CHAPTER XI

THE EFFECT OF INJURING ONE OF THE FIRST TWO BLASTOMERES

WE have seen that the plane of first cleavage corresponds as a rule with the median plane of the future embryo, so that one of the first two blastomeres gives rise to the cells that form one side of the body of the embryo, and the other blastomere produces the cells of the other side. It would seem then that even at the two-cell stage the axes of the future embryo are definitely laid down. But the most fundamental question remains unanswered; viz., has the egg after its first cleavage divided its material into qualitatively different parts (*i.e.* has the material of the right side of the body been separated qualitatively from that of the left side), or are the first-formed blastomeres still undifferentiated, and their subsequent fate dependent on the relative position they bear to each other as a part of a *whole?*

Roux tried to answer this question by the following ingenious experiment.

ROUX'S EXPERIMENT OF "KILLING" ONE OF THE FIRST TWO BLASTOMERES

As soon as the first furrow had passed through the egg, one of the resulting blastomeres was pierced with a hot needle. In order to carry out the experiment successfully, certain precautions must be taken. The eggs as soon as removed from the uterus are scattered over a glass plate (under water) so that they lie singly. Then water containing spermatozoa is added. After ten minutes this water, clouded by the spermatozoa, is poured off and fresh water is added. When the first furrow in the eggs appears, the water is again poured off. Each egg is held by a pair of forceps and then pierced by a hot needle. The needle is carefully sharpened, and is re-sharpened after each egg is operated upon. It is best to pierce the blastomere in the black hemisphere near the first cleavage-plane. The needle passes through about a half (or more) of the blastomere. When the needle is withdrawn, a greater or less amount of the contents of the blastomere protrudes where the blastomere has been injured. The egg after operation is returned to the water. It is necessary to keep the eggs under careful observation, because sometimes the blastomere has been only slightly injured and continues to develop more or less irregularly. Such eggs should be removed.

A B

FIG. 34. — A. Hemiembryo lateralis. B. Hemiembryo anterior. (After Roux.)

Roux found that in twenty per cent. of the eggs the uninjured blastomere lived and continued to develop. This blastomere by continued division developed into a form that may be called a "semimorula verticalis," since it is like the vertical half of a normal "morula." "That is to say, it is a hemispherical structure with small deeply pigmented cells above, and with larger non-pigmented cells below." The segmentation-cavity is often absent; sometimes it is represented by a few loosely aggregated cells, and sometimes by a cavity bordered in part by the injured half of the egg (Fig. 35, A). A "semiblastula verticalis" then develops with a well-defined segmentation-cavity. A "semigastrula" stage is next passed through. "Hemiembryones laterales" develop from most of these eggs, as seen in Fig. 34, A. This figure shows that the right half of an embryo has developed from the uninjured blastomere. Half a medullary plate is present along the line of separation of the injured and uninjured halves. Near the posterior end of the half plate, the yolk of the developed half is exposed over a small region and surrounded by half of a blastopore (?). A cross-section of such an embryo shows (Fig. 35, B) that the half plate has essentially the same form as half of the normal medullary plate; that beneath this half plate a notochord is present forming a rod, round or slightly oval in cross-section; that a small archenteron is present in the developing half, and that a mesodermal sheet is present over the side of the hemiembryo. It is interesting to note that while only half the medullary plate is present, yet the

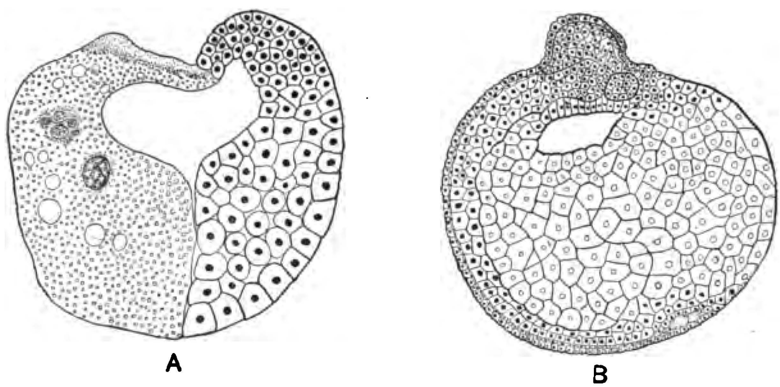

Fig. 35.—Cross-sections through two half-embryos of different stages. (After Roux.)

notochord and archenteron, which are also median structures, form whole structures but of smaller size than the corresponding normal organs. Roux thought that the notochord was very probably composed of only half the number of cells present in the normal notochord, but, owing to a great amount of variation in the latter, it was not possible to determine this relation definitely.

Pflüger, Roux, and Born have shown that sometimes in the normal development the plane of the first cleavage corresponds to the cross-plane of the body of the embryo, *i.e.* the plane of the first cleavage separates the anterior from the posterior end of the body. Under these circumstances, if one of the first two blastomeres had been killed, we should have anticipated, Roux says, that "hemiembryones anteriores" or "posteriores" would have appeared. Roux claims that such forms do really appear. The same result can be obtained, if, after the second cleavage of the egg, two of the four cells be killed, *i.e.* those two that lie on the same side of the second cleavage-plane. A hemiembryo anterior (?) is shown in Fig. 34, B. It has the anterior end of the medullary folds normally formed, also a normal chorda, mesoderm, and archenteron in this anterior end. In every respect it corresponds to the anterior end of a normal embryo, except that the archenteric cavity is small, resulting, Roux thinks, from the impossibility of pushing the yolk-mass posteriorly, as is done in the normal embryo when the archenteron enlarges. Roux is uncertain whether he has seen any "hemiembryones posteriores," although one embryo that he found, with thick and short blastoporic lips, may represent such a form.[1] Roux made some further experiments in which one of the first four blastomeres was killed, and other experiments in which three of the first four blastomeres were killed. In the first case he obtained three-fourth morulæ and three-fourth blastulæ; in the latter case, one-fourth blastulæ and one-fourth embryos. Roux concluded from his experiments, "that the development of the frog's gastrula and of the embryo immediately following the gastrula-stage is, after the second cleavage-period, a mosaic work of at least four vertical self-developing (or differentiating) parts." "How far this mosaic work is changed by a change in the position of material in the later development, cannot be determined."

In later stages in the development of the hemiembryos a new series of phenomena appear, that result in the "reorganization"

[1] We should expect, *following Roux's argument*, to get as many hemiembryones posteriores as anteriores, yet such does not seem to be the case. Hertwig ('93, A) has maintained that it is absurd to suppose the posterior end of the blastopore could appear when there is no anterior end; but this supposition rests, I think, on an erroneous idea of the way in which the blastopore forms, for I have shown in my experiments ('94) that the posterior lips of the blastopore may appear when the anterior lip has been destroyed. The experiment should be carefully repeated with the four-cell stage, where it is possible to distinguish the two anterior and the two posterior cells.

of the half operated upon, and in the subsequent "postgeneration" of the same.

Sections of eggs that have been successfully operated upon show the kind of change that has taken place in the injured blastomere as a result of the operation. The yolk is found much vacuolated in places, and the protoplasm in the immediate path of the needle has been killed, and much changed. After a time it is found that scattered nuclei or nuclear-like structures are also present in the injured half (Fig. 35, A). These have come from the regular or irregular division of the nucleus of the blastomere that has not in most cases been killed by the hot needle. The developed half is somewhat larger than the injured blastomere, and a sharp line of demarcation is at first present between the two halves. Even in the early stages of some eggs changes are found to take place that precede the "reorganization" of the injured half. Roux describes *three sorts of reorganization-phenomena.* The *first of these changes* involves the formation of cells in the injured half. Nuclei, surrounded by a finely granular protoplasm, appear in the injured blastomere. These nuclei seem to arise from two sources, — from the nucleus of the injured blastomere, and from nuclei (or cells) of the developing half that have transmigrated. Around the nuclei the yolk breaks up into cells. This cellulation of the yolk may take place at very different times. It may be absent in some cases in a semigastrula and be present in other cases in a semimorula or semiblastula. The cellulation of the injured half begins always near the developing half, and extends thence outward. The cells of the injured half are of various sizes, but generally larger than the cells of the uninjured half.

The cellulation of the yolk takes place only in the unchanged non-vacuolated parts. Where the yolk has been much changed, it is worked over by another method, *i.e.* by the *second method of reorganization.* These parts are revived or reorganized by the nuclei or the cells that have now appeared in the injured half. Such parts are either actually devoured by wandering cells or slowly changed under the influence of neighboring cells or nuclei so that they become a part of these cells.

In addition to the two preceding modes, *a third method of reorganization* takes place. When the yolk has been much injured, the surface may be subsequently covered by ectoderm that grows directly from the developing half over the injured portions. "*Postgeneration*" now begins in the cellulated injured half and ultimately the missing half of the embryo is formed. The surface ectoderm is first postgenerated either by direct overgrowth from the uninjured to the injured side, or by the formation of ectoderm from the cells of the newly cellulated yolk. The missing half of the medullary folds appears very quickly. Half a day or a night is often sufficient to change a hemiembryo lateralis into a whole embryo with a complete medullary plate. The mesoblast grows over to the injured half, but increases in length and breadth by the addition of new cells from the cellulated yolk. The formation of new mesoderm takes place only along the free edge of that already formed. The growth is in a dorso-ventral direction.

The archenteron is postgenerated in a way very different from the way in which the archenteron of the normal embryo is formed. The lacking half of the archenteron arises in connection with the half of the archenteron already present in the hemiembryo. The yolk-cells of the injured half become radially arranged and a slit appears in the postgenerated half extending out from the archenteron of the hemiembryo. The cells surrounding the slit arrange themselves into a lining layer and the slit opens to form the missing half of the archenteron. In general we may say that in the postgeneration of the organs of the injured half, the changes always proceed from the already differentiated germ-layers of the hemiembryo, and the postgeneration takes place where the exposed surfaces of the germ-layers touch the newly cellulated yolk-mass of the injured half.

FURTHER EXPERIMENTS

(By Hertwig, Endres and Walter, Schultze, Wetzel, Morgan)

We may next consider the work of others, who have, after Roux, repeated the same experiment and made further variations of it. Lastly, before a final conclusion can be reached as to the interpretation of the results, we must carefully examine the evidence from similar experiments on other forms. We shall be then in a position to understand more fully the results of the experiments on the frog's egg.

Hertwig ('93, b) was the first to repeat Roux's experiment, but reached results diametrically opposed to those of Roux. At the two-cell stage, one of the blastomeres was stuck with a hot needle,[1] but unfortunately a detailed description of the method employed is not given by Hertwig. After the operation[2] the egg so turns itself that the uninjured part rotates upward, while the injured half is below. This is owing, Hertwig says, to the development of a blastula and gastrula cavity, within the uninjured and segmented half. The cleavage-stages of the egg are not described! Sections of the blastula stage show that in the cellulated half a segmentation-cavity, having a thin roof, has appeared. This cavity lies, in the present case, in the centre of the developing half. In other embryos, the cavity may lie excentrically, and in some cases *a part of the floor of the cavity may be bounded by the yolk-substance of the undeveloped half.* Hertwig interprets these results to mean that when one of the first blastomeres is injured, the method of development of the other blastomere is very much altered. The injured half lying in contact with the active half plays only a passive rôle in the further development.

The injured blastomere is closely applied to the developing half, and in places passes continuously into the latter. Hertwig thinks that the yolk of the injured blastomere exerts on the developing half an influence similar to that which the food-yolk of meroblastic eggs exerts on the protoplasmic portion that forms the embryo. This injured yolk-material comes to lie in the ventral and posterior portion of the embryo.

Hertwig ventures further to prophesy that if the injured yolk-mass had been taken altogether out of the egg-coat (*i.e.* from its contact with the living half), then there would be formed a normal embryo without defect and like the normal embryo in every respect except its smaller size.

It is of importance to note that Hertwig describes other

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[1] In a few cases a galvanic stream was used to kill the blastomere.

[2] How soon after is not stated.

embryos that he obtained by Roux's methods, and contrasts these with those described above. Some of the embryos showed the condition of spina bifida, *i.e.* with both sides of the body developed and with a large yolk-exposure in the mid-dorsal line.[1] Others of the embryos were only slightly injured by the operation and developed nearly normally. In these the entire dorsal region was well developed and the blastopore closed to a small ring. Only on the ventral side was a small defect found where the outer and middle germ-layers were absent. In these latter embryos, and in those showing spina bifida, Hertwig believes the injured blastomere was not killed or even sufficiently injured to prevent its partial development. That this is the true explanation cannot be doubted; for it is not at all unusual to find after the operation that the injured blastomere may separate off small portions of itself as cells that develop along with the cells from the uninjured half. Here, it seems to me, is the uncertain part of Hertwig's work. He has not observed, as far as stated, the segmentation of each egg on which he has operated, and consequently his results are open to the objection that in many cases, where he does not suspect it, the *injured cell has also continued to divide* and to form a part of the later embryo.

In nearly all of the embryos described by Hertwig the medullary folds are unequally developed.[2] Hertwig's attempts to meet this fact do not seem to me altogether satisfactory. A large number of the embryos have developed unsymmetrically. The ventral and posterior yolk-mass lies higher up on one side than on the other. In consequence of this, one side of the medullary fold lies nearer to the injured yolk than does the other, and as a result the two sides of the body are unevenly developed. The asymmetrical position of the blastopore on the living part is assumed to be the underlying cause of the later asymmetrical position of the medullary folds; but for the primary reason of the lack of symmetry of the blastopore itself Hertwig gives really no explanation, and to state that it

[1] Among these embryos Hertwig describes one that seems to have been an excellent example of Roux's "hemiembryo lateralis."

[2] There are a few exceptions.

is due to the "yolk lying higher up on one side" is only begging the question. Roux has not failed to notice the incompleteness of Hertwig's explanation, and has interpreted all of Hertwig's results as due to a sudden postgeneration of the injured half of the embryo; *i.e.* Roux believes a half-embryo to have first formed, and then to have been quickly followed by an imperfect formation of the other half. Hence the asymmetry of the embryos.

It is impossible to say how far postgeneration has played a part in the development of the embryos described by Hertwig, but that postgeneration will explain all the difference between the results of Roux and of Hertwig seems highly improbable. Further, as I have said, it seems not unlikely that many of the embryos described by Hertwig have come, not only from the uninjured blastomere, but also from a part of the *injured blastomere.* If this latter supposition be true, we can better understand why the injured yolk forms in many cases an integral part of the developing embryo.

Hertwig has made a most formidable attack on Roux's explanation of postgeneration of the embryo. The subject itself is of secondary importance as compared with the main problem involved in the experiment, and yet of sufficient interest to warrant careful examination. Roux describes the blastomere into which the hot needle has been plunged as dead, and speaks of a later revivification of the dead half of the egg. Hertwig believes that all of that part of the operated blastomere that is later divided up into cells (to be used in the development) is not dead, but only more or less injured. Only a small portion of the injured blastomere is really *dead*, and that is the portion which has become coagulated by the hot needle. This portion cannot later be broken up into cells, but may be either thrown out by the living embryo or assimilated, owing to the power of digestion of neighboring cells. The injured blastomere behaves in the same way that a portion of the body of an animal would if a needle had been stuck into it. The place injured might quickly heal, and the comparatively small region that had been pierced and killed would be reabsorbed again. If the needle had been first heated, the region of injury would only be larger, and the necrotic tissue would be either thrown off or absorbed. It has been shown by Roux that when a blastomere has been pierced by a *cold* needle, there is a small outflow of yolk, and the injured blastomere continues to divide at the same rate as the uninjured cell. When the needle is heated, the cleavage-process is delayed or prevented, while it continues on the uninjured side; but after a time the injured blastomere may also begin to divide in an irregular way. After two or three days one gets generally from such eggs quite normal gastrulæ and embryos, differing in little or no respect from embryos from uninjured eggs.

The nucleus of the uninjured blastomere may continue to divide, although the protoplasm, owing to its injury, may not be able to do so for some time. The nuclei may scatter themselves through the protoplasm (and yolk), and subsequently take part in the division of this into cells. In extreme cases Hertwig admits that when the needle is very hot, the whole of the protoplasm of the blastomere may be killed, and also the nucleus. Furthermore, it is possible that occasionally the heat may radiate from the one blastomere into the other and *partially* kill this other one also. If the last condition is brought about, the development of the partially injured blastomere may take place only very slowly, if at all. In most cases, therefore, Hertwig believes a "reorganization" of the injured cell takes place, and not a "revivification" of the dead half. In this reorganization, Hertwig thinks that the nucleus of the injured cell itself plays the main part, while Roux believed the process was brought about largely by an immigration of cells (or nuclei) from the uninjured into the injured half. Hertwig's conclusion here seems based rather on *a priori* probability, while Roux's statements rest directly on his own observations. Recently the same ground has been worked over by Endres and Walter, whose results substantiate Roux in every respect.

Endres and Walter ('95) have obtained the typical half-blastulæ and half-gastrulæ and half-embryos which Roux has described. They deny that *whole embryos* develop from one of the first two blastomeres, as Hertwig affirmed. Their figures show in the most conclusive way that *half-embryos* do develop under the conditions of Roux's experiment. The subsequent postgeneration of the injured half of the egg has also been studied by these authors. They confirm in every detail the method of reorganization and postgeneration of the injured half as described by Roux. *The reorganizing cells have migrated from the uninjured to the injured side*, and there have caused the protoplasm to break up into cells. The injured blastomere is also overgrown *directly* by the ectoderm of the uninjured and developing side. In many of these embryos the right and left side (one side has postgenerated) are separated from each other by a protruding yolk-mass, forming spina-bifida embryos. The reorganization of the *much changed* mass of the injured blastomere is brought about by being assimilated by the cells that have migrated into that region, by the second and third methods of reorganization described by Roux. When the material of the injured half is only incompletely reorganized, there is formed, after postgeneration, a more or less pronounced spina bifida. When the injured material is completely worked over or reorganized and postgenerated, a perfect embryo may be formed.

Schultze ('94, b, d) has made an interesting modification of one of the experiments of Pflüger and obtained most unexpected results. The eggs of Rana fusca removed from the uterus were placed singly upon slides. On each slide had been stuck two thin glass rods from 1.65 to 1.35 mm. in thickness. Between these rods, which are separated from each other by the width of the slide, an egg is placed with the *white pole uppermost*. The egg is then fertilized in this position. After three minutes the spermatozoa may be supposed to have entered, and a glass cover is placed over the egg and brought down into contact with the two glass rods above-mentioned, and there fixed with rubber rings. The egg is by this means slightly compressed and held more or less firmly in position. Each slide is then turned over, *i.e.* through 180 degrees, so that the dark pole of the compressed egg is brought upward. The eggs now in the normal position are put into a dish of water, to remain in this position until the *first furrow* has appeared or even until it has passed through the egg. Then the slide and its egg *are again rotated through* 180 *degrees*, so that the white pole is once more turned uppermost. Owing to the compression, the eggs retain their inverted position.

After twenty-four hours at 17 degrees C., the gastrulation begins. The rubber bands are then removed from the slide,

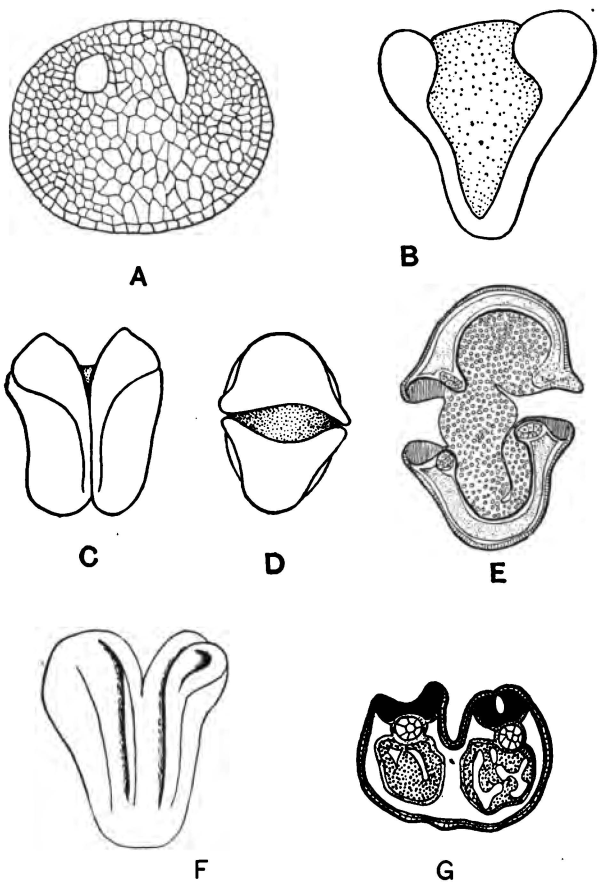

FIG. 36.—Double embryos. A. Section through segmenting egg. (After Wetzel.) B. Double embryos united ventrally. C, D. Double embryos united dorsally. (After Schultze.) E. Cross-section through C. (After Wetzel.) F. Double embryos united laterally, and G, cross-section of same. (After Wetzel.)

the cover-slip carefully cut away from the jelly of the egg, and the slide and egg returned to the water.

If eggs that have been inverted after the two-cell stage are watched during the later cleavage-period, it will be found that the upper white surface disappears, and often a whitish band is found in the position of the first furrow. Continuous observation also shows that the white hemisphere may slowly sink to one side. At thirty hours the blastopore has appeared in the normal eggs, while on the inverted eggs *two gastrula-invaginations* are found. From each half of the egg a more or less complete embryo may develop (Fig. 36, B, C, D). The two "double monsters" are united to each other in various ways, often with the two ventral surfaces united in one common yolk-mass, as shown in Fig. 36, B. Another of these double forms is shown in Fig. 36, C, D, and a cross-section through the body in Fig. 36, E.

The details of these experiments of Schultze have not yet been published. The method of gastrulation of the halves is not clearly explained, nor does Schultze explain the changes that take place in the interior of the blastomere after the rotation. The results show, however, in the clearest way that each half of the egg, after the first division, has the power to develop all the organs of a single embryo.

Wetzel ('95) has more recently studied the gastrulation-process in some of these embryos and has given a fuller description than Schultze of the origin of the archenteron. A cross-section through the blastula-stage of one of these eggs is shown in Fig. 36, A. Two distinct segmentation-cavities are present in the upper or white hemisphere of the egg. The centre of the double blastula is filled with large yolk-cells. The sides are formed of smaller cells richer in protoplasm and pigment. The structure of this double blastula shows that, in all probability, the contents of each of the first two blastomeres have rotated after the inversion of the egg so that the more protoplasmic portions have come to lie at the outer and upper sides of each blastomere; while the heavier yolk has sunken down to the lower surface along the cell-wall that separated the first two blastomeres from each other.

At a later stage a depression appears on the surface of the egg in the region of the plane that separated the first two blastomeres from each other, *i.e.* approximately in the plane of the first cleavage. This depression or groove on the surface may divide at either end into two distinct and independent grooves. Cross-sections through such an egg show that the groove on the surface is the result of an invagination to form an archenteron in each half. This means that each half-blastula has begun to invaginate along the common line of contact of the halves. Since the halves are in contact, the overgrowth of each blastopore is impossible. The lips of the blastopore of each half, therefore, have extended around the equator of the egg as in the spina-bifida embryos. A medullary fold appears later along *each* blastoporic rim, and then it becomes apparent that two embryos are present, each a spina bifida, and united by a common central yolk-mass (Fig. 36, C, D, E). The open dorsal surfaces of these two embryos are turned toward each other (Fig. 36, E).

This seems to be the more common type of double monster produced from these eggs. If, however, the blastoporic invaginations begin at different regions of the two hemispheres, many possible variations of the method described will be introduced; Schultze and Wetzel have in fact, as we have seen, described several forms of these double monsters. (Fig. 36, B, F.)

It seemed to me not improbable that Schultze's results explain in part the difference in the results of the experiments of Roux and of Hertwig. If, on the one hand, the uninjured blastomere retain its normal position after the operation, *i.e.* with the black pole turned upward, then there should develop a half-embryo, in Roux's sense. On the other hand, if, after the operation, the position of the egg be reversed so that the white pole of the uninjured blastomere is turned upward, then a whole embryo of half-size might develop. In Roux's experiment it is probable (although not explicitly stated) that the black hemisphere always remained upward after the operation. Hertwig does not say in what position the eggs lay in his experiments. He only says that in the blastula and gastrula stage the heavier injured yolk was down, and the lighter uninjured blastomere was above. If, immediately after the operation, the eggs lay with the injured blastomere below, we should expect some change to take place in the interior of the uninjured blastomere as a result of its oblique or even inverted position; hence the uninjured blastomere might develop differently than it would have done had it retained its normal position (as in Roux's experiment). In this way we might attempt to reconcile, in part, the different results of Roux and Hertwig. I cannot but think, however, that the main difference is due to the partial development of the injured blastomere in many of Hertwig's experiments, so that cells split off from the injured blastomere took part in the formation of the embryo.

In 1894 I made the following experiments to determine whether one of the first two blastomeres could give rise to a half or to a whole embryo, according to the conditions of the experiment. One of the first two blastomeres was killed with a hot needle in the way described by Roux ('93, c).[1]

In some of the eggs the black pole remained upward after the operation; other eggs were rotated after the operation, so that the white pole was turned upward. The eggs were closely watched for several hours, in order to ascertain with certainty whether the injured half divided or not. In those cases in which this happened, the eggs in question were eliminated from the experiment.

The eggs were placed at first on a moistened glass plate and kept for a time in a moist atmosphere, or else simply thrown into water. The results seemed to be the same. When the black pole of the uninjured blastomere remained up, the blastomere developed, in all the cases observed, into a *half-embryo*. Conversely, those eggs in which the white pole was turned upward, formed, in most cases, *whole embryos of half-size*. In the latter case the cleavage was modified in consequence of the reversed position of the egg. The upturned white hemisphere produced smaller cells than the lower black hemisphere, pointing unmistakably to a rotation of the fluid contents of the blastomere.

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[1] The needle was heated each time before piercing an egg. This made a greater injury to the blastomere much more certain. On the other hand, it lowered the percentage of embryos obtained, because in many cases the other blastomere was probably injured also by the heat.

The *half-embryos* and the *whole embryos of half-size* developed independently of the yolk-mass of the injured side. In this respect my results differed very materially from the results of Hertwig. Many of Hertwig's embryos developed in connection with the injured blastomere; mine, on the contrary, developed independently of the injured blastomere. I suspect, as I have said, that this difference may be in part due to this, that Hertwig did not carefully remove from his experiment those eggs in which the injured blastomere continued to segment, and that cells from the injured blastomere took a direct part in the subsequent development.

In one of my experiments, in which the uninjured blastomere had been *reversed* after the operation, it developed into a half-embryo, and not into a whole embryo of half-size. Moreover, in this embryo the medullary folds appeared on the white surface of the egg, showing that a rotation of the contents of the blastomere must have taken place. We must, therefore, conclude that the simple fact of the rotation of the blastomere-contents is not, in itself, the determining factor as to whether a whole or a half-embryo will result, but probably the *kind* of rotation determines this result. The result may also depend in part, I think, upon how far the contents of the uninjured blastomere have retained, after the operation, their organic connection with the other injured blastomere.

In later papers Roux stated that he has often obtained in his experiment other sorts of embryos than those he first described, which he calls "hemiooholoplasten." These are *whole* embryos that have come from the uninjured blastomere without the postgeneration of the other injured blastomere. Roux interprets these as embryos "completely postgenerated," with only a partial use of material from the other side, or even with no material from the injured side. Roux affirms that he has seen all intermediate stages between those embryos that have used all of the yolk-material of the injured side, those that have used only a part of the material of the injured side, and those that have not used any of this material. These embryos differ from one another only in point of size. Roux does not call the embryos that have developed entirely from the material of the non-injured side, whole embryos of half-size, but he believes that at first there formed a half-gastrula, then a half-embryo. Later this half-embryo completed itself without using material from the injured side! That is to say, by using "wandering cells" the half-embryo has *postgenerated* the other half of its body!