

## CHAPTER IV

## MULTIPLICATION BY GEMMATION

## I. THE PROCESS OF GEMMATION IN ANIMALS

IF, with von Wagner, we look upon gemmation as 'a process in which entire individuals are formed anew,' and which depends 'exclusively on a special (differential) growth differing from the normal one,' we must include under this term the processes of asexual multiplication which occur in most of the *Cœlenterata*, the *Polyzoa*, and the *Tunicata*.

*A. — Cœlenterata*

Hitherto it has been considered that we were fully acquainted with the process of gemmation in the *Cœlenterata*, especially in the case of the *Hydrozoa*. It had been observed that the two layers of cells which form the body-wall of these animals are present even in very young buds of Medusæ and Hydroid-polypes. These layers surround the digestive-cavity just as they do in the parent animal, and since the body-wall as well as the cavity it encloses are in direct connection with those of the parent, nothing was more natural than to suppose that the bud arises as an *evagination of the body-wall of the parent, both layers of the latter taking part in its formation from the first*. A doubt as to the correctness of this statement was less likely to arise owing to the fact that even in the youngest buds of a Hydroid-polype, before they become hollow, the ectoderm and endoderm were seen to consist of a number of cells engaged in active multiplication. I myself made such a statement in connection with my investigations on the formation of the sexual cells in Hydroids,\* and no doubt has yet been raised as to its correctness, or rather as to its interpretation.

The assumption that both germinal layers of the parent take part in the formation of the bud is nevertheless an incorrect one; *for the bud arises from the ectoderm only, and the young cells*

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\* 'Die Entstehung der Sexualzellen bei den Hydromedusen' (with 25 plates), Jena, 1883.

which form the endoderm in these buds are not derived from the endoderm of the parent, but have migrated from the ectoderm.

Purely theoretical considerations first led me to suppose that *this must be so*. The origin of the process of gemmation in the idioplasm can only be brought into agreement with the theory of the continuity of the germ-plasm, if the cells of the parent-*organism from which buds arise collectively* contain all the determinants of the species as accessory idioplasm. If this were not the case, an entire animal, capable of reproduction, could never arise from the bud. If, now, a certain cell of the ectoderm contained all the determinants for the outer, and one of the endodermal cells all those for the inner layer, a bud could only be formed when these two cells happened to lie exactly opposite to *one another in the body-wall*. As, however, the endoderm cells form a definite and continuous epithelial layer, and have a fixed relative position, and, moreover, the position of the ectoderm cells, although not quite so definite, is still on the whole a fixed one, I found it difficult to imagine how budding could take place at perfectly definite parts of the polype and of the stock in such a regular manner as actually occurs in many cases. The assumption that *all the cells of the ectoderm and endoderm are equally* provided with the necessary accessory idioplasm is excluded by the fact that budding occurs in such a regular manner. I am therefore led to suppose that the distribution of the 'blastogenic \* germ-plasm' might possibly be confined to *one* germinal layer only; and since it is known that in Hydroids the germ-cells are always developed from the ectoderm, it is natural to conclude that the *blastogenic idioplasm is contained in the cells of this layer*.

This conclusion has now been confirmed by investigations carried out by Mr. Albert Lang, in the Zoological Institute at Freiburg. In various Hydroid-polypes (*Eudendrium*, *Plumularia*, and *Hydra*) the bud arises in the following way. The cells in a certain small circumscribed region of the ectoderm first begin to multiply, the 'supporting lamella,' which separates the two layers of the body-wall, *gradually becoming thinner and softer* at the same time, and then a few of the newly-formed cells penetrate into the endoderm through this membrane. Here they

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\* The term 'blastogenic idioplasm' is here used in the special sense of 'Knospungs-Idioplasm,' and not in the more general sense in which it is usually used by the author (cf., e.g., the chapter on 'The Supposed Transmission of Acquired Characters').—W. N. P.

form a layer of young actively dividing cells, such as I had formerly observed in very young buds: this layer forces the older endoderm cells away from the supporting membrane, in consequence of which they loosen their connection with the rest of the endoderm, undergo disintegration, and gradually become absorbed. The cells, however, which have migrated from the ectoderm then give rise to the endoderm of the bud.

Now that these facts have been proved by Lang's investigations,\* it is easier to give a theoretical explanation of the process

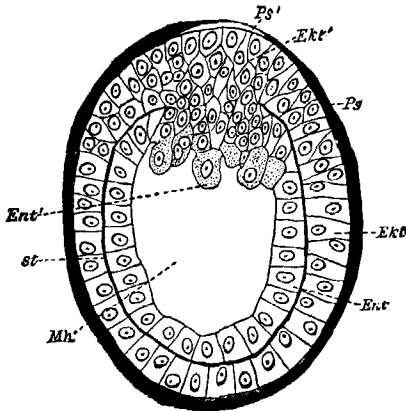


FIG. 6. — Diagrammatic section through the rudiment of a bud of *Eudendrium*. (Modified from a figure by Albert Lang.) *Ps'*, the horny perisarc; *Ps*, portion of the perisarc which has become very thin owing to the proliferation of the underlying ectoderm (*Ekt'*); *Ent'*, the region of the endoderm, in which a number of proliferating ectoderm cells have broken through the supporting lamella (*st*), migrated into the endoderm, and caused the latter to project into the gastric cavity.

of gemmation in Hydroids. We must, however, still assume that certain cells and series of cells in the ectoderm are provided with an accessory idioplasm, which contains all the determinants of the species, and which is therefore a kind of germ-plasm, though perhaps not quite identical with the germ-plasm proper:

\* Albert Lang, 'Ueb. die Knospung bei Hydra u. einigen Hydropolypen,' Zeitschr. f. wiss. Zool., Bd. 54, 1892, p. 365.

I therefore speak of it as 'blastogenic idioplasm.' It cannot be stated with certainty *which* cells of the ectoderm contain this idioplasm; it seems, however, that the growth of the bud originates in the deeper layer, *i.e.*, in the 'interstitial' cells. We may therefore suppose that some of these interstitial cells contain inactive blastogenic idioplasm, which, after a certain series of cell-divisions necessary for the growth of the polype, obtains the control of one of the offspring of these cells, and so causes budding to take place. Each bud must originally arise from *one* cell only, although this fact has not as yet been actually proved; and in the first division, or at any rate in the early divisions of this cell, the group of determinants of the ectoderm must become separated from that of the endoderm, the 'bearers' of the latter group migrating into the old endoderm through the disintegrating supporting lamella. The remaining details of the process require no further explanation.

*In the Hydromedusæ, then, each bud originates in a single cell,* and the process of multiplication by gemmation therefore differs essentially from that of reproduction by fission. For gemmation owes its origin to the entire mass of the determinants of the species, which only undergo disintegration at a later stage; while the new structures which arise by fission originate simultaneously from numerous smaller groups of determinants, corresponding with those of the later stages of ontogeny.

We should nevertheless be mistaken in supposing that the essential difference between fission and gemmation is due altogether to this difference as regards the group of determinants concerned in the two processes. This is rendered evident by a comparison with the processes of budding in other groups of animals. It still remains to be shewn whether the process of gemmation in other Cœlenterates, *viz.*, in the *Actinozoa*, the higher *Medusæ*, and the *Ctenophora*, also only apparently originates from both layers of the body-wall, or whether it actually arises from *one* layer only. As the possibility of the latter mode of origin has not till now been considered, it is very possible that the migration of cells may have been overlooked in this case also.

If we now turn our attention to the other groups of the animal kingdom in which gemmation occurs, *viz.*, to the *Polyzoa* and *Tunicata*, we shall find that we possess the results of very excellent investigations on which our arguments can be based; and the histological structure of these animals is such as to render

it unlikely that any oversight as regards the migration of cells can have occurred.

### B.—*Polyzoa*

The small stocks or colonies formed in the *Polyzoa* arise by a process of gemmation; and even the small number of species which do not form stocks multiply vigorously by budding, but in these cases the buds become detached from the parent sooner or later.

The process of gemmation seems to be essentially similar in all *Polyzoa*. A proliferation, which primarily originates in *one* cell, takes place in a certain region of the epidermis; the masses of cells which are thus produced form a hollow invagination, which extends into the body-cavity of the animal and gives rise to the entire alimentary canal—including the fore-, mid-, and hind-guts, as well as to the preoral 'atrium' with the tentacles ('lophophore'). Certain 'free mesoderm cells' are then said to migrate from the body-cavity of the parent into the bud, in which they give rise to the muscles and sexual organs, and also in certain groups of *Polyzoa* to the outer (serous) layer of the intestine; while in others again they form a subcutaneous layer of cells. This is at any rate the case according to the recent observations made by Seeliger,\* which are undoubtedly very accurate and trustworthy. But one point, however, still seems to be doubtful, viz., whether the sexual organs may not perhaps, after all, arise from the primary proliferation of the epidermic cells.

These processes of gemmation interfere very considerably with the ordinarily accepted and extremely conventional ideas of the germinal membranes; for the epithelium of the alimentary canal, which characteristically belongs to the inner germinal layer, here arises from the ectoderm. This, however, causes no difficulty from the point of view of the theory of the germ-plasm: we need only assume that the group of determinants for the endoderm is passed on to certain cells of the epidermis as accessory idioplasm. This transference must take place at an early stage in embryogeny, before the separation of the primary endoderm and ectoderm occurs.

Nitsche, whose means of observation were comparatively im-

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\* O. Seeliger, 'Die ungeschlechtliche Vermehrung der endoprokten Bryozoen,' and 'Bemerkungen zur Knospenentwicklung der Bryozoen,' Zeitschr. f. wiss. Zool., Bd. 49 and 50, 1889 and 1890.

perfect, but whose researches are nevertheless of great value, concluded that the *whole* bud was derived from the proliferation of the ectoderm. Had his statement proved correct, the explanation of the process of budding in the Polyzoa, based on the idioplasm, would be just as simple as in the case of Hydroids: it would then only have been necessary to suppose that the cell in which proliferation first began contained accessory idioplasm in the form of 'blastogenic idioplasm.' Seeliger was, however, unable to support Nitsche's statements, and the most recent observations of Oka,\* Davenport,† and Braem,‡ prove beyond doubt that the 'mesoderm cells' of the parent take part in the formation of the buds. We must therefore suppose that certain mesoderm cells, provided with definite groups of determinants for muscles, endothelia, and sexual organs, migrate into the bud. It is quite conceivable that muscles, and more especially endothelia, should be developed in this manner, but it would be difficult to understand how free cells from the body-cavity of the parent could migrate into the bud, and there give rise to sexual organs at *perfectly definite regions*: were this so, we must suppose that in reality *certain* of the cells only, and not *any* of them, are concerned in the migration. Such an assumption is, however, contradicted by the abnormal processes of budding which occur, for instance, in *Pedicellina*. I therefore do not consider that the question of the origin of the sexual organs is yet decided, but I suspect, nevertheless, that one or two of the mesoderm cells of the bud are derived from the primary proliferation of the ectoderm. This view is supported by Seeliger's statement that he considers such a derivation of individual mesoderm cells of the bud possible, at any rate, in the case of *Loxosoma*.§

As, however, we are not specially concerned with the process of budding in the Polyzoa in particular, but are only making

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\* A. Oka, 'Observations on Freshwater Polyzoa, Journ. of College of Science, Imperial University, Japan, Vol. iv., Pt. 1, 1890.

† C. B. Davenport, 'Observations on Budding in Paludicilla and some other Bryozoa,' Bull. of the Museum of Comp. Zool. at Harvard College, Vol. xxii., No. 1, 1891.

‡ F. Braem, 'Untersuch. über d. Bryozoen des süssen Wassers, Bibl. Zool., Cassel, 1890.

§ Seeliger, 'Bemerkungen zur Knospentwcklung der Bryozoen, Zeitschr. f. wiss. Zool., Bd. 50, p. 564.

use of it as an example of gemmation in which two germinal layers are primarily concerned, we can leave this question aside. It is at any rate true that in the Polyzoa parenchymatous cells, as well as a certain ectoderm cell, take part in each process of budding. We must therefore assume that the determinants of the species cannot be contained altogether in *one* cell as blastogenic idioplasm, as in the case of the Hydrozoa, but that a number of them — including those for the muscles, endothelia, blood-corpuscles, and perhaps those for the sexual organs also — are supplied to certain mesoderm cells of the parent. The development of sexual cells renders it necessary that those cells from which they arise shall also contain germ-plasm; and the formation of the epidermis of the bud, which results to some extent on purely mechanical grounds, presupposes the existence of determinants for the ectoderm in the epidermic cells of the parents.

The disintegration of the determinants, which is necessary before budding can take place, is obviously, however, of a very different kind from that which occurs in embryonic development. Seeliger, indeed, has called attention to the fact that the ontogeny which results from gemmation is a much shorter process than that which occurs when an embryo and larva are formed. In the former case, not only are the whole series of stages of segmentation and development of a free-swimming larva absent, but even in the later periods of development none of the stages in embryogeny and in gemmation exactly correspond to one another. Without following out these two processes in detail, I should be inclined to explain them in general by assuming that the groups of latent supplementary determinants, with which certain cells are provided in the course of embryogeny, contain combinations of determinants different from those which lead to the development of the embryo.

### C. — *Tunicata*

The fixed Ascidiæ usually multiply very extensively by gemmation, and thus give rise to stocks, the individual persons of which are more or less closely connected with one another.

We owe our detailed knowledge of the process of budding in the genus *Clavelina* to the researches of Seeliger.\* The

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\* O. Seeliger, 'Zur Entwicklungsgeschichte der Ascidiæ; Eibildung u. Knospung von *Clavelina lepadiformis*,' Sitzungsber. d. Wien, Akademie, Bd. 85, 1882.

parent, which was developed from an ovum, produces long stalk-like processes or stolons, on which new animals are produced by budding. Each of these stolons is made up of three layers of cells—an outer ectoderm, an inner endoderm, and an intermediate layer of motile ‘mesoderm cells.’ The ectoderm layer gives rise merely to the epidermis of the bud; the epithelium of the alimentary canal and its accessory organs, the branchial sac (‘peribranchial tube’), and the pericardial tube, being developed from the endoderm; and the muscles, ganglion (?), and sexual glands from the ‘free mesoderm cells.’

The endodermal tube mainly determines the form of the animal in these processes: it becomes definitely segmented, and on it the growing ectodermal tube is moulded, so to speak. We may thus conclude that a series of homologous formative zones of structure are to be found in the endodermal tube of the stolon, each of which may consist originally of a *single* circular layer of cells. At the point where a bud will arise, the corresponding zone of cells grows out to form a bladder-shaped enlargement, which becomes detached from its point of origin on the endodermal tube of the stolon and regularly differentiated, so as to give rise to the peribranchial tube, the intestine, and so on. The cells of this endodermic vesicle cannot all be equivalent, nor can they contain exactly similar determinants: were that the case, such a differentiation could not occur, and the walls of the peribranchial chamber could not arise from one part, and the intestine from another. But even as regards the primitive intestinal vesicle itself, one cell must contain the determinants of the stomach, another those of the hind-gut, and so on. In short, we must assume that—just as occurs in principle, if not as regards actual details in the case of embryogeny—*a disintegration of the idioplasm and a distribution of the groups of determinants among the different cells takes place during development.* The determinants of all parts arising in connection with each endodermal vesicle, must be collectively contained in each zone of cells of the endodermal tube from which such a vesicle is developed.

The formation of those organs which arise from the ‘free mesoderm cells’ of the stolon is the most difficult to understand. There is certainly no reason why we should not suppose that these cells contain very different kinds of idioplasm: one, for instance, might contain ‘muscle-determinants,’ another ‘nerve-



determinants,' and a third 'blood-corpuscle determinants.' Various kinds of these cells may easily be distinguished while they still float freely in the blood of the stolon. The difficulty only consists in ascertaining the *exact* part they play in the formation of the developing bud. Those which are to give rise to the longitudinal muscles become arranged in rows, which, diverging obliquely from one or two definite points, extend over the animal from behind forwards, and are attached at more or less definitely fixed points anteriorly. The ganglion and the sexual glands have also perfectly definite positions in the animal. In embryogeny, as well as in the development of the endodermal vesicle of the bud, the position of every cell is assigned to it mechanically, in consequence of its origin from previous cell-generations,—that is, by the rhythm of the cell-divisions. In the case, however, of the ganglion for instance, the cells of which it is composed must come together at the right place by means of their power of locomotion. A similar process is known to occur in embryogeny in the case of several groups of animals, such as the *Echinodermata*, for instance; and until we know more of the actual facts concerned, we can only—however unsatisfactory such an assumption may be—attribute to the cells a tendency to become attached at definite points according to the manner in which they have previously been determined. The reverse assumption—that these cells develop into muscle-, nerve-, or sexual-cells according to their point of attachment—seems to me at any rate a less likely one.

If we compare the processes of gemmation and embryogeny in Ascidians, important differences are seen to exist between them. In the former, all the stages of segmentation of the egg and gastrulation, together with the formation of the mesoderm, are omitted; and many parts, again, arise from the ectoderm in the embryo and from the mesoderm in the bud. These differences are perhaps still more marked in the free-swimming *Salpæ*. These animals also multiply by buds produced on a kind of stolon; and, as in the other Ascidians referred to, the ectoderm forms practically nothing except the epidermis, and the endoderm gives rise to only a few structures, by far the greater number of parts arising from the 'mesoderm-cells.' Seeliger\* explains this by supposing that 'the mesoderm

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\* Seeliger, 'Die Knospung der Salpen,' Jena, 1885.

of the mother-animal which passes into the buds, practically corresponds only to the future sexual apparatus.' This, however, can merely be taken as an explanation of the fact in so far as it indicates the possibility of the 'mesoderm cells' of the stolon and bud containing the groups of determinants required for these different structures. For *all* the determinants must be present in the sexual cells, and, owing to their disintegration during cell-division, they may become arranged in very varied groups, so that certain mesoderm cells may become furnished with one group and others with another. This certainly presupposes that the process of the distribution of the determinants in this case is entirely different from that which takes place during embryogeny, and this difference, again, can only depend on a difference in the original architecture of the idioplasm. In discussing the process of alternation of generations I shall once more return to this point, which, from a theoretical point of view, is a very fundamental one.

## 2. THE PROCESS OF GEMMATION IN PLANTS

Our conception of the process of gemmation has been in the first instance derived from the vegetable kingdom: all the higher plants correspond to stocks or corms which arise by copious and regular budding, much as occurs in the case of such animal-stocks as those of the Hydrozoa, for instance. Although the physiological individuality of separate 'persons' in a plant is often less defined than in the case of many animal colonies, there can nevertheless be no doubt as to the morphological value of a shoot as a 'person,' in the sense in which Haeckel uses the term.

Although as regards animal colonies, it has not yet in all instances been possible to ascertain with absolute certainty the actual origin of the processes of budding in connection with the cell-generations of the first person of the colony, this has been done very accurately in the case of plants; a theory of heredity can therefore be much more safely applied to the process of gemmation in plants than to that in animals.

In many plants, at any rate, budding originates from a *single* cell, situated at the apex of the growing shoot, and known as the '*apical cell*.' This cell grows and undergoes a series of divisions, much as occurs in the development of the ovum, and thus gives rise to a group of cells, the number, form, and arrangement of

which is perfectly definite. The primary constituents of the entire new shoot are contained in this group, and it is possible to predict what parts of the shoot will be formed from each of its cells. The successors of this group of cells continue to multiply up to a certain limit, and have then only to become elongated in one or more directions, and more highly differentiated, in order to give rise to a fully developed 'person' of the stock. This person does not undergo any further essential changes, but it is capable of giving rise to a new person from its apical cell;

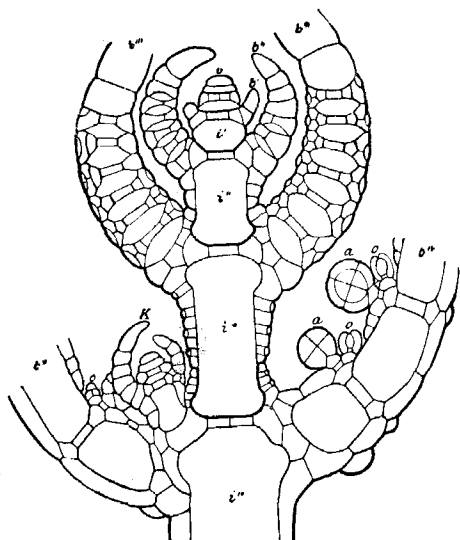


FIG. 7. — The apex of a shoot of *Chara*, in longitudinal section. (From Sachs' 'Lectures on the Physiology of Plants.')

for the latter is always being renewed, or, in other words, it always remains the same.

Let us take as an example the alga *Chara*. A glance at Fig. 7 will at once make it apparent that the idioplasm of the apical cell (*v*) cannot undergo separation into different groups of determinants in the first division, because one of the resulting two cells remains as the apical cell, while the other, or 'segmental cell,' gives rise to an entire shoot, — that is to say, to that very structure which the apical cell is capable of producing. The

next division of the lower of the two daughter-cells, however, separates the determinants into two dissimilar groups, for it results in the production of an upper biconcave 'nodal cell,' from which the leaves ( $b^I, b^{II}, b^{III}, b^{IV}$ ), the lateral shoot ( $k$ ), and the sexual organs ( $a$  and  $o$ ), will subsequently arise; and of a lower biconvex cell, which does not undergo further division, but only grows considerably in length, so as to form a segment of the main axis ( $i^I, i^{II}, i^{III}, i^{IV}$ ). The idioplasm of this 'internodal cell' does not therefore undergo further disintegration; the nodal cell, however, divides vertically, so as to form cells which, since they give rise to other parts of the shoot, must contain various groups of determinants. Thus a comparison of the younger with the older segments of the shoot, shows that the outer of the five nodal cells in the figure gives rise to a whole leaf, together with the sexual organs, the inner ones forming the actual node. The division of the outer cell is accompanied by constant though usually unimportant changes as regards its idioplasm: a glance at the structure of the leaf, in which similar segments are repeated many times over, will make this evident. If we now leave out of consideration the accessory idioplasm which is present in the cells along with the primary idioplasm, it will be seen that the distribution of the group of determinants derived from the apical cell must simply take place so as to result in each cell, as it is formed, receiving that group of determinants only, the individual constituents of which are required by its successors for the control of the individual cells. We must therefore suppose that the internodal cells of the stem only contain their own specific idioplasm, composed of 'internodal determinants,' for they do not give rise to any other structures. The primary nodal cell, on the other hand, must contain an entire group of determinants, as it gives rise to a number of cells which have various forms and perform various functions.

Although the cells of plants are often apparently very much alike, and no essential difference can be observed between them, such a difference must exist if the origin of the specific leaf, stem, and reproductive organs can be proved theoretically at all. For the origin of these structures can only be explained, at any rate in principle, by supposing that each of these centres of vitality is controlled by a specific idioplasm; that is, by a determinant which differs in some way or other from those in the other cells.

### 3. COMPARISON OF THE PROCESS OF GEMMATION IN ANIMALS AND PLANTS

Various stages may be recognised in the different kinds of gemmation with regard to the kind of idioplasm concerned in the process. The simplest form of budding is seen in those plants in which the production of a new 'person' by budding always originates from a single cell. We must therefore assume that the idioplasm of this cell contains all the determinants of the shoot, and very probably those of the root also. For most of the shoots of a plant, when they have been cut off from the stem, are capable of giving rise to roots under favourable circumstances. This does not as a rule occur under normal conditions, — that is to say, while the shoot is still connected with the parent-plant. The 'blastogenic idioplasm' cannot be quite identical with germ-plasm proper; for although precisely the same parts may arise from it as from the fertilised egg-cell, the different succession of cells which results in embryogeny and in gemmation indicates that the determinants must at any rate be differently arranged in the idioplasm, and that possibly their proportional number is also different. '*Blastogenic idioplasm*' and *germ-plasm* may in a sense be regarded as '*isomeric idioplasms*', using the term in an analogous sense to that of isomeric chemical compounds.

The same would be true as regards such animals as Hydroids, in which the formation of a bud originates from a *single* cell. In this case, again, the resemblance between embryonic development and the process of gemmation, although to a certain extent approximate, is not a complete one; and it must again be assumed that the *whole* of the determinants of the species are contained in the blastogenic idioplasm, — not only those which as a rule undergo development, but also those required for the formation of the attached ends in the case of Hydroids, or of roots in the case of plants. This conclusion is supported by the phenomena of budding in polypes like *Hydra*, in which the buds regularly become detached, and carry on an independent existence. In such cases the daughter-polypes do not develop a 'foot' until they become detached from the parent.

The next stage in the process of budding is seen in the Polyzoa. All the determinants of the species from which the bud is formed are no longer contained in a *single* cell, but are

arranged into main groups, one of which is supplied as accessory idioplasm to one cell of the ectoderm, and the other to one or more cells of the mesoderm. The *single* ectoderm cell gives rise to the entire endoderm, but it must nevertheless not be considered equivalent to those cells of the embryo which give rise to the endoderm by invagination, for it forms parts which are either not developed at all in the embryo, or else arise from other ectoderm cells. Without entering into details here, the facts may be expressed in terms of the idioplasm by supposing that the ectoderm-cell from which the bud arises is provided with an idioplasm which contains the whole of the determinants for the endoderm, as well as a number of others, and that this combination of determinants does not occur in embryogeny. The mesoderm-cells of the parent which gives rise to the endothelia, muscles, &c., of the bud, must also contain a peculiar combination of determinants which is not exactly similar to that which occurs in embryogeny. The gemmation must therefore be prepared for in embryogeny by certain series of cells in the ectoderm and mesoderm being provided with these groups of determinants in the form of accessory idioplasm.

A third stage is represented by the gemmation of fixed Ascidians and Salps. In these the bud originates—in the fully-formed animals, or in those which are still undergoing development—from three kinds of cells, viz., those of the ectoderm, mesoderm, and endoderm. And here again those groups of determinants which must be supposed to exist in the three kinds of cells do not correspond exactly to those which must be contained in the primary ectoderm, endoderm, and mesoderm cells. In fact, no group of cells which occurs in embryogeny can contain precisely the same group of determinants as does the endoderm cell of the bud. A collection of determinants especially adapted for budding must therefore be provided on a large scale during embryogeny in this case, so that eventually certain cells may receive their supply from it in the form of accessory idioplasm.

This last kind of budding resembles regeneration very closely as regards the idioplasm concerned in the process. It must not, however, be therefore implied that the former process has been derived phylogenetically from the latter. The resemblance only consists in the formation of a new 'person,' which in both cases originates in several cells provided with

different groups of determinants, these eventually completing one another, and interacting in such a manner that a fully-formed person must result.

#### 4. THE PHYLOGENY OF THE PROCESS OF MULTIPLICATION BY GEMMATION

In all probability the phylogeny of gemmation has taken place along different lines. The process most likely arose independently in animals and in plants, and perhaps even in different groups of animals it has had a different origin.

In many of the lower plants, the cells and organs of which are only slightly differentiated, all, or at any rate many, of the cells can individually give rise to a new plant under certain circumstances. In such cases we might be inclined to suppose that each cell contained originally, *i.e.* at the time of its phyletic origin, the entire mass of determinants of the species, or, in other words, contained germ-plasm. The various differentiations of the cells on the upper and lower surfaces, for instance, would consequently depend on the different determinants becoming active in response to different external stimuli: some, for instance, might be stimulated by a bright light, and others by a dim light.

This explanation would hardly suffice in the case of the higher plants, the differentiation of which is far too complicated to be due to the effect of external causes. A large number of the cells must nevertheless contain germ-plasm, which, however, is in the unalterable ('gebundenen') state,—that is to say, it is not merely inactive, but is incapable at the time of undergoing disintegration. This stage in the phylogeny of gemmation may be derived from the earliest stage. As the plant underwent an increasing differentiation, cells appeared which only contained special determinants, in addition to those with germ-plasm proper; and this may have led to the condition which we now find in the highest plants, and which is distinguished by the fact that many cells only contain specific determinants, while a large number of others possess in addition germ-plasm in the unalterable condition, which only becomes active under certain influences. I shall have occasion to return to this subject later on.

In the case, again, of the various groups of the lower animals

which multiply by gemmation, we cannot assume that this process has a common origin. But although it may have arisen independently in the various subdivisions of the animal kingdom, the history of its origin will have been essentially the same in all cases, for 'blastogenic' idioplasm must have become differentiated from the germ-plasm even in the egg-cell, as all the determinants of the species are contained only in the latter. Even at the present day the blastogenic idioplasm must be present as such in the germ-plasm, for otherwise it could not have undergone independent and hereditary variation: the formation of medusæ from polypes by gemmation, and many other cases of alternation of generations, prove that this has actually occurred.

Balfour attempted to derive the process of budding from a division of the fertilised ovum into two separate parts, such as has been observed in certain animal forms, and which leads to the formation of two individuals. He imagined that if this process of doubling were transferred to a later ontogenetic stage, budding would result, and expressed his views as follows:— 'While it is next to impossible to understand how production of a bud could commence for the first time in the adult of a highly organised form, it is not difficult to form a picture of the steps by which the fission of the germ might eventually lead to the formation of buds in the adult state.'\* Unfortunately this gifted observer did not work out this idea in detail: it seems to me, however, that the derivation of budding from the doubling of the fertilised ovum by division is not so simple or self-evident as we might expect at first sight.

Let us suppose that a fertilised ovum became capable of dividing into two parts: these two first segmentation-cells would not then be blastomeres, but would correspond to egg-cells, each of which could give rise to an entire animal. But this could not be called gemmation, nor would the latter process occur if the doubling were transferred to a later stage:—this would only cause a multiplication of the egg-cell, which would result in the formation of four, eight, sixteen, &c., ova, instead of two.

If, however, we suppose that the division of the egg is of such a kind that the two halves at first remain together so as to form

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\* F. M. Balfour, 'Comparative Embryology,' Vol. i., Introduction, p. 13.



only one embryo, the condition observed in a certain earth-worm (*Lumbricus trapezoides*) by Kleinenberg would result. In this animal the development is *apparently* single up to the gastrula stage, at which the separation of the two embryos first occurs. Did this separation take place at a much later stage, perhaps not until the two individuals are fully developed, the process would not be one of budding, but only of a doubling of the embryo.

An essential modification of this process is indispensable if gemmation is to result from it, and this consists in the *postponement of the development of one half of the egg*. Let us suppose that one of the two equivalent blastomeres of an ovum did not at once undergo development at the same time as the other, but remained in a unicellular condition enclosed within the embryo formed from the active blastomere, and subsequently began to develop when the latter had already given rise to a full-grown animal: this would be a true process of gemmation. I do not wish to assert definitely that the phylogeny of budding might not have taken place on similar lines. A postponement and subsequent transference to a later stage of ontogeny of the development of one of the blastomeres is not actually inconceivable. But such a transference must have undergone a still further modification, before even the simplest form of budding with which we are acquainted could arise. The shifting must have occurred in a backward as well as in a forward direction; that is to say, *the division of the egg into two separate ones must have been suppressed, and represented by the mere division of the germ-plasm*.

Thus in Hydroids and other animals which multiply by budding, we see, in fact, that one of the two blastomeres into which the egg-cell divides does not serve, so to speak, as a reserve cell for subsequent gemmation; both blastomeres, on the contrary, continue to divide, and together give rise to the embryo: and even in the latter none of the cells can be distinguished as 'blastogenic-cells': the cells which take part in the formation of the buds only appear at a much later stage, when the polype is fully formed. If therefore gemmation has in this case originated from the doubling of the egg, the latter process must itself have become degenerated, only the essential part of it remaining: the germ-plasm concerned in it must have remained associated with that of the egg-cell in the form of '*unalterable*' germ-plasm, and

must then have been passed into certain series of cells in the course of ontogeny.

Whether the process of budding has actually been derived from that of the doubling of the egg or not, it seems to me to be certain at any rate that the first process undergone by the idioplasm *must have been that of the doubling of the ids of the germ-plasm in the fertilised egg-cell*, and that this was not connected with the division of the egg-cell; one half of the germ-plasm consequently remained in an unalterable and inactive condition, in which, however, it was capable of development. This blastogenic germ-plasm was then supplied to one of the first segmentation-cells in the form of accessory idioplasm; and from these it was passed on through certain series of cells in an unalterable condition, only becoming active when it had reached certain parts in the fully formed animal, in which it then caused gemmation to occur.

It does not seem to be inconceivable that the process of budding owes its origin phyletically to such a spontaneous division and doubling of the germ-plasm, and that this was originally connected with the inactivity of half the germ-plasm: its connection with the doubling of the ovum was consequently not such as was indicated above, — that is to say, gemmation did not owe its origin to the doubling of the egg, but *both processes originated primarily in the division and doubling of the germ-plasm of the egg-cell*, to which in any case the doubling of the egg must be due. The difference between the two processes would then consist in the fact that in budding one-half of the germ-plasm would pass into the inactive condition, while in the doubling of the egg both halves would at once become active.

The modifications of the idioplasm which result in gemmation must become more complex as soon as two, or all three, of the germinal layers take part in the process, instead of one only. In such cases the blastogenic germ-plasm must undergo disintegration at certain ontogenetic stages, *e.g.*, at the separation of the ectoderm from the endoderm, and again at the separation of the mesoderm from one of the two primary germinal layers. Precisely the same combination of determinants need not necessarily be produced by the disintegration of the accessory germ-plasm into two or three groups of unalterable accessory idioplasm, such as are formed in embryogeny. We can thus explain the origin of endodermal organs from the ectoderm cells

of the bud, as occurs in the Polyzoa for instance, and also even the co-operation of three germinal layers in the formation of the bud.

It seems to me to be improbable that the phylogeny of gemination in animals has taken place in the reverse manner. We might assume that in the lowest Metazoa, which no longer exist at the present day, all or many of the cells also contained germ-plasm proper, just as in the case of the lower multicellular plants. Under certain circumstances a perfect animal might have been produced from each of these cells. But this assumption would only suffice as long as the individual formed by budding was exactly similar to that arising from the egg. Even the slightest difference between these would necessitate the presence of special ids in the germ-plasm. For such a difference can only depend on the fact that the two kinds of individuals are capable of independent variation from the germ onwards. We should therefore have to assume further, that in the course of phylogeny the germ-plasm of these somatic cells from which the buds originated became doubled in the earlier stages of ontogeny, and that it was consequently present in the germ-plasm of the egg-cell in the form of a special group of ids. But this, to say the least, is a very involved assumption, and can hardly be considered very probable: that which presupposes a primary doubling of the ids of germ-plasm is certainly far preferable to it. The following chapter will make this point still more evident.