

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.

Almost every writer on cleavage has a nomenclature of his own, and not only must one learn a new system every time he reads a new paper, but the difficulties of comparing the work of one author with that of another become constantly greater and greater. If it were possible to invent a system, as some have attempted to do, which would be simple, convenient, and *universally applicable*, it could, and of course would, be accepted by every one who writes upon this subject; but the differences in cleavage are so great that such a consummation seems to me almost hopeless. Besides, there are peculiar features in the cleavage of every egg upon which nature seems to lay emphasis, and such features deserve some special recognition in the nomenclature. Perhaps the most serious objection to any of the systems of nomenclature which have been proposed is the fact that it is almost impossible to recall cells by letters and figures when they differ from each other only in the value of one out of many exponents, *e.g.*, it is practically useless for an ordinary reader to attempt to remember the differences in the position, shape, and history of the cells called  $b''_2$  and  $b'''_2$  of Blochmann's ('81) system, or  $d^t$  and  $d^{t.4}$  of Wilson's ('92), whereas it is comparatively easy to recall these cells if they are known as the basal and terminal cells in the posterior arm of the cross. It is not always possible to designate cells by colloquial names which shall be of any help in forming a mental image of them, but wherever it is possible it should be done. At the same time some brief and accurate system of nomenclature is necessary in order to show the derivation of cells, and also for the purposes of comparison and reference.

I have, therefore, concluded to employ, so far as possible, a double system of names for every blastomere, one of which shall be, if you please, its common name, the other its scientific designation. Regarding the latter, which alone needs to be mentioned in this place, I shall, in the main, follow Wilson's system, given in his work on "The Cell Lineage of Nereis," modifying it only to this extent, that the quartettes<sup>1</sup> of cells, separated at various times from the macromeres will be desig-

<sup>1</sup> I use the term *quartette*, as employed by Kofoed ('94), to designate a group of four cells of the same generation, one of which belongs to each of the quadrants

nated by coefficients rather than by exponents ; *e.g.*, the first quartette of micromeres and all their derivatives are designated by the coefficient 1 (1a, 1d, 1a<sup>1.2</sup>, 1c<sup>2.2</sup>, etc.), the second quartette and its progeny by the coefficient 2 (2a, 2d, 2c<sup>3.1</sup>, etc.), the third quartette by the coefficient 3 (3a, 3d, etc.), and the fourth quartette by 4 (4a, 4d, etc.). I emphasize this difference between the quartettes of micromeres because in general their histories are very different, and also because it is only by following the different quartettes that I have been able to trace the cell lineage in the more advanced stages.

Another and an all-sufficient reason for emphasizing in the nomenclature the different groups or quartettes separated from the macromeres, is the fact that, so far as known, the same number of quartettes with essentially the same destiny is separated in all annelids and mollusks with holoblastic segmentation. This is certainly a feature of great morphological importance, and deserves special recognition in the nomenclature. This system of nomenclature will be better understood by reference to the following cytogenetic table.

The animal and vegetal poles are considered the fixed points in the egg. In the ectoblast the stem or parent cell is in all cases the upper one. The stem cell in the entoblast and mesoblast is in every case the lower one. If, in any case, the cleavage is perfectly meridional (an exceedingly rare thing), the right moiety is considered the stem cell. The terms *right* and *left* are employed in the usual sense, *i.e.*, right is clockwise, left is anti-clockwise. A cleavage is oblique to the right, or, following Lillie ('95), *dexiotropic*, when the upper moiety lies to the right of the lower ; it is oblique to the left, or *laeotropic*, when the upper moiety lies to the left of the lower. The direction of a cleavage refers to the direction of the nuclear spindle, not to the plane of the division wall.

of the egg. In numbering the different quartettes, however, I have departed somewhat from Kofoid's system. The four macromeres are the basal quartette ; the first group of ectomeres separated from these are the first quartette, the second group the second quartette, etc.





## THE UNSEGMENTED OVUM (FIG. 1).

The spermatozoa meet the ova in the oviduct and are inclosed with them in the egg capsules, but the maturation and fecundation of the ova do not take place until after the capsules have been laid. I have reserved for another paper the study of the nuclear phenomena which underlie these processes.

Two polar bodies are extruded : they are clear and vesicular, and each contains a small nucleolus-like sphere of chromatin. The chromatin in the first-formed polar body usually divides, though the body itself frequently does not. Both polar bodies remain attached exactly at the centre of the ectodermal area, frequently until the ectoderm cells have extended more than halfway around the egg, Figs. 49 and 50. In all these later stages the chromatin is not surrounded, as in earlier stages, by a clear vesicular layer of cytoplasm, but seems to have dissolved and spread throughout the whole body, so that it stains quite uniformly. Sooner or later the polar bodies fall off and disappear, and in sections of embryos of the stage shown in Fig. 93, I have, in several cases, found them in the mesenteron, having been drawn in with the nutrient fluid surrounding the embryos.

The unsegmented ovum is nearly spherical in *C. plana* and *C. fornicata*, though in the larger eggs of *C. convexa* and *C. adunca* it is generally elongated in one diameter, so that when seen from either pole the outline is elliptical.<sup>1</sup> The protoplasmic portion in all of these species is small as compared with the yolk, but much smaller relatively in the last two than in either of the first two. There is no sharp boundary line between the protoplasmic and deutoplasmic portions ; on the contrary, the former sends out pseudopodia-like branches between the yolk spheres, and the spheres themselves grow smaller and more indistinct as one approaches the protoplasmic portion. Fig. 1, the earliest stage drawn, shows the male and female pronuclei lying close together but still distinct. Each nucleus contains, besides several bands or loops of chromatin, a homogeneously staining nucleolus of considerable size, from which the bands of chromatin seem to radiate. In the figure the female pro-

<sup>1</sup> McMurrich has pointed out that the eggs of *Fulgur* are elongated.

nucleus is slightly larger than the male, and this continues to be true as long as the pronuclei can be recognized as such.

Two polar bodies are shown in the figure at the upper pole, of which the first formed is much the larger ; the chromatin in this has already divided into two masses, though the cell body is still undivided.

At the vegetal pole of the egg there is frequently found a rounded mass of hyaline substance, which stains homogeneously. It persists until after the first two cleavages, lying in the furrow between the macromeres, but apparently attached to one of them only. I am not satisfied as to the significance of this body, but am inclined to believe that it is a remnant of the stalk of attachment by which the ovum was fastened to the basal membrane of the ovarian follicle. If this view be correct, the polarity of the egg is determined in the ovary, the vegetal pole lying next the membrane, the animal pole next the lumen of the follicle. This is precisely the condition in *Unio* (Lillie ('95), p. 10), where the point of attachment marks the position of the micropyle. There is no micropyle in *Crepidula*, and no need of any, since there is no egg membrane, but this hyaline mass suggests the micropyle, not only because it is located at the vegetal pole, and seems to be formed in the same way, but still more remarkably, because the spermatozoan usually, though not invariably, enters the egg at this spot. In all cases the polarity of the egg is definitely established long before the polar bodies are formed, and if my interpretation of the hyaline mass is correct, the animal and vegetal poles of the egg are established at a very early stage in the ovary.<sup>1</sup>

<sup>1</sup> Since the above was written a brief study of the eggs of *Fulgur carica* and of *Sycotypus canaliculatus* shows that a similar body, though very much larger than that in *Crepidula*, is present in these animals. In both *Fulgur* and *Sycotypus* this body contains a considerable amount of yolk and yet stains quite uniformly, as it does in *Crepidula*.

I am convinced that this peculiar body is homologous with the problematical lobe which is described by Mead ('95) in the egg of *Chaetopterus*, and further, it is probably identical with the polar rings observed by Whitman ('78) in *Clepsine*, and since then by various authors in different annelids.