sults, though many other stains were useful, particularly the Biondi-Erlich mixture and the iron haematoxylin of Heidenhain.

One other thing ought to be mentioned in this connection. I have in no instance been able to follow any one lot of eggs throughout any considerable part of their development. When removed from the mantle cavity of the mother they do not develop normally for more than two or three days. I tried keeping some of the eggs in small dishes, changing the water twice a day; others were placed in a large jar, in which the water was continually aerated by a stream of air; still others were placed in a jar, the mouth of which was covered by silk netting, and the jar was then inverted in a tank of flowing water; the most successful method, however, was to put the eggs in open bottles, which were then placed in an aquarium through which water was constantly flowing. Yet by none of these methods could the eggs be kept normal for more than a few days. It would seem that the circulation of water within the mantle chamber of the mother is more perfect and gentle than could be obtained by any method which I could devise. It was necessary, therefore, to take eggs from a large number of individuals in order to get a complete series, since all the eggs laid by one individual are in nearly the same stage of development. Fortunately, there are such vast numbers of fertile females during the breeding season as to make this an easy task.

B. THE GENUS CREPIDULA.

1. *Natural History.*

At least three species of the genus Crepidula are found on the Atlantic coast of the United States,[1] *viz.*, C. fornicata Lam., C. plana Say, and C. convexa Say, all of which are quite abundant along the shores of New England. All these species are more or less completely sedentary, and they show the most remarkable individual differences in the shape of their shells due

[1] Other species have been described, *viz.*, C. unguiformis Stimson, C. glauca Say, C. acuta Lea. Concerning the first of these there is no doubt that it is identical with C. plana, and I am convinced after a careful anatomical and embryological examination of the last two that they are only local varieties of C. convexa (cf. Verrill '74) Invertebrate Animals of Vineyard Sound.

to the character of the surfaces upon which they are attached. Upon a smooth, plane surface the shell is regular and unusually broad and flat; on a convex surface it is deep and highly arched; on a concave surface it is concave, sometimes to the extent of being almost semicircular; on a twisted surface, like the columella of Neverita, it is twisted; on an irregular surface, such as a rough stone, it is irregular; if pressed upon from the sides the animal and shell become long and narrow; if growth is limited in front the shell becomes short and broad; if limited on all sides the shell may increase greatly in thickness but remains small, filling the space in which it is found. In such cases the lines of growth are crowded closely together and the very edge of the shell may be as thick as any other portion. In small places, such as the interior of Illyonassa shells, C. plana may be dwarfed to one twenty-fifth the size of normal specimens. These individual variations in the shape and size of the animals and shells appear in all the species of Crepidula, but they are most marked in C. plana. The cause of the variations in the *shape* of the shells is not far to seek, though the great differences in the *size* of individuals is more difficult to understand: the shape of the shell is conditioned by the shape and position of the mantle edge; the mantle is moulded over the surface upon which the animal rests; and consequently the shape of the shell comes in time to correspond to any sort of a surface upon which the animal is attached.

C. fornicata, the "slipper limpet" or "boat shell," is a common object to all visitors at the sea-shore. It occurs in great numbers on the shells of the king crab, Limulus polyphemus, where it is firmly attached to the ventral side of the carapace and abdomen; sometimes it is found on the appendages, the gill plates, or even the dorsal surface of the crab. After it has reached a certain size, about half that of the adult, it never moves about. It thenceforth leads a perfectly passive existence, being carried about by the king crab, and obtaining all its food by merely sweeping into its mantle chamber currents of water containing particles of food, which are in large part the crumbs which have fallen from the king crab's table. This species is also found abundantly on muddy sea bottoms a short distance below low-water mark, where it usually occurs in curious chains often containing ten or twelve individuals. In these chains the foot of one individual is firmly fastened to the dorsal side of the shell of the next one, and the heads of all the animals are turned in the same general direction; the first or oldest individual in a chain is usually attached by its foot to a stone or dead shell. Even those which live upon Limulus sometimes show a tendency to pile one upon another, though in this case there are seldom more than two or three in a pile. C. fornicata also occurs, but in comparatively small numbers, on submerged portions of stones, buoys, and wharves. In none of these cases, however, is it able to change its position after it is about half grown, and it obtains all its food from the particles which float to it in the water. The fact that the large Crepidulas are immovably fixed to one spot is shown not only by the shells, which have in many cases become greatly distorted in order that they may perfectly fit the spot of fixation, but I have again and again observed that in old Crepidulas the sole of the foot secretes a calcareous substance by which the animal is so firmly fixed that the foot is often torn to pieces before it can be freed from its attachments. Unlike most prosobranchs, the foot in Crepidula is plainly divided into two portions, a broad and thin *propodium* which is deeply notched in the middle, and a thick, muscular *mesopodium* or sole, by which the animal is attached. The sole of the foot forms a powerful sucker, and when the animal is removed from its attachment so as not to injure the foot, the latter immediately becomes deeply concave on the ventral side, showing that considerable muscular tension was being exerted in order to produce the suction.

C. plana is smaller and much flatter than C. fornicata, and its shell, which is quite fragile, is nearly white in color. It is found most abundantly within those gasteropod shells (Neverita, Lunatia, etc.) inhabited by the larger hermit crab, Eupagurus Bernhardus, and while it may be found in this position either at the outer or inner lip of the shell, it is nearly always so situated that its head is directed toward the opening of the shell in which the crab lives. It is evident that in this case also the Crepidula has taken this position in order that it may be carried about and supplied with food by the hermit, for here again the Crepidula is unable to move about or change its position in the least after it has reached adult size. When a hermit dies, or leaves one shell for another, the Crepidulas in that shell remain attached for some time, but sooner or later perish without attempting to find another shell. Some doubt has been expressed as to whether C. plana is a true species.[1] It has been held that it belongs to the species fornicata, and that those individuals living inside other shells have been slightly modified by their environment, the shell becoming thinner and flatter. There is no doubt, however, that C. plana is a well-marked species, as is shown by its embryological as well as its anatomical differences from C. fornicata.

A very interesting variety of C. plana is found within those gasteropod shells (Illyonassa, Litorina, etc.) inhabited by the smaller hermit crab, Eupagurus longicarpus. This variety resembles the type in all respects save size, being usually less than one-thirteenth the size of adult female specimens found within the larger shells. That this difference in size is not due merely to age is shown by the fact that the dwarfs are sexually mature, and they show by the shape and character of their shells that they are several years old. Apparently, all the organs are perfectly formed, and differ from those of the larger variety only in size. The ova are of the same size as those laid by the larger form, but are fewer in number. The same thing is true of the cells constituting the other organs of the body, so that it may be said that the difference in size between those two varieties is due to the smaller number of cells of which the body of the dwarf variety is composed, rather than to the smaller size of those cells.

There are many evidences that this dwarf form is not a permanent or persistent variety, but only a physiological one.[2] It, like the typical form of this species, is sedentary, and cannot move about after it has reached a certain size. The shape of the shell and body are modified, so that they fit one particu-

[1] Cf. Gould: The Invertebrata of Massachusetts.

[2] It may be doubted whether the word "variety" should be used in this connection at all. However, for lack of a better term, it is employed in its colloquial meaning rather than in a strictly scientific sense.

lar spot and no other ; therefore, the animal cannot migrate to larger quarters after it has grown to its maximum size in the smaller ones. The eggs, embryos, and larvae of the two varieties cannot be distinguished, and since both live together on the same beach, under about the same conditions of food, temperature, and water, it seems probable that the later development of both would be the same if one was not forced by the smaller size of the shell which it inhabits, or by the smaller quantity of food supplied to it, to remain smaller than the typical form. But what is absolutely conclusive is the fact that the dwarfs, when placed in positions where they can obtain a new foothold and increase in size, become almost, if not quite, as large as the common form. A few specimens were found which showed by the shape and character of their shells that for several years they had lived in the shells inhabited by the smaller hermit crab, and had been typical dwarfs; afterward, having been detached, they by rare good fortune gained a new foothold on a larger surface, and their shells began to increase in size, the new portions of the shell becoming shaped so as to fit the surface upon which they had found a new home. In every such shell one can recognize both the dwarf and the normal forms. The dwarfs are what they are by reason of external conditions, and not because of inheritance. In such a case the *shape* and *size* of the body, and the *number of cells* in the entire organism are greatly modified by the direct action of environment. There is no evidence, however, that these modifications of the shape and size of the body and the number of cells have become in the least degree heritable.

C. convexa is smaller than either of the preceding species, and as its name indicates, its shell is more convex, while its color is much darker than either of the others. It is found upon the *outside* of those gasteropod shells (chiefly Litorina and Illyonassa) inhabited by the smaller hermit crab, Eupagurus longicarpus ; and it undoubtedly obtains its food, as do the others, from the fragments left by its messmate. Unlike the others, however, it can move about to a limited extent, and, if removed from the surface to which it is fastened, can attach itself again, though so far as I could observe it never voluntarily leaves the shell upon which it is carried about. It is also said[1] to be found in numbers on blades of eel grass, though I have not seen it in such positions.

C. adunca, a species abundant along the Pacific coast, is remarkably like C. convexa in size, shape, and color of shell, as well as in habits and development. Keep, in his *West Coast Shells*, says of it: "The most common species is C. adunca Sby., hooked slipper shell. The apex is strongly recurved, giving the shell a hooked appearance. Its color is brown, but the deck is white. Living specimens may often be found growing upon rocks or upon other shells. Common length from one-half to three-fourths of an inch. Abundant." Mr. Harold Heath, who has been kind enough to send me specimens of this species, together with material for a study of its embryology, writes me that individuals are found in about equal numbers upon the shells of the "black turban" (Chlorostoma funebrale), and upon shells inhabited by hermit crabs. "The individuals found upon the 'black turbans' seem to come to sexual maturity earlier than upon the hermit shells. Several times on pulling off shells of adunca from the 'black turbans,' I was surprised to find eggs under very small shells, very much smaller than are found with eggs on the hermit crab shells." It seems to me that we have here a case parallel with C. plana and its dwarf variety, though the difference between the two forms in C. adunca is very much less striking than in the case of C. plana. That the phenomena in the two species are similar is still further borne out by the fact that the average number of eggs laid by each individual of C. adunca found upon the "black turbans" is 173.3, while the average number laid by those on hermit crab shells is 201.1. Concerning the habits of C. adunca, Mr. Heath writes: "Their shape indicates that they never leave the spot to which they first become attached. Sometimes surrounded by Bryozoa, the shell is clear within the Crepidula shell. Still, when taken off, they can, and sometimes do, regain a foothold. Many that I placed loose in the aquarium have attached themselves to the 'black

[1] Cf. Gould: The Invertebrata of Massachusetts.

turbans' living there. They appear to breed throughout the whole year."

2. *Breeding Habits.*

The breeding season of C. fornicata lasts on the New England coast from early summer until about August 15. A large proportion of the individuals of this species, examined late in June, were found to have laid their eggs, while none were found with eggs later than the middle of August, though many from widely separated localities were examined. At that time, however, the shells from all these localities were covered by the very small young, or spat, of this species. It may be worth while to remark that the breeding season is always earlier with those individuals found on the shells of Limuli than with those which exist in chains on the sea bottom. This is due, I think, to the fact that in early summer the Limuli are found on shallow, sandy beaches, where the temperature of the water is higher than at a depth of one to six fathoms, where the others are found. The breeding season of C. plana begins somewhat later and lasts longer than that of C. fornicata; several of the former species were found with newly laid eggs as late as September 7. The egg-laying season of C. convexa lasts through nearly the same period as that of C. plana.

As is well known, the sexes are separate in these gasteropods, and the males are fewer in number and smaller than the adult females. Chains of Crepidulas are sometimes found in which there is not a male individual, while isolated females, with from ten to twenty thousand perfectly fertilized eggs, are of frequent occurrence. Considering the sedentary character of these mollusks, the manner of sexual union is an interesting question. There is no doubt that the spermatozoa mingle with the ova before the egg capsules are formed within the oviduct of the female, and yet the mature females are absolutely fixed to one spot, and the largest males have very little, if any, power of movement. The smaller the individual is, however, the greater its power of locomotion. The young of both sexes are freely motile, but as they grow larger they lose this power. In C. plana all the males are much smaller than the females, and all are motile. In C. fornicata the males may become almost as large as the females, in which case they become immovably fixed to one spot, and cannot, therefore, perform the sexual function unless they are attached near to or upon a female. In C. convexa and in C. adunca all the males are smaller than the females, and are motile. I have carefully taken the volume of a number of alcoholic specimens, and find that the following ratios exist between the males and females of the different species: in C. plana the males are about one-sixteenth the size of the females ; in C. adunca, one-eighth ; in C. convexa, one-fifth ; in C. fornicata, three-quarters. The small males are able to move about more or less freely ; if they are detached they readily find a new foothold, and their shells are rarely distorted to fit irregular surfaces, as is the case with the females. There is, then, a marked sexual dimorphism in these mollusks, the mature females being generally much larger than the males ; the females are sedentary, the males locomotive, and at the breeding season, or perhaps once for all, the females are visited and fertilized by these motile males. In all mature females, the seminal receptacle, which is a convoluted tubule communicating with the oviduct, is at all times filled with mature spermatozoa. These spermatozoa are attached to the walls of the receptacle by their apices, while their tails project into the lumen exactly as they do in the seminiferous tubules of the male. I believe that the spermatozoa receive nutriment from the walls of the seminal receptacle, and that they can live in this position indefinitely. Since there are myriads of spermatozoa in the receptacle, and furthermore, since none are wasted, so far as I have been able to observe, it might well be that copulation occurs only once in a lifetime.

In C. plana the shell of the male has a characteristic shape, being more nearly round than that of the female, and having a rather sharply pointed apex. This shape is so characteristic that it is generally easy to distinguish a male from an immature female. I have observed a good many cases in which the older part of the shell had the male characters while the newer part was like that of the female. In such animals the penis is usually very small, and in some cases has almost entirely disappeared. Quite a complete series of stages in the degeneration of this organ was observed, from the fully formed organ on the one hand to a minute papilla on the other. Sections of such animals show that neither male nor female sexual cells are produced at this time. Although the evidence seems to favor the view that we have in these cases an example of successive hermaphroditism, I am not able to assert that this is really the case, although I have spent considerable time in attempting to decide it.

3. *Types of Development in C. fornicata, C. plana, C. convexa, and C. adunca.*

All the ova produced by one individual are laid at about the same time, and the development proceeds very slowly. In C. plana and C. fornicata it is about four weeks from the time the ova are laid until the fully formed veligers escape from the egg capsules, and in C. convexa and C. adunca the period preceding the escape of the young is probably much longer. How long the veligers of the two former species lead a free-swimming life I do not know, since I found it impossible to keep them alive until they were transformed into the spat, or young Crepidulas. From circumstantial evidence, however, I am convinced that in C. fornicata the veligers do not swim about for more than three weeks, probably about two. On July 23, 1890, Mr. Vinal Edwards, collector for the United States Fish Commission, brought me a large number of C. fornicata, dredged from the mouth of the New Bedford river. A large proportion of these were carrying egg capsules, many of which contained fully formed veligers, while most of them were in an advanced stage of development. On August 11, nineteen days later, another lot of Crepidulas were taken at the same place, but no eggs or egg capsules could be found; the parent shells, however, were covered with the very small spat of this species. During July of the next year (1891) I kept a lot of veligers of this species in a wooden box, the bottom of which was covered by silk netting. The box was anchored in the "codfish pool," a place where there was a large supply of fresh and pure sea-water, and yet where the surface was generally calm. In this box some of the veligers lived for almost two weeks, but although there were stones and shells in the box, I could not find any spat upon them at the end of that time. From these facts it seems probable that the free-swimming life of the veligers lasts not less than two weeks nor more than three. The whole course of development, therefore, from the time the eggs are laid to the close of the larval life and the assumption of adult characters and habits, is from six to eight weeks.

The fertilized eggs in all four species are laid in capsules, which are formed by secretions from the wall of the uterus or nidimental organ.[1] These capsules are united into a bunch, like a cluster of grapes, by a common stem, which is fastened to the shell, stone, or other object upon which the Crepidula lives. This bunch is attached between the two folds of the propodium, and within the mantle cavity of the mother, and since the adults do not move about, it follows that the eggs are always covered by the parent's shell. As a result of this protection the walls of the egg capsules are thin and delicate; very unlike the tough, leathery capsules of most marine prosobranchs. Within the capsules is an albuminous fluid, in which the eggs are immersed, and which is absorbed by the embryos in the course of development. Salensky ('**72**) has described similar capsules and egg-laying habits in Calyptraea, a sedentary prosobranch nearly related to Crepidula.

The approximate number of capsules and eggs deposited by the mature females of the different species is shown in the following table:

[1] The capsules in Urosalpinx cinerea are marked on the outside by faint spiral lines, and show a tendency to tear in a spiral direction. The same is true of the capsules of Crepidula, though in a less marked degree than in Urosalpinx. This spiral structure is caused, I think, by the rotation of the capsule as it passes through the uterus, in the same way that the spiral character of the egg membranes of birds and reptiles is produced.

TABLE I.

	NUMBER OF CAPSULES.	EGGS IN EACH CAPSULE.	TOTAL NUMBER OF EGGS LAID.
C. fornicata,	55	240[1]	13,200
C. plana (type),	51	176	9,000
C. plana (dwarf),	48	64	3,070
C. convexa,	20	11	220
C. adunca,	10	18	180

These figures are but rough averages made from counting the capsules and the eggs in many of the capsules laid by a large number of mature females ; I have no doubt that in another lot of individuals the numbers would be found to vary a little from those given above. In general, however, these figures may be taken as approximately accurate. In all cases the smaller the individual of a species the smaller the number of eggs laid, so that two specimens scarcely ever lay the same number of eggs.[2]

This great difference in the number of eggs laid is the result of the different modes of development in the different species. In no species which is not rapidly increasing or decreasing in numbers are more or less ova produced and fertilized than are just sufficient to insure the continuance of that species in its present numbers. There is no reason to believe that any of these species of Crepidula are rapidly increasing or decreasing in numbers at present ; so far as one can judge, each is just about holding its own. If, therefore, one species produces sixty or seventy times as many eggs as another, it must be that in the one case each fertilized ovum has sixty or seventy times as many chances of reaching maturity as in the other case. The history of the development

[1] By a typographical error in a former paper ('**92**) it is recorded that "about 50 eggs are laid in each pouch or capsule" of C. fornicata. It should read "about 250."

[2] Herrick ('**91**) showed that the number of eggs laid by the American lobster varies greatly, depending upon the size of the lobster. More recently ('**95**) he has published an extensive series of measurements of female lobsters and computations of the number of eggs laid by them, from which he constructs the curve of the fecundity of the lobster. He concludes that "the number of eggs produced by female lobsters at each reproductive period varies in a geometrical series, while the lengths of the lobsters producing these eggs vary in an arithmetical series."

in each of these species shows that this is probably the case, for associated with these differences in the number of ova produced are profound differences in the later stages of development. C. plana and C. fornicata pass through a long larval or veliger period, but C. convexa and C. adunca have no free-swimming larval stage at all, the young crawling directly out of the egg capsules in a condition practically adult. Since vast numbers of the free-swimming veligers of C. plana and C. fornicata must be destroyed before reaching that stage of development at which the young of C. convexa and C. adunca first issue from the egg capsules, it is evident that vastly more eggs must be produced by the two former species than by the latter if these different species are to continue in the same relative numbers in which they are now found.

Correlated with the different number of ova produced by the three species are noteworthy differences in the size of the ova, as is shown by the following tables and diagram :

TABLE II.

ABSOLUTE MEASUREMENTS OF THE UNSEGMENTED EGGS OF CREPIDULA. (APPROXIMATE.)

(All measurements were made on eggs preserved in alcohol and mounted in Canada balsam.)

Species.	Diameter.	Volume.	Number of Eggs Laid.
C. plana (type),	.136 mm.	.00131709 cu. mm.	9000
C. plana (dwarf),	.136 "	.00131709 " "	3070
C. fornicata,	.182 "	.00315655 " "	13200
C. convexa,	.280 "	.01149406 " "	220
C. adunca,	.410 "	.03608703 " "	180

TABLE III.

RELATIVE MEASUREMENTS OF THE UNSEGMENTED EGGS OF CREPIDULA. (APPROXIMATE.)

Species.	Diameter.	Volume.	Number of Eggs Laid.
C. plana (type),	1	1	50
C. plana (dwarf),	1	1	17
C. fornicata,	$1\frac{1}{3}$	$2\frac{2}{5}$	73
C. convexa,	2	$8\frac{3}{4}$	$1\frac{1}{3}$
C. adunca,	3	$27\frac{2}{5}$	1

This dissimilarity in the size of the eggs is due to the differences in the larval history — the species with the most pronounced larval period having the smallest eggs, because but a small amount of nutritive yolk is necessary to carry the development to the free-swimming stage where the larva can take care of itself, while in the species without any larval history enough yolk must be stored in the egg to carry the development clear through to the adult condition.

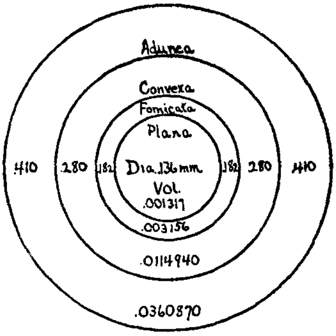

DIAGRAM I. — Showing the relative size of the eggs of C. plana, C. fornicata, C. convexa, and C. adunca. The actual diameter and volume of each is given in millimeters and cubic millimeters.

The larger size of the eggs in C. adunca and C. convexa as compared with C. fornicata and C. plana, is due chiefly to the greater amount of yolk stored in the entoderm cells of the two former species; and it is worthy of note that this increased quantity of yolk is equally distributed, so that the four macromeres produced by the first two cleavages are nearly equal in size and bear the same relation to each other in the larger eggs that they do in the smaller ones, though in many other molluscan eggs, *e.g.*, Aplysia, Urosalpinx, Unio, and Ostrea, one of the macromeres is very much larger than the other three.

In spite of this vast difference in the size of the eggs in these different species of Crepidula the cleavage, gastrulation, and formation of organs is very similar in all of them. In the large eggs of C. adunca and C. convexa the entoderm cells are, relative to the ectoderm cells, much larger than in C. fornicata, and C. plana; therefore, at the time of the closure of the blastopore there are more ectoderm cells in the large eggs than in the small ones. A count of the nuclei of the ectoderm cells in the species plana, fornicata, and convexa at this stage, shows that they are to each other as two, three, and five respectively, while a comparison of adunca with the other species at an earlier stage (just before the division of the three smaller entoderm cells, see p. 156), shows that it has a larger number of ectoderm cells than either of the others.

The cleavages are precisely the same in all the species up to the 52-cell stage. At this point the ectoderm cells begin to grow more numerous in adunca, though the divisions continue the same until a still later period in the other species.

In all the species the number of mesoderm and entoderm cells remains the same as far as they can be recognized.

There can be no doubt that C. plana and C. fornicata, with their larval types of development, represent a more ancestral condition than C. convexa and C. adunca with their suppressed larval or foetal type.[1] It must be considered that the larval type of development is the more ancestral, from which the foetal type has been derived. The small number of eggs and the direct development of C. convexa and C. adunca are correlated with the small size of the adult in these species, and this in turn may be due to the action of environment through natural selection. These species live upon small objects, chiefly those small gasteropod shells like Litorina or Chlorostoma, which are inhabited by the small hermit crab, and only those individuals could survive in these positions which are small enough to become firmly attached to these shells, while all larger ones would be torn off, and would sooner or later perish. The dwarf variety of C. plana furnishes evidence that the cause here assigned for the small size of C. convexa and C. adunca is not purely imaginary. The ability which all the members of this genus show to adapt themselves to large or small places, and to modify the shell so that it will fit plane, convex, concave or angular surfaces indicates, that the body is very plastic.

But whatever the cause of the smaller size of C. convexa and C. adunca may be, it is evident that the total mass of germinal matter must be less in these than in the larger species, provided that all the other organs are developed in about the same relative proportions, as appears to be the case.

[1]The use of the expression "foetal type of development" in this case is, I think, justifiable. It is true that in these four species various stages in the suppression of the larval development are shown, and even in that species in which the larval development is most completely suppressed, *viz.*, C. adunca, there are many rudiments of larval organs; yet these are only rudiments and they completely disappear before the young escape from the capsules.

Clearly two methods of reducing the total amount of germinal matter are possible : (*a*) the germ cells, while remaining the same in number, may decrease in size, or (*b*) the germ cells may decrease in number, provided a larger proportion of them produce adults. Both of these methods are illustrated within the genus Crepidula. (*a*) The typical form of C. plana, which is about one-third the size of the average C. fornicata, produces almost as many eggs as the latter, but each egg is only about one-third the size of the eggs of C. fornicata. In this case the total amount of germinal matter has been decreased (or increased, according as one or the other species is taken as a standard) by the decrease in *size* of the individual cells. (*b*) In the dwarf variety of C. plana, which is only one-thirteenth the size of the type form, the eggs are of the same size as in the common variety, but much *less numerous*. The method of development in the two varieties is exactly the same, and therefore it follows that unless the typical variety is rapidly increasing in numbers, which does not appear to be true, the dwarf variety must be rapidly disappearing. I think it altogether probable that the eggs laid by the dwarfs are not numerous enough to continue the dwarf variety in its present numbers, and it would rapidly disappear if it were a true or morphological variety. However, since it is merely a physiological variety of C. plana, due to the smaller size of the shell in which the young take up their residence, the continuance of the dwarf variety is not dependent upon the number of eggs produced by the dwarfs ; rather it depends upon the number of the young of C. plana, whether of the common or dwarfed form, which make their abode in the smaller shells.

In C. convexa and C. adunca the amount of germinal matter is reduced in the same way that it is in the dwarfed form of C. plana, *i.e.*, by reducing the number of cells. Since, however, these are true species which are neither rapidly increasing nor decreasing in numbers, it follows that if they produce a smaller number of eggs than the other species, the chances that each egg will produce an adult must be proportionately increased. In C. convexa and C. adunca this is done simply by lengthening the period during which the young organism remains under the protection of the mother, *i.e.*, by the suppression of the larval type of development.

Since the yolk is almost the only nutriment furnished the young organisms by the mother, it follows that the sooner they can begin to take care of themselves the less yolk will be needed, while the longer they remain in the egg capsules the more yolk will be required. While it is true, therefore, that in the foetal type of development the number of germ cells may be decreased, it is also true that the size of each ovum must be increased. However, in C. convexa and C. adunca the decrease in the number of eggs more than overbalances their increase in volume, so that the total volume of eggs laid is greatly reduced as compared with the other species. The following table gives a basis for comparing the approximate volume of the body of a mature female in each species with the total volume of the eggs laid:

TABLE IV.

COMPARISON OF VOLUME OF ADULT WITH VOLUME OF EGGS LAID.

SPECIES.	RELATIVE NO. OF EGGS.	RELATIVE VOL. OF SINGLE EGG.	RELATIVE TOTAL VOL. OF EGGS LAID.	RELATIVE VOL. OF ADULT FEMALE.
C. convexa,	$1\frac{1}{3}$	$8\frac{3}{4}$	1	$1\frac{1}{4}$
C. plana (dwarf),	17	1	$1\frac{1}{2}$	1
C. adunca,	1	$27\frac{2}{5}$	$2\frac{1}{3}$	$4\frac{1}{6}$
C. plana (type),	50	1	$4\frac{1}{4}$	$13\frac{1}{3}$
C. fornicata,	73	$2\frac{2}{5}$	15	30

The first series of measurements which I made showed a close correspondence between the relative total volume of eggs laid and the relative volume of the adult in these different species. Later and more careful measurements have given the results set down in the above table. The fact is that the sexually mature females of a species vary so much in size, and the eggs laid by them vary so greatly in number, that unless one measures a very great number of individuals of all sizes, no satisfactory ratio between the eggs laid and the volume of the adult can be determined for a given species. However, all measurements and enumerations show that the volume of eggs laid is, in general, directly proportional to the volume of the adult. This is very plainly the case within a single species where the *number* of eggs laid always stands in direct relation to the size of the animal which lays them. When one species is compared with another this same thing is generally true of the total *volume* of eggs laid, *i.e.*, the species with the largest individuals lays the largest volume of eggs, though the number and size of the eggs in the various species differs immensely. For example, C. convexa, which is about one-twentieth the size of C. fornicata, produces only about one-sixtieth as many eggs of one-fifteenth the total volume of those laid by the latter species. The great reduction in the number and total volume of eggs in C. convexa and C. adunca, as compared with the other species, is made possible by their foetal type of development. At the same time the wide distribution of individuals brought about by the free-swimming veligers of C. fornicata and C. plana is partially secured in C. convexa (I do not know whether this is true of C. adunca or not) by the freely moving young or spat of this species, which are much more active than the spat of either of the other species.

It is very evident that the foetal type of development in C. convexa and C. adunca is correlated with the smaller size of the adult in these species, and for the reasons given above, it seems to me probable that the former may be in some way the *result* of the latter.[1]

4. *General Sketch of the Embryology.*

The First and Second Cleavages.—The chief axis of the ovum corresponds to the future dorso-ventral axis of the embryo.

[1] Although I do not suppose that these relations between the size of the adult and the number, size, and volume of the eggs produced, is a general law applicable to all larval and foetal types of development, neither do I think that such relations are wholly isolated, *i.e.*, true only of this one genus, Crepidula. I believe they will be found to be quite generally true of the gasteropods. Long ago, Fol (**'76**) called attention to the fact that among the heteropods the smallest species lay the largest eggs. He says, "The smallest heteropods lay relatively the largest eggs, but infinitely fewer than the larger species." He did not observe that the largest eggs had a foetal or suppressed larval development, but I think it would be safe to assume that this is true, and that here also the foetal type, and consequently the larger eggs, are due in part to the smaller size of the adult.

The first cleavage is transverse to the long axis of the embryo, exactly as it is in the case of Teredo, Nereis, and Umbrella, and divides the ovum into an anterior and a posterior half; the second cleavage coincides with the antero-posterior axis of the future embryo, and divides the ovum into right and left moieties. The four macromeres formed by the first two cleavages are nearly equal in size, and each contains the elements of both ectoblast and entoblast, and the left posterior macromere contains, in addition, most of the future mesoblast.

Formation of the Ectoblast. — The whole of the ectoblast is separated from the macromeres by three successive divisions, which separate twelve micromeres from the four macromeres. The four cells first separated from the macromeres constitute the first quartette of micromeres, while those separated by the two following divisions are respectively the second and third quartettes. The first quartette forms the upper hemisphere (umbrella or head vesicle) of the larva, the brain, an apical sense organ, an apical plate of ciliated cells, and a portion of the velum. The second quartette gives rise to the larger part of the velum, the shell gland, and at least a part of the foot. The third quartette I have not been able to follow satisfactorily; its derivatives lie wholly outside of the velar area, and form a considerable part of the lower hemisphere.

Formation of Mesoblast and Entoblast. — Soon after the ectoblast has been segregated, and at the stage when there are twenty-four cells, the left posterior macromere divides obliquely, forming the first member of the fourth quartette, which later comes to lie in the second cleavage furrow at the posterior side of the egg. This cell then divides into right and left portions, and each half again divides into a dorsal and ventral part. The two ventral moieties form a part of the intestine or hinder portion of the alimentary canal. The two dorsal moieties are still mesentoblasts, and the mesoblast is not completely separated from the entoblast until after two more divisions. There are finally formed two mesoblastic teloblasts, each of which gives rise to a mesoblastic band, from which a part of the middle layer is derived. The rest of the middle layer comes apparently from one additional mesoblast cell in each quadrant, except the left posterior one. These three cells are derived from the advancing edge of ectoblast, and from them the scattered mesoblast cells around the blastopore apparently originate. The other three members of the fourth quartette are purely entoblastic, and they form the lateral and ventral walls of the mesenteron. The residue of the four macromeres is entirely entoblastic, and after they have given rise to a fifth quartette of large yolk cells they form the dorsal wall of the mesenteron.

Gastrulation. — The gastrula is formed by epibole associated with a flattening of the macromeres ; there is no invagination. The blastopore closes near the middle of the ventral side, and at this point the mouth soon afterward appears.

The Ectoblastic Cross. — When the stage with forty-two cells has been reached, there appears at the upper pole of the egg a cross of ectoblast cells ; the centre of the cross lies exactly at the animal pole, while each of the arms lies between the first and second cleavage planes. Later the whole cap of ectoblast shifts position so that the arms of the cross lie approximately over those cleavage furrows ; thus one arm comes to be anterior, one posterior, one right, and one left. In the further development all the arms lengthen, and all save the posterior one divide longitudinally into two parallel rows of cells. All the cells of the cross are derived from the first quartette save the "tip," or terminal cell, of each arm, which comes from the second quartette. A single ectoblast cell, which is at one time the smallest in the egg, but which afterwards becomes the largest, lies in the angle between adjacent arms of the cross. There is one of these in each quadrant, and because of their position and shape they are called for the present the "turret cells." In later stages at least two of them contribute to the formation of the velum.

Change of Axes. — During the later stages of cleavage and throughout gastrulation, the whole of the ectoblast at the upper pole moves gradually forward through an angle of about 90°, so that the centre of the cross, which originally lay at the middle of the future dorsal region, comes to lie at the anterior end of the long axis of the embryo. The entoblast seems to take no part in this shifting, and the ectoblast on the postero-ventral side of the ovum moves in an opposite direction, *i.e.*, forward on the ventral side. There is thus a stationary point in the ectoblast on the posterior side of the egg, in front of which the ectoblast cells are shoved forward, both on the dorsal and ventral sides. This stationary point is just ventral to the region of the future shell gland, and probably corresponds to the posterior growing-point of the annelids.

Organs formed from First Quartette. — Those cells of the first quartette which lie posterior to the lateral arms of the cross, grow very large and become covered by fine cilia, which protrude through a thin cuticula. These are the cells of the posterior cell plate, and they form the principal part of the walls of a large head vesicle.

The four central or apical cells give rise to an apical sense organ. Each cerebral ganglion is formed at least in part from the cells of the "rosette series" lying on each side of the mid line and between the bases of the anterior and lateral arms of the cross; secondarily the ganglia become connected with the apical organ and with the pedal ganglia and otocysts. The eyes are formed in connection with the cerebral ganglia. All the turret cells lie in the velum, and at least the two anterior ones contribute to the formation of the first velar row. The cells of the lateral arms of the cross divide repeatedly, and some of them form part of the velum. The anterior arm forms a plate of seven large cells reaching from the apical cells to the velum.

Organs formed from the Second and Third Quartettes. — A portion of the velum completely surrounds the first quartette. That part of the first velar row which lies at the ends of the arms of the cross, is formed from the second quartette; the intervening portions, on the anterior side, come from the first quartette (turret cells). The velum is many cell-rows wide, and consists of a preoral and postoral ridge bearing long flagellae and an adoral ciliated groove lying between the two. Dorsally the velum divides into anterior and posterior branches, which are separated by the posterior turrets and the other cells of the posterior plate. The anterior branch runs in on each side toward the apex, and ends on each side of the apical organ;

it traverses the cells of the transverse arms from tip to base. The posterior branch, which is never functional, surrounds the first quartette. When first formed the velar cells are not ciliated, and they lie at the same level as the surrounding cells. Later they are raised into a well-marked ridge, and are finally drawn out into a very extensive wheel-shaped lobe, the long velar cilia being borne around its margin.

The shell gland appears on the postero-dorsal surface just dorsal to the growing-point. It arises as a prominence of ectoderm cells, which from their position seem to be derived from the posterior member of the second quartette. In the place of this prominence an invagination afterward appears ; the margins of the invagination extend rapidly, and a thin cuticle, the first indication of the shell, is secreted by the invaginated cells. As development proceeds the shell becomes asymmetrical, developing more rapidly on the left side than on the right. This asymmetry extends to all the organs posterior to the foot and head vesicle.

The foot arises as a single median protuberance on the ventral side of the body just posterior to the mouth, and in front of the anal or growing region. In later stages the foot becomes more and more prominent posteriorly, until it turns forward and lies ventral to the mouth, though still attached to the body posterior to the mouth.

At the posterior end of the embryo three or four large ciliated anal cells appear very near the growing-point, and at this place the distal end of the intestine is in contact with the ectoderm. The proctodeal invagination does not occur until late in development.

Later Changes. — The intestine is a tube with a distinct lumen, its walls being formed of small cells free from yolk. Its posterior end is formed first, and it grows in length chiefly by the addition of cells at its anterior end, where it opens into the space between the yolk cells. In the course of development, the distal end of the intestine is carried forward on the ventral side, and at the same time the whole hinder portion of the embryo undergoes laeotropic torsion. By the continuance of these two movements the distal end comes to lie in front of the central end, and the latter is found successively on the right side, the dorsum, and the left side of the embryo. In the end the course of the mesenteron is like a figure 8 open at the top.

In well-advanced embryos the head vesicle and the velar folds become separated by a deep constriction from the posterior part of the embryo. The latter contains all the yolk, and it alone becomes asymmetrical ; the head vesicle, velar lobes, and foot, all of which lie anterior to this constriction, retain their bilateral symmetry.

At the point of constriction there is a large spherical prominence on each side, just dorsal to the foot ; this is the primitive excretory organ ("urniere").

On the right side of the embryo, just posterior to this constriction, a depression appears in the ectoderm which becomes the branchial cavity.

The formation of the gills, permanent kidney, pericardium, and heart does not occur until a later period than is shown in the figures.

In later stages the head vesicle decreases rapidly in size, the velum is largely, if not entirely, absorbed, the foot becomes relatively very large, and the shell, which during the veliger stage was of the spiral type, takes on the form characteristic of the adult.

In this condition the young or spat resemble the adult forms in all essential respects, and the embryology may be considered as finished.

5. *Abnormalities.*

Under entirely normal conditions all the eggs of C. fornicata and C. plana develop into perfect embryos and veligers (I have not studied C. convexa and C. adunca with reference to this point) ; still it is not uncommon to find one or two small, abnormal embryos in each egg capsule, even though taken from an individual living in what seems to be a normal environment. But when the adult Crepidulas are removed to the laboratory, and kept in the best possible conditions, the percentage of these abnormalities increases, and when the egg capsules are removed from the mantle cavity of the mother, and kept in dishes of sea-water, the monstrosities increase to such an extent that after a few days not a single normally developing egg or embryo can be found.

These abnormalities may appear in the early stages of cleavage, or they may be found in any of the later stages of development, even up to the fully formed veliger. When present in the early stages the blastomeres are more spherical and less compact than usual. The four macromeres are frequently separated from each other far enough to leave a cavity between them, and into the depression thus formed the overlying ectoderm cells dip down, forming a pit. A similar invagination has been described by Blochmann ('81) for Neritina and by McMurrich ('86) for Fulgur. Both of these authors supposed that this was a normal feature of development, but from the loose character of the cell aggregate and the rounded outlines of each of the cells in Blochmann's figures of Neritina, I believe that the ova there described were segmenting abnormally, and this view is rendered all the more probable when the large proportion (eighty to one) of abnormal as compared with normal eggs in Neritina is taken into account. In fact, Figs. 52–56 of Blochmann's paper represent very well the abnormally segmenting eggs of Crepidula, and I believe the ectodermal pit is in Neritina, as in Crepidula, an abnormal formation.

I have studied the cleavage in Fulgur and find that the ectodermal invagination which McMurrich describes is the shell gland which appears at an early stage, some distance posterior to the apical pole ; it is therefore a wholly different feature from the invagination in Neritina, which lies exactly at the apical pole.

Heymons ('93) found that in Umbrella, one of the Opisthobranchiata, the egg capsules contain thirty to forty eggs, and that some of these, though evidently no definite number, do not develop normally. He says : "Von letzeren kommen nicht alle zur normal Entwicklung, indem ein Theil von ihnen gleich nach der ersten Stadien abweichende Verhältnisse und Missbildungen zeigt und später dem Zerfalle unterliegt. Nicht selten sind auch Doppel- oder gar Mehrfachbildungen zu beobachten, die durch Aneinanderwachsen der Eier zu Stande kommen, wie sich im zwei- oder vierzelligen Stadium leicht nachweisen lässt, und die demgemäss auch die doppelte resp. mehrfache Grösse besitzen. Solche Doppelbildungen sind häufig noch ziemlich spät, noch nach Anlage des Fusses und der Schalendrüse anzutreffen und können bis auf die Berührungsstelle ganz normal ausgebildet sein."

Such double or multiple formations sometimes occur in Crepidula and many other prosobranchs, though so far as I have observed they never reach so advanced a stage as Heymons mentions. Among the later stages in Crepidula the abnormal forms are sometimes nearly like the normal ones, the chief difference being due to irregularities of form, which often take the shape of protrusions or wart-like prominences. A more marked form of degeneration is shown by those embryos which have divided into two or more pieces, each of which may move about independently. It is not an uncommon thing to see a little embryo consisting largely of velum and foot, and entirely disengaged from the yolk cells, swimming actively about in the most amusing fashion. Still greater degrees of degeneration are shown by small fragments, which move about rapidly and are nothing more than little masses of ciliated cells.

It might be considered that in all such cases these abnormal forms were the result of unfavorable conditions, such as imperfect aeration, varying density of the sea-water, or rough mechanical treatment, were it not for the fact that in some forms (*e.g.*, Neritina) even under the most perfectly normal conditions a definite number of abnormalities are always found. McMurrich ('**86**) has given a pretty complete series of forms showing the varying tendency to produce abnormalities which different species possess. In Fulgur and Urosalpinx all the eggs are said to develop ; in Purpurea floridana all do not develop, but a considerable number (not definitely stated) break down and are used as food : in Purpurea lapillus there are five hundred to six hundred eggs in a capsule, only twelve to thirty of which develop, while in Neritina fluviatilis there are seventy to ninety eggs in each capsule, only one of which undergoes regular development. In each of these cases the eggs which do not develop, break down and are used as food by the normal embryos. Such cases cannot be accounted for by assuming merely that the environment is unfavorable. Such a cause would give no such definite results as are said to exist, *e.g.*, in

Neritina. Nor can it in all cases be explained by assuming that in each egg capsule there is a struggle for existence, and that the fittest survive while those less hardy are destroyed, since in some forms, *e.g.*, Neritina, the development does not proceed far enough to introduce such a struggle. From the very beginning of development the ova are divided into two classes, those which segment regularly and develop into normal embryos, and those which divide irregularly and never form embryos at all. Blochmann thinks that in Neritina the eggs which do not develop have not been fertilized, while McMurrich believes that too little yolk was furnished for the number of eggs produced, and that, therefore, some of the eggs broke down and were used as food by the embryos which survived. "This process," he says, "might have been seized upon by natural selection, and increased by it until it became a regular process of development."

I am inclined to believe that in different species different causes may have been operative in producing these abnormal forms. In Neritina, Purpurea and all other forms in which the development of some of the ova goes no farther than a few irregular cleavages, the most probable cause of such non-development seems to be the lack of fertilization, for if McMurrich's supposition is the correct one we should expect to find the ova which undergo development larger than those which do not, but there is no evidence of such disparity in size. On the other hand, in those forms in which the abnormalities do not appear at an early stage and with great regularity, *e.g.*, Crepidula or Urosalpinx, in which they may or may not be present, and if present may occur at any stage, in such cases I am convinced that the abnormal forms are the result of unfavorable environment, *e.g.*, lack of oxygen, presence of bacteria, mechanical pressure, etc.

C. HISTORY OF THE CLEAVAGE.

NOMENCLATURE.

The question of an accurate and convenient nomenclature for the various cells of the cleaving ovum, while of no scientific value, is, nevertheless, of considerable practical importance.