

*Citation:*

Delsman, H.C., The egg-cleavage of *Vovox globator* and its relation to the movement of the adult form and to the cleavage types of Metazoa, in:

KNAW, Proceedings, 21 I, 1919, Amsterdam, 1919, pp. 243-251

**Anatomy.** — "*The egg-cleavage of Volvox globator and its relation to the movement of the adult form and to the cleavage types of Metazoa.*" By Dr. H. C. DELSMAN. (Communicated by Prof. J. BOEKE).

(Communicated in the meeting of June 29, 1918).

For the zoologist still more than for the botanist *Volvox* is an interesting object. Already in this organism, where it is still dubious whether we have to consider it as a plant or as an animal, we see indicated the main lines along which the phylogenetic development of the Metazoa has taken its course. BUTSCHLI<sup>1)</sup> rightly observes that *Volvox* is no longer to be considered as a colony of Protozoa, but as a pluricellular organism of simple structure. Not only do the cells communicate with each other by plasmodesms, forming thus one single mass of protoplasm, but also there is a difference between mortal somatic and potentially immortal propagation cells as is characteristic of Metaphyta and Metazoa. Between these two *Volvox* holds an intermediate position, reminding one more of the former by the possession of chlorophyll but pointing more in the direction of the animal kingdom by the rest of its organisation.

Long ago the first stage of development in Metazoa, the blastula, has been compared to *Volvox* and was termed by HUXLEY<sup>2)</sup> e.g. "the animal Volvox". The resemblance afterwards appeared to be still greater than HUXLEY could have suspected, for *Volvox* is by no means a homaxone sphere rotating indiscriminately in all directions, but shows a distinct opposition between an animal and a vegetative pole. The line joining them can be described as the main axis of the organism, which is not strictly globular, but a little elongated in the direction of the main axis. With the animal pole directed forwards it swims with a rotary movement round the main axis just as is the case with the pelagic larvae of lower Metazoa and also still of *Amphioxus*. At the animal pole the cells are smaller and further from each other and contain also less chlorophyll than those at the vegetative pole which are darker green, by reason of the higher

<sup>1)</sup> O. BUTSCHLI, 1883—1887, Protozoa II, p. 775, in BRONN's Klassen und Ordnungen des Thierreichs.

<sup>2)</sup> T. H. HUXLEY, 1877. The Anatomy of Invertebrated Animals, p. 123, 678.

proportion of chlorophyll, and communicate by more numerous and broader plasmodesms. The cells at the animal pole each contain a red stigma as characteristic of flagellates sensible to light (to which also the Volvocineae belong), whilst those at the vegetative pole are lacking them. The two kinds of cells pass quite gradually into each other. The propagation cells are restricted to the vegetative half. Any one having an opportunity to study *Volvox* can easily verify all this.

The propagation occurs either by means of egg-cells and spermatozoa, or parthenogenetically by so-called parthenogonidia. The latter mode occurs, just as in Rotatoria and Infusoria, during a number of generations, the former mode at the close of such a period, the encysted egg being the result. The cleavage stages of the egg and of the parthenogonidia in which development proceeds in a similar manner, exhibit again a striking resemblance to those of Metazoan eggs. The figures given of these stages for *Volvox*, *Pleodorina*, *Eudorina*, *Pandorina*, and *Gonium*, remind one especially of stages of the spiral cleavage type, which probably we may designate as the original cleavage type of the Zygoneura or Protostomia, and which is still found with Polyclads, Nemertines, Polychaetous Annelids and most Molluscs. It therefore seemed to me very interesting to find out how far the cleavage of *Volvox* corresponds to the spiral type. The statements made by former investigators appear to be insufficient and too contradictory to answer this question in a satisfactory way<sup>1)</sup>.

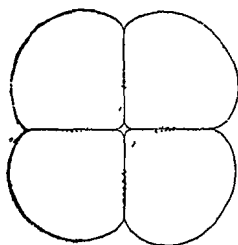


Fig. 1. *Volvox globator*, parthenogonidium, four-celled stage, seen from the vegetative side.

When, therefore, the opportunity presented itself to study more closely the cleavage of the parthenogonidia in *Volvox*, which appeared

<sup>1)</sup> Statements on the cleavage of *Volvox* are found in:

J. GOROSHANKIN, 1875, Genesis im Typus der palmellenartigen Algen. Versuch einer vergleichenden Morphologie der Volvocineae. Mitt. Kaiserl. Ges. naturf. Freunde in Moskau, Bd. 16 (Russian, an extract is found in Botan. Jahresber. f. 1875, p. 27).

E. OVERTON, 1889, Beitrag zur Kenntniss der Gattung *Volvox*. Botan. Centralbl., Bd. 10, p. 177.

L. KLEIN, 1890, Vergleichende Untersuchungen über Morphologie und Biologie der Fortpflanzung bei der Gattung *Volvox*. Ber. naturf. Ges. Freiburg, Bd. 5, p. 15.

to occur in considerable number in the *Victoria regia*-basin of the Leyden botanical garden, I readily seized it. The study was made on living material. During development the parthenogonidium, which continues to communicate by plasmodesms with the surrounding cells, considerably increases in size<sup>1)</sup>, so that the older stages are often easier to study than younger ones, for which the use of oil-immersion as a rule is to be preferred.

By two meridional cleavages the parthenogonidium is first divided into four equal cells, which each will give rise to a quadrant. The eight-celled stage has already been figured repeatedly for *Volvox* and other Volvocinea, but not the transition of the four- into the

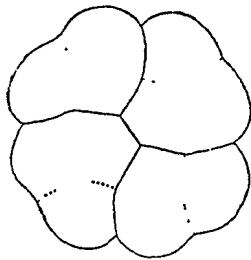


Fig. 2. Beginning of the third cleavage, animal side

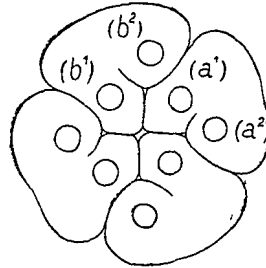


Fig. 3. Transition 4—8, vegetative side

eight-celled stage. Figs. 1, 2, and 3 teach us that during this cleavage a torsion amounting to  $45^\circ$  occurs between what we may call for the sake of shortness the four vegetative cells and the four animal cells. In the terminology of the spiral cleavage type we should call this torsion a dextrotropic one since, if we look at the egg from the side of the animal pole, the four animal cells appear to lie to the right of the four lower cells.

It seemed to me interesting to make out if this third cleavage always takes place in the same way or if, as could equally be imagined, it is sometimes dextrotropic and sometimes laetotropic. In the cleavage of *Balanus*, which shows a similar torsion, I found e.g. both possibilities occurring indiscriminately<sup>2)</sup>. In the spiral cleavage type the third cleavage is always dextrotropic with the exception of inversely wound Gasteropoda where the whole cleavage proceeds in an inverse manner. So not only the adult form but equally the earliest cleavage stages present the reflected image of what we find in dextral Gasteropods.

<sup>1)</sup> All the figures in this article have been drawn the same size.

<sup>2)</sup> H. C. DELSMAN, 1917. Die Embryonalentwicklung von *Balanus balanoides* Linn Tijdschr. Nederl. Dierk. Ver. (2), Dl. 15.

I found that in *Volvox* the third cleavage always proceeds in a dextrotropic manner, and the suggestion lies at hand that here too some peculiarity of the adult form might stand in a certain relation to this phenomenon. What, for example, is the direction in which *Volvox* rotates round the main axis, is this always the same or at one time dextrotropic and at another laeotropic? As has been already observed by earlier investigators and as I can confirm here once more, the rotation always occurs in this way that, seeing it from the animal pole, we may designate it as clockwise, i.e. in the direction of the hands of a clock or dextrotropic. It lies at hand to suggest a relation between these phenomena, as has been stated equally in *Gasteropods*. That in the latter there can be no question of a direct causal relation between the torsion of the adult animal and that of the cleavage cells will be evident at once if we bear in mind that the spiral cleavage type occurs equally well in forms that are not wound at all, as *Lamelibranchiata*, *Chitons*, *Polychaetous Annelids* etc. We will revert to the question whether possibly in *Volvox* we might think of a more direct relation between the torsion during cleavage and the direction of the rotation during movement.

In the eight-celled stage (fig. 4, 5) which has been figured already

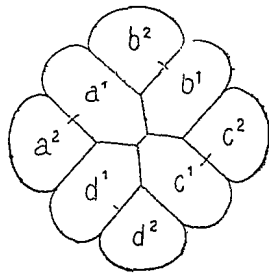


Fig. 4. Stage 8,  
animal side.

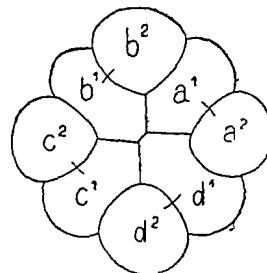


Fig. 5. Stage 8,  
vegetative side.

more than once, the four vegetative cells alternate with the four animal cells. They constitute together a little cell-plate representing phylogenetically the *Gonium*-stage, but which at the border already begins to curve in. This curving in accentuates itself during the transition into the 16-celled stage and in *Volvox* evidently manifests itself somewhat earlier than in *Pleodorina*, *Eudorina*, and *Pandorina*, where also in the stage 16 the cells are still lying in a concave little plate, while in *Volvox* it has then already passed into a hollow globule with an opening, the "phialoporus". The eggs always have the vegetative side, with the phialopore, directed to the surface of the maternal organism.

The passage of the eight- into the sixteen-celled stage, which in the spiral type is always performed by a laeotropic cleavage, is characterised in *Volvox* by a progressive torsion of the cells of the vegetative side with regard to those of the animal side and this in

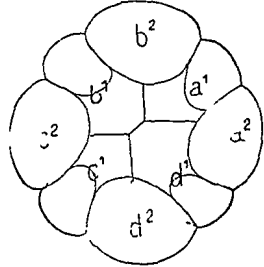


Fig. 6. Beginning of the fourth cleavage, vegetative side.

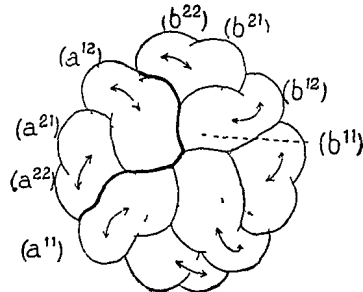


Fig. 7. Transition 8—16, animal side

the same direction in which it has already manifested itself in the foregoing cleavage, which is what we may call dextrotropic. This expresses itself in the shape of the cells immediately when the fourth cleavage sets in, as fig. 6 teaches us. The torsion here has already become a little greater than  $45^\circ$  as becomes evident if we compare the situation of the inferior parts of the vegetative cells ( $a_4$ — $d_4$ ) with regard to the cross of the cleavage furrows at the animal pole. The fourth cleavage (fig. 7, 8), therefore, under the influence of

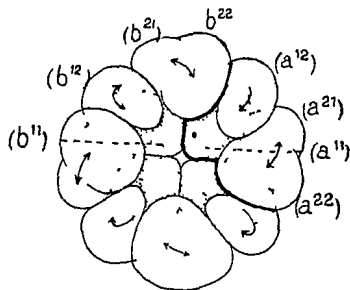


Fig. 8. Transition 8—16, vegetative side.

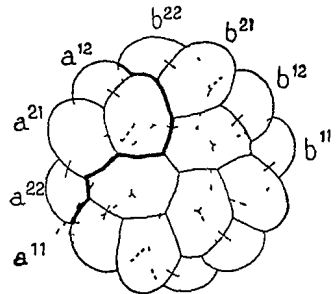


Fig. 9. Stage 16, animal side.

the above torsion, must be described as dextrotropic. For this reason, and in regard to the further cleavage, I think it inadvisable to apply here the nomenclature proposed by CONKLIN for the spiral type, but will modify this a little. I call the cells of the four quadrants resp.  $a$ ,  $b$ ,  $c$ , and  $d$ , and to their descendants I give each time the exponent 1 to the cell that lies to the animal side, and the exponent 2 to that lying to the vegetative side. Thus all the cells with the letter  $a$  are descendants of the cell  $a$  of the four-celled stage, forming

together one quadrant which, moreover, I have surrounded with a thick line in the figures. Now fig. 9 answers wholly to the image presented by a 16-celled stage of the spiral cleavage type, however, one would expect the cells  $a^{11}$ ,  $a^{12}$ ,  $b^{21}$  and  $b^{22}$  to represent together one quadrant. This has been shown not to be the case, and if one takes a view of figs. 8 and 9, the dextrotropic torsion that has occurred during the cleavage, at once strikes the eye. Between  $a^{11}$  and  $a^{22}$  this torsion now amounts to between  $45^\circ$  and  $90^\circ$ . The phialopore is surrounded by the cells  $a^{22}-d^{22}$  and  $a^{12}-d^{12}$ , the former constituting the four longer, the latter the four shorter sides of the octangular phialoporic border. Sometimes one of the cells  $a^{21}-d^{21}$  also reaches the border, the latter then being formed by nine cells.

The fifth cleavage, leading to the 32-celled stage, is again laeotropic, as is shown as well by a view from the animal (fig. 10) as from the vegetative side (fig. 11). Thus the dextrotropic torsion is again

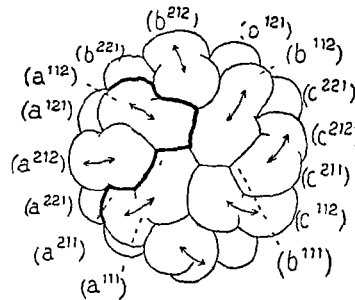


Fig. 10. Transition 16—32,  
animal side.

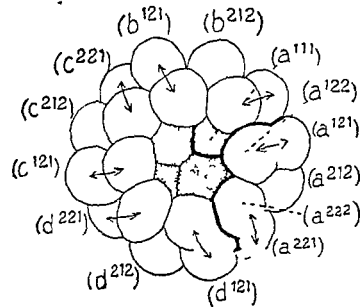


Fig. 11 Transition 16—32,  
vegetative side.

continued here, and as fig. 11 and especially fig. 13 shows, this torsion of the vegetative extremity of each quadrant with regard to the animal extremity (the cell  $a^{111}$ ) now amounts to nearly  $90^\circ$ . While the cell  $a^{212}$  forces itself between  $a^{12}$  and  $a^{22}$ , as was already the case in the 16-celled stage, so that  $a^{221}$  is pushed aside a little (figs. 11, 13),  $a^{12}$  while dividing is pushed to the phialoporic border by  $a^{11}$ , which also divides. As a consequence  $a^{122}-d^{122}$  now form the longer,  $a^{222}-d^{222}$  the shorter sides of the octangular phialopore. Often also all eight sides are of equal length.

The arrangement of the cells in the 32-celled stage is so regular (figs. 12 and 13) that no doubt one would not suspect from it the torsion stated here by watching the cleavages.

The last cleavage studied by me is the one that leads from the 32-celled to the 64-celled stage (figs. 14 and 15). The direction of

the divisions gradually becomes subject to more variation, yet the equatorial direction just as in former cleavages — though with a

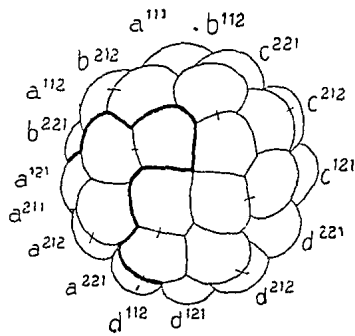


Fig. 12. Stage 32, animal side.

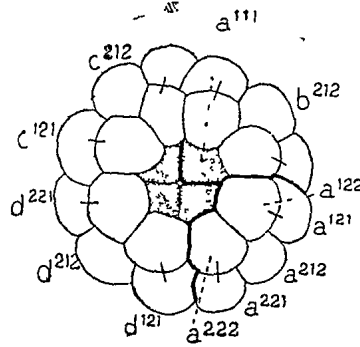


Fig. 13. Stage 32 (the same egg), vegetative side.

deviation caused by the torsion — continues to predominate. That the torsion still proceeds is evident from fig. 15, which shows that it is already more than 90°.

At the beginning of this investigation I almost expected to find that *Volvox* divides according to the spiral cleavage type. The figures given by some investigators seemed to me to point in this direction. No doubt this result would have been interesting with regard to the derivation of the different cleavage types of Metazoa and their mutual relation. A more direct relation between *Volvox* and the lowest forms with a spiral cleavage type would not then appear improbable, since, as shown above, there are other points of agreement. That *Volvox* possesses chlorophyll would be no insuperable obstacle

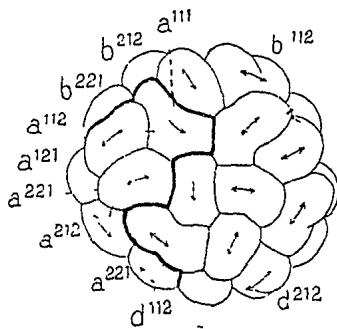


Fig. 14. Transition 32—64, animal side.

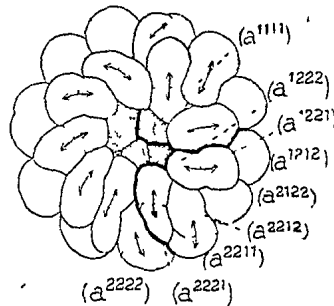


Fig. 15. Transition 32—64, vegetative side.

since it can hardly be doubted that animals must descend from organisms with chlorophyll. No production of organic from inorganic substance would have been possible otherwise.



We have seen, however, that the cleavage of *Volvox* may not be counted as belonging to the spiral type in the form in which it occurs in Metazoa, though the arrangement of the cells is more in a spiral than it is with the latter. Though there are certain points in common I yet refrain from further speculations in this direction.

In another respect, however, the results reached seem to me to be interesting. We have been able to state during the cleavage a progressive torsion of the vegetative cells with regard to the animal cells which becomes especially manifest from a comparison of figs. 2, 4, 7, 9, 10, 12, and 14 and of figs. 3, 5, 6, 8, 11, 13, and 15. So we have every reason to assume that in the adult form also a similar arrangement of the cells prevails. In the spiral cleavage type the succeeding dextrotropic and laetotropic divisions nearly annul the effect of each other, so that in the blastula the cells belonging to one quadrant nearly occupy an area situated between two meridians distant  $90^\circ$  from each other, as is represented fig. 16a. Fig. 16b shows the situation of the cells belonging to one quadrant in the case where the torsion does not surpass  $90^\circ$ . How great the latter has become in the adult *Volvox* cannot be made out. Now in the same dextrotropic direction also the rotation occurs, as we have seen, and it seems to me probable that in this case we may look for a more direct relation between the two phenomena than with the torsion of Gasteropods. Let us assume to this end that not only the colony but also each of the cells of *Volvox* has a certain polarity and thus a main axis in the direction from the animal to the vegetative pole of the colony. This polarity of the cells e.g. manifests itself in the corresponding direction in which all the flagella beat causing a water current from in front backwards, which makes the organism move

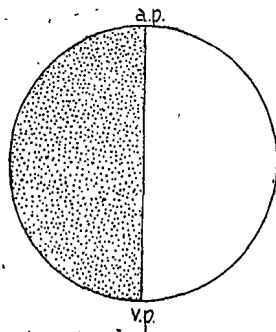


Fig. 16a.

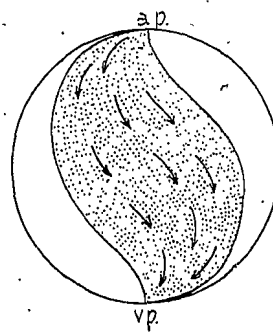


Fig. 16b.

in the direction of the animal pole. If a *Volvox* be pressed between a cover-slip and an object-slide so that it cannot move anymore, this

water current can easily be demonstrated by watching the little particles suspended in the water. If further we assume that by the dextrotropic torsion, during the cleavage the direction of the main axis of the cells undergoes a dextrotropic deviation and the flagella thus beat in the direction of the arrows in fig. 16b, then the dextrotropic rotation of the colony follows directly from this assumption. That indeed the flagella beat in this way needs no further proof, but follows from the rotation itself.

It would be interesting no doubt if a variety of *Volvox globator* rotating to the left, were discovered. It can hardly be expected otherwise than that the cleavage here will equally belong to the inverse type.

Have we accounted now for the rotating movement of *Volvox* by the torsion presenting itself during the cleavage? In a causal sense we have, if our suggestion is right. But how is the torsion of the cleavage cells to be accounted for? Phylogenetically now I should feel inclined to consider the torsion during the cleavage rather as a consequence of the rotation of the adult animal than as its cause. The study of ontogeny ever anew teaches us that we must not consider the structure of the adult animal phylogenetically as a product of the developmental processes, but we rather must account for the latter by the structure of the adult animal. Thus I would see also in the torsion during the egg cleavage of *Volvox* nothing but a very precociously appearing character of the adult form related to the movement of the latter. This character, which cannot be demonstrated in the adult form, could be revealed only by the study of its development.

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