CHAPTER XI

DIMORPHISM AND POLYMORPHISM

1. Normal Dimorphism

The phenomena of reversion discussed in the last chapter depend on the capacity possessed by organisms of conveying in their idioplasm characters which they do not themselves possess in the form of 'latent' primary constituents, and of transmitting these to their descendants, in which they may, under favourable circumstances, undergo development.

It has hitherto been supposed that all the individuals of a species possess these latent primary constituents in the same degree; and that, consequently, characters which are capable of becoming occasionally manifest at all in any organic form exist in a latent condition in all individuals of the species, their subsequent appearance or non-appearance depending solely on certain developmental conditions. Even Darwin was of this opinion, as is shown by many passages in his works. He imagined that latent 'gemmules' existed, for instance, of stripes like those of the zebra in every horse, of the slate-blue coloration of the rock-pigeon in every domesticated pigeon, and of the two parental species in every hybrid. In the last chapter I attempted to show that this may be true in many cases, — such as, for instance, in the races of pigeons, — but that it is by no means necessarily so always, and that in numerous instances certain latent ancestral characters are not present in all, but only in a larger or smaller number of individuals of the form in question. We have seen that the reducing division may, indeed, from one generation to another, divide the germ-plasm of the parent in such a manner that the germ-plasm of some of the offspring receives no portions of the idioplasm of one of the grandparents at all. The most striking example is seen in plant-hybrids, in which reversion to one of the parental forms may even occur amongst the offspring of the hybrid. In spite of the nearness of the generations between such descendants and the parental forms, none of the characters of one of the parents are present in a latent condition.

Such a rapid removal of characters from the germ of individual descendants is, however, only possible if — as in the case of these hybrids — they belong to one parent only. Thus in the human race, any individual traits of the mother or father may not only be absent in certain of the children, but the corresponding determinants may even be wanting in their germ-plasm, so that these traits cannot reappear in the grandchildren or great-grandchildren. The case, however, is very different with regard to those characters which are possessed by both parents. These cannot disappear from the germ-plasm of individual descendants from one generation to the next, for their determinants constitute a majority in the maternal as well as in the paternal half of the germ-plasm. As long as these characters are present in *all* the individuals of the group of forms in question, the determinants for these characters will predominate in most of the idants, and it will then hardly be possible for them to dwindle into a minority in consequence of successive reducing divisions. But let us take the case of a gradually disappearing character, and select as an example the wing-bars characteristic of the rock-pigeon which are present in the domesticated breeds. The absolute number of the 'wing-bar' determinants in the germ-plasm must have been diminished gradually in the course of the processes of selection which led to the formation of the various races, owing to many of them becoming transformed into differently constituted or 'modern' determinants. The smaller the number of 'ancestral' determinants, the more liable are they to be totally eliminated from *one* half of the germ-plasm in the reducing division. When, however, they are entirely wanting in individual germ-cells, two of these cells may possibly come together in conjugation; and an animal would then be produced which possessed no 'wing-bar' determinants, or, in other words, *which no longer contained this character in a latent condition.* In proportion as such individuals became more frequent, the average number of 'bar' determinants in the germ-plasm of the race must still further decrease, owing to the constant interbreeding of these individuals with others, until finally only a small percentage of individuals would contain such determinants at all.

I do not think that the above argument can be strictly applied in the case of this particular character of the pigeon. The frequent appearance of bars in crosses of different races of pigeons indicates, on the contrary, that most individuals still contain a number of these 'bar'-determinants. We may, however, conclude with regard to the occurrence of stripes like those of the zebra on horses and asses, that the infrequency with which reversion occurs, even in the case of crosses, is probably due to the fact that the character in question has long ceased to be present in a 'latent' condition in all individuals of both species, and that the germ-plasm usually no longer contains 'zebra'-determinants.

We certainly cannot ascertain whether some few ancestral determinants may not nevertheless still be present occasionally, for even in crosses their cumulative effect might no longer be apparent; but general considerations compel us to assume that even these sporadic old determinants must ultimately disappear. They will be contained in the germ-plasm of a gradually decreasing number of individuals, and as these derive no benefit from their presence, they will presumably become less and less frequent.

We must therefore take into consideration, on the one hand, the dwindling specific or racial characters, which may be present in a latent condition, though all of them need not by any means necessarily occur in all individuals; and on the other, the individual characters, which may exist in a latent condition in a varying number of individual descendants.

The actual specific characters are, however, transmitted to every individual, though they also do not always become manifest, for some regularly remain latent when another opposing group of characters becomes apparent. I am here alluding to *primary and secondary sexual characters*: but all characters — even the non-sexual ones due to *dimorphism* and *polymorphism* — come under this category. I must now attempt to explain these phenomena in accordance with my theory.

In considering this problem, we must naturally begin with the simplest case of sexual differentiation, in which the originally monomorphic germ-cells become differentiated into male and female. The question then arises as to *the origin of this differentiation in the idioplasm, and how it has arisen phyletically.*

Let us take a definite example. The *Volvocineæ* are lowly organised multicellular algæ of a globular form, which rotate and are propelled through the water by the movement of their cilia. In addition to multiplication by means of asexual germ-cells, several genera of this order, such as *Eudorina* and *Pandorina*, exhibit a sexual mode of reproduction, consisting in the conjugation — *i.e.* complete fusion — of two germ-cells which are apparently quite similar to one another.

As long as this is the case in all individuals, we might suppose that the reproductive-cells are controlled by the idioplasm which directs the development of the species in general, — that is, by the germ-plasm, which is composed of a varied number of similar determinants. This will, however, no longer be the case as soon as the conjugating germ-cells become differentiated into male and female, as has occurred in the allied genus *Volvox*. The utilitarian motive for this differentiation is not far to seek, for it must be advantageous for the germ-cells to contain the greatest possible accumulation of nutritive material; and this could only occur to a very slight extent as long as the two germ-cells destined to undergo amphimixis retained a marked power of movement, as is the case in *Pandorina*. They consequently become differentiated into the stationary egg-cell, containing a large quantity of nutritive material, and the small motile sperm-cell, in which very little food-material is present. On what process in the idioplasm, then, does this differentiation depend?

The idioplasms of the egg- and sperm-cells evidently cannot be precisely similar. They cannot simply consist of germ-plasm; but the egg-cell must contain a determinant which gives it the histological character by which it is distinguished from the sperm-cell, which latter must also contain a determinant controlling its histological development. The germ-plasm of *Volvox* must therefore contain *spermatogenetic* and *oogenetic* determinants besides those for the ciliated somatic cells, only one or the other of which, however, becomes active, and impresses the male or female character on the germ-cell. I imagine that these sexual determinants are *double*, each of the two parts always occurring together and being closely united, but so regulated that only one of them becomes active at a time. We might represent this figuratively by supposing that each id of the germ-cells consists of a central globular mass of germ-plasm, surrounded by a layer composed of this sexual double-determinant, either the male or female part of which may be external, and consequently dominant.

This is only a metaphor, and is not intended to represent the actual occurrences. We are ignorant of the forces and substances which are here concerned, but we at any rate know that the idioplasm of the primary germ-cells in the higher animals is still capable, in by far the most cases, of giving rise to *either* kind of germ-cells, and that the decision as to whether the germ-cells will develop into ova or spermatozoa occurs at some early stage in embryogeny: in the eggs of the bee it takes place at the beginning of embryonic development, long before the first primary germ-cell is differentiated, while in other animals it perhaps occurs at a later stage. The well-known researches of Siebold and Leuckart, prove that at any rate in the case of bees, this decision undoubtedly rests upon the occurrence or omission of fertilisation, — it occurs, that is, at the time when the germ-plasm which controls the new organism is constituted; and this fact seems to me to be of great importance. If fertilisation takes place, the organism develops into a female, and if not, a male will result. This at least proves that the decision *may* take place at such an early stage, and I doubt whether it can in any case occur later: in some animals, at any rate, it occurs still earlier, during the period of maturation of the egg. The *Phylloxera* lays large eggs which produce females, and small ones from which males arise. Both become fertilised, so that in this case fertilisation takes no part in the determination of sex.

These questions cannot be discussed more fully here. We are only concerned in making it clear that sexual determinants in the sense indicated must be assumed to exist, and that both kinds are contained in the primary germ-cells. The following considerations will render it apparent why we have assumed these determinants to be double, — *i.e.*, to consist of two groups of biophors of a common origin lying close to one another. Even apart from such low organisms as *Volvox*, it is well known that the male and female individuals only differ from one another as regards the kind of sexual cells they produce in many of the lower Metazoa — viz., the sponges and Hydromedusæ. In these forms the sexual determinants alone are double. In most other animals, however, the difference of sex is not confined to the germ-cells, but affects the soma itself to a greater or less extent. Hence in all *sexually dimorphic* organisms the germ-plasm must contain a varied number of double primary constituents of somatic characters, — namely, those which represent characters which differ in male and female individuals. These in the first instance concern the organs in which the sexual cells are developed, nourished, stored, and removed, — that is to say, the so-called sexual glands and their ducts; then follow the active and passive copulatory organs, and the structures connected with oviposition; and, finally, special sexual characters arise with regard to the organs for supporting and nourishing the offspring — such as mammary glands, teats, and uterus, — or they may refer to the instinct of carrying the eggs in the mouth, as in the male of a tropical species of frog, or to that in the female butterfly, which deposits its eggs in a definite manner on a certain plant. In the last two instances, the structure of the body and the nerve-centres must also be different in the two sexes, and the male and female type of these parts must exist in a latent condition in every germ-plasm. Under this head, moreover, '*secondary*' *sexual characters* must be included, such as the various tracking and alluring organs of the males, the gorgeous colours of male birds and butterflies, the scent-producing organs of the latter, which exhale perfume, and the song of male birds and insects.

In the human race we know that all the secondary sexual characters are transmitted by individuals of the opposite, as well as of the corresponding sex. A fine soprano voice, for instance, may be transmitted from mother to granddaughter through a son, and a black beard from the father to the grandson through a daughter. And in other animals, the sexual characters of both sides must be present in every sexually differentiated organism, some of them becoming manifest and others remaining latent. This fact can only be proved in certain cases, for we seldom notice the individual differences of these characters with sufficient accuracy; it can, however, be shown to be true, even in tolerably simply organised species, and we must therefore suppose that *latent characters belonging to the other sex* are always present *in each sexually differentiated organism*. In bees, the males developed from unfertilised eggs possess the secondary sexual characters of the grandfather; and in the water-fleas, in which several generations of females arise from one another, the last of these generations produces males with the secondary sexual characters of the species, which must consequently have been present in a latent condition in an entire series of female generations.

The germ-plasm of the fertilised egg-cell must therefore contain the primary constituents of all the secondary male and female sexual characters, as well as those of the male and female germ-cells. We might, then, suppose that this would be accounted for by the assumption that the determinants of both kinds of characters are contained in the germ-plasm, and that the decision as to sex is not only determined with regard to the sexual determinants, — so that the germ-cells take on a male or a female character, — but also as regards the somatic determinants, in order that the secondary sexual character of the male or of the female may take the lead in the building up of the body.

This assumption is certainly indispensable, and it suffices as far as the latent transference of secondary characters of both kinds from the germ-plasm of one generation to that of the next is concerned, but it still requires an essential addition. A number of facts indicate that the latent primary constituents of secondary characters of both kinds are not only present in the germ-plasm from which the organism arises, *but also in the fully developed body of the organism*. The fact that the characters of both sexes can be transmitted to descendants, proves that the germ-plasm must contain the corresponding primary constituents of both; and in the sixth chapter it has already been shown how this transmission may be accounted for by a continuity of the germ-plasm from one generation of germ-cells to the next. We are now concerned with the fact that mature individuals may also contain the primary constituents of secondary sexual characters of both kinds, and that those of the female may be present in the body as well as in the germ-cells of a male organism, and conversely those of the male may exist in the female. The well-known facts to which I refer have been carefully collected and fully discussed by Darwin, and are briefly as follows: — the secondary sexual characters of one sex may, under special circumstances, become developed subsequently in fully-developed individuals. This results in both sexes, especially in the case of castration. The removal of the sexual 'glands' from young mammals and birds prevents the development of secondary male sexual characters. Castrated cocks, for example, retain the appearance of hens, and do not develop the beautiful tail or the large comb and spurs of the male bird, nor do they crow; and conversely, when hens become sterile from age, or if their ovaries become degenerated, they take on the external sexual characters of cocks. I possess a duck which no longer lays eggs, and has assumed the coloration of the drake. Men who have been castrated in their youth retain a high voice like that of the other sex, and the beard does not become developed.

These facts obviously compel us to assume that the capacity for the development of secondary female characters exists in a latent condition in the body of the male, and *vice versâ*, and that these are ready to undergo development under certain conditions. Darwin also arrived at the same conclusion. The only argument which might be advanced against its correctness is that a change of secondary sexual characters in any particular individual has only been observed in rare instances, and in very few species of the higher animals, such as birds and mammals. It might, therefore, be doubted whether it is possible to draw a general conclusion from such isolated observations. These instances nevertheless remain to be accounted for, and we must attempt to explain them in accordance with our theory.

Let us take a very simple example. In many butterflies of the family *Lycænidæ*, the upper surface of the wings is brown in the females, and blue in the males; and it seems very probable that brown was the original colour, as species of *Lycæna* exist at the present day in which both sexes are of this colour. The process which took place in the idioplasm in order that the change of colour may have occurred, must have consisted in the primary determinants of those cells which decide the colour of the wings — which we will speak of as 'brown' determinants — becoming transformed into 'blue' determinants in the germ-plasm, this change only occurring after they had become doubled and in such a manner that only one of the twin-determinants in each case remained brown, an arrangement also taking place which only allowed each to become active alternately. We thus arrive at the assumption of *double determinants*, just as in the case of the determination of sex in the germ-cells. I at first believed that it was indispensable to assume the existence of determinants with different halves, merely because the presence of inactive determinants in the corresponding part of the body could not be otherwise explained. As the adoption of the characters of the opposite sex cannot possibly be of any use to the species, natural selection can have taken no part in the addition of male determinants to the somatic cells of the female body, or *vice versâ*. Such a transference must therefore depend on an unintentional secondary effect of existing arrangements and forces. I soon, however, recognised that such arrangements actually exist, and that the assumption of mechanically unseparable double-determinants is not necessary in order to explain the presence of the *two* sexual determinants in the region where one of them undergoes development. I therefore attach no value to the idea of the material connection of the two dimorphic halves of the primary determinants in question. In fact I shall have occasion to show presently that these halves *must*, in any case, sooner or later become separated as independent determinants in the course of phyletic development.

The reason that such double determinants must, however, always remain close together, even after their separation, results simply from the mechanism for the ontogeny of the idioplasm, which we suppose to consist in the gradual disintegration of the mass of determinants of the germ-plasm into smaller groups. They divide according to a definite law into smaller and smaller groups in the course of the embryonic cell-divisions. None of them remain unused or undergo destruction, but each passes through a definitely prescribed course, and the determinants for any particular part or region of the body *must* necessarily remain together, even when they are not inseparably connected mechanically. In a *physiological* sense, therefore, they are still *double* determinants, — *i.e.*, each half controls the same region, — and in this sense I shall now use the term.

A transfer of the secondary sexual characters, such as occurs in birds, cannot take place in the *Lycænidæ*, because the wing-scales are never formed more than *once* in the course of life, and consequently we have no means of proving the presence of double determinants in the cells of the wing. Other observations on insects indicate, however, that their idioplasm is nevertheless capable of producing such a sexual transference.

This is especially shown in the case of the occasional hermaphrodite forms of insects, the most instructive instance — which has been very accurately investigated by Leuckart * and von

* R. Leuckart, 'Sitzungsberichte der deutschen Naturforscherversammlung,' 1864.

Siebold,* and more recently by Kraepelin — being furnished by bees. The male and female secondary sexual characters are combined in the most wonderful manner in these hermaphrodite forms: in some bees, the *right side was female and the left male;* in others, the anterior half of the body was male and the posterior female; while in others, again, the entire trunk was male and one side of the head female. As Leuckart remarks, 'the male and female characters' in these hermaphrodite bees 'have been intermingled in the most varied and unsystematic manner, so that it is difficult to discover two individuals with perfectly similar characteristics.'

We are indebted to Kraepelin for an excellent account of the external sexual parts in these hermaphrodite bees,† including the copulatory apparatus. His description shows that the blending of the male and female characters even affects very small parts. It not only often happens, for instance, that half the entire stinging apparatus of the left side is female, while an intromittent organ is developed on the right, but certain chitinous plates on the ventral side of the last abdominal segment, which is almost male in character, also display a distinct tendency to take on the form of the corresponding plates of the female stinging apparatus; in other words, *these chitinous plates are intermediate in form between those of the male and female.* Their formation must therefore have been controlled by a combination of 'male' and 'female' determinants. It would be incredible that these harmonising determinants could have met together at the right point in the extremely complex combination of determinants in the germ-plasm if they had not been arranged together from the first, and if an arrangement of male and female double determinants had not previously existed in every such region of the germ-plasm, so that they reached the corresponding part of the body *together* in the course of ontogeny, either the male or the female half then becoming active.

In the determination of sex in the normal development of bees, all these somatic double determinants must be correspondingly determined. We do not know to what factor the prevention of the determination of sex in a similar manner in the formation

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* C. Th. von Siebold, 'Zeitschrift für wissenchaftliche Zoologie,' Bd. xiv., 1864, p. 73.

† Kraepelin, 'Zeitschr. f. wiss. Zoologie,' Bd. xxiii., 1873, p. 326.

of the hermaphrodites is due. Siebold attempted to explain this difficulty by supposing that the eggs which produced hermaphrodites were imperfectly fertilised. He found that in the queen, after producing hermaphrodites, the receptaclum was almost empty; and as drones arise from unfertilised, and females from fertilised eggs, the view that imperfect fertilisation must produce hermaphrodites appeared to be a plausible one. It was not known at that time that a single spermatozoon suffices for fertilisation, and at the present day we are no longer justified in using such an expression as 'imperfect fertilisation.' Whenever a living spermatozoon enters an egg, the latter becomes fertilised; and an imperfect fertilisation could only be supposed to occur if the spermatozoon is abnormal — if, for instance, it contains too few idants. But even if such a case occurred, it would be of very little value theoretically, and we could only state that the determination of sex did not take place in all the double determinants at once, but only in certain larger or smaller groups, — in the case of the germ-cells as well as of the dimorphic parts of the body. Besides the ordinary case, in which the sexual gland of an individual was developed on the female type on the right side and the male type on the left, other instances occurred in which female and male germ-follicles were formed on the same side, seminal tubules and ovarioles being present close together. With reference to this fact, von Siebold remarks that 'the hermaphroditism of the sexual apparatus hardly ever corresponded to that observable in the external form;' and this seems to me to be of special theoretical interest, as it allows us to conclude with certainty that *the harmony of the normal condition is due to a simultaneous decision respecting the double determinants of the germ-cells and those of the body*, and not to a primary determination of sex in the sexual glands, from which the somatic male or female sexual characters would only be determined secondarily. The existence of double determinants in the germ-plasm can be actually proved in the case of bees. For if any egg can develop into a male or female according to whether it is fertilised or not, it *must* contain both kinds of determinants.

Although this assumption is undoubtedly a correct one, it alone is insufficient, because the secondary differences of sex do not always only concern single cells or groups of cells which correspond exactly in the two sexes, such as, for example, the brown and blue scales of the *Lycænidæ; and because in many, and perhaps in most cases, the dimorphic parts correspond only partially or not at all.*

The degree of sexual differentiation is very different in the various groups of the animal kingdom. In the lower and higher Crustacea the males commonly possess more 'olfactory setæ' on their antennæ than do the females. In the large water-flea, *Leptodora hyalina*, for instance, the anterior antennæ are represented in the female by short stumps provided with five olfactory setæ, while the male has long rod-like feelers, which bear about eighty setæ. This difference evidently cannot be referred to one double determinant. Each olfactory seta must be represented by a special determinant in the germ-plasm; even if the first five corresponded, and the differences between them could be attributed to the double determinants, more than seventy determinants for these setæ — which occur in the male sex only — would still be left, quite apart from those for the feeler itself. These seventy determinants are not double, because the corresponding parts are absent in the female, and consequently two *groups* of determinants must exist side by side in the germ-plasm, — those, namely, for the antennæ in the male and in the female, — only *one* of which becomes active in each case. We might imagine that the two groups pass, in close proximity to one another, through the cell-series of embryogeny up to the formation of the rudiments of the antennæ, and then become separated, the inactive group remaining in an 'undifferentiated' cell at the base of the feeler, while the other causes the development of the antennæ of the sex in question by continued cell-division.

The same must be true in numerous other and much more complicated cases. If a tail feather in a male humming-bird, for instance, is six times as long as the corresponding feather in the female, the colour of the former being of a brilliant ultramarine, and that of the latter greyish, we must assume that two groups of determinants are present, which differ in number and in nature. The two groups are situated close together in the germ-plasm, pass through the same cell-series in ontogeny, and ultimately reach the same part of the skin covering the last caudal vertebra. Here, however, one of them remains inactive, the other alone causing further cell-divisions and the consequent development of a feather to take place.

The greater the extent to which sexual dimorphism occurs, and the larger the parts which it affects, the larger the two groups of determinants must be, and the earlier in ontogeny will one of them remain inactive in a cell and cease to undergo further division, while the other gives rise to further cell-divisions.

Sexual dimorphism largely consists in *the arrest of development in an organ in one sex.* In many female butterflies, for instance, wings are wanting. This must be due to the group of determinants for the wings, which existed in a double condition, — *i.e.*, were male and female in the earlier phyletic stages, — becoming arrested as regards their male portion. Such females commonly possess rudiments of the wings, and in this case the two groups of wing-determinants must pass through ontogeny together up to the stage in the caterpillar in which the formation of the imaginal disc of the wing arises from a cell of the hypodermis. If the animal is a female, the arrested group, and if a male, the perfect group of wing-determinants will then become active. It is, however, also conceivable that the development of the group of determinants in the female might continue to be arrested until they disappeared completely, as in the case of female *Psychidæ*, in which the wings are altogether wanting.

But the highest degree of sexual dimorphism is not reached even when certain parts disappear completely. In various groups of the animal kingdom *species exist in which the males differ from the females in nearly all their characters.* In many Rotifers the males are very much smaller than the females, and exhibit an entirely different structure; the alimentary canal, moreover, is entirely wanting. In *Bonellia viridis*, a marine gephyrean worm, the male differs so much from the female that one might be tempted to class it with an entirely different group — the Turbellaria. The difference in the sizes also of the two sexes is still more marked in this instance, the length of the male being 1–2 mm., and that of the female 150 mm.; the former, moreover, lives as a parasite within the latter. In this case the eggs which give rise to males cannot be distinguished from those which develop into females, even in size; and the relatively enormous bulk of the female simply results from subsequent growth. Even the young male and female larvæ cannot be distinguished from one another, and their development only begins to differ when metamorphosis of the larva into the sexually mature animal takes place. The larva is of an elongated oval shape, is furnished with two bands of cilia by means of which it swims about, and possesses an alimentary canal with a mouth and anus. The transformation into the definitive form of the species begins with the loss of the posterior band of cilia,

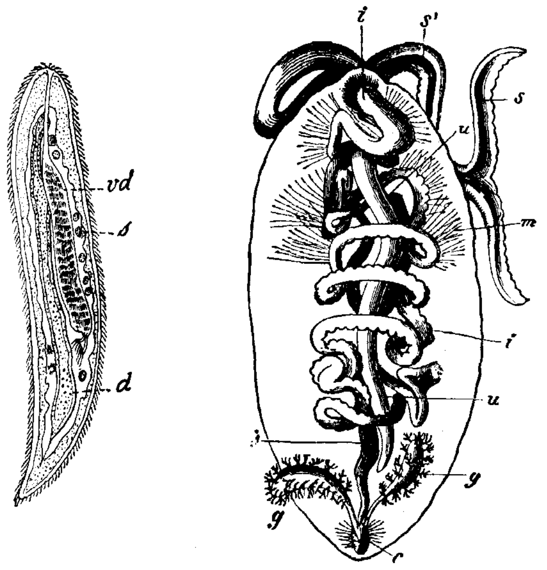

FIG. 24. — *Bonellia viridis.* (After Huxley, from R. Hertwig's "Zoology.") On the left hand the male is shown, considerably magnified; and on the right the female, about natural size. *d*, Rudimentary intestine of the male; *vd*, Sperm duct; *i*, Intestine of the female.

and from this point onwards the mode of development is different in the two sexes. The females grow rapidly, develop a 'proboscis' at the anterior end, and the intestine increases in length; the males, on the other hand, become entirely covered with cilia, and the mouth and anus, as well as the fore- and hind-gut disappear, the mid-gut, filled with yoke-granules, alone being retained. Notwithstanding their great diversity, the two sexes are formed on the same plan; the male, however, may be said in general to remain stationary at a certain stage of organisation, while the female continues to develop, and reaches a much higher stage of organisation, at any rate as regards many organs, such as the nervous and vascular systems, which are altogether wanting in the male. But neither is this the full extent of the difference between them, for the testes, as well as the skin and certain hooked organs of attachment are only developed in the male at a later stage in a peculiar manner. A certain correspondence still remains in the most essential points of structure of the body, in spite of the great difference between the adult sexual animals; so that, as Sprengel says, the male is also 'a Gephyrean possessing all the known structural characteristics of the group.'

In terms of the idioplasm, this course of development may be described somewhat as follows: the determinants which direct the development of the larvæ are single, and consequently *monomorphic* larvæ are produced. The idioplasm of all or most of the cells, however, which constitute the organs of these larvæ, contain double determinants or double groups of determinants, of which those for the female are, in most cases, far the larger: in fact, the group for the female will usually not be opposed by any for the male at all, — in the case, that is, of such organs as the long proboscis, of which there is no homologue in the male. It is certainly very remarkable that these groups of determinants, although present in the male and unopposed by others, do not become active; but, even although we do not in the least understand how it comes about that this inactivity is enforced, the case is not more surprising than that of the determination of sex as a whole, and the inactivity of existing individual primary constituents. Why do the wings first appear at the pupal stage of the caterpillar, and not long previously, since they must be present all along in rudiment — *i.e.*, in the form of a group of determinants in certain cells of the hypodermis? Or why does a boy not grow a beard, seeing that the necessary determinants must be contained in certain cells of the skin? We can no more account for all these cases than for the inactivity of sexually differentiated determinants. All that can be said is, that these determinants have the peculiarity of only becoming active at a certain ontogenetic stage; but this scarcely gives any further insight into the matter than does the statement that sexually differentiated determinants become active or remain inactive, according to the sex of the organism in question.

The ids of the germ-plasm must contain more determinants in sexually dimorphic than in monomorphic species, the number increasing in proportion to the increase of difference between the sexes. They must also increase in size; and the question therefore arises as to whether dimorphism may not perhaps increase to such an extent and finally involve all parts of the body, that *double ids* arise; that is to say, each id of the germ-plasm comes to consist of a male and a female half, in which all the determinants are different. This seems to be practically the case in some animals: in the *Rotifera*, for instance, the males commonly differ so much from the females that they, like the sexual form of *Phylloxera*, arise from special eggs, smaller than those which develop into females. But it would nevertheless be incorrect to suppose that each of these two kinds of eggs contained either male or female ids only. The number of common determinants present must certainly be small, but even here the germ-plasm of each egg must nevertheless contain all the male and female determinants. This is proved by the interpolation of generations consisting of females only in the cycle of generations which is passed through each year, the parthenogenetic females eventually producing males.

We must now return to the question of *sexual reversion* — if I may so call it — which has already been referred to; that is to say, the appearance of characters of the opposite sex after castration or degeneration of the sexual glands. Hitherto this has always been considered a universal phenomenon, but I do not think that such a conclusion is justified. As already mentioned, observations with regard to such cases of 'sexual reversion' have practically been confined to birds and mammals, and even in these do not always refer to all the parts which are sexually dimorphic in the species in question. Cases have certainly been observed in which, for instance, an old 'hen which had ceased laying, assumed the plumage, voice, spurs, and warlike disposition of the cock.' * This proves that in these birds all the secondary sexual characters of the male are present in a latent condition in the soma of the female. We might, however, suppose that this form of reversion only takes place when the characters concerned are completely homologous in the two sexes; that is

* Darwin, 'Animals and Plants under Domestication,' Vol. II., p. 26.

to say, when they exactly correspond with regard to the time and place of their ontogenetic origin and the number of their determinants: but if this is not the case, such a 'reversion' to the characters of the other sex can hardly be possible, because the foundation is wanting from which the reverted organ could arise. Let us suppose that the same conditions as apply to fowls hold good in the case of butterflies: — that is to say, that the secondary sexual characters are present in a latent condition in the soma of the other sex, and undergo development on removal of the sexual glands. The male of *Lycæna alexis*, for example, which has blue wings, would then develop brown ones on being castrated. This would take place by the shedding of old scales and the growth of new ones; or if castration had been effected in the caterpillar stage, the scales in the growing wing would be brown from the first. The scales are homologous structures in the male and female, and each of them is controlled by a single determinant. If, therefore, a cell containing the determinant for a brown scale of the female is situated at the base of the already developed scale of the male, a reversion to the colour of the scales in the female might occur under such circumstances, which are of course purely imaginary.

The matter would, however, be entirely different if the female *Lycæna* had no wings at all, as is the case in females of some *Bombycidæ*. The character of the blue scales in the male would then have no homologue in the female, and an inactive cell, with the determinant of a brown scale, could not possibly be situated at the base of the blue scales in the male. This may be expressed in general terms as follows: — *double-determinants, possessing a definite male and female character, can only be present up to the phase and point in ontogeny in which the development of the two sexes is exactly homologous*. We can therefore only expect a reversion to the secondary characters of the other sex to occur when this point remains permanent. In *Lycæna* the divergence would occur at the formation of the wing-scales; in *Psyche* (the female of which is wingless), in a certain group of cells in the hypodermis of the thorax; in *Bonellia*, in all the cells of the larva; and in the Rotifera, in the egg itself. If our view is a correct one, a female *Bonellia* would consequently be incapable of developing male characters in consequence of castration, because it has long since passed that stage of ontogeny in which the divergence into a male or female occurs; and in the case of the Rotifera, it is not to be expected that any influence could cause a male to produce female characters.

In the part treating of sexual reproduction — including the section on the struggle of the paternal and maternal hereditary tendencies which takes place during the development of the offspring — no mention was made of a very general, and, in my opinion, erroneous conception of sex; and it will be as well to explain this omission before proceeding further.

The transference of sex has hitherto usually been looked upon as an act of transmission. This cannot be the case, inasmuch as every germ-plasm contains the primary constituents for both sexes, and the process of transmission itself has evidently nothing to do with the determination of sex. As already mentioned, it does not by any means follow that because a child is a female, its secondary or primary sexual characters will resemble those of its mother. This, indeed, has long been known, but has not led to a general recognition of the fact that sex is not transmitted at all; and that, on the contrary, the primary constituents of both sexes are always passed on from both sides: the decision as to which of them are to become active depends on secondary factors, which have not yet been clearly recognised in any case. The male halves of the sexual double-determinants of the mother are just as capable of undergoing development as are the female halves, and *vice versâ*: — the 'law of sexual transmission,'* which was propounded by Haeckel some time ago, is not tenable. Expressed in a purely empirical manner, the facts have been more correctly formulated by Déjerine † according to Darwin's (?) views, in his valuable work on the heredity of nervous complaints: — 'the prepotency of *one* of the parents in transmission may be direct, and follow the sex, or may cross over, and become manifest in the opposite sex.'

For this reason the so-called 'transmission of sex' was entirely left aside in the section on the struggle of the parental characters during the formation of the child; transmission of the primary and secondary sexual characters occurs, but sex itself cannot be transmitted.

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* Ernst Haeckel, 'Generelle Morphologie der Organismen,' Bd. II., Berlin, 1866, p. 183.

† J. Déjerine, 'L'Hérédité dans les maladies du système nerveux,' Paris, 1886, p. 17.

2. Pathological Dimorphism: Hæmophilia.

In connection with the attempt to trace sexual dimorphism to its origin in the idioplasm, I will now make a few remarks with regard to a certain disease — or rather structural anomaly — which affects the human race, and which, I believe, will be better understood from this point of view; the analysis of it may, moreover, possibly throw a new light upon the causes of sexual dimorphism.

This anomaly is known as *hæmophilia*, and although of rare occurrence, it has been very accurately observed in a number of cases, and is known to be transmitted in a marked degree and in a very peculiar manner. It only occurs in the *male* members of a family, but is transmitted by the female members, and in this respect *resembles a secondary sexual character*.

The disease, however, is apparently not connected with the sexual organs, or with those parts which differ in the two sexes. It consists in an abnormal flaccidity of the walls of the blood-vessels, in consequence of which slight injuries cause serious hæmorhage, which cannot be easily stopped. As the blood-vessels are developed from certain cells of the so-called mesoblast or 'parablast,' hæmophilia is described in many text-books on pathological anatomy as an anomaly of the 'parablast' or 'Bindegewebekeim.' It must certainly be assumed that this disastrous variation in the blood-vessels — or rather of the cells from which the blood-vessels are formed — is due to some variation in certain mesoblast cells which cannot be more definitely defined at present. The determinants for the cells of the blood-vessels must in this case have varied in some way or other in the germ-plasm of the individuals affected, *and the anomaly must originally have occurred in a male individual*. There is apparently no reason why a similar variation of the determinants should not take place in a female, and cases of women exhibiting the hæmorrhagic diathesis may perhaps still be ascertained. The exclusive transmission of this anomalous condition to the male sex seems to me, however, to indicate that the determinants for the blood-vessels differ in men and women, in spite of the apparent similarity of the vessels themselves: — *these determinants must be double*.

On this assumption, we can easily account for the otherwise mysterious phenomena of heredity observed in these cases. As this disease only appears in men, the pathological variation must affect the 'male' half of the determinants for the cells of the blood-vessels of the person affected, and we may compare it with the variation which occurs in the cells constituting the larynx, the determinants of which must certainly be regarded as being double, and as undergoing variation in the 'male' half. The decision as to which halves of the double-determinants in the idioplasm are to be active during embryogeny and which passive, takes place simultaneously with that as to the sex of the embryo, as is proved by the case of hermaphrodite bees. It is therefore self-evident that this disease must remain latent—*i.e.*, no diseased formation of the tissues whatever can be produced—in the case of every female descendant of a 'bleeder,' for in them the 'female' untransformed halves of the determinants for the cells of the blood-vessels become active. If, however, the offspring develops into a male, the pathologically transformed 'male' halves of these determinants become active, and the disease can develop, provided that a stronger hereditary influence is not exerted in the formation of the blood-vessels of the healthy maternal side, so that the tendency to disease, which has been derived from the father, is overcome by the healthy tendency inherited from the mother. This was the case in four generations of a family of 'bleeders,' observed by Chelius, Mutzenbecher, and Lossen,—* the sons were not affected. In another case described by Thulasius-Grandidier, on the other hand, the disease was transmitted from the father to the male members of three generations. We can understand both cases from our point of view, for in no instance is an individual variation due to the variation of the corresponding determinants in *all* the ids of the germ-plasm, but only in the *majority* of them. But this majority may become reduced to a minority at every 'reducing division' and every time amphimixis occurs, the variation thus ceasing to manifest itself. As soon therefore as only a small majority of the ids contain 'hæmorrhagic determinants,' a considerable number and hereditary force of the healthy maternal determinants for the blood-vessels would preponderate over the morbid paternal ones, and consequently the male descendants would not inherit the disease. If, however, a considerable majority of 'hæmorrhagic determinants' were present

* Klebs, 'Lehrbuch der pathologichen Anatomie.'

in the germ-plasm of the father, a favourable reducing division is necessary if the son is to remain free from the disease. We can, moreover, even account for those cases in which several female members of a hæmorrhagic family in which the fathers were healthy, bear sons all of whom suffer from the disease. For the 'male' halves of the double-determinants in almost all the ids might have undergone a pathological change in the germ-plasm of the mothers, without producing any apparent result in them; in the sons, on the other hand, this would lead to the development of the disease, unless an unusually favourable reducing division had counteracted the marked preponderance of the morbid determinants. Hæmophilia, which remains latent in the mother, is just as liable to be transmitted by the mother to her male descendants as is any other masculine characteristic of the grandfather, such as the colour of his beard, or the quality of voice.

It seems to me that we cannot overlook the indication afforded by this agreement between the mode of transmission of ordinary sexual characters and of hæmophilia that *all, or nearly all, the determinants in the human germ are double*, half being 'male' and half 'female,' so that a determinant for any particular part may cause the development of the male or female type of the corresponding character.

The facts which Prosper Lucas * brought forward, and illustrated by numerous examples, concerning the occasional transmission of new characters to *one* sex only, — even when they have nothing to do with secondary sexual characters in the strict sense, — may be understood by this assumption of a wide distribution of double-determinants in the germ. The modification affects only the 'male' or the 'female' halves of these determinants of the germ-plasm in such instances. This is true as regards the disease we have just considered, inasmuch as it must have made its first appearance at some time or other, — as well as in numerous instances of colour-blindness, of the possession of supernumerary fingers, of the absence of certain fingers or of segments of fingers, and so on. Even the peculiar nature of the epidermis in the well-known case of Lambert, the 'porcupine-man,' was only transmitted to the male descendants.

* 'Traité philosophique et physiologique de l'hérédité naturelle,' Tom. II., Paris, 1850, p. 137.

In certain instances, polydactylism is known to be transmitted to the male members of a family only, while in others it passes from the mother to the daughters exclusively.

It appears, however, that such modifications of the one half in the double-determinants may in the course of time be transferred *to the other half, even though, in the first instance,* this only occurs to a slight extent; for cases are known in which an abnormality first arose (?) in the male sex, and afterwards passed over to certain individual female descendants. These cases have certainly not been followed out with sufficient accuracy to enable us definitely to deny that a modification of both halves of the double-determinants in question might possibly *have taken place from the first, and that it only affected those* in the one half (the homologous determinants) in a smaller number of ids.

Numerous instances in which an abnormality appears, sometimes in the male, and sometimes in the female members of a family, prove that both halves may become modified at the same time. Prosper Lucas mentions several instances of this kind, such as that of the *family Ruhe:—in the first generation observed,* the mother transmitted her polydactylism to the daughter, and in the second this peculiarity was passed on from the mother to the son, while in the third it was transmitted from the father to the son. Numerous facts in zoology indicate the correctness of the assumption that modifications in one half of a double-determinant exert an influence on the other half, so as to result in a similar transformation. *It is well known that* many secondary sexual characters of the male in birds and insects appear in a slighter degree in the female. Amongst the *Lycænidæ*—which are called 'blues,' on account of the preponderance of this colour in the members of the family—some species exist in which both sexes are brown, while in most the male is blue and the female brown, and in a small number of southern species, again, both sexes are *blue. There can be no doubt that* brown was the original colour of these species, and that the blue tint first appeared in the males, while the females remained brown; and that, finally, in certain species, the females also became blue, although not so markedly so as the corresponding males. The *males therefore preceded the females as regards the change of* colour; and if, with Darwin, we attribute the impulse to this change to sexual selection, *it follows that the blue colour of the* females must have been introduced mechanically, owing to its previous existence in the males, and that this secondary sexual character affected the other sex in the course of a great number of generations. According to our theory, this must have been due to the modification of the 'male' halves of the determinants having gradually caused a similar, if less marked, modification of the 'female' halves. We can thus also to some extent understand how it has been possible for certain females to precede the others as regards this modification, as the influence which produced it would not take effect to the same extent and at a similar rate in all individuals. In many species of *Lycænidæ* in which the females are brown, individuals of this sex occur more or less frequently which are clouded with blue, or even exhibit this colour in a marked degree.

3. Polymorphism

Sexual trimorphism is of frequent occurrence in the animal kingdom. I will here refer to certain instances amongst butterflies, which were first discovered by Alfred Russel Wallace, and will begin with a case in which apparently the first step towards polymorphism has been taken.

The male of a common North American butterfly, *Papilio turnus*, resembles the ordinary 'swallow-tail,' having yellow wings ornamented with black transverse stripes; while the females sometimes resemble the males, and are sometimes quite black, and may thus differ markedly from one another. The yellow females occur in the eastern and northern parts of the United States, and the black ones in the west and south; we must therefore suppose that two local varieties of this butterfly exist, in the northern of which the two sexes have a similar coloration, while the southern form is dimorphic. This indicates, in terms of the idioplasm, that the determinants for the wing-scales are single in the northern, and double in the southern variety. Describing these determinants according to the colour which they produce, we may say that the last-named variety possesses double-determinants, the 'male' half of which is 'yellow' and the 'female' half 'black'; while the single-determinants of the northern form are 'yellow.' This species is properly speaking, therefore, not trimorphic, but includes two local varieties, one of which is dimorphic. If the two varieties interbreed, — as is actually the case at the junction of the districts in which the two forms are respectively distributed, — the double-determinants of the southern form will meet with single-determinants of the northern form in the germ-plasm of the offspring. The male descendants of such a cross would remain unmodified, but the females would be either black or yellow according to the power of transmission of the 'female' halves of the determinants, or — as was observed by Edwards * — a combination of both these colours. Such combinations might either arise from the cross between a yellow female and a yellow male of the dimorphic variety, or from that between a black female and a yellow male of the monomorphic form; for in the dimorphic variety the germ-plasm contains double-determinants in the males as well as in the females. If we suppose that these crosses occur frequently, the number of females of an intermediate form in the borderland of the two districts would gradually increase, and might ultimately result in the production of a constant intermediate female form. But if the males exhibited a preference for the females corresponding to them, the female forms would remain essentially distinct from one another. This seems to be the case in *Papilio turnus*, at least Edwards states that the intermediate forms are rare.

The dimorphic and polymorphic females in many butterflies may perhaps be looked upon as belonging to *sexually dimorphic local forms which have subsequently spread and occasionally crossed.* In places where the varieties merely exist side by side without interbreeding, each of them also contains either single- or double-determinants, according to whether it is sexually monomorphic or dimorphic; but when interbreeding occurs, the determinants of the two races come together, and then several homologous double-determinants may even meet in the same germ-plasm, — some in certain ids and some in others.

In *Papilio turnus* the case is not quite so simple as I have stated it: as a matter of fact, this species exhibits a *double dimorphism*, for the yellow females do not exactly resemble the males, but differ considerably from them as regards the shade of yellow and the pattern on the wings: — thus they possess an orange-coloured eye-spot on the posterior wings, which is absent in the male. We must therefore assume that double-deter-

* W. H. Edwards, 'Butterflies of North America.'

minants are present in the yellow variety also. If we imagine that the two sexes were identical as regards the wing-marking in the immediate ancestors of *Papilio turnus*, as they are in the closely allied European species *Papilio machaon*, and that this monomorphic ancestral form had persisted — in California, let us say, — we should have an instance of that kind of polymorphism which Wallace has described in the case of *Papilio memnon*, in which there are one male and three female forms. In this case we must suppose that the first and oldest form possessed *single*-determinants for the wings; while in the second and third forms the determinants were double, and their 'male' halves retained their original nature, the female halves becoming modified in two different directions.

It is therefore not necessary, as might have been supposed, to assume the existence of triple determinants from the fact of the trimorphism of a species alone, or of quadruple or quintuple ones in the case of polymorphism.

The *polymorphism of animal and plant stocks* rests on a different basis, as it concerns the physiologically dissimilar members of a higher stage of individuality — that of the stock. This kind of polymorphism has already been treated of as a phenomenon of development in connection with alternation of generations. We must, however, take the closely allied *polymorphism of animal communities* into consideration.

The differences between the male and female individuals in bees has already been referred to the existence of double-determinants. But a third form of individual, the *worker*, occurs in the honey-bees. These workers differ from the females in the slight development of the ovaries, the ovarioles not only being fewer in number than in the 'queen,' but even frequently containing no eggs at all, and at most only very few. The receptaculum seminis is also more or less reduced, and the abdomen is much shorter and thinner than that of the queen bee. If these were the only differences between the two forms, there would scarcely be any need to assume the existence of special determinants for these parts in the germ-plasm of the workers: we might imagine that the determinants of the ovarioles, for example, were so constituted as to become active in consequence of abundant nourishment, and to cause the development of ovarioles; while a smaller supply of nutriment would not always be sufficient for this purpose, and thus the complete formation of the sexual organs would be prevented. We know, indeed, that a fertilised egg may develop into a queen or a worker, according to whether the larva arising from it is fed on royal diet or with the less nutritious food supplied to the workers.

This explanation, however, even if correct as regards the degenerated parts of the workers, does not sufficiently account for the other differences between the two kinds of females. For the workers are not inferior to the queen bee in all respects: on the contrary, the worker's sting is straighter, longer, and stronger, and is provided with more teeth, than the queen's; the wings, moreover, are longer, the tarsal segment of the hind-limb is provided with the well-known brush, and the tibia has a depression known as the pocket, for carrying the masses of pollen which the insect collects. These two characteristic parts are wanting in the queen. Important differences must also exist as regards the minute structure of the brain, for the instincts of the queen are very different from those of the workers. After fertilisation has taken place, the queen lays eggs, but she neither gathers honey from flowers, excretes wax, nor makes the honeycomb. It is therefore incredible that the queen and workers should be formed by the agency of similar determinants. The germ-plasm must contain double-determinants for certain parts of the body of the queen and workers respectively. But as we have already assumed the existence of double-determinants for the formation of male and female bees, or at any rate for the development of those parts which differ in the two sexes, we can only make the further assumption that *the 'female' halves of the double-determinants may themselves consist of two halves*, corresponding to the queen and worker respectively, and that each of these halves must naturally be looked upon as a complete determinant as regards size and structure. It is of no consequence whether they are regarded as being closely connected together, or as independent structures in close proximity with one another: in either case they must have arisen by the doubling or tripling of a single ancestral determinant. The terms '*double-determinant*' and '*half-determinant*' are simply used for the sake of simplicity. Their relation to one another is similar to that existing between the homologous but heterodynamous determinants of different ids.

In the case of bees, the factor that determines which of the two halves of the 'female' determinants is to become active, seems to be the quality of the food supplied to the larva, so that the critical moment only arrives long after the termination of embryogeny, and before the chrysalis stage is reached. It is well known that when the queen is lost, another one is produced by feeding a larval worker with royal diet. Thus the sex depends on the occurrence or omission of fertilisation, but the modification into a queen or worker takes place much later, when the animal has reached the larval stage. The idea of the trimorphism of certain determinants thus becomes much less difficult to realise. We must look upon them as double-determinants contained in the ids of the germ-plasm, the female hemisphere of which is again composed of two dissimilar quarter-spheres. If the egg becomes fertilised the male half becomes inactive, and we have already represented this figuratively as taking place by the 'female' hemisphere extending over the 'male' hemisphere, and enveloping it like a mantle. This 'female' 'determinant mantle' consists of two halves, representing the queen and worker respectively, and we may suppose that the subsequent determination during the larval stage as to which half is to control the cell, takes place in such a manner that the 'worker' half extends over the other when the nourishment is poor, while with more abundant food the 'queen' half grows more rapidly, and prevents the 'worker' half from exerting any influence on the cell. I naturally do not in the least suppose that this figurative representation of the process represents the actual facts of the case, but it at any rate shows that the existence of trimorphic determinants — or more accurately, of double-determinants each possessing a dimorphic half — is conceivable.

We might, however, also assume the existence of three independent determinants side by side, so arranged that they become active under other definite influences; and this conception would better agree with the unavoidable assumption that the three determinants which act vicariously are of a similar size.

The differentiation of the determinants into several equivalent parts, each of which prevents the others from becoming active, may take place to a still further degree *by the 'male' half of the double-determinants becoming differentiated into two dissimilar* *halves*. The Termites, in addition to the workers or stunted females, possess 'soldiers' or males, in which the sexual organs are stunted, which possess very strong mandibles, and differ in other important structural details from the ordinary males. In this case, therefore, four determinants must be present, each capable of being substituted for another, and only one of which can be active at a time.

Apart from local dimorphism, a temporary dimorphism occasionally occurs, and is especially well known amongst butterflies as *seasonal dimorphism*. In this case the individuals of the same generation, hatched at the same time of year, are alike, but the summer and spring generations differ from one another.

In the European species *Vanessa levana-prorsa*, the individuals of the spring generation are characterised by a yellow and black pattern on the upper side of the wings; while the summer form (*prorsa*) has black wings, with a broad white transverse band, and delicate yellow lines running parallel to the margins. Were we to superpose these two patterns, it would be seen that the black parts in *prorsa* do not correspond to the yellow ones in *levana*, and that the white band in the former does not correspond to a yellow or black part in the latter. This band is, on the contrary, entirely wanting in *levana*, and is represented by both black and yellow regions.

These cases of dimorphism can also, it seems to me, only be accounted for in terms of the idioplasm by the assumption of double-determinants, which, however, are concerned in this case merely with the wing-scales, and essentially with those on the upper side of the wings only; for the lower surface, though not precisely similar, differs far less in the two forms than does the upper side. We will speak of the halves of these double-determinants as 'winter' and 'summer' determinants, and may suppose that the influences of temperature which affect them at the beginning of the pupal stage determine which of the two halves is to predominate over the other. Nearly twenty years ago I showed that it is possible to compel the pupæ of the summer-generation to assume the winter form by exposing them to a low temperature, so that the butterfly emerged as a *levana* instead of a *prorsa*. The converse experiment was also occasionally successful, the pupæ of the winter-generation being forced to assume the summer form by the influence of a higher temperature during, or shortly after, pupation. We may perhaps therefore suppose that an increase of temperature prevents the 'winter' halves of the double-determinants in question from developing, while it is beneficial to the 'summer' halves; and that conversely, the development of the 'summer' halves remains stationary when the temperature is lowered, while the 'winter' halves continue to develop. This may be illustrated, as in the case of ordinary sexual dimorphism, by supposing a determinant of the germ-plasm to be spherical, and to consist of a 'summer' and a 'winter' half. This determinant would remain unchanged throughout embryogeny, and even during the entire caterpillar stage; and the increased or diminished temperature would only determine which half should outgrow the other and prevent it from controlling the cell, at the beginning of pupation, when the wings are formed.

In *Vanessa levana* the males and females resemble each other so closely in the pattern of the wings that they cannot be distinguished from one another with any degree of certainty; but in many other seasonally dimorphic butterflies, sexual dimorphism is exhibited in the pattern and coloration of the wings, and we must therefore assume that they possess double-determinants consisting of 'male' and 'female' halves, each of which is again subdivided into a 'summer' and a 'winter' half. We do not know what factors determine the sex of butterflies, but in many cases the determination is effected early, for ovaries and spermaries can be distinguished from one another in the full-grown caterpillar. Thus, as in the case of Termites, the decision concerning the subdivisions of the double-determinants takes place subsequently to that with regard to the primary halves.

4. Dichogeny in Plants

De Vries has made use of the term 'dichogeny' to describe that form of dimorphism which becomes manifest when a young vegetable tissue, under normal conditions, is capable of developing in different ways according to the external influences to which it is exposed. Shoots of ivy bear leaves on the side which is exposed to the light, and roots on the opposite side; but if the plant is rotated, the same shoot will grow leaves on the side which previously bore roots, and *vice versa*. The stimulus due to light therefore apparently causes a group of cells, which would have formed roots if they had been in the shade, to give rise to leaves.

The assumption, which is in accordance with de Vries's ideas, that all the hereditary tendencies of the species are contained in every cell of the ivy-shoot, and that those which concern the leaves only undergo development in response to the stimulus caused by the light, and those corresponding to roots only to that produced by the shade, does not materially help us in the solution of the problem. In point of fact, the *same* cells are not capable of forming roots and leaves; the leaves are much less numerous than the short and closely aggregated roots, and therefore a large number of cells, or groups of cells, which give rise to roots when shaded, do not develop leaves when exposed to the light; they consequently contain no 'leaf-determinants.' Hence the same idioplasm cannot produce roots when shaded from, and leaves when exposed to, the light; but the determinants for the roots or leaves respectively must be distributed very differently in the cells.

The predisposition to form either of these two structures is obviously determined in the growing point or apex of the shoot. The cells which are continually being produced by the apical cells are destined at a very early stage to form the rudiments of roots or leaves; only a certain number of cells on the illuminated side are provided with leaf-determinants, while much more numerous cells on the shaded side are furnished with root-determinants. The determination therefore takes place at a very early stage, when the shoot is actually in an embryonic condition; and the degree of illumination determines which side is to be provided with leaf- and which with root-determinants, — each kind being distributed in accordance with a different law, — as well as the side to which the groups of each kind of determinants are to pass during the nuclear divisions in the cells arising from the apical cells. This case is analogous to that of the inversion of the viscera in man, except that we do not know the cause of this change of position. Some influence, however, must in this case also be exerted during the early embryonic stages, and cause the liver to take up a position on the left side, and the spleen and heart on the right, long before these parts are actually formed. No subsequent influences could cause the liver to become shifted from the right to the left side, or could transform the liver into the spleen; just as in the ivy-shoot no influences can lead to the formation of leaves on the shaded side when it is once covered with roots.

It therefore seems to me that the *same* cells cannot give rise to two kinds of structures in this case, but that some groups form roots, and others leaves; and that, moreover, the idioplasms of these groups of cells differ from, and cannot be transformed into, one another, but that the sides of the shoot which produce roots and leaves respectively, are determined by the influence of the light as soon as the first embryonic rudiments of the shoot is formed.

The fact that rudiments of roots can actually be proved by the aid of the microscope to exist in the tissue of the stem in some plants, seems to me substantially to support this view. This is the case in the willow, in which the power of producing roots from cuttings exists in a high degree. But numerous other plants are also capable of multiplying by means of cuttings, and we may suppose that in them, in spite of the absence of visible root-germs, the determinants for the tissue of the roots are present, and are ready to develop into germs whenever external influences leading to the formation of roots come into play.

All cases of dichogeny, however, cannot be explained in this manner. In some instances the *same* cells may actually develop in different ways, and the idioplasm may therefore become transformed by external influences. A transformation as regards the dorso-ventral arrangement of the parts in a young shoot of *Thuja* takes place when it is turned round so that the relative positions of the upper and under surfaces are reversed.*
The cells which, under ordinary conditions, take on the form of palisade cells, then assume the structure of the cells on the lower surface, and *vice versa*.

It appears to me that this fact is to be explained by supposing that the determinants of these two forms of cells are both present in each cell, but that only one or the other of them becomes active, according to the degree of illumination. I can, however, form no idea as to why such an arrangement is met with in this case.

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* Compare the statements made on this subject by Detmer, Biolog. Centralblatt, Vol. VII., No. 23.