APPENDICES.

APPENDIX I. FURTHER CONSIDERATIONS WHICH OPPOSE NÄGELI'S EXPLANATION OF TRANSFORMATION AS DUE TO INTERNAL CAUSES [1].

WHEN I describe Nägeli's theory of transformation as due to active causes lying within the organism, as a phyletic force of transformation, I do not mean to imply that it is one of those mysterious principles which, according to some writers, constitute the unconscious cause which directs the transformation of species. Nägeli's idioplasm, which changes from within itself, is conceived as a thoroughly scientific, mechanically operating principle. This cause is undoubtedly capable of theoretical conception: the only question is whether it has any real existence. According to Nägeli, the growing organic substance, the idioplasm, not only represents a *perpetuum mobile* rendered possible as long as its substance continually receives from without the matter and force which are necessary for continuous growth, but it also represents a *perpetuum variabile* due to the action of internal causes [2]. But this is just the doubtful point, viz., whether the structure of the idioplasm itself compels it to change gradually during the course of its growth, or whether it is *not rather the external conditions which compel the* ever slightly varying idioplasm to change in a certain direction by the summation of small differences. It has been shown above that we do not gain anything by adopting Nägeli's theory, because the main problem which organic nature offers for our solution, viz. adaptation, remains unsolved. Hence this theory does not explain the phenomena of nature, and I believe that there are also certain facts which are directly antagonistic to it.

If the idioplasm really possessed the power of spontaneous variability ascribed to it by Nägeli; if, as a result of its own growth, it were compelled to undergo gradual changes, and thus to produce new species, we should expect that *the duration of species, genera,*

---

[1] Appendix to page 257.

[2] l.c., p. 118.

orders, &c. would be of approximately equal length respectively, at least in forms of equal structural complexity. The time required by the idioplasm to undergo such changes as would constitute transformation into a new species ought to be always the same at equal heights in the scale of organization, that is, with equal complexity in the molecular structure of the idioplasm. It appears to me to be a necessary consequence of Nägeli's theory that the causes of transformation lie solely in this molecular structure of the idioplasm. If nothing more than a certain amount of growth, and consequently a certain period of time during which the organism reproduces itself with a certain intensity, is required to produce a change in the idioplasm, then we must conclude that the alteration in the latter must take place when this certain amount of growth has been reached, or after this certain period has elapsed. In other words, the time during which a species exists—from its origin as a modification of some older species, until its own transformation into a new one—must be the same in species with the same degree of organization. But the facts are very far from supporting this consequence of Nägeli's theory. The duration of species is excessively variable: many arise and perish within the limits of a single geological formation, while others may be restricted to a very small part of a formation; others again may last through several formations. It must be admitted that we cannot estimate the exact position of extinct species in the scale of organization, and the differences may therefore depend upon differences of organization: or they may be explained by the supposition that certain species may have become incapable of transformation, and might, under favourable conditions, continue to exist for an indefinite period. But this reply would introduce a new hypothesis in direct antagonism to Nägeli's theory, which assumes that the variability of idioplasm takes place as the consequence of mere growth, and necessarily depends upon molecular structure. Nägeli himself asserts that the essential substance (idioplasm) of the descendants of the earliest forms of life is in a state of perpetual change, which would continue even if the series of successive generations were indefinitely prolonged[1]. Hence there can be no rest in the process of change which the idioplasm must undergo; and this is as true of each single species as it is of the organic world taken as a whole. We

---

[1] l. c., p. 118.

could, perhaps, find shelter in the insufficiency of our geological knowledge, but the number of ascertained facts is too great for this to be possible. Thus it is well known that the genus *Nautilus* has lasted from Silurian times, through all the three geological periods, up to the present day; while all its Silurian allies (*Orthoceras*, *Gomphoceras*, *Goniatites*, &c.) became extinct at a comparatively early period.

A keen and clever controversialist might still bring forward many objections against such an argument. I do not therefore place too much dependence upon the geological facts by themselves, as a disproof of the self-variability of Nägeli's idioplasm ; for it must be admitted that the facts are not sufficiently complete for this purpose. For instance, in the case of *Nautilus* it might be argued that we do not know anything about the fossil Cephalopods of pre-Silurian times, and that it is therefore possible that the above-mentioned allies of *Nautilus* may have existed previously for as long a period as that through which *Nautilus* has lived in post-Silurian time. However this may be, it will be at least conceded that the geological facts do not lend any support to Nägeli's theory, for we can see no trace of even an approximately regular succession of forms.

APPENDIX II. NÄGELI'S EXPLANATION OF ADAPTATION [1].

In order to explain adaptation Nägeli assumes that, under certain circumstances, external influences may cause slight permanent changes in the idioplasm. If then such influences act continually in the same direction during long periods of time, the changes in the idioplasm may increase to a perceptible amount, i. e. to a degree which makes itself felt in visible external characters [2]. But such changes alone could not be considered as adaptations, for the essential character of an adaptation is that it must be a purposeful change. Nägeli, however, brings forward the fact that external stimuli often produce their chief effects at that very part of the organism to which the stimuli themselves were applied. 'If the results are detrimental, the organism attempts to defend itself against the stimulus: a confluence of nutrient fluid takes place towards the part upon which the stimulus has acted, and new tissues

---

[1] Appendix to page 258.

[2] l. c., p. 137.

are formed which restore the integrity of the organism by replacing the lost structures as far as possible. Thus in plants the healthy tissues begin to grow actively around the seat of an injury, tending to close it up, and to afford protection by impenetrable layers of cork.' Purposeful reactions of this kind are certainly common in the organic world, occurring in animals as well as in plants. Thus in the human body an injury causes a rapid growth of the surrounding tissues, which leads to the closing-up of the wound; while in the Salamander even the amputated leg or tail is replaced by growth. An extreme example of these purposeful reactions is afforded by the tree-frog (*Hyla*), which is of a light-green colour when seated upon a light-green leaf, but becomes dark brown when transferred to dark surroundings. Hence this animal adapts itself to the colour of its environment, and thus gains protection from its enemies.

Admitting this capability on the part of organisms to react under certain stimuli in a purposeful manner, the question remains whether such a power is a primitive original quality belonging to the essential nature of each organism. The power of changing the colour of the skin in correspondence with that of the surroundings is not very common in the animal kingdom. In the frog this power depends upon a highly complex reflex mechanism. Certain chromatophores in the skin are connected with nerves[1] which pass to the brain and are there brought into relation, by means of nerve-cells, with the nervous centres of the organ of vision. The relation is of such a kind that strong light falling upon the retina constitutes a stimulus for the production of an impulse, which is conducted, along the previously mentioned motor nerves, from the brain to the chromatophores, thus determining the contraction of these latter and the consequent appearance of a light-coloured skin. When the strong stimulus (of light) ceases, the chromatophores expand again, and the skin becomes dark. That the chromatophores do not themselves react upon the direct stimulus of light was proved by Lister[2], who showed that blind frogs do not possess the power of altering their colour in correspondence with that of their environment. It is quite obvious that in this case we are not dealing with a primary, but with a secondarily produced character;

---

[1] Compare Brücke, 'Farbenwechsel des Chamäleon.' Wien. Sitzber. 1851. Also Leydig, 'Die in Deutschland lebenden Saurier,' 1872.

[2] 'Philosophical Transactions,' vol. cxlviii. 1858, pp. 627-644.

and it has yet to be proved that all the purposeful reactions mentioned by Nägeli are not similarly secondary characters or adaptations, and thus very far from being primitive qualities of the organic substance of the forms in which they occur.

I do not by any means doubt that some of the reactions witnessed in organisms do not depend upon adaptation, but such reactions are not usually purposeful. Curiously enough, Nägeli mentions the formation of galls in plants among his instances of purposeful reactions under external stimuli. I think, however, that it can hardly be maintained that the galls are of any use to the plant: on the contrary, they may even be very injurious to it. The gall is only useful to the insect which it protects and supplies with food. The recent and most excellent investigations of Adler[1] and of Beyerinck[2] have shown that the puncture made by the *Cynips* in depositing its eggs is not the stimulus which produces the gall, as was formerly believed to be the case, but that such a stimulus is provided by the larva which developes from the egg. The presence of this small, actively moving, foreign body stimulates the tissue of the plant in a definite manner, always producing a result which is advantageous to the larva and not to the plant. It would be to the advantage of the latter if it killed the intruding larva, either enclosing it by woody tissue devoid of nourishment, or poisoning it by some acrid secretion, or simply crushing it by the active growth of the surrounding tissues. But nothing of the kind occurs: in fact an active growth of cells (forming the so-called 'Blastem' of Beyerinck) takes place around the embryo, while it is still enclosed in the egg-capsule; but the growth is not such as to crush the embryo, which remains free in the cavity, the so-called larval chamber, which is formed around it. It would be out of place to discuss here the question as to how we can conceive that the plant is thus compelled to produce a growth which is at any rate indifferent and may be injurious to it; and which, moreover, is exactly adapted to the needs of its insect-enemy. But it is at all events obvious that this cannot be an example of a self-

---

[1] Adler, 'Beiträge zur Naturgeschichte der Cynipiden,' Deutsche entom. Zeitschr. XXI., 1877, p. 209; and by the same author, 'Ueber den Generationswechsel der Eichen-Gallwespen,' Zeitschr. f. wiss. Zool., Bd. XXXV. 1880, p. 151.

[2] Beyerinck, 'Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen,' Verhandl. d. Amsterd. Akad. d. Wiss. Bd. XXII. 1883.

protecting reaction under a stimulus, and that therefore an organism does not always respond to external stimuli in a manner useful to itself.

But even if we could accept the suggestion that the purposeful reaction of an organism under stimulation is a primary and not a secondarily produced character, such a principle would by no means suffice for the explanation of existing adaptations. Nägeli attempts to explain certain selected cases of adaptation as the direct results of external stimuli. He looks upon the thick hairy coat of mammals in arctic regions, and the winter covering of animals in temperate regions, as a direct reaction of the skin under the influence of cold. He considers that the horns, claws, and tusks of animals have arisen directly as reactions under stimuli applied to certain parts of the surface of the body in attack and defence[1]. This interpretation is similar to that offered by Lamarck at the beginning of this century. At first sight such a suggestion appears to be plausible, for the acquisition of a thick hairy covering by the mammals of temperate regions is actually contemporaneous with the cold season of the year. But the question arises as to whether the production of a larger number of hairs at the beginning of winter is not merely another instance of a secondary character, like the assumption of a green colour by the tree-frog under the stimulus exerted by strong light.

In the case of the hairy coat it is only necessary to produce a larger number of structures such as had existed previously; but how can it have been possible for the petals of flowers, with their peculiar and complex forms, to have been developed from stamens as a direct result of the insects which visit them in order to obtain pollen and nectar? How could the creeping of these insects and the small punctures made by them constitute stimuli for the production of an increased rate of growth? And how is it possible in any way to explain, by mere increase in growth, the origin of a structure in which each part has its own distinct meaning and plays a peculiar part in attracting insects and in the process of cross-fertilization effected by them? Even if the manifold peculiarities of form could be explained in this way, how can such an explanation possibly hold for the colours of flowers? How could the white colour of flowers which open at night be explained as the direct

---

[1] l. c., p. 144.

result of the creeping of insects? How can the suggestion of such a cause offer any interpretation of the fact that flowers which open by day are tinted with various colours, or of the fact that there is often a bright or highly coloured spot which shows the way to the hidden nectary?

There are, moreover, a large number of very striking adaptations in form and colour, for which no stimulus acting directly upon the organism can be found. Can we imagine that the green caterpillar[1], plant-bug, or grasshopper, sitting among green surroundings, is thus exposed to a stimulus which directly produces the green colour in the skin? Can the walking-stick insect, which resembles a brown twig, be subject to a transforming stimulus by sitting on such branches or by looking at them? Or again, if we consider the phenomena of mimicry, how can one species of butterfly, by flying about with another species, exercise upon the latter such an influence as to render it similar to the first in appearance? In many cases of mimicry, the mimicked and the mimicking species do not even live in the same place, as we see in the moths, flies, and beetles which resemble in appearance the much-dreaded wasps.

The interpretation of adaptation is the weak part of Nägeli's theory, and it is somewhat remarkable that so acute a thinker should not have perceived this himself. One very nearly gains the impression that Nägeli does not wish to understand the theory of natural selection. He says, for instance, in speaking of the mutual adaptation observable between the proboscis, the so-called 'tongue' of butterflies, and flowers with tubular corolla[2]:—'Among the most remarkable and commonest adaptations observable in the forms of flowers, are the corollas with long tubes considered in relation to the long "tongues" of insects, which suck the nectar from the bottom of the long narrow tubes, and at the same time effect the cross-fertilization of the plant. Both these arrangements have been gradually developed to their present degree of complexity—the long-tubed corollas from those without tubes, and from those

---

[1] It is now known that many such caterpillars are actually modified in colour by their surroundings, but the process appears to be indirect and secondarily acquired by the operation of natural selection, like that of the change of colour in the chamaeleon, frogs, fish, etc.; although the stimulus of light acts upon the eyes of the latter animals and upon the skin of the caterpillar. See the seventh Essay (pp. 394-397) for a more detailed account.—E. B. P.]

[2] l. c., p. 150.

with short ones, the long "tongues" from short ones. Undoubtedly both have been developed at the same rate so that the length of both sets of structures has always remained the same.'

No objection can be raised against these statements, but Nägeli goes on to say:—'But how can such a process of development be explained by the theory of natural selection, for at each stage in the process the adaptation was invariably complete. The tube of the corolla and the "tongue" must have reached, for instance, at a certain time, a length of 5 or 10 mm. If now the tube of the corolla became longer in some plants, such an alteration would have been disadvantageous because the insects would be no longer able to obtain food from them, and would therefore visit flowers with shorter tubes. Hence, according to the theory of natural selection, the longer tubes ought to have disappeared. If on the other hand the "tongue" became longer in some insects, such a change would be superfluous and should have been given up, according to the same theory, as unnecessary structural waste. The simultaneous change in the two structures must, according to the theory of natural selection, be due to the same principle as that by which Münchhausen pulled himself out of a bog by means of his own pig-tail.'

But, according to the theory of natural selection, the case appears in a very different light from that in which it is put by Nägeli. The flower and the insect do not compete for the greater length of their respective organs: all through the gradual process, the flower is the first to lengthen its corolla and the butterfly follows. Their relation is not like that between a certain species of animal and another which serves as its prey, where each strives to be the quicker, so that the speed of both is increased to the greatest possible extent in the course of generations. Nor do they stand in the same relation as that obtaining between an insectivorous bird and a certain species of butterfly which forms its principal food; in such a case two totally different characters may be continually increased up to their highest point, e.g. in the butterfly similarity to the dead and fallen leaves among which it seeks protection when pursued, in the bird keenness of sight. As long as the latter quality is still capable of increase, so long will it still be advantageous to any individual butterfly to resemble the leaf a little more completely than other individuals of the same species; for it will thus be capable of escaping those birds which possess a rather keener sight than others. On the other hand, a bird with rather keener sight will have the greatest chance of catching the better protected butterflies. It is only in this way that we can explain the constant production of such extraordinary similarities between insects and leaves or other parts of plants. At every stage of growth both the insect and its pursuer are completely adapted to each other; i. e. they are so far protected and so far successful respectively, as is necessary to prevent that gradual decrease in the average number of individuals which would lead to the extermination of the species[1]. But the fact that there is complete adaptation at each stage does not prevent the two species from increasing those qualities of protection and of pursuit upon which they respectively depend. So far from this being the case, they would be necessarily compelled to gradually increase these qualities so long as the physical possibility of improvement remained on both sides. As long as some birds possessed a rather keener sight than those which previously existed, so long would those butterflies possess an advantage in which the resemblance to leaf-veining was more distinct than in others. But from the moment at which the maximum keenness of eyesight attainable had been reached, at which therefore all butterflies resembled leaves so completely that even the birds with the keenest eyesight might fail to detect them when at rest,—from this very point any further improvement in the similarity to leaves would cease, because the advantage to be gained from any such improvement would cease at the same time.

Such reciprocal intensification of adaptive characters appears to me to have been one of the most important factors in the transformation of species: it must have persisted through long series of species during phylogeny: it must have affected the most diverse parts and characters in the most diverse groups of organisms.

In certain large butterflies of the Indian and African forests —*Kallima paralecta, K. inachis*, and *K. albofasciata*—it has been frequently pointed out that the deceptive resemblance to a leaf is so striking that an observer who has received no hint upon the subject believes that he sees a leaf, even when he is looking at the butterfly very closely. The similarity is nevertheless incomplete; for out

---

[1] In order to make the case as simple as possible, I assume that the insectivorous bird feeds upon a single species of insect, and that the insect is only attacked by a single species of bird.

of sixteen specimens in the collections at Amsterdam and Leyden, I could not find a single one which had more than two lateral veins on one side of the mid-rib of the supposed leaf, or more than three upon the other side; while about six or seven veins should have been present on each side. But from two to three lateral veins are amply sufficient to produce a high degree of resemblance; in fact so much so that it is a matter for wonder as to how it has been possible for such a relatively perfect copy to have been produced; or how the sight of birds can have become so highly developed that while flying rapidly they could perceive the vein-like markings; or to state the case more accurately, that they could detect those individuals with a less number of veins than others. It is possible that the process of increase in resemblance is still proceeding in the species of the genus *Kallima*; at all events, I was struck by the rather strong individual differences in the markings of the supposed leaf.

On the other hand, the cause of the increase in length of the tubular corolla and of the butterfly's 'tongue,' lies neither in the flower nor in the butterfly, but it is to be found in those other insects which visit the flower and steal its honey without being of any assistance in cross-fertilization. It may be stated shortly, that non-tubular corollas, with the honey freely exposed—for it must be assumed the ancestral form was of this kind—gradually developed into corollas with the honey deeply concealed. The whole process was presumably first started by the flower, for the gradual withdrawal of the honey to greater depths conferred the advantage of protection from rain (Hermann Müller), while larger quantities of honey could be stored up, and this would also increase the number of insects visiting the flower and render their visits more certain. As soon as this withdrawal occurred, the mouth-parts of insects began to be subjected to a selective process whereby these organs in some of them were lengthened at the same rate as that at which the honey was withdrawn. When once the process had begun, its continuance was ensured, for as soon as flower-frequenting insects were divided into two groups with short and with long mouth-parts respectively, a further increase in the length of the corolla-tube necessarily took place in all those flowers which were especially benefited by the assured visits of a relatively small number of species of insects, viz., those flowers in which cross-fertilization was more certainly performed in this way than by the uncertain visits of a great variety of species. This would imply that a still further increase in length would take place, for it is obvious that the cross-fertilization of any flower would be more certainly performed by an insect when the number of species of plants visited by it became less; and hence the cross-fertilization would be rendered most certain when the insect became completely adapted—in size, form, character of its surface, and the manner in which it obtained the honey—to the peculiarities of the flower. Those insects which obtain honey from a great variety of flowers are sure to waste a great part of the pollen by carrying it to the flowers of many different species, while insects which can only obtain honey from a few species of plants must necessarily visit many flowers of the same species one after the other, and they would therefore more generally distribute the pollen in an effective manner.

Hence the tube of the corolla, and the 'tongue' of the butterfly which brings about fertilization, would have continued to increase in length as long as it remained advantageous for the flower to exclude other less useful visitors, and as long as it was advantageous for the butterfly to secure the sole possession of the flower. Hence there is no competition between the flower and the butterfly which fertilizes it, but between these two on the one side, and the other would-be visitors of the flower on the other. Further details as to the advantages which the flower gains by excluding all other visitors, and the butterfly by being the only visitor of the flower, and also as to the manifold and elaborate mutual adaptations between insects and flowers, and as to the advantages and disadvantages which follow from the concealment of the honey—will be found in Hermann Müller's[1] work on the fertilization of flowers, in which all these subjects are minutely discussed, and are clearly explained in a most admirable manner.

APPENDIX III. ADAPTATIONS IN PLANTS[2].

It is well known that Christian Conrad Sprengel was the first to recognise that the forms and colours of flowers are not due to

---

[1] English Edition, translated by D'Arcy W. Thompson, B.A. London, 1883, p. 509 et seqq.

[2] Appendix to page 260.

chance, that they are not the mere sport of nature, and that they are not made for the enjoyment of man, but that their purpose is to attract insects for the performance of cross-fertilization. It is also well known that this discovery—which was made at the end of the last century, and which caused much excitement at that time—was completely forgotten, and was brought to light again by Charles Darwin when attacking the same problem.

In his work entitled 'The Solution of Nature's Secret in the Structure and Fertilization of Flowers' ('Das entdeckte Geheimniss der Natur im Bau und der Befruchtung der Blumen'), published at Berlin, in 1793, Sprengel showed, in several hundred cases, that the peculiarities in the structure and colours of flowers were calculated to attract insects, and to ensure the fertilization of the flowers by their instrumentality. But it was due to his successor in this line of investigation that the whole significance of the cross-fertilization effected by insects was made clear. Darwin[1] showed that in many cases, although not in all, the intention of nature was to avoid self-fertilization, and he showed that stronger and more numerous descendants are produced after cross-fertilization.

After Darwin, several investigators, such as Kerner, Delpino and Hildebrand, have paid further attention to the subject, but it has been especially studied in a most thorough manner by Hermann Müller[2]. He looked at the subject from more than one point of view, and showed by direct observation the species of insects which effect cross-fertilization in various species of our native flowers: he also studied the structure of insects in relation to that of flowers, and attempted to establish the mutual adaptations which exist between them. In this way he succeeded in throwing much light upon the process of transformation in many species of flowers, and in proving that certain insects, although unconsciously, are, as it were, breeders of certain forms of flowers. He not only distinguished the disagreeably smelling, generally inconspicuous flowers ('Ekelblumen') produced by Diptera which live on putrid substances, and the flowers which are produced by butterflies; but he also distinguished the flowers bred by saw-flies, by

---

[1] Ch. Darwin, 'On the fertilization of Orchids by Insects.' London, 1877.

[2] Compare Hermann Müller, 'Die Befruchtung der Blumen durch Insekten und die gegenseitigen Anpassungen beider.' Leipzig, 1873. See also many articles by the same author in 'Kosmos,' and other periodicals. These later articles are included in the English translation by D'Arcy W. Thompson.

Fossoria, and by bees. He even believes that in certain cases (*Viola calcarata*) he can prove that a flower which owed its original form to being bred by bees, was afterwards adapted to cross-fertilization by butterflies, when it had migrated into an Alpine region where the latter insects are far more abundant than the former.

Although there must of course be much that is hypothetical in the interpretations of the different parts of flowers offered by Hermann Müller, the majority of these explanations are certainly correct, and it is of the greatest interest to be able to recognise the adaptive character of details, even when apparently unimportant, in the structure and colours of flowers.

Sachs has offered a very convincing explanation as to the meaning of leaf-veining, and of its significance in relation to the functions of leaves[1]. He shows that the venation of a leaf is in every case *exactly adapted for the fulfilment of its purpose.* It has, in the first place, to conduct the nutrient fluid in both directions, and in the second place to support the thin layers of assimilating chlorophyll cells, and to stretch them out so as to expose as large a surface as possible to the light; lastly, it has to toughen the leaf as a protection against being torn. He shows in a very convincing manner that the whole diversity of leaf venation can be understood from these three principles. Here, again, we meet with purposeful arrangements in a class of structures in which it was formerly thought that there was only a chaos of accidental forms, or, as it were, the mere sport of nature with form.

APPENDIX IV. ON THE SUPPOSED TRANSMISSION OF ACQUIRED CHARACTERS[2].

When I previously maintained that the proofs of the transmission of artificially produced diseases are inconclusive, I had in mind the only experiments which, as far as I am aware, can be adduced in favour of the transmission of acquired characters; viz. the experiments of Brown-Séquard[3] on guinea-pigs. It is well

---

[1] 'Lectures on the Physiology of Plants,' translated by H. Marshall Ward, Oxford, 1887, p. 47.

[2] Appendix to page 267.

[3] *Brown-Séquard, 'Researches on epilepsy; its artificial production in animals and its etiology, nature, and treatment.'* Boston, 1857. Also various papers by the same author in 'Journal de physiologie de l'homme,' Tome I and III, 1858, 1860, and in 'Archives de physiologie normale et pathologique,' Tome I–IV, 1868–1872.

known that he produced artificial epilepsy in these animals by dividing certain parts of the central and also the peripheral nervous system. The descendants of the animals which acquired epilepsy sometimes inherited the disease of their parents.

These experiments have been since repeated by Obersteiner[1], who has described them in a very exact and entirely unprejudiced manner. The fact itself cannot be doubted: it is certain that some of the descendants of animals in which epilepsy has been artificially produced, have also themselves suffered from epilepsy in consequence of the disease of their parents. This fact may be accepted as proved, but in my opinion we have no right to conclude from it that acquired characters can be transmitted. Epilepsy is not a morphological character; it is a disease. We could only speak of the transmission of a morphological character, if a certain morphological change which was the cause of epilepsy had been produced by the nervous lesion, and if a similar change had re-appeared in the offspring, and had produced in them also the symptoms of epilepsy. But that this really occurs is utterly unproved; and is even highly improbable. It has only been proved that many descendants of artificially epileptic parents are small, weakly, and very soon die; and that others are paralysed in various parts of the body, i. e. in one or both of the posterior or anterior extremities; while others again exhibit trophic paralysis of the cornea leading to inflammation and the formation of pus. In addition to these symptoms, the descendants in very rare cases exhibit upon the application of certain stimuli to the skin, a tendency towards those tonic and clonic convulsions together with loss of consciousness which constitute the features of an epileptic attack. Out of thirty-two descendants of epileptic parents only two exhibited such symptoms, both of them being very weakly, and dying at an early age.

These experiments, although very interesting, do not enable us to assert that a distinct morphological change is transmitted to the offspring after having been artificially induced in the parents. The injury caused by the division of a nerve is not transmitted, and the part of the brain corresponding to that which was removed from the parent is not absent from the offspring. The symptoms of a disease are undoubtedly transmitted, but the cause of the disease in the offspring is the real question which requires solution. The

---

[1] 'Oesterreichische medicinische Jahrbücher.' Jahrgang, 1875, p. 179.

symptoms of epilepsy are by no means invariably transmitted; they are in fact absent from the great majority of cases, and the very small proportion in which they do occur, exhibit the symptoms of other diseases in addition to those of epilepsy. The offspring are either quite healthy (thirteen out of thirty cases) or they suffer from disturbances of the nervous system, such as the above-mentioned motor and trophic paralysis,—symptoms which are not characteristic of epilepsy: however in some of the latter epilepsy is also present.

If therefore we wish to express the matter correctly we must not state that epilepsy is transmitted to the offspring, but we must express the facts in the following manner:—animals which have been rendered epileptic by artificial means, transmit to some of their offspring a tendency to suffer from various nervous diseases, viz. from motor paralysis, to a less degree from sensory, and to a high degree from trophic paralysis; in rare cases, when the symptoms of paralysis are very marked, epilepsy is also transmitted.

If we now remember that a considerable number of diseases are already known to be caused by the presence of living organisms in the body, and that these diseases may be transmitted from one organism to another in the form of germs, ought we not to conclude from the above-mentioned facts, that the symptoms are due to an unknown microbe which finds its nutritive medium in the nervous tissues, rather than to suppose that they are due to morphological changes, such as a modification of the histological or molecular structure of certain parts of the nervous system? At all events, it would be more difficult to understand the transmission of such a structural change, than the passage of a bacillus into the sperm- or germ-cell of the parent. There is no ascertained fact which supports the former assumption, but it is very probable that the transmission of syphilis, small-pox and tuberculosis[1] is to be explained by the latter method, although the bacilli have not yet been detected in the reproductive cells. Furthermore, this method of transmission has been rigidly proved in the case of the mus-

---

[1] A direct transmission of the germs of disease through the reproductive cells has lately been rendered probable in the case of tuberculosis, for the bacilli have been found in tubercles in the lungs of an eight-months' fœtal calf, the mother being affected at the time with acute tuberculosis. However it is not impossible that infection may have arisen through the placenta. See 'Fortschritte der Medicin,' Bd. III, 1885, p. 198.

cardine disease of the silkworm. At all events we can understand in this way how it happened that the offspring of artificially epileptic guinea-pigs were affected with various forms of nervous disease, a fact which would be quite unintelligible if we assume the occurrence of a true hereditary transmission of a morphological character, such as a pathological change in the structure of some nervous centre.

The manner in which artificial epilepsy becomes manifest after the operation, is also in favour of the explanation offered above. In the first place epilepsy does not result from any one single injury to the nervous system, but it may follow from a variety of different injuries. Brown-Séquard produced it by removing a portion of the grey matter of the brain, and by dividing the spinal cord, although the disease also resulted from a transverse section through half of the latter organ, or from the section of its anterior or posterior columns alone, or from simply puncturing its substance. The most striking effects appeared to follow when the spinal cord was injured in the region between the eighth dorsal and the second lumbar vertebrae, although the results were sometimes also produced by the injury of other parts. Epilepsy also followed the division of the sciatic nerve, the internal popliteal, and the posterior roots of all nerves which pass to the legs. The disease never appears at once, but only after the lapse of some days or weeks, and, according to Brown-Séquard, it is impossible to conclude that the disease will not follow the operation until after six or eight weeks have passed without an epileptic attack. Obersteiner did not witness in any case the first symptoms of the disease for several days after the division of the sciatic nerve. After the operation, sensibility decreases over a certain area on the head and neck, on the same side as the injury. If the animal be pinched in this region (which is called the epileptic area, 'zone epileptogène') it curves itself round towards the injured side, and violent scratching movements are made with the hind leg of the same side. After the lapse of several days or even weeks, these scratching movements which result from pinching in the above-mentioned area, form the beginning of a complete epileptic attack. Hence the changes immediately produced by the division of a nerve are obviously not the direct cause of epilepsy, but they only form the beginning of a pathological process which is conducted in a centripetal direction from the nerve to some centre which is apparently situated in the pons and medulla oblongata, although, according to others [1], it is placed in the cortex of the cerebrum. Nothnagel [2] considers that certain changes, the nature of which is still entirely unknown, but which may be histological or perhaps solely molecular in character, must be produced, leading to an increased irritability of the grey matter of the centres concerned.

Nothnagel thinks it possible or even probable that in those cases in which the division of nerves is followed by epilepsy, a neuritis ascendens—an inflammation passing along the nerves in a central direction—is the cause of the changes suggested by him in the epileptic centre. All our knowledge of bacteria and of the pathological processes induced by them, seems to indicate that such a neuritis ascendens, as is assumed by Nothnagel, would render important support to the hypothesis that the artificial epilepsy is due to infection. But when we further consider that the offspring of artificially epileptic animals may themselves become epileptic, although in most cases they suffer from a variety of other nervous diseases (in consequence of trophic paralysis), I hardly see how the facts can be rendered intelligible except by supposing that in these cases of what I may call traumatic epilepsy, we are dealing with an infectious disease caused by microbes which find their nutritive medium in the nervous tissues, and which bring about the transmission of the disease to the offspring by penetrating the ovum or the spermatozoon.

Obersteiner found that the offspring were more frequently diseased when the mother was epileptic, rather than the father. This is readily intelligible when we remember that the ovum contains an immensely larger amount of substance than the spermatozoon, and can therefore be more frequently infected by microbes and can contain a greater number of them.

Of course, I do not mean to assert that epilepsy always depends upon infection, or upon the presence of microbes in the nervous tissues. Westphal produced epilepsy in guinea-pigs by striking

---

[1] Compare Unvericht, 'Experimentelle und klinische Untersuchungen über die Epilepsie.' Berlin, 1883. With regard to the question of hereditary transmission, the part of the brain in which the epileptic centre is placed is of no importance.

[2] Compare Ziemssen's 'Handbuch der spec. Pathologie und Therapie.' Bd. XII. 2. Hälfte; Artikel 'Epilepsie und Eklampsie.' Leipzig, 1877.

them once or twice sharply upon the head: the epileptic attack took place immediately and was afterwards repeated. It is obvious that the presence of microbes can have nothing to do with such an attack, but the shock alone must have caused morphological and functional changes in the centres of the pons and medulla oblongata, identical with those produced by microbes in the other cases. Nothnagel also distinctly expresses the opinion that epilepsy 'does not depend upon one uniform and invariable histological change, but that the symptoms which constitute the disease may in all probability be caused by various anatomical alterations, provided that they take place in parts of the pons and medulla which are morphologically and physiologically equivalent[1].' Just as a sensory nerve produces the sensation of pain under various stimuli, such as pressure, inflammation, infection with the poison of malaria, etc., so various stimuli might cause the nervous centres concerned to develope the convulsive attack which, together with its after-effects, we call epilepsy. In Westphal's case, such a stimulus would be given by a powerful mechanical shock, in Brown-Séquard's experiments, by the penetration of microbes.

However, quite apart from the question of the validity of this suggestion, we can form no conception as to the means by which an acquired morphological change in certain nerve-cells—a change which is not anatomical, and probably not even microscopical, but purely molecular in nature—can be possibly transferred to the germ-cells: for this ought to take place in such a manner as to produce in their minute molecular structure a change which, after fertilization and development into a new individual, would lead to the reproduction of the same epileptogenic molecular structure of the nervous elements in the grey centres of the pons and medulla oblongata as was acquired by the parent. How is it possible for all this to happen? What substance could cause such a change in the resulting offspring after having been transferred to the egg or sperm-cell? Perhaps Darwin's gemmules may be suggested; but each gemmule represents a cell, while here we have to do with molecules or groups of molecules. We must therefore assume the existence of a special gemmule for each group of molecules, and thus the innumerable gemmules of Darwin's theory must be imagined as increased by many millions. But if we suppose that the theory

---

[1] l. c., p. 269.

of pangenesis is right, and that the gemmules really circulate in the body, accompanied by other gemmules from the diseased parts of the brain, and that some of these latter pass into the germ-cells of the individual,—to what strange results would the further pursuit of this idea lead? What an incomprehensible number of gemmules must meet in a single sperm- or germ-cell, if each of them is to contain a representative of every molecule or group of molecules which has formed part of the body at each period of ontogeny. And yet such is the unavoidable consequence of the supposition that acquired molecular states of certain groups of cells can be transmitted to the offspring. This supposition could only be rendered intelligible by some theory of *preformation*[1], such as Darwin's pangenesis; for the latter theory certainly belongs to this category. We must assume that each single part of the body at each developmental stage is, from the first, represented in the germ-cell as distinct particles of matter, which will reproduce each part of the body at its appropriate stage as their turn for development arrives.

I will only briefly indicate some of the inevitable contradictions in which we are involved by such a theory. One and the same part of the body must be represented in the germ- or sperm-cell by many groups of gemmules, each group corresponding to a different stage of development; for if each part gives off gemmules, which ultimately reproduce the part in the offspring, it is clear that special gemmules must be given off for each stage in the development of the part, in order to reproduce that identical stage. And Darwin quite logically accepts this conclusion in his provisional hypothesis of pangenesis. But the ontogeny of each part is in reality continuous, and is not composed of distinct and

---

[1] It is generally known that the earlier physiologists believed in what was called the 'evolutionary theory,' or the 'theory of preformation.' This assumes that the germ contains, in a minute form, the whole of the fully-developed animal. All the parts of the adult are preformed in the germ, and development only consists in the growth of these parts and their more perfect arrangement. This theory was generally accepted until the middle of the last century, when Kaspar Friedrich Wolff brought forward the theory of 'epigenesis,' which since that time has been the dominant one. This assumes that no special parts of the germ are preformations of certain parts of the fully-developed animal, and that these latter arise by a series of changes in the germ, which gradually gives rise to them. In modern times the theory of preformation has been revived in a less crude form, as is shown by the ideas of Nägeli, and by Darwin's 'pangenesis.'—A. W., 1888.

separate stages. We imagine these stages as existing in the continuous course of ontogeny; for here, as in all departments of nature, we make artificial divisions in order to render possible a general conception, and to gain fixed points in the continuous changes of form which have in reality occurred. Just as we distinguish a sequence of species in the course of phylogeny, although only a gradual transition, not traversed by sharp lines of demarcation, has taken place, so also we speak of the stages of ontogeny, although we can never point out where any stage ends and another begins. To imagine that each single stage of a part is present in the germ, as a distinct group of gemmules, seems to me to be a childish idea, comparable to the belief that the skull of the young St. Laurence exists at Madrid, while the adult skull is to be found in Rome.

We are necessarily driven to such conceptions if we assume that the transmission of acquired characters takes place. A theory of preformation alone affords the possibility of an explanation: an epigenetic theory is utterly unable to render any assistance in reaching an interpretation. According to the latter theory, the germ does not contain any preformed gemmules, but it possesses, as a whole, such a chemical and molecular constitution that under certain circumstances, a second stage is produced from it. For example, the two first segmentation spheres may be regarded as such a second stage; these again possess such a constitution that a certain third stage, and no other, can arise from them, forming the four first segmentation spheres. At each of these stages the spheres produced are peculiar to a distinct species and a distinct individual. From the third stage a fourth arises, and so on, until the embryo is developed, and still later the mature animal which can reproduce itself. No one of the parts of such an animal was originally present as distinct parts in the egg from which it was developed, however minute we may imagine these parts to be. If now an inherited peculiarity shows itself in any organ of the mature animal, this will be the consequence of the preceding developmental stages, and if we were able to investigate the molecular structure of all these stages as far back as the egg-cell, we should trace back to the latter some minute difference of molecular constitution which would distinguish it from any other egg-cell of the same species, and was destined to be the cause of the subsequent appearance of the peculiarity in the mature animal. It is only by the aid of some such hypothesis that we can conceive the cause of hereditary individual differences and the tendencies towards hereditary diseases. Hereditary epilepsy would be intelligible in this way, that is, when the disease is congenital and not due to the presence of microbes, as is presumably the case with artificially induced epilepsy.

The question now arises as to whether we can conceive the communication of such traumatic and therefore acquired epilepsy to the germ-cells. This is obviously impossible under the epigenetic theory of development described above. In what way can the germ-cells be affected by molecular or histological changes in the pons varolii and medulla oblongata? Even if we assume, for the sake of argument, that the central nervous system exercises trophic influences upon the germ-cells, and that such influences may consist of something more than variations in nutritive conditions, and may even include the power of altering the molecular constitution of the germ-plasm in spite of its usual stability; even if we concede these suppositions, how is it conceivable that the changes produced would be of the exact nature and in the exact direction necessary in order to confer upon the germ-plasm the molecular structure of the first ontogenetic stage of an epileptic individual? How can the last ontogenetic stage of the ganglion cells in the pons and medulla of such an individual, stamp upon the germ-plasm in the germ-cells of the same animal—not indeed the peculiar structure of the stage itself—but such a molecular constitution as will ensure the ultimate appearance of epilepsy in the offspring? The theory of epigenesis does not admit that the parts of the full-grown individual are contained in the germ as preformed material particles, and therefore this theory cannot allow that anything is added to the germ-plasm; but in accepting the above-made supposition, we are compelled to assume that the molecular structure of the whole of the germ-plasm is changed to a slight extent.

Nägeli is quite right in maintaining that the solid protoplasm alone, as opposed to the fluid part, i. e. that part of the protoplasm which has passed into solution, can act as the bearer of hereditary tendencies. This appears to be undoubtedly proved by the fact that the amount of material provided by the male parent for the development of an embryo is in almost all animals far smaller than the amount provided by the female parent.

In Mammalia the share contributed by the father probably only forms about one hundred-billionth part of that contributed by the mother, and yet nevertheless the influence of the former in heredity is on an average equal to that exerted by the latter[1]. Now, from the point of view of epigenesis, no molecule of the brain of an epileptic animal can reach the germ-cell except in a state of solution, and therefore no direct increase in the germ-plasm can be referred to such molecules, quite apart from the fact that such addition, even if possible, could not be of any value, because the last stage of the epileptic tendency must be represented in the nerve-cells and nerve-fibres of the diseased brain, while the first stage ought to be represented in the germ-cell.

It may be safely asserted that according to the theory of epigenesis the germ-cells cannot be influenced except as regards their nutrition. Nutritive changes may be imagined to occur through the varying trophic influence of the nervous system upon the sexual organs, but the structure of the germ-plasm cannot be altered by mere nutritive changes, or at all events it cannot be altered in that distinct and definite direction which is required by the supposed transmission of acquired epilepsy.

Thus the transmission of artificially produced epilepsy can neither be explained upon the epigenetic theory, nor upon the theory of preformation; it can only be rendered intelligible if we suppose that the appearance of the disease in the offspring depends upon the introduction and presence of living germs, viz. of microbes. The supposed transmission of this artificially produced disease is the only definite instance which has been hitherto brought forward in support of the transmission of acquired characters. I believe that I have shown that such support is deceptive, not because there is any uncertainty about the fact of the transmission itself, but because it is a transmission which cannot depend upon heredity, and is in all probability due to infection.

Ever since I began to doubt the transmission of acquired characters, I have been unable to meet with a single instance which could shake my conviction. There were many instances in which hereditary transmission was clearly established, but in none of them

---

[1] Nägeli, l. c. p. 110.

was there any reason to suppose that the characters transmitted were really acquired. For example, Fritz Müller has recently informed me of an instance in which he believes that there can be no doubt of the transmission of acquired characters. His observations are so interesting in several respects that I will quote them here. He says in his letter, 'Among the bastards of two species of *Abutilon*, in which I had never observed hexamerous flowers, there was a single plant with a few such blossoms. As these flowers are sterile with the pollen of the same plant, I was obliged to fertilize it with pollen from another plant bearing only pentamerous flowers, in order to obtain seeds from the former. For three weeks I examined all the flowers from a plant grown from such seed, finding 145 pentamerous, 103 hexamerous, and 13 heptamerous flowers. I examined similarly the flowers of another plant produced from seed obtained from pentamerous flowers from the same parent plants. There were 454 pentamerous and 6 hexamerous flowers, and hence only 1·3 per cent. of the latter kind.'

It must certainly be admitted that the large proportion of abnormal hexamerous flowers depends upon heredity in the instance first quoted; but the hexamerous condition is not an acquired character; it is merely the first appearance of a new innate character. It is not due to the reaction of the vegetable organism under some external stimulus, for it appeared in a plant exposed to conditions similar to those which acted upon the other plant which only produced the normal pentamerous flowers. It must therefore have resulted from the tendencies which were present in the germ from which the plant itself developed, either as a spontaneous change in the germ-plasm or through the combination of two parental germ-plasms—a combination which may lead to the appearance or the reality of a new character. We know that the germ-plasm of each individual is not a simple substance, but possesses a very complex composition, for it consists of a number of ancestral germ-plasms represented in very different proportions. Now, although we cannot learn anything directly about the processes of growth of the germ-plasm, and its resulting ontogenetic stages, yet we do know, chiefly from observations upon man, that the characters of ancestors appear in the offspring in very different combinations and in very different degrees of strength. This may, perhaps, be explained by assuming that in the union of parental germ-plasms which takes place at fertilization, the contained ancestral germ-plasms unite in different ways, and thus come to grow with different strengths. Certain ancestral germ-plasms will meet and together produce a double effect: other opposed germ-plasms will neutralize each other; and between these two extremes all intermediate conditions will occur. And these combinations will not only take place at fertilization, but also at every stage of the whole ontogenetic history, for each stage is represented by its idioplasm, which is itself composed of ancestral idioplasms.

We do not yet know enough to be able to prove in detail the manner in which new characters may arise from such a combination of different kinds of germ-plasm. And yet it appears to me that such a view, e. g. in the case of the variation of buds, is by far the most natural. There is indeed a single example in which we can, to some extent, understand how it is that a new character may arise by these means. Certain canary-birds have a tuft of feathers on the head, but if two such birds are paired, their descendants are generally bare-headed, instead of having larger tufts[1]. The formation of a tuft depends upon the fact that the feathers are scanty and in fact absent from part of the skin of the head. Now when the scanty plumage of both parents is combined in the offspring the latter is bare-headed. Hence by the combination of ancestral characters a new character (bare-headedness) is produced, and one which is hardly likely to have ever occurred in the ancestors of existing canaries.

We do not know the causes which have been in operation when a flower possesses one petal more than the usual number, any more than we can explain why it is that one star-fish has five and another six rays. We cannot unravel the details of the mysterious relationship between two parent germ-plasms, each of which is composed of a countless number of ancestral germ-plasms from the first and second back to the *n*th degree. But we can nevertheless maintain in a general way that such irregularities are the result of this complex struggle between the germ-plasms in the ovum and the idioplasms in the subsequent stages of the developing organism, and that they are not the result of external influences.

---

[1] See Darwin, 'The Variation of Animals and Plants under Domestication.' 1875. Vol. I. p. 311.

If, however, acquired characters are brought forward in connexion with the question of the transformation of species, the term 'acquired' must only be applied to those characters which do not arise from within the organism, but which arise as the reaction of the organism under some external stimulus, most commonly as the consequence of the increased or diminished use of an organ or part. We have then to learn whether the altered conditions of life, by forcing an organism to adopt new habits, can by such means lead directly, and not indirectly through natural selection, to the transformation of the species; or whether the effects of increased or diminished use of certain parts, implied by the new habits, are restricted to the individual itself, and therefore powerless to effect any direct modification of the species.

Fritz Müller's observation is also interesting in another respect: it appears to controvert my views upon heredity as expressed in the theory of the continuity of the germ-plasm. If a single flower can transmit to its descendants special peculiarities which were not possessed by its ancestors, we seem to be driven to the conclusion that the ancestral germ-plasm has not passed into the flower in question, but that new germ-plasm has been formed, inasmuch as the new characters are derived from the flower itself, and not from any of its ancestors. I think, however, that the observation admits of another interpretation: a specimen of *Abutilon* with many hundred flowers is not a single individual, but a colony consisting of numerous individuals which have arisen by budding from the first individual developed from the seed.

I have not hitherto considered budding in relation to my theories, but it is obvious that it is to be explained from my point of view, by supposing that the germ-plasm which passes on into a budding individual consists not only of the unchanged idioplasm of the first ontogenetic stage (germ-plasm), but of this substance altered, so far as to correspond with the altered structure of the individual which arises from it—viz. the rootless shoot which springs from the stem or branches. The alteration must be very slight, and perhaps quite insignificant, for it is possible that the differences between the secondary shoots and the primary plant may chiefly depend upon the changed conditions of development, which takes place beneath the earth in the latter case, and in the tissues of the plant in the former. Thus we may imagine that the idioplasm, when it developes into a flowering shoot, produces at the same time the germ-cells which are found in the latter. We thus approach an understanding of Fritz Müller's observation; for if the whole shoot which produces the flower arises from the same idioplasm which also forms its germ-cells, we can readily understand why the latter should contain the same hereditary tendencies which were previously expressed in the flower which produced them. The fact that variations may occur in a single shoot depends upon the changes explained above, which occur in the idioplasm during the course of its growth, as a result of the varying proportions in which the ancestral idioplasms may be contained in it.

Fritz Müller's observation affords a beautiful confirmation of this view, for if the flower itself transmitted the hexamerous condition to its germ-cells, we could not understand why some of the extremely rare hexamerous flowers were produced by the crossing of two pentamerous flowers, in the control experiment. An explanation of this fact can only be found in the assumption that the germ-plasm contained in the mother plant, during its growth and consequent distribution through all the branches of the colony, became arranged into a combination of idioplasms, which, whenever it predominated (as it did at certain places), necessarily led to the formation of hexamerous flowers. I will not consider here the question as to whether this combination is to be looked upon as an instance of reversion, or whether it represents something new. Such a question is of no importance for our present purpose; but the hexamerous flowers of the control experiment prove, in my opinion, that germ-plasm containing the requisite combination was distributed in the mother plant and also existed, but in insufficient amount, in shoots which did not produce any hexamerous flowers.

APPENDIX V. ON THE ORIGIN OF PARTHENOGENESIS[1].

The transformation of heterogeny into pure parthenogenesis has obviously been produced by other causes as well as by those mentioned in the main part of this paper. Other and quite different circumstances have also had a share in its production. Pure parthenogenesis may be produced without the intermediate condition of heterogeny.

---

[1] Appendix to page 290.

Thus, for example, the pure and exclusive parthenogenesis with which the large Phyllopod crustacean, *Apus*, is reproduced at most of its habitats, has not arisen from the loss of previously existent sexual generations, but simply from the non-appearance of males, accompanied by the simultaneous acquisition of the power, on the part of the females, of producing eggs which do not require fertilization. This is proved by the fact that males occur in certain scattered colonies of this species, and sometimes they are even present in considerable numbers. But even if we were not aware of these facts, the same conclusions might nevertheless have been drawn from the fact that *Apus* produces eggs of only one form —viz. resting eggs with hard shells. In every case in which parthenogenesis has been first introduced in alternation with sexual reproduction, the resting eggs are produced by the latter generations, while the parthogenetic generations produce eggs with thin shells, in which the embryo developes and hatches very rapidly. In this way parthenogenesis leads to a rapid increase of the colony. In *Apus* such increase in the number of individuals is gained in an entirely different manner, viz. by the fact that all the animals become females, which produce eggs at a very early age, and continue producing them in increasing fertility for the whole of their life. In this manner an enormous number of eggs collects at the bottom of the pool inhabited by the colony, so that after it has dried up, in spite of loss from various destructive agencies, there will still remain a sufficiency of eggs to reproduce a numerous colony, as soon as the pool has filled again.

This form of parthenogenetic reproduction is especially well suited to the needs of species inhabiting small pools which entirely depend upon rain-fall, and which may disappear at any time. In these cases the time during which the colony can live is often too short to permit the production of several generations even from rapidly developing summer-eggs. Under these circumstances the pool would often suddenly dry up before the series of parthenogenetic generations had been run through, and hence before the appearance of the sexual generation and resting eggs. In all such cases the colony would be exterminated.

This consideration might lead us to think that Crustacea, such as the *Daphnidae*, which develope by means of heterogeny, would hardly be able to exist in small pools filled by the rain ; but here also nature has met the difficulty by another adaptation. As I have shown in a previous paper[1], the heterogeny of the species of *Daphnidae* which inhabit such pools is modified in such a manner, that only the first generation produced from the resting eggs consists of purely parthenogenetic females, while the second includes many sexual animals, so that resting eggs are produced and laid, and the continuance of the colony is secured a few days after it has been first founded; viz. after the appearance of the first generation.

But it is also certain that in the *Daphnidae*, heterogeny may pass into pure parthenogenesis by the non-appearance of the sexual generations. This seems to have taken place in certain species of *Bosmina* and *Chydorus*, although perhaps only in those colonies of which the continuance is secured for the whole year; viz. those which inhabit lakes, water-pipes, or wells in which the water cannot freeze. In certain insects also (e. g. *Rhodites rosae*) pure parthenogenesis seems to be produced in a similar manner, by the non-appearance of males.

But the utility which we may look upon as the cause of parthenogenesis is by no means so clear in all cases. Sometimes, especially in certain species of Ostracoda, its appearance seems almost like a mere caprice of nature. In this group of the Crustacea, one species may be purely parthenogenetic, while a second reproduces itself by the sexual method, and a third by an alternation of the two methods: and yet all these species may be very closely allied and may frequently live in the same locality and apparently with the same habit of life. But it must not be forgotten that it is only with the greatest difficulty that we can acquire knowledge about the details of the life of these minute forms, and that where we can only recognize the appearance of identical conditions, there may be highly important differences in nutrition, habits, enemies and the means by which they are resisted, and in the mode by which the prey is captured—circumstances which may place two species living in the same locality upon an entirely different basis of existence. It is not merely probable that this is the case; for the fact that certain species have modified their modes of reproduction is in itself a sufficient proof of the validity of the conclusions which have just been advanced.

---

[1] Weismann, 'Naturgeschichte der Daphnoiden,' Zeitschrift f. wiss. Zool. XXIII. 1879.

The fact that different methods of reproduction may obtain in different colonies of the same species, although with thoroughly identical habits, may depend upon differences in the external conditions (as in *Bosmina* and *Chydorus* mentioned above), or upon the fact that the transition from sexual to parthenogenetic reproduction is not effected with the same ease and rapidity in all the colonies of the same species. As long as males continue to make their appearance in a colony of *Apus*, sexual reproduction cannot wholly disappear. Although we are unable to appreciate, with any degree of certainty, the causes by which sex is determined, we may nevertheless confidently maintain that such determining influences may be different in two widely separated colonies. As soon, however, as parthenogenesis becomes advantageous to the species, securing its existence more efficiently than sexual reproduction, it will not only be the case that the colonies which produce the fewest males will gain advantage, but within the limits of the colony itself, those females will gain an advantage which produce eggs that can develope without fertilization. When the males are only present in small numbers, it must be very uncertain whether any given female will be fertilized: if therefore the eggs of such a female required fertilization in order to develope, it is clear that there would be great danger of entire failure in this necessary condition. In other words:—as soon as any females begin to produce eggs which are capable of development without fertilization, from that very time a tendency towards the loss of sexual reproduction springs into existence. It seems, however, that the power of producing eggs which can develope without fertilization is very widely distributed among the Arthropoda.

APPENDIX VI. W. K. BROOKS' THEORY OF HEREDITY[1].

The only theory of heredity which, at any rate in one point, agrees with my own, was brought forward two years ago by W. K. Brooks of Baltimore[2]. The point of agreement lies in the fact that Brooks also looks upon sexual reproduction as the means employed by nature in order to produce variation. The manner in which he supposes that the variability arises is, however, very different from

---

[1] Appendix to page 277.

[2] Compare W. K. Brooks, 'The Law of Heredity, a Study of the Cause of Variation and the Origin of living Organisms.' Baltimore, 1883.

that suggested in my theory, and our fundamental conceptions are also widely divergent. While I look upon the continuity of the germ-plasm as the foundation of my theory of heredity, and therefore believe that permanent hereditary variability can only have arisen through some direct change in the germ-plasm effected by external influences, or following from the varied combinations which are due to the mixture of two individually distinct germ-plasms at each act of fertilization, Brooks, on the other hand, bases his theory upon the transmission of acquired characters, and upon the idea which I have previously called 'the cyclical development of the germ-plasm.'

Brooks' theory of heredity is a modification of Darwin's pangenesis, for Brooks also assumes that minute gemmules are thrown off by each cell in the body of the higher organisms; but such gemmules are not emitted always, and under all circumstances, but only when the cell is subjected to unaccustomed conditions. During the persistence of the ordinary conditions to which it is adapted, the cell continues to perform its special functions as part of the body, but as soon as the conditions of life become unfavourable and its functions are disturbed, the cell 'throws off minute particles which are its germs or gemmules.'

These gemmules may then pass into any part of the organism; they may penetrate the ova in the ovary, or may enter into a bud, but the male germ-cells possess a special power of attracting them and of storing them up within themselves.

According to Brooks, variability arises as a consequence of the fact that each gemmule of the sperm-cell unites, during fertilization, with that part of the ovum which, in the course of development, is destined to become a cell corresponding to that from which the gemmule has been derived.

Now, when this cell developes in the offspring, it must, as a hybrid, have a tendency to vary. The ova themselves, as cells, are subject to the same laws; and the cells of the organism will continue to vary until one of the variations is made use of by natural selection. As soon as this is the case, the organism becomes, *ipso facto*, adapted to its conditions; and the production of gemmules ceases, and with it the manifestation of variability itself, for the cells of the organism then derive the whole of their qualities from the egg, and being no longer hybrid, have no tendency to vary. For the same reason the ova themselves will also cease to vary, and the favourable variation will be transmitted from generation to generation in a stereotyped succession, until unfavourable conditions arise, and again lead to a fresh disposition to vary.

In this way Brooks[1] attempts to mediate between Darwin and Lamarck, for he assumes, on the one hand, that external influences render the body or one of its parts variable, while, on the other hand, the nature of the successful variations is determined by natural selection. There is, however, a difference between the views of Brooks and Darwin, although not a fundamental difference. Darwin also holds that the organism becomes variable by the operation of external influences, and he further assumes that changes acquired in this way can be communicated to the germ and transmitted to the offspring. But according to his hypothesis, every part of the organism is continually throwing off gemmules which may be collected in the germ-cells of the animal, while, according to Brooks, this only takes place in those parts which are placed under unfavourable conditions or the function of which is in some way disturbed. In this manner the ingenious author attempts to diminish the incredible number of gemmules which, according to Darwin's theory, must collect in the germ-cells. At the same time he endeavours to show that those parts must always vary which are no longer well adapted to the conditions of life.

I am afraid, however, that Brooks is confounding two things which are in reality very different, and which ought necessarily to be treated separately if we wish to arrive at correct conclusions: viz., the adaptation of a part of the body to the body itself, and its adaptation to external conditions. The first of these adaptations may exist without the second. How can those parts become variable which are badly adapted to the external conditions, but are nevertheless in complete harmony with the other parts of the body? If the conditions of life of the cells which constitute the part in question must become unfavourable, in order that the gemmules which produce variation may be thrown off, it is obvious that such a result would not occur in the case mentioned above. Suppose, for example, that the spines of a hedgehog are not sufficiently long or sharply pointed to afford protection to the animal,

---

[1] l. c., p. 82.

how could such an unfavourable development afford the occasion for the throwing off of gemmules, and a resulting variability of the spines, inasmuch as the epidermic tissue in which these structures arise, remains under completely normal and favourable conditions, whatever length or sharpness the spines may attain? The conditions of the epidermis are not unfavourably affected because, as the result of short and blunt spines, the number of hedgehogs is reduced to far below the average. Or consider the case of a brown caterpillar which would gain great advantage by becoming green; what reason is there for believing that the cells of the skin are placed in unfavourable conditions, because, in consequence of the brown colour, far more caterpillars are detected by their enemies, than would have been the case if the colour were green? And the case is the same with all adaptations. Harmony between the parts of the organism is an essential condition for the existence of the individual. If it is wanting, the individual is doomed; but such harmony between any one part and all others, i.e. proper nutrition for each part, and adequate performance of its proper function, can never be disturbed by the fact that the part in question is insufficiently adapted to the outer conditions of life. According to Darwin, all the cells of the body are continually throwing off gemmules, and against such an assumption no similar objection can be raised. It can only be objected that the assumption has never been proved, and that it is extremely improbable.

A further essential difference between Darwin's theory of pangenesis and Brooks' hypothesis lies in the fact that Brooks holds that the male and female germ-cells play a different part, and that they tend to become charged with gemmules in different degrees, the egg-cell containing a far smaller number than the sperm-cell. According to Brooks the egg-cell is the conservative principle which brings about the permanent transmission of the true characters of the race or species, while he believes that the sperm-cell is the progressive principle which causes variation.

The transformation of species is therefore believed to take place, for the most part, as follows:—those parts which are placed in unfavourable conditions by the operation of external influences, and which have varied, throw off gemmules which reach the sperm-cells, and the latter by fertilization further propagate the variation. An increase of variation is produced because the gemmules which reach the egg through the sperm-cell may unite or conjugate with parts of the former which are not the exact equivalents of the cells from which the gemmules arose, but only very nearly related to them. Brooks calls this 'hybridization,' and he concludes that, just as hybrids are more variable than pure species, so such hybridized cells are also more variable than other cells.

The author has attempted to work out the details of his theory with great ingenuity, and as far as possible to support his assumptions by facts. Moreover, it cannot be denied that there are certain facts which seem to indicate that the male germ-cell plays a different part from that taken by the female germ-cell in the formation of a new organism.

For example, it is well known that the offspring of a horse and an ass is different when the male parent is a horse from what it is when the male parent is an ass. A stallion and a female ass produce a hinny which is more like a horse, while a male ass and a mare produce a mule which is said to be more like an ass[1]. I will refrain from considering here the opinion of several authors (Darwin, Flourens, and Bechstein) that the influence of the ass is stronger in both cases, only predominating to a less extent when the ass is the female parent; and I will for the sake of brevity accept Brooks' opinion that in these cases the influence of the father is greater than that of the mother. Were this so in all cross-breeding between different species and in all cases of normal fertilization, we should be compelled to conclude that the influences of the male and female germ-plasms upon the offspring

---

[1] This seems to be the general opinion (see the quotation from Huxley in Brooks' 'Heredity,' p. 127); but I rather doubt whether there is such a constant difference between mules and hinnies. Furthermore, I cannot accept the opinion that mules always resemble the ass more than the horse. I have seen many mules which bore a much stronger likeness to the latter. I believe that it is at present impossible to decide whether there is a constant difference between mules and hinnies, because the latter are very rarely seen, and because mules are extremely variable. I attempted to decide the question last winter by a careful study of the Italian mules, but I could not come across a single hinny. These hybrids are very rarely produced, because it is believed that they are extremely obstinate and bad-tempered. I afterwards saw two true hinnies at Professor Kühn's Agricultural Institute at Halle. These hinnies by no means answered to the popular opinion, for they were quite tractable and good-tempered. They looked rather more like horses than asses, although they resembled the latter in size. In this case it was quite certain that one parent was a stallion and the other a female ass.—A. W. 1889.

differ at any rate in strength. But this is by no means always the case, for even in horses the reverse may occur. Thus it is stated that certain female race-horses have always transmitted their own peculiarities, while others allowed those of the stallion to preponderate.

In the human species the influence of the mother preponderates quite as often as that of the father, although in many families most of the children may take after either parent. There is nevertheless hardly any large family in which all the children take after the same parent. If we now try to explain the preponderating influence of one parent by the supposition of a greater strength in hereditary power, without first inquiring after some deeper cause, I think the only conclusion warranted by the facts before us is that this power is rarely or never equal in both of the conjugating germ-cells, but that even within the same species, sometimes the male and sometimes the female is the stronger, and that the strength may even vary in the different offspring of the same individuals, as we so frequently see in human families. The egg-cells of the same mother which ripen one after the other, and also the sperm-cells of the same father, must therefore present variations in the strength of their hereditary power. It is then hardly to be wondered at that the relative hereditary power of the germ-cells in different species should vary, although we cannot as yet understand why this should be the case.

It would not be very difficult to render these facts intelligible in a general way by an appeal to physiological principles. The quantity of germ-plasm contained in a germ-cell is very minute, and together with the idioplasms of the various ontogenetic stages to which it gives rise, it must be continually increased by assimilation during the development of the organism. If now this power of assimilation varied in intensity, a relatively rapid growth of the idioplasm derived from one of the parents would ensue, and with it the preponderance of the hereditary tendencies of the parent in question. Now, it is obvious that no two cells of the same kind are entirely identical, and hence there must be differences in their powers of assimilation. Thus the varying hereditary powers of the egg-cells produced from the same ovary become explicable, and still more easily the varying powers of the germ-cells produced in the ovaries or testes of different individuals of the same species; most easily of all the differences observable in this respect between the germ-cells of different species.

Of course, this hereditary power is always relative, as may be easily proved by cross-breeding between different species and races. Thus when a fantail pigeon is crossed with a laugher, the characters of the former preponderate, but when crossed with a pouter the characters of the latter preponderate [1]. The facts afforded by cross-breeding between hybrids and one of the pure parent species, together with a consideration of the resulting degree of variability, seem to me to be even more unfavourable to Brooks' view. They appear to me to admit of an interpretation different from that brought forward by him; and when he proceeds to make use of secondary sexual characters for the purpose of his theory, I believe that his interpretation of the facts can be easily controverted. It is hardly possible to conclude that variability is due to the male parent, because the males in many species of animals are more variable, or deviate further from the original type, than the females. It is certainly true that in many species the male sex has taken the lead in processes of transformation, while the female sex has followed, but there is no difficulty in finding a better explanation of the fact than that afforded by the assumption 'that something within the animal compels the male to lead and the female to follow in the evolution of new breeds.' Brooks has with great ingenuity brought forward certain instances which cannot be explained with perfect confidence by Darwin's theory of sexual selection, but this hardly justifies us in considering the theory to be generally insufficient, and in having recourse to a theory of heredity which is as complicated as it is improbable. The whole idea of the passage of gemmules from the modified parts of the body into the germ-cells is based upon the unproved assumption that acquired characters can be transmitted. The idea that the male germ-cell plays a different part from that of the female, in the construction of the embryo, seems to me to be untenable, especially because it conflicts with the simple observation that upon the whole human children inherit quite as much from the father as from the mother.

---

[1] Darwin, 'Variation of Animals and Plants under Domestication,' 1875, Vol. II. p. 41.