Notes on the Post-Larval Development of the Giant Chiton, *Cryptochiton stelleri* (Middendorff)[1)]

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(*With 18 Textfigures*)

Breeding habits: *Crytochiton stelleri* is one of the largest species of chitons and is rather commonly found along the north-eastern coast of Hokkaido. It lives on or aside rocks below the low tide-line or at greater depths. In spring a large number of *Cryptochiton* gather on rocks exposed at low tide, presumably ascending from deep water for spawning. The breeding season of this chiton is relatively short. In Akkeshi the spawning begins about May 10th, or a few days later, and continues until the end of the same month, and it takes place on calm day when low tides occur in the early morning. The females never release their eggs until the males have liberated their sperms into the water. Like *Ischnochiton* as described by Heath the eggs of the present species are also laid in a remarkably giant jelly-mass to form a spiral string. A pair of the strings thus emerged from the genital pores opened in the mantle groove are simply laid on the algae or the rocks between the sub-littoral zone, i.e. they are not fastened to the substratum by any adhesive apparatus, and hence a heavy wave easily washes them away and soon breaks them into fragments. In the laboratory the female lays such a string at the rate of about 50 cm per hour, occupying nearly three hours in laying the entire eggs. Each one of these two strings measures 1–1.4 m in length and 2–2.5 cm in width. The jelly strings freshly laid are cinamon red owing to the coloration of the eggs seen through a gelatinous membrane.

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1) Contributions from the Akkeshi Marine Biological Laboratory, No. 44.

Development within the jelly-mass: The egg is nearly spherical, measuring about 250 μ in diameter and appears orange brown due to the abundant yolk supply. It is surrounded by a chorion about 4μ thick. The first cleavage of the egg occurs two hours after fertilization. The segmentation is total and blastomeres are nearly equal. In about one hour the second cleavage furrow appears at right angles to the macromeres, and micromeres are now distinguishable. The present species develops slowly than *Chaetopleura*. In *Chaetopleura* the hatching of the trochophore occur usually from twenty-five to thirty hours after fertilization depending upon the temperature. In the present species the trochophore does not hatch

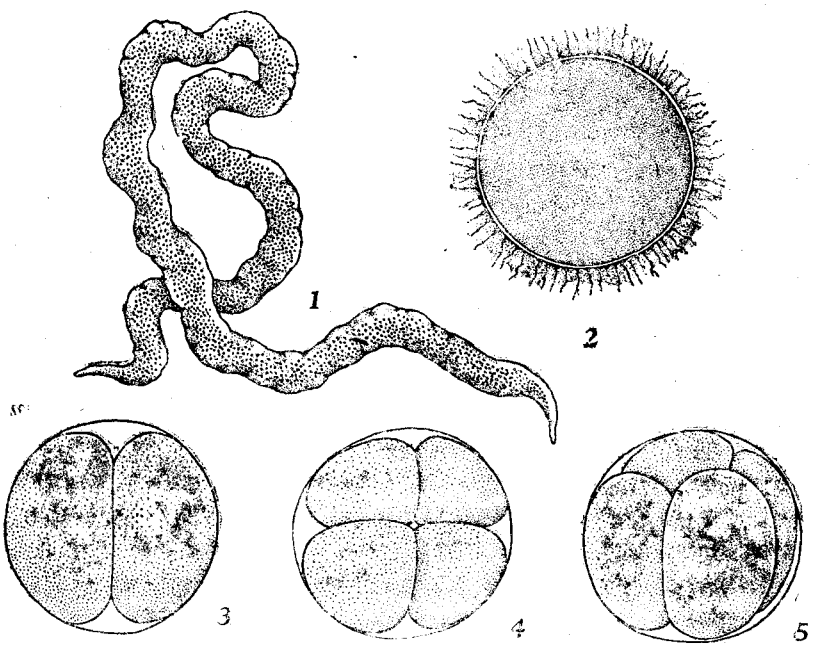

Fig. 1. Jelly-string packed with fertilized eggs. Actual length approx. 1.2 m. Fig. 2. Fertilized egg. Actual length 250μ in diameter. Fig. 3. Two-cell stage seen from above. Figs. 4–5. Four-cell stages.

out before seventy hours after fertilization. Eighteen or twenty hours later the embryos show the first signs of movement and commence to beat with cillia within the egg-membrane. The early trochophore (Fig. 6) measures about 0.35 mm in length and 0.25 mm in width at the prototroch. Just anterior to the equator there is a

complete ring of fine cilia, the first sign of the prototroch. The prototroch consists of two rows of cilia, of which the anterior is shorter, about 20μ in length and the posterior 70–80μ in length. At the anterior pole a few very fine long cilia form an apical tuft. The cilia of the apical tuft are usually directed forwards and twisted together. The gastric cavity remains opaque in the central body region. The mouth cannot as yet be seen from a surface view, and its relation to the ciliated band is therefore uncertain. The entire body is beset with fine short cilia. As the embryo develops the prototrochal cilia lengthen and become more powerful, and the larva rotates actively inside the chorion. After the larva has reached the trochophore stage represented in Fig. 6, no further marked differentiation of the soft tissue is observed for the time being. During this period the body of the larva only becomes slightly larger.

The larva drawn in Fig. 7 is about four days old. The whole body is ovoid in shape, slightly flattened dorso-ventrally. They are 0.35–0.4 mm long and 0.2–0.25 mm broad. Both of the cilia of the apical tuft and prototroch slightly lengthen, measuring 0.15 mm long in the former and 0.09 mm in the latter. The eyes are pigmented and now appear as a pair of red round spots situated laterally just behind the prototroch. The most obvious distinction from the trochophore stage is the appearance of the segmentation of the body by the seven transverse bands of clear cells filled apparently with granules. These seven narrow rows of darkly staining cells occupy the positions between the future valves and thus divide the dorsal body surface behind the prototroch into eight segments. The slight depression in the region of the future mouth deepens a little. The central gut region is dense than rest. A broad band of fine cilia runs along the ventral median surface. The larva is very active and rotates within chorion.

Development in the plankton: About a day or so later the larvae are liberated from the jelly mass and swim about in the sea-water. They do not show a very active reaction towards light, but they tend to keep on the side of the bowl or dish furthest from the window whenever the light is strong. They swim with the ciliary band of the prototroch and the fine cilia borne on the body surface. While swimming the apical tuft is kept to the direction of movement. Often they spend most of the time in crawling. In the last

stage of the pelagic life, just before metamorphosis, the larva shows an increasing tendency to crawl about on the bottom, and after crawling about for some time a larva may suddenly swim again, and then settles down before long. The larva just liberated from the jelly-mass (Figs. 8–9) measures about 0.5 mm in length and 0.25 mm in width. The entire body is slender cocoon-shaped, with a prominent hemispherical cephalic portion. An apical tuft arising from a slightly depressed portion of the anterior end consists of three to five long flagella. The stomodaeum or mouth is situated at the inverted V-shaped median area of the ventral prototrochal region and is surrounded by the fine cilia. The prototroch is well developed, consisting of two bands of fine cilia which encircle the

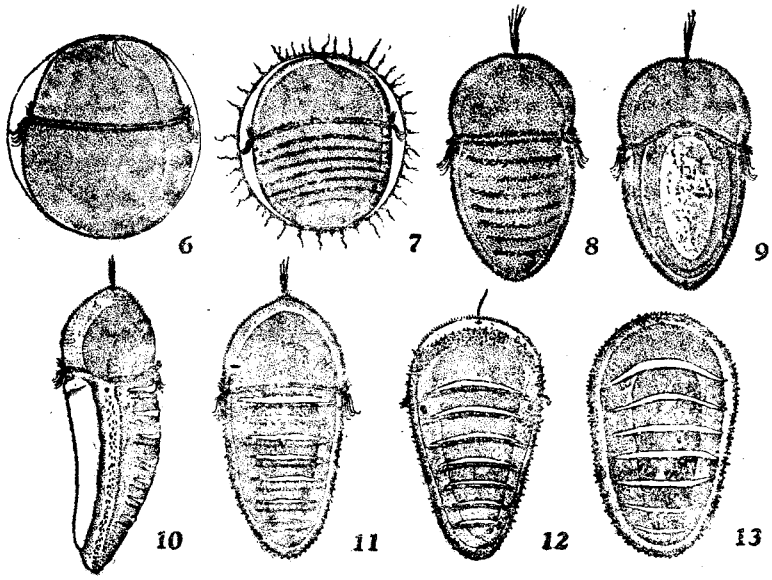

Fig. 6. Early trochophore about twenty-four hours after fertilization. Dorsal view. Actual length approx. 0.35 mm. Fig. 7. The larva just before hatched out. Dorsal view. Actual length approx. 0.35 mm. Fig. 8. Free-swimming larva just liberated from jelly-string. Dorsal view. Actual length approx. 0.5 mm. Fig. 9. The same. Ventral view. Fig. 10. The larva just before metamorphosis. Seven valves are formed. The larva may creep as well as swim. Lateral view. Actual length approx. 0.55 mm. Fig. 11. The same. Dorsal view. Fig. 12. Dorsal view of metamorphosing larva. Actual length approx. 0.55 mm. Fig. 13. Just metamorphosed larva. Apical tuft and prototroch have fallen off. Dorsal view.

body completely, but it turns forwards in position. A pair of eyes is now well marked on each ventro-lateral side just behind the prototroch. Each eye-spot consists of numerous reddish globules aggregated into a round cluster. The trunk is much bigger in proportion to the cephalic portion than formerly and is divided into eight segments by the seven transverse rows of granulated cells as described above. The entire body surface is finely ciliated excepting the dorsal portion posterior to the prototroch. In general, there has been no great change in structures since the larva four-days old of the preceding figures. During further development the rudiment of the foot is well demarcated as a median broad ovate folding on the ventral surface and is bounded by a shallow surrounding groove. At the anterior end of the foot-portion is a more or less backwardly projecting fold beset with fine cilia. About at the close of the free-swimming period the shell plate first arises on the dorsal surface of the body between the transverse row of the densely stained cells. The shell is at first confined to the trunk region posterior to the prototroch and then it gradually extends into the head vesicle. The shell plates do not appear simultaneously or subsequently, and not in definate order. During the pelagic even in the early bottom stages the last or the eighth shell plate does not make its appearance, and it is first added to a considerably advanced larva after metamorphosis. Each shell plate is merely a white, thin calcareous piece transversely elongated, and adheres closely to the ectoderm at certain interval, i.e. there remains a broad space between each of the neighbouring valves. There is no nautiloid shell or velum as shown in the other molluscs, accordingly, the free-swimming larva carrying shell plates is quite different from the true veliger. The rudiment of the mantle formed from the larval ectodermal epithelium is well differentiated and its outer border is uniformly covered with a number of spicules. In the cephalic portion the spicules on the hemispherical mantle edge are densely borne. The foot is now well separated by a narrow mantle groove. The larvae have now reached the end of the pelagic development, and appear to be no longer affected by light. They often still swim by means of their cilia, but spend a good deal of time in creeping upon the bottom. While thus crawling they adhere very tenaciously, apparently by a secretion of mucus from the foot-gland, and are very difficult to

dislodge by squirting water at them. The larvae while creeping, flex suddenly the body ventrally so as to bring the head vesicle close to the foot in the region of the mouth.

Metamorphosis and early bottom stages: The duration of pelagic life seems to be varied in individuals to some extents. Reared larvae take from twelve hours to the twenty hours from the time of liberation before they begin to metamorphose. It is possible that in the sea the period is shorter. After a larva has reached the stage drawn in Fig. 12, it shows an intense tendency to crawl about on the bottom. This it does with the head downwards by applying the foot to the substratum, on which the foot is spread out and flattened. In the finger-bowl they generally settle on high up the sides, just below the meniscus. They show apparently negative phototropic reaction. The change in habits is accompanied by changes in structure. The prototrochal cilia gradually disappear and the apical tuft also commences to fall off. The body is markedly flattened dorso-ventrally, and the anterior cephalic portion becomes broad and short than in the preceding stage. There are seven shell plates and all of them become broad and stout than in the previous stage. The first shell plate or head valve shifts forwards and occupies the position anterior to the prototroch previously located. The larval eyes are now situated between the first and second shell plates and are carried ventralwards. After the cilia of the apical tuft have gone, the prototrochal cilia of the dorsal body disappears subsequently, but a narrow band on the ventral body remains for a while. The mouth is now opened on a folding in front of the foot. The mantle projects beyond the body and its outer margin is densely beset with minute papilliform spicules. The mantle groove is shallow, running round the ventral body excepting the anterior head portion. The foot occupies the greater part of the ventral surface, and is ellipsoid and broad flattened in shape. It is now sufficiently powerful to be enable the young to glide over the substratum. The anterior region of the foot is finely ciliated and quite contractile, bending now and then ventralwards. In general appearance the young resembles well the adult except for the shell plates. The time taken to metamorphose varies, but appears to be normally about two days; it is often shorter. The metamorphosis is now completed.

The young chitons after metamorphosis were found to be living

at rest on the bottom of the bowl in which they had been reared. To the surface of the body debris of various sorts was attached, especially masses of living diatoms. They were so firmly attached to the substratum that the body could not easily be detached with a needle. A specimen a few days after completion of metamorphosis is seen in Figs. 15 and 16. The body is elongated oval, ellipsoidal and measures about 0.55 mm in length and 0.4 mm in width. The mantle completely hides the head which is transferred to the ventral

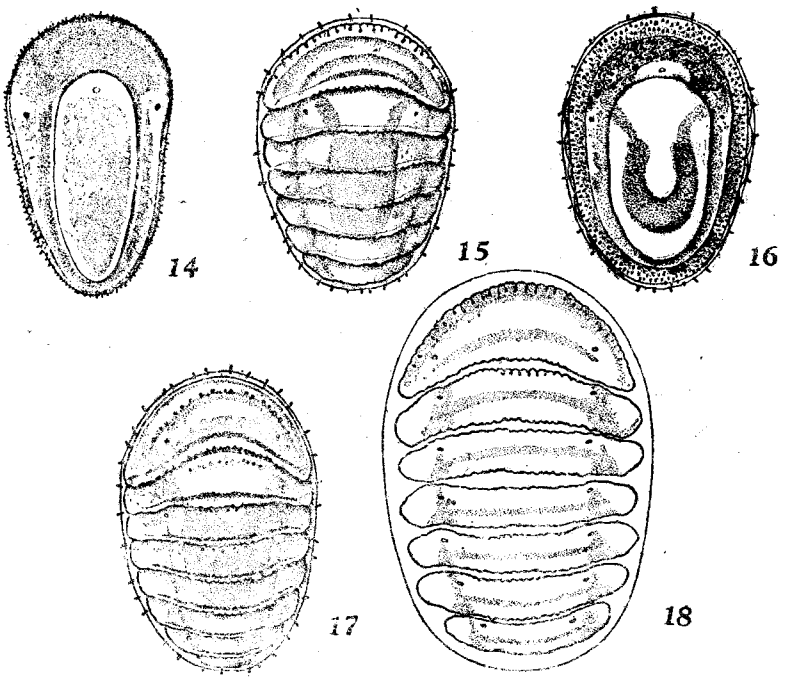

Fig. 14. The same larva as Fig. 13. Ventral view. Fig. 15. The larva of early bottom stage; five days after metamorphosis. Actual length approx. 0.55 mm. Fig. 16. The same. Ventral view. Fig. 17. The young about eight days after metamorphosis. Actual length approx. 0.6 mm. Dorsal view. Fig. 18. The same larva as Fig. 15, showing valves magnified. A pair of tegumental sense organs is shown on each valve.

side. The dorsal body surface is covered entirely with the seven shell plates. The eighth or the tail valve is not still appeared at this stage. The first or the head valve is the largest, nearly semicircular in outline and the anterior border is weakly undulated. A

row of the small round pores is arranged along the anterior wavy margin. The median valve is more or less hexagonal and situated at the posterior margin. The last or the sixth median valve is the smallest. Each of these shell plates has the tegumental sense organs (aesthetes) and, accordingly, the part of the valve first to be formed seems to be tegumentum. Each valve is arranged one behind the other and the posterior border of the one overlaps partially the anterior edge of the next. The mantle fold enclosed a shallow groove which becomes deeper than in the preceding stage and appears in the head vesicle below the shell. Thus, the mantle groove now extends all around the ventral body. The mantle is covered with short oblong cone-shaped spicules. The mouth is placed on a head in front of the foot. The presence of the anus could not yet be detected. A pair of reddish eyes is still present on each lateral side of the anterior portion of the foot. It becomes small and indistinct. The foot with a broad flat sole is well developed. The internal structure is not visible except the gut.

After this stage no marked structure is observed in the sequence of development. It proceeds steadily as before. About three days later the young has first acquired the last or tail valve. It is narrow and very small in comparison with the median valves. The head valve measures 0.15 mm in length and 0.38 mm in breadth, and while the tail valve is 0.05 mm long and 0.12 mm broad. Apart from the new addition of the valve the body structure is almost identical with the preceding stage. The development of the girdle is still quite indistinct, and the shell plates are nakedly exposed. The presence of the eyes becomes more obscure. No branchiae are visible. The young with the finger-bowl spends most of its time quiescently and rarely creeps sluggishly.

The most important study of the development of the chiton is carried out by Heath (1899) who has observed throughly the embryology of *Ischnochiton magdalenensis*. In this species the process of the egg-laying is quite similar to that of *Cryptochiton*, i. e. unlike any chitons described the eggs are laid in giant jelly-masses which take the form of spiral strings nearly a yard in length. The development of *Ischnochiton* proceeds with considerable rapidity. At the end of twenty-four hours, the larvae begin to rotate within the membrane and six days later become free and swim about. The

free swimming stage lasts no longer than three hours and the larvae settle down upon the rocks or seaweed, there to undergo the metamorphosis. In ten to twelve days, though small, they resemble the adult in form. In *Chaetopleura apiculata* described by Grave (1932) the trochophore hatches from twenty-five to thirty hours after fertilization and enters into the pelagic life, and it settles to the bottom and metamorphoses into the adult form after six to ten days. The eggs of *Chaetopleura* are enclosed in a bristly chorion. In *Chiton polii* observed by Kowalevski (1879) the eggs are carried and kept in the mantle groove of the parent. The tail valve makes its appearance simultaneously when the remaining valves have been formed in *Ischnochiton* and *Chaetopleura*, while its development is delayed for some time in *Chiton* and *Cryptochiton*. In conclusion I wish to express my hearty thanks to Prof. Dr. T. Uchida for his kind guidance.

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