CHAPTER III

MULTIPLICATION BY FISSION

1. PRELIMINARY REMARKS

UNTIL a short time ago the process of multiplication by gemmation was looked upon as having been derived phyletically from the corresponding process by fission, and the two were thought to be closely related, and connected by gradual transitions. Von Wagner * has, however, recently attempted to contest this opinion, and to show that the two processes should be more distinctly separated from one another than they have hitherto been, and that they are, in fact, genetically distinct. By the term (fission), Wagner means to indicate a process of multiplication which is preceded by a symmetrical growth of the parent organism, by means of which the individuality of the latter becomes changed and to a certain extent abolished: the term (gemmation), on the other hand, he takes to mean a process of multiplication which is preceded by an unsymmetrical (differential) growth of the parent organism, in which the individuality of the latter is not abolished and its place taken by a new individual.

This view I agree with in so far as I am convinced that in multicellular organisms the processes of multiplication by fission and budding have not arisen *genetically* from one another: these processes differ so essentially that it will be advisable to discuss them separately.

Following von Wagner's example, I shall include under this head of fission all the processes of asexual multiplication which occur in the flat-worms (*Turbellaria, Cestoda*), the annelids proper (*Syllidæ, Naidæ, Tubificidæ,* &c.), and also in the higher Medusæ (strobilation). In all these cases multiplication is effected by the division of the parent animal into two or more

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* Franz von Wagner, 'Zur Kentniss der ungeschlechtlichen Fortpflanzung uon Microstoma nebst allegemeinen Bemerkungen über Thielung u. Knospung im Thierreich,' Zool. Jahrbücher, Abth. f. Anat. u. Ontogenie, Bd. iv., Jena, 1890.
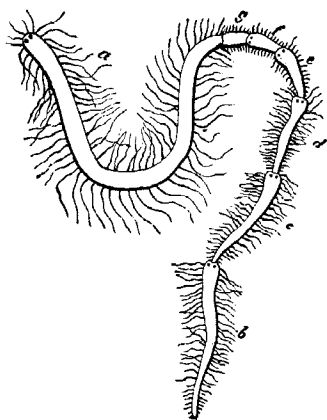
Fig. 4. — *Myrianida*, a marine worm which multiplies by fission (after Milne-Edwards, from Hatschek's ' Lehrbuch der Zoologie '). The letters *a—g* indicate the relative ages of the daughter-individuals resulting from the division of the parent.

parts : this therefore necessitates a regeneration of one or of the other end of the body, or even of both ends. This process may begin to take place either after (*Lumbriculus*) or before the division has taken place, and in the latter case is more or less complete before the fission begins. The actual process of the formation of the new organism is essentially the same in both cases, and important differences only occur as regards the various groups of animals.

We are particularly well acquainted with these processes of regeneration — which may either precede or succeed fission — in the case of various kinds of worms, and we will therefore first illustrate them in their main features by reference to these animals.

2.   The Process of Fission in the Naidæ

The process of fission in these small fresh-water segmented worms has been very accurately followed out by Semper. An individual undergoes division into two, or usually into several, daughter-individuals at the same time, the fission being regularly preceded by a circular growth of cells taking place around the circumference of the body at one or more definite regions, each of such ring-like thickenings eventually giving rise to a new head- and tail-end respectively. These rings of cells have hitherto been spoken of as ' zones of gemmation ; ' but it would be better to call them ' zones of regeneration,' as they are not concerned with budding in the true sense of the word. Two of these rings are as a general rule formed in each animal, and when the anterior and posterior ends of each of the resulting three sections are fully developed, the separation into the corre-

sponding three daughter-individuals takes place by a construction in the middle of each zone of regeneration.

In *Nais* the zones of regeneration are always formed at the boundary line of two segments: that is to say, they arise from the contiguous margins of two segments, in the following way. Cells of the epidermis first begin to multiply, and give rise to a circular layer of small stratified cells, which is thickest on the ventral side. The cells have at first no definite histological character. At the same time an increase in the length of the internal organs takes place: this is rendered necessary by the growing zone penetrating between the segments from which it arises and thus forcing them apart. The alimentary canal, however, is the only internal organ which becomes regenerated from its own cells: all the other new formations, including the ventral nerve cord, muscles, blood-vessels, 'liver'-cells, and excretory-organs, are developed from the ring of proliferating epidermic cells.

As Semper has pointed out, the process of the reconstruction of the anterior and posterior ends which prepares the way for fission, may in a sense be compared with the embryonic development of the animal subsequent to the gastrula stage, in which the two primary germinal layers are already distinct.

In these regenerative processes two layers of formative cells are likewise produced, owing to the proliferation of the ectoderm cells on the one hand, and those of the alimentary canal on the other; the epithelial lining of the latter only is formed from the internal layer, the outer layer giving rise to all the other organs, including the mesodermic structures as well as those which belong to the ectodermic part of the integument. In fact the resemblance between the processes which take place in embryogeny and in regeneration is so close, that in both cases the mesoderm becomes split off from the mass of formative ectoderm cells in the form of two longitudinal bands, from which the blood-vessels, muscles, &c., are then differentiated.

In order to explain these processes theoretically from our point of view, we must suppose that those cells of the epidermis from which the formative cells arise possess an '*accessory idioplasm*,' containing the determinants of those organs which are formed from them in regeneration in addition to their own specific idioplasm. The rate of division of each of these cells. as well as the manner in which the groups of determinants con-

tained in them becomes disintegrated in the course of the sub-
sequent divisions, is strictly definite, and determines the number
of successors which each cell produces, as well as the relative
position and combination into organs, and histological differen-
tiation of the cells. When the process of proliferation begins,
the newly-formed cells no longer retain the specific epidermic
character, and their successors may, indeed, be said to possess
an 'embryonic character,' in the sense in which that term has
usually been used, — if it is not thereby understood that they
must all contain similar primary constituents. Their further
development shows that this cannot be so: the cells of one
particular region give rise, for instance, to the dorsal vessel;
those of another to the nerve-cord; those of a third region to
certain muscles, and so on.

We must therefore suppose that the various epidermic cells
of the parent animal are pro-
vided with active accessory
idioplasm, somewhat in the
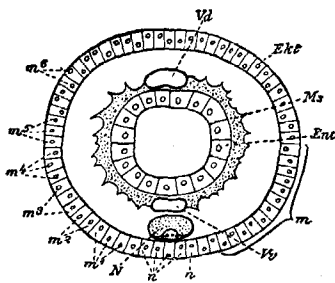manner I have indicated in
the accompanying diagram.
The cells marked n, for in-
stance, would contain the
groups of inactive determi-
nants for the formation of the
ventral nerve-cord; those of
the epidermis marked m,
groups of determinants for
the mesoderm structures, in
addition to their own proper
idioplasm, — m^1 containing
those for the lateral muscles,
m^2 those for the ventral
blood-vessel, m^3 those for the
'liver-cells' and mesodermic
part of the intestine, m^4 those

FIG. 5. — Transverse section through a Nais
in the region of the zone of regeneration
(modified from Semper): Ekt, Integu-
ment; Ent, Epithelium of the ali-
mentary canal; N, Nerve-cord; Ms,
Visceral mesoderm; Vd, Dorsal blood-
vessel; m, Cells with accessory deter-
minants for the mesoderm; n, Cells
with accessory determinants for the
nerve-cord.

for the segmental organs and the adjacent system of muscles,
m^5 those for the dorsal vessel, m^6 those for the dorsal muscles,
and so on. For the sake of simplicity I have supposed that the
epidermis consists of only *one* layer of cells, although in reality
there are two layers in many parts: the diagram, in fact, is not
by any means intended to represent the actual structure of the

animal in detail, or even to indicate accurately the part which the individual cells take in the process of budding.

The question of the *origin of the supplementary determinants* which we have assumed to exist in the cells of the epidermis, does not stand in the way of this explanation of the regenerative process; for, as already stated, a similar course is in the main followed both in embryogeny and regeneration. In both processes the primary mesoderm arises from the primary ectoderm. The definitive ectoderm cells have therefore an opportunity during their embryonic development of taking over certain primary mesoderm determinants as accessory idioplasm from the primary ectoderm cells : these can then become separated into several groups during the multiplication of the ectoderm cells, so that the epidermic cells around the circumference of the body are provided with an accessory idioplasm consisting of various mesoderm determinants.

It must, however, also be borne in mind that the growth in length of the worm only takes place at the posterior end of the body, just as occurs in the regeneration which prepares the way for division. In both cases a new body-segment is formed between the last segment and the last but one, in which process the epithelium of the intestine alone arises from the endoderm, the integument and all the mesodermic structures being formed from the ectoderm. Thus the accessory determinants which we have assumed to exist in the epidermic cells, and which render the subsequent regeneration possible, are not derived from the embryo directly, but from the zone of growth in the tail-end, into which again they have passed during embryogeny.

3. THE PROCESS OF FISSION IN THE MICROSTOMIDÆ

It is not, then, in the nature of every ectoderm cell to give rise to all the possible kinds of cells and organs with the exception of the epithelium of the alimentary canal: each one must be specially equipped for the purpose. This is proved by the fact that the ectoderm by no means always performs this function in animals which multiply by fission : even in some worms this is not the case.

According to von Wagner's * excellent researches, the cells of the epidermis in a certain flat-worm, *Microstoma lineare*, take

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* *Loc. cit.*

a very small share in the reconstruction of the anterior and posterior ends of the animal during the process of fission, the restoration being effected in this case chiefly by the mesoderm, or so-called 'connective tissue' cells, which 'are suspended in large numbers in the perivisceral fluid between the supporting trabeculæ.' These cells begin to increase in number when the animal is preparing for division, and by their multiplication they form a ventral mass of so-called 'embryonic' cells, which gives rise to the pharynx, the pharyngeal and prostomial glands, all the parts generally known as 'parenchymatous' or 'mesodermic structures,' and also apparently to certain parts of the nervous system. Kennel * found that a similar mode of development of these parts occurs in a Planarian. In such cases we must therefore suppose that the accessory determinants required for regeneration are supplied to the mesoderm cells, instead of to those of the ectoderm. We cannot at present determine whether this is effected by each of these cells being provided with all the supplementary determinants for the mesoderm, which only become disintegrated and distributed amongst the other cells when these begin to multiply, or — as we assumed in the case of the ectoderm cells of *Nais* — by the distribution of the different determinants to a number of these cells *before* proliferation occurs.

The regularity with which all organs are formed in the proper position and mutual relation, may perhaps be taken as a proof of the assumption that they contain latent determinants which are from the first separate, and which differ according to the topographical position of the organ. It is hardly possible that the contrary assumption can be the correct one, for this would render it necessary to suppose that although all the determinants are certainly present in every formative cell, only that one can undergo development which corresponds to the region in which the cell happened to be situated.

Here, again, we meet with no serious difficulty as regards the derivation of the required supplementary determinants in ontogeny: in fact there is less difficulty in this case than in that of *Nais*, for the cells of the different layers of the body contain the determinants for the *corresponding* organs.

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* J. Kennel, ' Untersuchungen an neuen Turbellarien,' Zool. Jahrbücher, Bd. 3. Abth. f. Anat. u. Ontog. d. Thiere, p. 447.

4. THE PHYLOGENY OF THE PROCESS OF MULTIPLICATION BY FISSION

There can be little doubt that the process of spontaneous division which occurs in flat-worms and in annelids is to be derived phylogenetically from regeneration, as Kennel* has recently attempted to prove. He has rightly, I believe, shown that multiplication by a spontaneous separation into parts, such as occurs regularly in the freshwater worm *Lumbriculus*, must be looked upon as a preliminary stage of that kind of fission, accompanied by regeneration, which occurs in the *Naidæ*, for instance. The difference between the two processes consists essentially in the fact that in *Nais* the separation into parts is preceded and prepared for by the formation of new head- and tail-ends, which appear between the old segments at the point at which the separation is to take place. Such a preparatory process does not occur in *Lumbriculus :* the region in which division will take place in this worm cannot previously be distinguished, and the new head- and tail-ends are formed subsequently, after the division has occurred.

The capacity for division of an individual into parts must naturally be looked upon as an adaptation, and it presupposes some kind of histological and physiological arrangement of which we are at present ignorant. It is, however, quite conceivable that when fission had once occurred in a species, it may have been advantageous for a more thorough preparation for the process to take place, and for the structures necessary for the completion of the individuals thus formed to become developed beforehand. Such a capacity for multiplication by spontaneous division necessitates, moreover, the previous possession of the power of regeneration. Hence the latter must have existed in the animal before spontaneous division could take place regularly in the species, and we must thus conclude that the capacity for regenerating portions of the body which had been accidentally torn asunder was first acquired very early in the philogeny of multicellular animals ; and that the special arrangements for multiplication by fission subsequently originated from this capacity for regeneration, and was followed by the formation of new head- and tail-ends. The formation of the new parts pre-

* J. Kennel, ' Uber Theilung u. Knospung der Thiere,' Dorpat, 1888.

viously to the division must be looked upon as a still later modification of the process.

This conclusion receives further support from the fact that, as already shown, the capacity of regeneration is not by any means an inherent quality of the organism: that is to say, it is not a direct and inevitable result of a particular degree of organisation, but is due to an adaptation produced by natural selection, and constitutes a special arrangement which may exist in different degrees of perfection, or which may, again, be entirely absent. If an earthworm is cut into two, the anterior portion develops a new tail-end, but the posterior portion does not give rise to a new head-end: the arrangement existing in *Lumbriculus* and *Nais* is therefore absent in this case. This fact I should explain by assuming that in the last-named animals the determinants required for the formation of the head-end are supplied to the cells of the integument and alimentary canal as accessory idioplasm, while in the earthworm these cells only possess the determinants required for the formation of the tail-end.

It is very possible that the arrangement for the regeneration of the tail-end may have taken place more easily than that for the restoration of the head in the case of segmented worms, owing to the fact that the last segment possessed the power of giving rise to entire new segments. The growth of the animal is effected by the formation of new segments at the posterior end of the body, which would therefore be already provided with the requisite accessory determinants, and it would then only be necessary that these should be transferred to the corresponding cells of the other body-segments. This might have taken place in a relatively simple manner in the course of philogeny, by a portion of the accessory determinants being left in the cells of each new body-segment as it became formed. The determinants of the head-end, on the other hand, can only have been supplied to the respective cells as accessory idioplasm before or during embryonic development; we can therefore understand why the capacity for forming a new head-end was only acquired later, and that some worms are able to regenerate the posterior, but not the anterior end by the body when it is cut in half.

We can therefore trace a series of stages of gradually increasing complexity in the development of the process of regenera-

tion in worms, beginning with the formation of segments at the growing tail-end, and then passing from the regeneration — first of the tail, and then of the head-end, to the actual fission of *Lumbriculus*, and finally to that of *Nais*. And according to our view, this course of development depends on the regular distribution of certain accessory determinants to particular tissue-cells, and the gradual increase in the complexity of this distribution.

The regenerative process which renders fission possible must be traced to the doubling of certain groups of determinants in the idioplasm, so that the half of them remain latent. I imagine that this doubling need not necessarily take place and be followed by the subsequent multiplication of the inactive groups of determinants in the germ-plasm itself: such a multiplication would, in fact, be a useless encumbrance to the germ-plasm. The latter need only contain the determinants for fission when this process leads to an alternation of generations; that is to say, when the animals formed by division have a different structure from those which arise directly from the ovum : for in the latter case the forms which arise by fission are independently variable hereditarily. This must be the case in the alternation of generations in certain marine annelids, such as the *Syllidæ*, and also in the strobilation of polypes, which will be discussed later on. In all such cases, two kinds of ids must be assumed to exist in the germ-plasm. In the ordinary kind of fission which occurs in the fresh-water annelids, on the other hand, the separation of the groups of determinants necessary for the regeneration of a part may take place during embryogeny: nothing definite, however, can be said on this point at present, but in any case the process of splitting off of the accessory determinants may conceivably be thrown back from the later to the earlier stages of ontogeny, until it finally takes place in the fertilised ovum, so that double ids are present in the germ-plasm. It will be assumed in the next section that certain forms of budding owe their origin to the presence of these double ids.