advisable. Tendency to make these technical and it might be wise to encourage this idea. Let affiliated societies here take the leading position.

E. P. Felt (15 April, '04, No. 485, pp. 622–623).

Two general sessions of association ought to meet every demand at the meetings; one to mark the opening of the meeting, the other to give the president opportunity to deliver his address. Notices for each day could appear on program, thus allowing unbroken day. Morning meetings devoted to general papers. Afternoon meetings to special papers before subsections or societies. Evenings to sessions of members for short addresses on topics of general interest. We would favor the continuing of the complimentary lecture to the people of the city where the meeting is held. All evening meetings should close by 9:30, leaving time for banquets, etc.

W. J. Beal (20 Mch., '04, No. 490, pp. 797–798).

"Let association keep up all its sections, possibly adding to the number, freely cooperating with special societies, each section showing a willingness to unite in preparing a program with any one or more special societies having a like object." Years ago Professor Cope, Mr. W. A. Rogers and Mr. E. S. Morse objected to presentation of popular papers. I have recently thought it desirable to have a number of selected speakers present some topic or series of topics in a popular way to attract 'outsiders.'

3. "Education, economics, but not philology."

4. "Once a year, preferably in winter, till this date has had a fair trial."

5. "Meet most of time in populous regions from Washington to Boston, Detroit to Chicago, where many people are most sure to attend."

AN ANALYSIS OF THE PHENOMENA OF ORGANIC 'POLARITY.'*

The so-called 'polarity' that is shown in the regeneration of animals and plants has always been regarded as an expression of a fundamental influence of the old upon the new growth. By polarity is meant in a general way that from the anterior end of a piece of an animal a new head regenerates, and from the posterior end a new tail. Many exceptions to this rule have been discovered in recent years, and in the light of these discoveries, I think, we are now in a position to undertake a more thorough analysis of the phenomena of organic polarity than was possible without these new facts to guide us.

I shall group the main points to be discussed under four artificial headings: (1) 'Regeneration when *no* Alternative Exists at a cut Surface,' (2) 'Regeneration when an Alternative does Exist,' (3) 'Regeneration when the Relative Rate of Growth Depends on Preformed Elements (Buds)' and (4) 'Lateral Regeneration.'

1. REGENERATION WHEN NO ALTERNATIVE EXISTS AT A CUT SURFACE.

If the tail of a tadpole is cut off a new tail regenerates at the posterior end of the tadpole. The tail that is cut off does not ordinarily regenerate at its anterior end, *because* it dies before regeneration can take place. If it is kept alive, either by grafting or by remaining partially attached, it regenerates from its anterior end, *not* a tadpole, but another tail, reversed in direction. The conditions are such that both at the anterior and at the posterior cut surfaces only a tail can develop. The new tail from the posterior cut surface is in the direction of the old polarity, while that from the anterior cut surface is in a reverse direction.

In the earthworm a similar condition has been found. If the worm is cut in two at any level behind the gizzard, both cut ends regenerate a tail. Anterior to this level, however, the posterior piece regenerates a head on its anterior end. It is

* Read before the National Academy of Science, November 16, 1904.

not improbable that the anterior piece also, if kept alive, would regenerate a head on its posterior cut surface.

I have obtained a similar result with the leg of one of the salamanders, *Spelerpes ruber*. If the foot is first cut off and then the skin of the foreleg is loosened, so that a piece of the internal parts can be cut out, and if this piece is turned round, and grafted in the pocket made by the loosened skin, there regenerates from the free end a new foot (and not a salamander).

A few other examples might be given, but these will suffice to illustrate the main points. The new part has in these cases only one possibility, and the same structure regenerates from the anterior and from the posterior cut surface, regardless of the 'polarity' of the old part.

The interpretation of these facts is, I believe, not difficult in the light of certain other results that are now known. Only one kind of structure develops because the group of new cells that appears over the cut end is such that out of it only one kind of organ can be formed. This may sound paradoxical, but my meaning will, I hope, be clearer when we have considered the next category, when an alternative exists.

2. REGENERATION WHEN AN ALTERNATIVE EXISTS.

The worm *Lumbriculus* furnishes the most striking instance of this sort. If the worm is cut in two *at almost any level* a head regenerates from the anterior end and a tail from the posterior end. Since the two cut ends are identical, each must have both potentialities. Nevertheless, a head forms at one end and a tail at the other. Planarians give the same results. Pieces of *Hydra* also behave in the same way. Another hydroid, *Tubularia,* often produces a head (hydranth) at one (apical) end and a stolon at the other; but also quite frequently produces a head at both ends. It has been shown, in fact, in all these forms, except *Lumbriculus,* that a head may regenerate on the posterior end under certain conditions.

Thus, if the apical end of *Tubularia* be tied or stuck into the sand, a head develops on the basal end. If a piece is sharply bent the same result happens.

If very short cross-pieces of *Planaria maculata* be cut out, a head often develops on both ends. If two pieces of hydra are grafted together by their anterior ends, one piece being longer than the other, the 'polarity' of the shorter piece will be reversed, and a single hydra regenerate.

Several recent writers have attempted to account for these cases of reversal on the old Bonnet-Sachs hypothesis that formative stuffs migrate in definite directions. Loeb, for example, has tried in a recent paper on *Tubularia* to rehabilitate this view, but, I believe, without success. During the past summer I have carried out a large number of experiments on *Tubularia,** which I think show that the assumption of the migration of stuffs in definite directions is not needed to explain the results, and there is in reality nothing in the experiments to support such an idea.

It would take me too long to go into the details necessary to substantiate this statement; but in a forthcoming paper I shall hope to discuss the question more fully. It must suffice here to state that, in my opinion, the development of a head on the apical or on the basal end of *Tubularia* may be explained if we assume that the amount of nutritive substances present at a given moment represents one of the internal factors and the stimulus of the sea water on the *more responsive* free end (which is always that nearer to the old head) represents the external factor that calls forth the regeneration of the hydranths.

The third category applies only to plants.

* In collaboration with N. M. Stevens.

3. REGENERATION WHEN THE RELATIVE RATE OF GROWTH DEPENDS ON PRE-FORMED ELEMENTS.

If a piece of a willow be cut off and suspended in a moist atmosphere the apical buds produce new shoots (the basal buds hardly developing at all). Roots develop around the basal end of the piece from preformed root-buds. This phenomenon is so similar to what takes place in the regeneration of animals that the same term, 'polarity,' has been applied here also. Now I believe it can be shown that the phenomenon is not the same in the two groups and is the outcome of quite different factors. An examination of the results in plants will show that the first buds to develop are the most vigorous ones, which are usually the largest. In the case of the willow the largest buds are those nearer, although not at, the distal ends of the branches. If these buds once begin to develop they will use up the available food stuffs in the piece, and thus hold in check the development of the more basal buds. Hence the latter fail to develop. In some other plants the basal buds are the most vigorous ones and these develop first. Whether the same explanation will account for the root development can not be stated, because, so far as I can discover, no one has shown whether the root-buds nearer the base are more advanced than are those nearer the apex. If this should prove to be the case the explanation used for the shoots will also account for the development of the roots. These phenomena in the pieces of plants led Sachs to apply his stuff hypothesis to explain them. He not only assumed that formative stuffs are present, but also that they move, in response to gravity, in definite directions. His latter assumption was shown to be untenable by Vöchting. A number of recent investigators still continue, nevertheless, to make use of Sachs's hypothesis in one form or another. Goebel, for instance, intimates that the 'polarization' of the tissues themselves is the cause of some of the formative (or, in some cases, nutritive) stuffs moving in one direction and of others in the opposite direction. Thus, while Sachs started out to explain polarity as the result of fluids flowing in a given direction, Goebel, nominally using Sachs's view, assumes the polarity in order to make the substances flow in predestined paths.

I think we need assume neither formative suffs nor their movements in specific directions. I have stated above that we can account for the results by means of a simpler and, I believe, a more reasonable explanation.

4. LATERAL REGENERATION.

If we confine our attention to the regeneration of the head and of the tail alone we get a very incomplete conception of the phenomena that are to be included under the term polarity, for animals regenerate not only in the directions of the poles of a magnet, but laterally, dorsally, ventrally. In short, in all three dimensions of space, or combinations of them. One example of many that might be given will illustrate my point.

If a planarian is split lengthwise into two equal parts, each half regenerates laterally its missing part. If we examine carefully the method by which this takes place we find that a narrow edge of new material appears along the cut side and in this material the new structures are laid down. The chief point of interest here is that the lateral organs develop long before the new part has reached the size of the part removed. Furthermore, at the outer, new edge the distal ends of the branches of the digestive tract are produced, and along the line between the new and the old material the median organs are laid down. The intermediate parts are at first much shortened, perhaps even undeveloped. Thus there is no building outwards of the new organs from the cut edge, but, on the contrary, the differentiation is in large part centripetal in direction. Pflüger thought that the regeneration of a new part may take place in somewhat the same way that a crystal grows in a saturated solution, but the case that I have just given shows that this conception will not explain the main facts,* although it is not to be denied that to a limited extent the old organs along the cut edge may have some influence on the formation of the new organs besides that of proliferating new cells.

The same points that are illustrated by the last case are even more strikingly shown in a piece cut off far out to one side. In this case the structures exposed along the cut edge are not median structures, yet the new median organs are here also laid down between the old and the new tissues. The old parts in this case can not be supposed to determine the formation of the median organs, as was possible in the former instance, but the entire process of differentiation in the new material is rather centripetal, *i. e.,* from the surface inwards. At least, if the actual differentiation is not in point of time from without inwards, the influences that determine the extent and kind of organs that are laid down must be thought of as acting in this way.

In these pieces that regenerate laterally a new head appears at the anterior end of the new material and a new tail at the posterior end. The position of the pharynx in lateral pieces removed from different levels of the body gives a clue to one, at least, of the internal factors that must be at work. If the lateral piece is from the anterior region of the worm, the new pharynx develops near its posterior end; if the piece is from the middle of the worm the new pharynx develops near the middle; and if the piece is from the posterior region the new pharynx develops near the anterior end. Thus the location of the pharynx gives us a clue to certain conditions present in the new part. An analysis of the results leads to the following conclusions:

1. The new material is at every level totipotent, as shown by the fact that a new head will form near the anterior end of a piece at whatever level the piece has been removed.

2. The new material although totipotent is not homogeneous, or, more technically, not isotropic, as shown, for example, by the position of the pharynx. We must conclude from this that the material is somewhat different at every level, and that this difference corresponds *in kind* to the character of the body at each level. Consequently there is in every piece a gradation in the new material from before backwards that gives us the phenomenon that we call polarity. With this difference, or polarity, as a basis the centripetal influence, acting from the surface inwards, determines the organization of the new part.* The action of this centripetal influence is on the new part as a whole, and determines the relative location of each organ.

By means of these three assumptions—of totipotence, of heterotropy and of organization-power—we can explain the main features in the result. Each assumption is, moreover, a direct deduction from an experiment or observation!†

This view will also account for the de-

* Pflüger's view does not explain those cases in the regeneration of a head or tail when the new part is shorter than the part removed.

* This idea of the action from without inwards was formulated by Morgan in 1899, and by Driesch more fully in 1900.

† The same explanation applies to the development of the egg.

velopment of a head at the anterior end and a tail at the posterior end of a cross piece of planaria, or of lumbriculus, or of hydra. In the planarians a head forms on the anterior end, because, on my view, the new material there is continuous with the new material throughout the old part and the difference in the character of the parts at each level gives the basis on which the organizing power acts. Similarly for the tail development at the posterior end. In *Lumbriculus* the same conditions hold. In both cases the old tissue may be so little differentiated that its regional differences may also furnish the basis for the organizing power to act. *Very short cross-pieces of Planaria maculata* often produce a head at each end. This result may be due, as I have explained elsewhere,* to the absence of sufficient difference between the ends on which as a basis the organization of the posterior end can take place. It must be assumed in this case that the external and internal factors, in the new part, have a stronger influence in calling forth a new head than a new tail—much as in *Tubularia.* In hydra no new tissue is produced at the cut ends, but the old part molds itself into the typical form. Here the old tissues are so little fixed that the organizing power acting along the lines of regional difference molds the old part into a new whole. In this respect the difference between hydra and the other forms is merely relative.

My view differs in many points from the stuff hypothesis. It assumes no specific stuff apart from the living material, and consequently it makes no assumption of the migration of such stuffs in multicellular organisms;† it assumes that the material at each level has in addition to its totipotence something also of the material basis characteristic of that level. Lastly, my view takes into account the organizing power of the living material which builds up its structure independently of cell boundaries on the basis of the totipotence and heterotropy of the new part. It is needless to point out further differences of minor importance.

Another example of lateral regeneration brings into the foreground the character of the organizing factors that are at work. If the arm of a salamander is cut off near the body new material appears over the cut end, and while the new material is still relatively small in amount (compared with the amount removed) a new limb, including parts of all the structures, is laid down. The humerus does not complete itself, and then the other parts form in order of succession from within outwards, but simultaneously the new material is proportionally subdivided or *segregated* into the typical elements. Subsequently the new parts all grow larger and longer, until the new limb reaches the size of the one on the other side.

The migration hypothesis is not needed in this case where no alternative exists to account for the location of the new part, and it is helpless to explain the phenomenon of segregation that takes place when the dif-

* 'The Control of Heteromorphosis in *Planaria maculata,' Roux's Archiv*, XVII., 04.

† It has been shown in the case of the egg of many forms (frog, sea-urchin, crepidula, ascidian) that movements of the protoplasm may occur. The differentiation that results appears to follow, to some extent at least, the regional differences in the protoplasm. Here we are not dealing with formative stuffs, in the original sense of the term, but with differences in the kinds of protoplasm, or perhaps only with quantitative differences, which become relegated to different cells. It is presumably the same differences of protoplasm in the cells of the fully formed animal that furnishes the basis for the regional differences in the new and old material in antero-posterior regeneration, etc., and which gives the basis on which the organizing changes go forward. In multicellular forms there is no extensive evidence of migration from cell to cell of the different kinds of protoplasmic materials, nor any necessity of making the assumption that they do migrate.

ferentiation occurs. In my view the material of the new stump is at first totipotent (at least for each kind of material); the surface and the ends of the old organs are the terminals between which the segregation of the new parts takes place.

Let us next turn our attention for a moment to the factors that determine the organization of the new structure.

The term *formative force* was formerly used to cover the changes that take place when the new organ 'crystallizes,' as it were, in the new material. Since no such force is known in the physical world, modern biologists have looked askance at the term. In one sense they are, of course, entirely justified in doing so, because no such creating force is known to us outside of the phenomena to be explained, and the term, therefore, only restates the changes and can not be used as a causal explanation of them. In another sense, however, the use of this term may come nearer to an expression of what is needed than any attempt to explain the results by known chemical or physical 'forces' or energies or principles; for it seems to me that we are dealing here with a phenomenon characteristic of living material—a phenomenon that is unknown to the physicist. This does not mean that I believe the phenomenon is not capable of a causal, *i. e.*, of a physical, explanation. In fact, I have every reason to believe it belongs to this category, but it is not a principle that the physicist meets with, or, at least, has yet met with outside of living material—unless, indeed, the so-called liquid crystals of Lehmann represent a similar phenomenon.

The term *'formative force'* is obnoxious also because of the dubious use of the word *force*. It has been pointed out that since no two animals develop in the same way, or regenerate identical structures, there would be as many kinds of formative forces as there are animals that develop or regenerate. In fact, there would be in *each* animal as many kinds of formative forces as there are *parts* that can regenerate. I believe the objection is well founded, at least, to the extent that it shows that we are not offering a causal explanation when we refer the phenomena to a formative force. On the other hand, no one knowing the facts can doubt that all the cases belong to the same general category; but since the composition of no two animals belonging to different species is the same we should not expect the egg or the newly formed materials to organize themselves in exactly the same way, although the *kind* of action may be the same in all of them.

We meet with the same problem in attempting to explain certain facts in inorganic nature. The salts of different substances crystallize each in its own peculiar way. It would, therefore, be just as misleading to speak of a *crystallizing force* as of a *formative force*, yet no one doubts that the crystallization of each salt depends on some property that all salts have in common.

We meet here with a philosophical principle that it would be out of place to discuss at this time, yet it is a point of as much importance to the practical, thinking experimentalist as to the theorist. I suggest that, for want of a better term, we may provisionally call the property of living material to assume a specific form the property of *formative organization*.

I may sum up my conclusions categorically as follows:

1. Where no alternative exists at a cut surface there is no question of polarity and we have simply to deal with the phenomenon of formative organization, which I would suggest, but can not prove, is in some way a phenomenon of contraction depending on the relative condition of tension in the parts.

2. When an alternative exists at the cut end we meet with the problem of polarity also. In the hydroid, *Tubularia*, an analysis of the conditions leads me to conclude: (1) That the hypothesis of stuffs moving in given directions does not explain the facts, (2) that the results can be accounted for on the ground of the amount of nutritive substance present in the pieces, taken in connection with the relative conditions of the stem at each level. Furthermore, in this case the stimulus of the water on the exposed end, calling forth hydranth regeneration, is an important factor in the result.

3. There is nothing in the phenomena to suggest that the old part has a stereometric influence, *i. e.*, a directive influence on the new part, as the term 'polarity' suggests. On the contrary, the influence is largely centripetal in direction, so far as there is any question of direction involved.

4. An analysis of the conditions present in lateral regeneration in planarians suggests that at least three separate factors are to be recognized in the changes that take place. I have put these factors into the categories of (*a*) totipotence, (*b*) heterotropy and (*c*) organization.

5. The ends of the old organs have also an influence on the regeneration, but a less important one in some cases than those just mentioned.

6. The same factors are also present in antero-posterior regeneration in which an alternative is present. When *no* alternative exists the totipotence has certain limitations, which depends, however, on the special combination of tissues in the new part, rather than on any limitations in each group of cells.

7. The organizing principle acts on the new and old part *as a whole* and determines the relative arrangement and proportions of the new organs.

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*MOSAIC DEVELOPMENT IN THE ANNELID EGG.**

Our general interpretation of the problem of development has been somewhat prejudiced by the fact that so much of the earlier experimental work dealt with such eggs as those of echinoderms, medusæ, *Amphioxus* or the nemertines, where any one of the first two or four cells may produce a perfect dwarf embryo; for such cases seem at first sight to be irreconcilably opposed to any theory of definite pre-localization or mosaic development. The collapse of the Roux-Weismann theory of differentiation by qualitative nuclear division discredited for a time the whole mosaic theory; but more recent experimental work, especially on the eggs of ctenophores and mollusks, promises to re-establish it on a new basis. In the course of the past year I have been able to show experimentally that the development of mollusks (*Dentalium, Patella*) conforms in its main features to the mosaic principle, and, furthermore, that the cleavage mosaic is foreshadowed by a very definite original pre-localization of specific protoplasmic materials in the undivided egg. During the past summer I have had an opportunity to extend these observations in some measure to the egg of an annelid, where the same general principle has been found to hold true.

The development of the annelids presents the problem in a very clear-cut form, since from the first cleavage onward the principal material of the segmented trunk-region lies in the posterior cell of the embryo, and this cell is in most species somewhat larger than the anterior, and hence may be immediately identified. The experiments here reported consist in a comparison of the development of the isolated posterior cell of the two-cell stage with

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