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STUDIES OF *CUCUMARIA CURATA* COWLES 1907

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Little has been done on the brooding habits of *Cucumaria curata* Cowles 1907 from the Pacific Coast of North America. Most of the embryological investigations of holothurians on this coast have been with species having free swimming larval forms (Johnson & Johnson, 1950). Since the majority of holothurians have planktonic larvae, a study of the direct development found in *C. curata* should be of value in comparing the ecological distribution of this species with those having planktonic larvae. The brooding type of development is found in polar species, but seldom found in those of warmer waters. This may have some direct effect on limiting the distribution of the species.

Most of the investigation of holothurians of the Pacific Coast has been of a taxonomic or physiological nature. Clark (1902) made some preliminary studies on *C. curata*. Some of the earlier work was conducted by Ackerman (1902) on *C. laevigata*. Ludwig (1897, 1908) was the first to describe the phenomenon of young adhering to the smooth part of the creeping sole of the adult in *Psolus antarcticus*. Wooton (1949) described the method by *Thyonepsolus nutriens* of placing the young on the dorsal surface. The principal articles on oviparous development are those of Metschnikoff (1870), Selenka (1876, 1883), Semon (1888), Ludwig (1891) and Edwards (1909). Those of Clark (1898, 1910) and Wootton (1949) are the most important in this particular case.

Important contributions to morphology and physiology are by Woodland (1906, 1907), Crozier (1915), Théel (1921), Verne (1926), and Millott (1950, 1952, 1953).

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Collection Data

Specimens of *C. curata* used in this study were collected in two areas along the coast near the Pacific Marine Station at Dillon Beach, California. The northern collecting area was Shell Beach, Sonoma County, which is some 15 miles north of the station, and the southern area was Second Sled Road, Marin County, about one mile north of the station. Embryological and ecological studies were carried out; the larval forms were raised and behaviour problems were investigated at Pacific Marine Station. Entire populations were taken to the laboratory for counting and identification.

Ecological and field studies were conducted from Hopkins Marine Station, Monterey, California, north to the mouth of the Russian River. Sample collections were made at each area visited between the two stations.

External Characters

In *Cucumaria curata* pentaradiate symmetry is externally evident by the presence of five equally spaced meridional ambulacra (Fig. 1). The mouth, terminal and of a circular shape, is surrounded by a thin area of body wall, bordered by a circlet of 10 tentacles. The tentacles are modified buccal podia or labial podia which contain extensions of the water-vascular system from branches of the radial canals.

A great number of individuals had sub-equal tentacles as observed in a population study conducted by Filice (1950); this is contrary to the definition of the species by Cowles (1907). In some keys of Pacific Coast holothurians this character is used to differentiate *C. curata* from *C. lubrica* Clark (1901), which has equal tentacles. Since this feature is highly variable in any single population it must be used with care in differentiating species.

The tentacles are extremely retractile and can be withdrawn by the closure of the adjacent body wall over them when fully contracted. The ten retractable tentacles are attached to a smooth, thin, collar-like region (introvert or aquapharyngeal bulb) which is pulled into the body cavity when the animal is disturbed. The introvert is retracted by a set of retractor muscles, and the rim of the body wall then closes over the retracted anterior end.

The general body surface is leathery, slightly slimy, and covered by tubercles and papillae. The podia occur in five rows, with only the three ventral rows taking the form of locomotory tube feet (pedicels). These pedicels extend the entire length of the animal. The pedicles are hollow tubular projections of the body wall containing part of the water-vascular system and terminate in a cup like expansion acting as a sucker and supported by skeletal spicules.

The average length is about 9 mm with a range of from 4 mm to 21 mm. This maximum size agrees with the original description (Cowles, 1907) though it is considerably larger than those recorded by Filice (1950). In general the dorsal surface is dark brown to black but can be light gray to white. The ventral surface is white or pinkish in color.

Body Wall

The epidermal cells occur in roundish clumps as described by Cuénot (1891) and are interspersed with gland cells (Fig. 3). Lying directly below the peripheral dermis is a thick layer of circular muscles. Between this muscular layer, and interspersed with the epidermal clumps, are branched pigment cells (Fig. 2). The pigments to which the body owes its coloration occur as free, brown to black granules, within these branched cells.

Black or brown pigments are common among echinoderms, and certain of them have been described as melanins (Millott, 1953). Briot (1906), Crozier (1915), Verne (1926) have all worked with holothurians and the melanin problem. However, as Millott (1953) has said, "their statements have not always been made clear."

The presence of melanin may have a direct bearing on the dark coloration of *C. curata*. Work has been done on the melanin in *Holothuria forskali* (Millott, 1952, 1953), and tests were devised to show the presence or possible presence of melanin.

Since a definitive test for melanin seems to be lacking, the following criteria established by Lison (1936) and adopted by Millott (1953) were used: (1) it occurs in the form of black, brown, or yellow granules; (2) it shows extreme resistance to solvents; (3) it is decolorized by oxidizing agents; (4) it reduces directly ammoniacal solutions of silver nitrate.

The results of these tests, when applied to *C. curata*, closely followed the reactions obtained by Millott (1953) for *H. forskali*. The pigment was insoluble in ethanol 90%, acetone, ether, and chloroform. It was slightly soluble in water, pyridine, and NaOH.

Pieces of the body wall were bleached by the following oxidizing agents: chlorine, hydrogen peroxide and potassium permanganate.

Only in the last test did the pigment show any deviation from the results obtained by Millott (1953). In the argentaffine reaction (Lison, 1936) the body wall reduced ammoniacal silver nitrate only slightly. However, in general, the behavior of the pigment toward the tests resembles the characteristics of melanin enough to conclude that it is present in *C. curata*.

Some work has been done on the role of the integumentary pigment in photo-reception in holothurians (Crozier, 1914, 1920; Pearse, 1908).

In *Holothuria captiva*, Crozier (1920) failed to show that the screen of dark pigments "protected" the animal to any degree from the stimulating action of light. The heavily pigmented *H. captiva* exhibits a pronounced photo-irritability while the equally pigmented *C. curata* is not photonegative. If the photochemical action effected by light is due to the absorbed wave-lengths, then in both of these species one would expect a low rate of photo-irritability. Yet in *H. captiva* the reaction is similar to specimens of *C. curata* containing little or no pigment. It would seem that the heavily pigmented specimens of *C. curata* were absorbing the

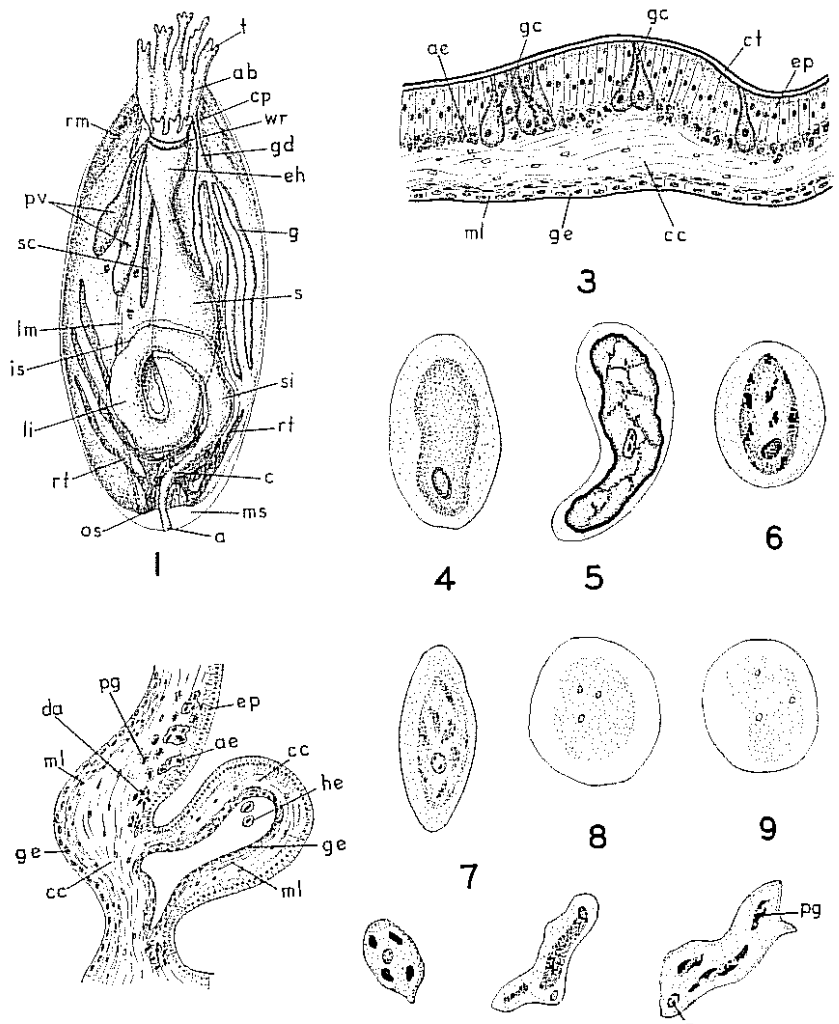

PLATE 1

Cucumaria curata. Fig. 1. Internal anatomy of the adult: a, anus; ab, aqua-pharyngeal bulb or introvert; c, cloaca; cp, calcareous ring; os, cloacal suspensors; eh, esophagus; g, gonad; gd, gonoduct; is, intestinal suspensors; li, large intestine; lm, longitudinal muscle band; ms, mesentery; pv, polian vesicles; rm, retractor muscles; rt, respiratory tree; s, stomach; sc, stone canal; si, descending small intestine; t, tentacles; wr, water ring. Fig. 2. Transerve section of the ventral body wall, showing amoebocytes and skin pigments. ae, amoebocytes; cc, connective tissue; da, disintegrating amoebocytes releasing pigment granules; ep, epidermal cell; ge, germinal epithelium; he, haemocytes; ml, muscle layer; pg, pigment granules. Fig. 3. Transverse section of the dorsal body wall. ae, amoebocytes;

stimulating radiation while the lightly pigmented specimens were not. The photodynamic activity of the heavily pigmented *C. curata* seems to be one of masking, perhaps to prevent an excess of light penetration. *C. curata* found on exposed rocky areas may be exposed to direct sun for three or four hours during low tide. These animals are heavily pigmented and dark brown to black in color. Yet, those found in protected areas, such as under *Mytilis californianus* beds, are lighter in color. Some are entirely colorless, being white or almost clear. These animals contain few or none of the pigment granules present in the animals found on the exposed rocks.

Coelom and Amoebocytes

A large coelom is present in *C. curata*, extending from the calcareous ring to the attachment of the cloacal muscles. This coelom is divided by perforated mesenteries of the digestive system. The periphery of the coelom is lined by a thin layer of flat epithelium of the same type surrounding the peripheral walls of the digestive tract. These same cells cover both sides of the connective tissue forming the mesenteries.

The coelom is occupied by most of the internal organs. When eggs are present in the ovaries the entire lower part of the coelom is filled with the lobes of the gonads. The respiratory tree is small and compact, and extends only a short distance into the coelom. The large loop of the intestine with its suspensor mesenteries takes up a great part of the coelom (Fig. 1).

The coelom is filled with a watery fluid containing a number of different types of free cells. Since reference is made to cells exhibiting amoeboid movement I shall refer to them as amoebcytes (Théel, 1921) and not the all-inclusive term coelomocytes (Hyman, 1955).

The richness of red-corpuscles is considerably less than in *C. elongata* and *C. hyndmani* (Théel, 1921). There is a great variation in the number of plasma-amoebocytes (Figs. 8, 9) in different individuals, and there is no direct relationship between the number of plasma-amoebocytes and red blood-corpuscles, contrary to the suggestion of Théel (1921).

The shape of the blood-corpuscles is irregular, and they vary from fusiform to disc-shaped (Figs. 4, 5, 6, 7). The size of the corpuscles also differs greatly, with a range of from 9 μ to 21 μ. This range compares closely with that of *C. hyndmani* (Théel, 1921).

The blood-corpuscles examined in the coelomic cavity exhibited no tendency to adhere to each other. This corresponds with the observations in *C. planci* (Howell, 1885).

In most of the animals examined the water-vascular system was stained a red or reddish-yelow color due to the presence of red corpuscles.

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cc, connective tissue; ct, cuticle; ep, epidermal cells; gc, gland cells; ge, germinal epithelium; ml, muscle layer. Fig. 4,5,6,7. Different types of red blood-corpuscles fixed in 30% formalin and stained. Fig. 8,9. Two different types of plasma-corpuscles fixed and stained. Fig. 10,11,12. Amoebocytes containing pigment granules. n, nucleus; pg, pigment granules.

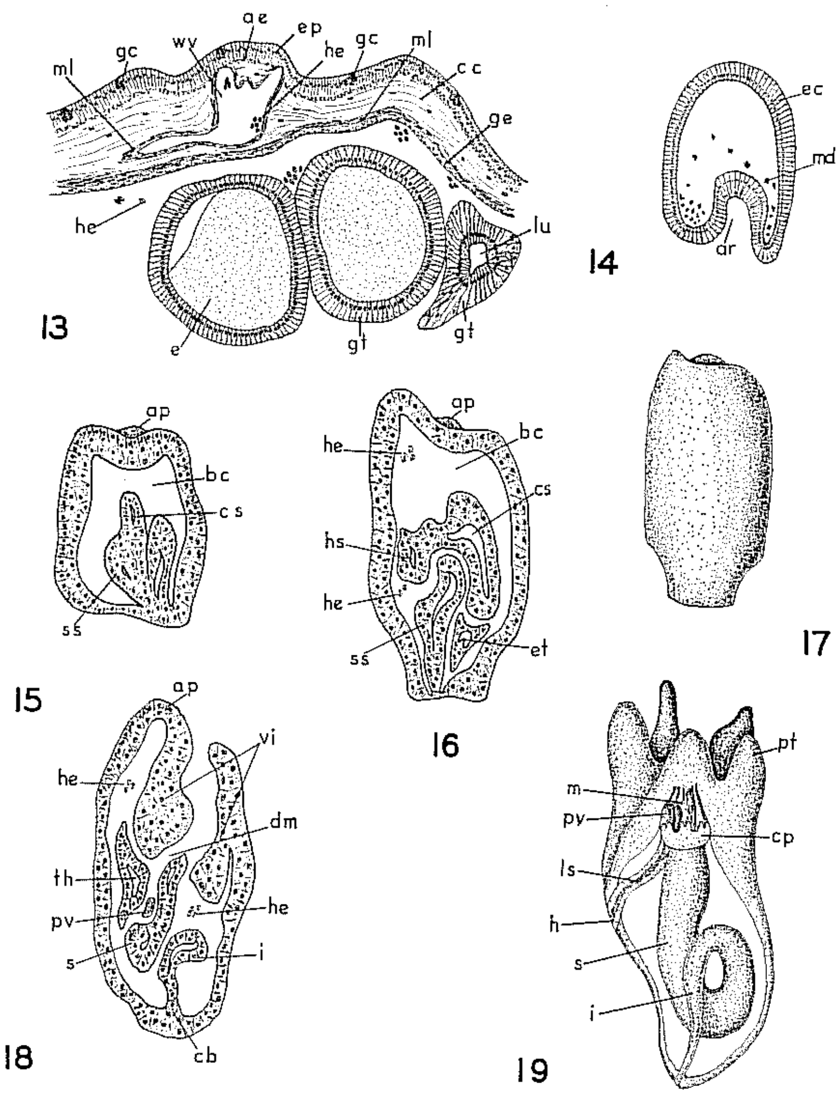

PLATE 2

Cucumaria curata. Fig. 13. Transverse section through part of the body wall and coelomic cavity containing oviducts and eggs. ae, amoebocytes; cc, connective tissue; e, egg; ep, epidermal cells; gc, gland cells; ge, germinal epithelium; gt, oviduct; he, haemocytes; lu, lumen of the oviduct; ml, muscle layer; wv, water vascular system. Fig. 14. Blastula stage. ar, archenteron; md, mesoderm; ec, ectoderm. Fig. 15. Gastrula stage. ap, apical sensory plate; bc, blastocoel; cs, coelomic sac; ss, somatocoel. Fig. 16. Late gastrula stage. ap, apical sensory plate; bc, blastocoel; cs, coelomic sac; et, enteric sac; he, haemocytes; he, hydrocoel; ss, somatocoel. Fig. 17. External view of the gastrula. Fig. 18. Elongated stage.

These red blood corpuscles were shown to contain haemoglobin (Hogben and Van der Lingen, 1928) though the chemical makeup differs from that of the vertebrates.

These hemocytes are capable of movement and may put out one or more pseudopodia. The degree of amoeboid movement is increased when the cells are removed from the body.

There is another group of amoebocytes found in the coelomic fluid and body wall. These cells were first observed in *Holothuria forskali* by Millott (1953). They were found in coelomic fluid of *Cucumaria curata* that had been removed from the animal and exposed to air for 15 hours (Figs. 10, 11, 12). A whitish-yellow clot was formed. Close examination of *Cucumaria curata* showed that free amoebocytes occurred within the loose connective tissue and the coelom. These contained brown to black pigment granules and spheroids. Many of the amoebocytes within the body wall were in different stages of decomposition (Fig. 2). These observations compare closely with those of Cuénot, 1891; Lison, 1930; Millott, 1950, 1953; Millott and Jacobson, 1952, and bear out the concept that the skin pigment is derived from amoebocytes. The released pigment granules from the decomposed amoebocytes were mixed within the connective tissue.

Development of *Cucumaria curata*

Unfertilized eggs were first observed in the ovaries of adults in November of 1957. These animals were sectioned and stained, and a detailed study was made. Fertilized eggs and brood were found from late January to April, 1958, in accord with the pattern of the more northern species, *C. frondosa* and *Psolus phantapus* (J. & S. Runnström, 1921), although MacGinitie (1949) found brood in *C. curata* during December at Pacific Grove. These eggs were removed from the adults, put in small culture dishes and placed in a soft-drink cooler which was adjusted to maintain a temperature comparable to that of local sea water.

The eggs contained a great amount of yolk material (Fig. 13). The egg-filled gonads occupied the lower part of the coelom and covered the intestine on the ventral side. In an adult, without developing eggs, the gonads occupy only a small area dorsal and anterior to the intestine.

C. curata is probably hermaphroditic, though no really conclusive evidence was found. Sperm was found in the gonadial tubules during October to December. However, it was not found along with developing eggs in later months. It was not ascertained whether the eggs and sperm are produced in the same gonadial tubule as in *Cucumaria crocea* (Ludwig, 1898), or perhaps follow the pattern of *C. laevigata* (Ackermann, 1902),

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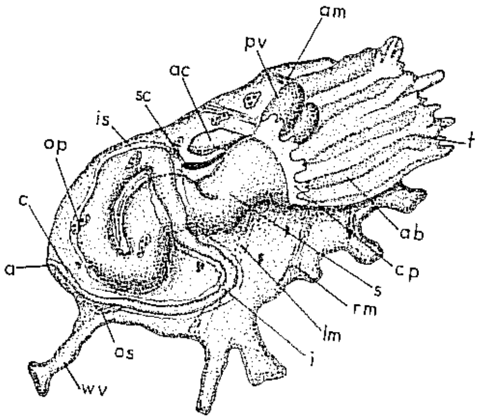
ap, apical sensory plate; cb, closed blastopore; dm, definitive mouth; he, haemocytes; i, intestine; pv, polian vesicles; s, stomach; th, tentacular hydrocoel; vi, vestibular invagination. Fig. 19. External view of the late elongated stage. cp, calcareous ring; h, hydropore; i, intestine; ls, larval stone canal; m, mouth; pt, primary tentacles; pv, polian vesicles.



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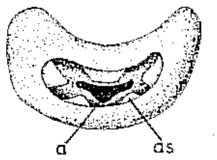

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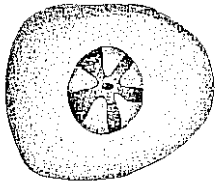

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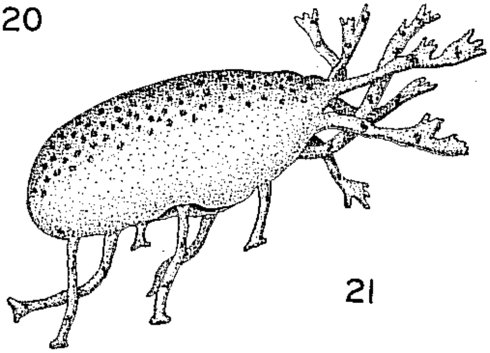

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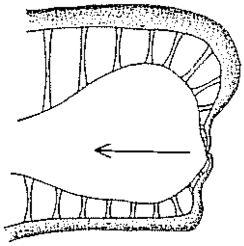

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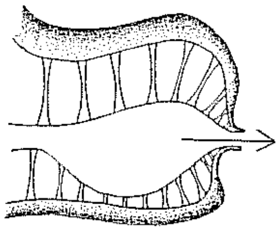

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PLATE 3

Cucumaria curata. Fig. 20. Internal anatomy of a two week old specimen. a, anus; ab, aquapharyngeal bulb; ac, axial complex; am, aquapharyngeal bulb retractor muscle; c, cloaca; cp, calcareous ring; i, intestine; is, intestinal suspensors; pv, polian vesicles; rm, retractor muscles; s, stomach; sc, stone canal; t, tentacle; wv, water vascular system. Fig. 21. External view of a three week old specimen. Fig. 22. Diagramatic longitudinal section through the cloacal end, showing the form of the anal brim during spouting. The arrow indicates the course of the water. Fig. 23. Diagram showing the form of the anal brim after the intake of water. Fig. 24. Posterior end during the pumping of water into the respiratory tree. Fig. 25. Posterior end during the spouting period.

where the gonadial tubules are first female, are then destroyed by phagocytic coelomocytes and replaced by sperm-producing tubules.

The eggs are brooded on the ventral side of the adult. The method of placing the eggs on the ventral surface is similar to that of *Thyonespolus nutriens* (Wootton, 1949). The spawning females arch their expanded tentacles to catch the extruded eggs. These eggs are then transferred to the ventral surface and arranged by the extensile podia located along the three ventral ambulacra. The eggs are very sticky when first released and are attached to the ventral surface at this time. *C. curata* secretes a mucus which covers the body and aids in the attachment of the eggs during development. It has a limited ability to clean itself, for many pebbles and other debris may cling to the surface of the animal, both ventral and dorsal, along with the eggs. There are no incubatory pockets as found in the antarctic *Psolus koehleri* (Vaney, 1914), but the eggs were attached to the ventral body between the rows of tube feet. Enough room is left between the body and the substrate for oxygenation of the developing young.

Eggs were removed from the animals after fertilization but before the blastula stage had developed. The cleavage is superficial, and the blastula consists of a surface layer of cells enclosing the yolk. There is a lack of cilia during gastrulation as development is direct in this species (Fig. 14). Mesenchyme is given off from the tip of the archenteron during the invagination and formation of the blastopore. The blastocoel becomes filled with endomesoderm in the form of mesenchyme. Hemocytes are formed from the endomesoderm at this time. The anterior part of the archenteron forms the coelom, while the posterior part forms the primordium of the digestive tract.

During the third day of development, the bell shaped gastrula (Fig. 17) is transformed into an elongated, tube-shaped stage (Fig. 18). There is no doliolaria nor auricularia stage during the development, and there seems to be no vitellaria stage, as occurs in some species of *Cucumaria* and *Labidoplax* (Fell, 1945). The hydrocoel begins to encircle the foregut; three lobes arise and soon divide to five. These lobes are the tentacle primordia and will soon form the five primary tentacles. A sixth lobe develops into the polian vesicle which forms rapidly after the formation of the primary tentacles.

During the fourth day, the stomach, intestine, pharynx and definitive mouth are visible in the elongated stage (Fig. 19). The buccal tentacles and calcareous ring have appeared along with the radial canals which have been formed by the hydrocoel. The number of hemocytes has increased and the introvert has developed.

During the fifth day, the buccal tentacles have branched and the first of the calcareous skeletal plates appear (Fig. 20). Podia develop from the precocious mid-ventral canal, along the posterior end. Now the young pentactula consists of five primary tentacles and one or two podia and is able to lead a semi-independent life on the dorsal side of the adult. After the second week of development, ten branched tentacles and many podia are present. The animal then leaves the dorsal surface of the adult and begins a completely independent life (Fig. 21).

Behavior

The withdrawing reaction is most often seen in *C. curata;* it consists of the withdrawal of the posterior end of the body and the closing of the cloacal opening.

During the extending reaction the posterior end becomes elongated and the introvert extended with tentacles attached. The animal may increase its length to more than three times its contracted size.

C. curata carries on a regular system of breathing movements by which water is taken into the cloacal chamber and expelled. Water is drawn into the cloacal chamber by closing the opening to the respiratory trees and contracting the radial muscles which extend from the cloaca to the body wall (Figs. 22, 23). The cloacal opening is then closed, the respiratory tree aperture is opened, and the contraction of the walls of the cloaca forces water into the respiratory tree. The lateral muscles control the contraction of the cloacal area. About 10 seconds is required to complete the contraction of the cloacal area. These contractions are rhythmic and regular.

When the water becomes stagnant or when conditions become otherwise unfavorable, the anterior end of the body is often cast off together with some of the visceral organs. The calcareous ring, part of the digestive system, and the tentacles, are lost in this manner.

C. curata is not extremely sensitive to contact with solid objects. However, it will attach itself after lying on the surface for some time. The reaction to touch by a probe is slow and no contraction is brought about by irritation of the tentacles. If the body is tapped slightly, the animal reacts slowly, reaching the contracted state in about 30 seconds. The animal remains contracted for about 5 minutes and then begins to expand its tentacles while the body remains in a state of contraction. After the tentacles are expanded for about one minute, the body becomes elongated and the animal assumes a normal feeding position.

A violent reaction was obtained by squirting the animal with a stream of sea water from an eyedropper. In this case the *Cucumaria* remained contracted for seven minutes. The stream of water was directed over the anterior end, which caused the introvert to retract within the coelom carrying the tentacles into the cavity. This was followed by the general contraction of the whole body.

C. curata is not extremely sensitive to change in light intensity. Tests were made to determine if *Cucumaria* had a linear light alignment as stated by Crozier (1915) for *Thyone*. Under normal daylight, coming through three large windows, animals that had been collected along the open coast did not orient themselves toward the source of light. However, when a high intensity light was placed 12 inches away (model 570, AO lamp, with an 18 amp, 6 volt ribbon filament bulb) the animals oriented themselves in non-linear groups to the source of the light. There was no contraction of the body when the light was directed on the body itself. When *Cucumaria* collected from *Mytilus* beds were used in the same tests a different set of reactions were recorded. These animals lacked pigment and seemed to be very sensitive to light. They moved away from any strong light source. These reactions are the opposite of the darker pigmented animals collected on the open coast.

C. curata is a more or less sedentary animal. It can move when light or other conditions are unfavorable, but under normal conditions it does not move. One *Cucumaria* was kept alive for two years in an aquarium without moving from its point of attachment (Pearse, 1908).

When an animal is placed on the bottom of a dish in sea water it remains contracted for a short time. Then the ventral tube-feet are protruded on all sides of the body and begin to wave about, and those which come in contact with a solid object attach themselves. The animal may move in any direction, but an interesting reaction was recorded when 22 of the animals were placed in a rectangular dish. After one hour they had formed into two groups in the corners opposite the windows. These animals formed tightly packed bunches, with some climbing on top of others.

Locomotion is brought about in several ways: by the shortening of the tube-feet after they have been extended and attached, by twisting and extending movements of the whole body, and by sharp waves of muscular contraction which travel from one end of the body to the other. The tube-feet act by pulling and were never observed to become rigid enough to lift the body from the surface on which it rested, nor was there any pushing action, such as Jennings (1907) described in the starfish.

During feeding, the circum-oral tentacles are extended and either waved in the water or swept over the surface of the substrate. They are then consecutively poked into the mouth and wiped off. This reaction has been briefly described by Grave (1905).

Distribution

C. curata has been found in three distinct habitats along the rocky shores near the marine station at Dillon Beach. In each case, the situation and the associates which form the community are different.

1. At Shell Beach, an exposed coast situation 15 miles north of Dillon Beach, the animals occur just below the *Mytilus* beds. The cucumbers occur in extensive beds on the leeward side of insular rocks at this level. The animals form an almost pure, densely packed population in this situation. They are very dark in color.

2. In the Second Sled Road area, the animals occur mixed through the mussel beds in groups of five to twenty. They may occur at higher levels than in the Shell Beach area, and are gray to white in color.

3. A third type of environment for *Cucumaria curata* is the undersides of rocks toward the lower limit of the mid-littoral zone in the Second

Sled Road area. The animals are as dark as those at Shell Beach, and occur in groups of densely-packed individuals.

Discussion

The most significant factor affecting the coastal distribution of *C. curata* and the occurrence of individuals within the community is the brooding habit. The varied and irregular pattern of compact communities along a moderately uniform rocky coast is also characteristic of the more northern brooding species (Ludwig, 1898). This variation in arrangement of populations is to be expected in an organism without free swimming larvae living exposed to heavy surf. The difference in disposition of a related species having free swimming larva, *Cucumaria miniata* (Brandt, 1835) along the same coast is marked. In the latter species, the distribution is rather even, encompassing a number of varied habitats.

The general behavior pattern of the adult is sedentary, with little or no movement. Distribution along the rocks is enhanced by the protection of the *Mytilus* beds, and where these beds bridge gaps between rocks *Cucumaria miniata* has formed extensive and abundant populations. This type of distribution may be seen in the Second Sled Road area as opposed to the isolated rock populations of the Shell Beach region lacking the interconnecting beds of *Mytilus*.

Undoubtedly, the influence of pigmentation and presence of melanin also determines to some extent the placement of individuals. The individuals lacking pigment seem adapted to life among the mussels, while the densely pigmented forms are better suited to the full exposure of the sun.

Summary

A brief description of the body wall, its structure, function and possible influence on the environmental distribution of the species is given. The presence of melanin is indicated by the use of tests on the pigment found in *C. curata*.

The integumentary pigment plays an important role in photo-reception and influences photo-irritability. The pigment seems to act as a masking agent effecting its behavioral pattern.

Amoebocytes carry and distribute skin pigment. There is no direct relationship between the number of plasma-amoebocytes and red blood-corpuscles.

Direct development occurs in *C. curata*. There is no doliolaria nor auricularia stage, and there seems to be no vitellaria stage.

A behavior study has been conducted in an attempt to correlate some of the behavior traits with the distribution of the species along a rocky coast. A difference in reactions is recorded for the two color groups. The lightly pigmented *C. curata* is very sensitive to light while the darkly pigmented animals are not sensitive.

Direct development has the effect of causing isolated populations except where *Mytilus* beds are present. These beds act as bridges for the movement of the holothurians between isolated rock populations.

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