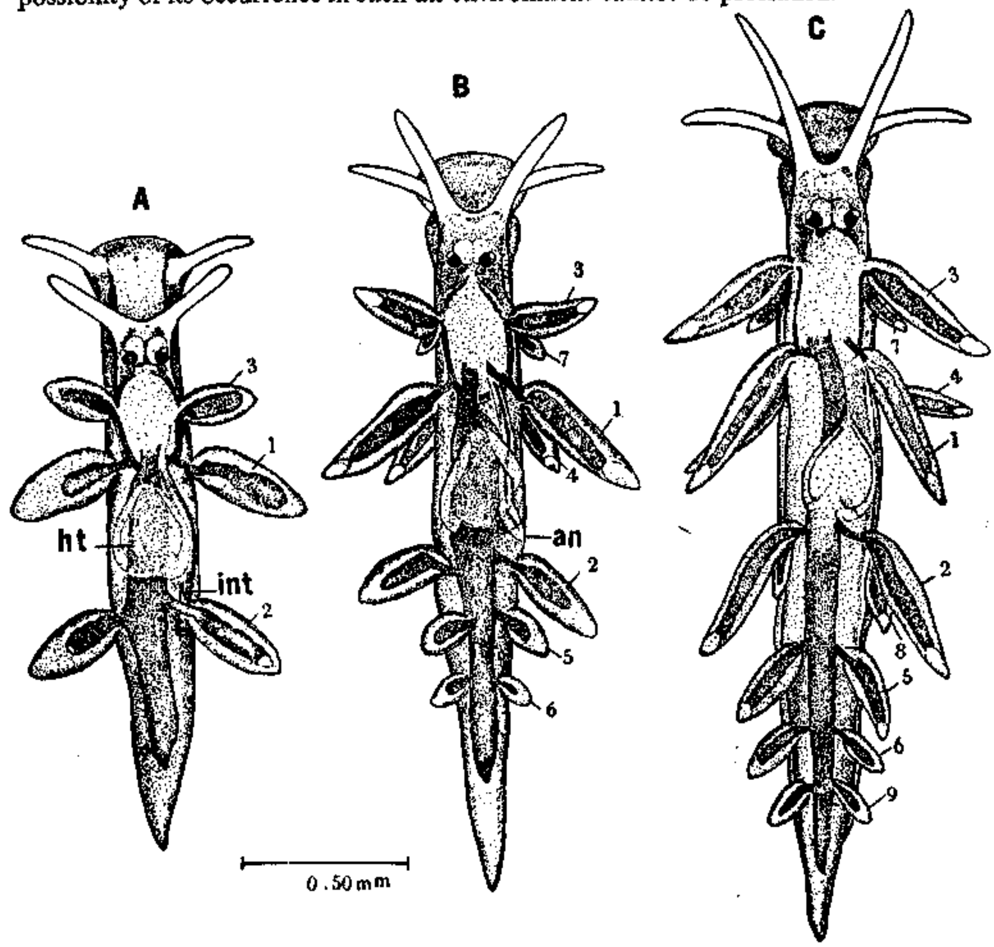
being broad. The head is prominent and the rhinophores are better developed than before, with scattered grayish pigment on their surfaces. Associated with the pharyngeal bulb is developed a pair of salivary glands, which extend from the former to a little distance hindwards on either side of the stomach. The left liver lobe instead of being an irregular mass has extended lengthwise. The cerata of the first pair have grown and a second pair of them have since appeared leaving an appreciable gap between them. The hepatic diverticula from the left liver lobe enter both the cerata of the posterior pair and of the left one only in the anterior pair, the right one of this pair having been supplied with a diverticulum of the right liver lobe. The diverticula are greenish except at the terminal regions where there are tiny clusters of clear vesicular cells. The anal opening is distinctly lateral lying beneath the right posterior cerata. The feeding activity of the form is a little greater than in the previous stage.

Post-larva with anterior tentacles and the heart.—By the end of 78 to 80 hours from the time it has dropped the shell and taken to creeping, the post-larva has grown fairly large, measuring 1430 μ long and 270μ broad (Text Fig. 3, F). It has now a pair of anterior tentacles and a distinct heart in addition to the structures described in the earlier phase. The anterior tentacles are budded off from the front region of the head. The heart which lies enclosed in the pericardium behind the region of the stomach consists of an auricle and a ventricle, the pulsations of them being visible clearly through the transparent body-wall beneath which they lie. In front of the earlier described anterior pair of cerata there has appeared another pair of them. The hepatic diverticula entering them are derived from the original liver lobes of the corresponding sides.

The juvenile stages.—Text Fig. 4, A represents a juvenile measuring 1.8 mm. in length which has resulted from the earliest creeping stage after the expiry of 120 hours. It has the same number of cerata as in the previous stage, but the formation of structures in the head and the general body contour are as in the adult. The first pair of tentacles and the rhinophores have become slender and long. The anterior region of the head is distinctly narrow and rounded in front of the first pair of tentacles. Two labial thickenings in the ventral aspect have appeared, at the sides of the mouth as in the adult. The cerebro-pleural and the pedal ganglia are well defined. The eyes reveal in each a distinct crystalline lens fitting to the pigmented retinal cup. The same juvenile has grown to 2.2 and 2.5 mm. in the next five and seven days respectively showing an increasing number of cerata which have become now grouped into clusters as represented in Text Fig. 4, B & C. The cerata are serially numbered in the order in which they have appeared during development. The well developed ones are slender, elongate, greenish gray with their tips white and provided with cnidosacs as in the adult. The anus opens laterally at the base of the third group of cerata on the right side.

CONCLUSION

The egg of *Cuthona adyarensis* is much larger and more yolky than those of most other Nudibranchs. Excluding the enclosing capsule the egg in this species measures 180 μ whereas the same is 80 μ in *Fiona marina* (Casteel, 1904), 110 to 150 μ in *Embletonia pallida* (Rasmussen, 1944), 70 μ in *Favorinus branchialis* (Rasmussen 1951) and 150 μ in *Eolidina (E.) mannarensis* (Rao & Alagarswamy, 1960). A variation in the diameter of the eggs was noticed by Rasmussen (1944) in *Embletonia pallida* from two localities, which differed in their salinity conditions, those from Isefjord (Sealand, Denmark) having higher saline waters of over 20‰ being smaller measuring 110 μ, in diameter than others ranging from 130 to 150 μ obtained from the South Harbour of Copenhagen where a low salinity of 12‰ prevailed. The largeness in the size of the eggs appears to be correlated with the estuarine or brackish water habitat in Adyar. Although this species has not so far been recorded, from a marine habitat the possibility of its occurrence in such an environment cannot be precluded.



TEXT FIG. 4, A. Juvenile stage five days after the larva had settled for creeping, *ht.* heart and *int.* intestine; B & C the same juvenile after 10 and 12 days respectively, *an.* anus; the cerata are serially numbered in the order in which they appear.

The early development of *C. adyarensis* is very rapid as is the general rule with all other invertebrate organisms from the warmer waters. At a temperature of 22°C to 24°C and in a salinity medium of 24‰ the veliger larvae are formed in seventy-two to eighty hours even though they are not liberated free from the capsules at least ninety-six hours after the deposition of the spawn. As compared with the present tropical species the British form, *Doris tuberculata* from the cooler waters, as remarked by Eliot (1910) has much slower rate of development, the larvae being liberated from the spawn not earlier than a fortnight after the eggs have been spawned. In *Embletonia pallida* from the South Harbour of Copenhagen the development from spawning to hatching at a temperature of 17.3°C took about nine days whereas in the same species from Isefjord this process was completed at 22°C to 25°C in four days (Rasmussen, 1944). In *Eolidina* (*E.*) *mannarensis* (Rao & Alagarswamy, 1960) the entire larval development, at 29 to 31° C and a salinity of 33.5 to 34.18 ‰, was completed in about seventy-two hours, a rate which is more rapid than that observed in *C. adyarensis*.

The briefness of the larval life in the species is a feature which it shares with all other Nudibranchs. The larvae of the Prosobranch Gastropods with comparatively larger and continuously growing shells having a greater capacity for displacement and by virtue of their possessing bigger velar lobes for vigorous propulsion in water are better fitted for a pelagic mode of existence than those of the Nudibranchs. Among the latter group the larvae with the inflated or egg-shaped type of shells are in a general way a little better suited for free swimming life than others with cup-shaped or spiral types of shells having comparatively lesser buoyancy as expressed by Thorson (1946), but this is not always true because in *Embletonia pallida* (Rasmussen, 1944) and in *C. adyarensis* described here the duration of larval life is extremely short although both these species possess the inflated type of larval shells. In both a relatively much abbreviated velum appears to be a limiting factor for a prolonged pelagic existence of the larva. It may also be stated here that the larva and the post-larval creeping stages in *C. adyarensis* are fairly robust and active and they quickly pass through their development to attain juvenile condition. The largeness of the eggs with plenty of reserve yolk, the briefness of the larval duration, the hardiness of the post-larvae and fastness in the rate of the pre-larval and post-larval development are factors conducive to successful completion of the life-history of a species living in a brackish water or an estuarine habitat where the environmental conditions being subject to very rapid changes are mostly adverse and only rarely favourable.

In regard to larval development and metamorphosis, Nordman's (1846) account of *Tergipes edwardsii* differs in some respects from Schultze's (1849) description of *T. lacinulatus* (probably synonymous with *Galvina exigua* as pointed out by Eliot, 1910). In the former species the heart was seen pulsating as early as the shelled larval stage and the anterior tentacles also appeared at the same time even before the velum was lost whereas in the latter species the heart was formed much later in the post-larva and the rhinophores appeared only after the obliteration of the velum but earlier than the formation of the anterior pair of tentacles. The sequence of these structures appearing in *C. adyarensis* is as in *T. lacinulatus*.

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SUMMARY

1. In an estuarine nudibranchiate mollusc, *Cuthona adyarensis* Rao of the family Tergipididae reared under laboratory conditions a complete series of developmental stages from the fertilized eggs to the juveniles has been traced.

2. The egg is fairly large, measuring about 180 μ in diameter and is enclosed in an oval, double-walled membranous capsule of about 270 μ by 200 μ. As a rule the individuals spawn only after pairing. However, juveniles isolated and reared to sexual maturity spawned without copulation.

3. After the extrusion of the polar bodies the first cleavage which has a spiral trend divides the egg into two equal halves. Subsequent cleavages are formed rapidly. Gastrulation is by invagination. The blastopore closes but the larval mouth appears subsequently in the same position. The fully formed veliger is liberated free from the spawn at the end of the fifth day.

4. The larva has an inflated or egg-shaped shell which is characteristic of the nudibranch families, Tergipididae and Flabellinidae. The soft body is plumpy and the velum is rather small. The duration of larval life is extremely short.

5. The larva begins to creep and discards its shell. Simultaneously the velum is reduced and the foot is enlarged for creeping. Jaws and radula begin to develop in the pharyngeal bulb. The earliest creeping phase has the eyes and the statocysts as in the larva. In the next twenty-four hours the post-larva develops rudiments of rhinophores and cerata.

6. In the subsequent stages the post-larvae have developed the oral tentacles and the salivary glands. The hepatic diverticula from the liver lobes show ramifications entering the cerata of which another pair has since appeared in front of the anterior pair. The heart begins to pulsate in the pericardium lying beneath the body-wall behind the region of the stomach. The anus shifts from its median position to the right side to lie close to the third pair of cerata.

7. The earliest juvenile stage is reached five days after the larva has settled for creeping. The head is narrow and rounded on front. The oral tentacles and rhinophores are slender and elongate. Eyes, the cerebro-pleural and the pedal ganglia are well developed. The cerata come to possess the enidosacs with nematocysts. As the juveniles grow more cerata are developed.

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