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Unisexual Inheritance

by

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(Schluss.)

It does not seem to me that much light is or can be, thrown on the problem of sexual dimorphism by the statistical methods of investigation now so much in vogue among biologists. Professor Karl Pearson, although not claiming to be a biologist himself, has taken a leading part in the development of the mathematical treatment of biological statistics. In his Grammar of Science[1]) he gives an outline of the science of biology from what he considers the physical point of view, as distinguished from the metaphysical. His exposition may be perfectly sound so far as it goes, but I have been unable to discover in it any discussion of the phenomena of unisexual inheritance. In considering inheritance in animals which reproduce sexually he states that there are three chief forms, blended inheritance, exclusive inheritance, and particulate inheritance.

By exclusive inheritance he does not mean unisexual inheritance, but merely the inheritance by an offspring of either sex, of any character exclusively from one parent[2]). In another place he con-

1) The Grammar of Science, 2nd Edition: London, A. & C. Black, 1900.

2) For example when a black mouse is paired with a white the offspring may be all black, or all white, or piebald black and white, or of a uniform intermediate colour. The first two cases are exclusive inheritance the third is parziculate inheritance, the last blended inheritance.

siders the various forms of sexual selection. Of this he distinguishes five forms, one of which termed apolegamic or preferential mating is stated to be selection in the narrower sense of Darwin, while another is assortative mating, the selection of like by like, preference not for a mate in which certain characters are most developed, but for a mate most similar to the seeker. He does not consider all the forms in detail, but in his own words „contents himself with some illustrations of how exact quantitative methods can be applied to the problems of apolegamic and homogamic mating".

His application of quantitative methods consists in ascertaining whether preferential mating is actually taking place with regard to given characters. In the whole of the discussion not a word is said as to the consequence of the selection, as to the interpretation or explanation of the existence of constant differences between the sexes. In fact, Professor Pearson seems to have in mind the question whether it is possible to demonstrate by measurements and numbers that both progressive change of type in a single race, and the differentiation of one race into two or more, actually take place as the result of variation and selection. He remarks that „without a barrier to intercrossing during differentiation the origin of species seems inexplicable". He considers sexual selection as merely forming a barrier to intercrossing: to quote his words: „By sexual selection I would understand something rather more than Darwin includes by that term, namely, all differential mating due to taste, habit, or circumstance, which prevents a form of life from freely intercrossing." But of sexual selection in the true Darwinian sense, as a part of the theory of sexual dimorphism, and the explanation of the evolution of conspicuous characters which are either useless or even harmful in ordinary life, Professor Pearson seems to have no conception whatever.

He takes the case of stature in the human race and ascertains from actual measurements what differences there are in type and variability between husbands, and men in general, or between wives and women in general. He finds that in no case, except in the type in the case of women, is there any certain difference, and in that exception the difference is not „significant". The statistics, he says, only run to a few hundreds, and were not specially collected for the purpose; still so far as they go they show no evidence in mankind of preferential mating with respect to stature, or of any character very closely correlated with stature. And yet stature is one of the characters in which human beings are most distinctly dimorphic sexually. If we take from Professor Pearson's figures the difference in type between husbands and wives instead of between husbands and men in general, it is 5.267 inches, while the difference in variability is very slight. Professor Pearson makes no remark on this.

He next considers eye-colour from the same point of view, and finds that there is a distinct difference of type between husbands and men in general. There is also a difference in type but of less magnitude between wives and women in general. The general tendency is for the lighter eyed to mate, the darker eyed being less frequently married. Whether the fact is due to actual preference on the part of the women is not certain, it may be due to greater philogamic instincts on the part of the blonde section of the population.

In this case then more light-eyed men get married than dark eyed men, and also more light eyed women than dark eyed women, but the selection is greater among the men. But what Professor Pearson does not discuss is the relation of these conclusions to the sexual dimorphism. Are men lighter eyed than women in type? The figures given show a considerable difference between the sexes in this respect, and apparently it does consist in the men being lighter in eye-colour. But what reason is there for supposing that the selection for marriage of the lighter-eyed men would have any effect in making men on the average lighter-eyed than women? Again we find the essential point ignored by Professor Pearson: sexual selection may have been proved to be taking place, but what is the relation of this selection to the sexual dimorphism?

Professor Pearson next proceeds to discuss assortative mating in mankind, and examines again the same two characters, namely, stature and eye-colour. He finds that there is a quite sensible tendency of like to mate with like, husband and wife are more alike for one of these characters than uncle and niece, and for the other more alike than first cousins. There is therefore according to this evidence, not only no sexual selection in relation to stature, but actually a selection in the opposite direction. Yet as I have already urged the difference in stature is one of the most marked of the secondary sexual differences in mankind. Professor Pearson's investigation with regard to this point therefore goes to prove that the sexual dimorphism in this character is not only not maintained by sexual selection or preferential mating, but is maintained in direct opposition to assortative mating which is the opposite of sexual selection in Darwin's sense.

Professor Pearson also finds that a quite sensible measure of homogamy or assortative mating exists with regard to eye-colour. This seems to be in contradiction to his previous result that preferential mating occurs in reference to this character. It is difficult to understand how women can at the same time prefer men with the lightest eyes, and those with eyes most like their own. The contradiction is apparently explained by the fact that the lightest-eyed women are also more frequently married. But it seems to me that if this is the case sexual selection in Darwin's sense does not take place in

reference to this character. Yet as I have said there would seem to be some sexual dimorphism in eye colour in mankind. I am not concerned however to interpret Professor Pearson's results, but merely to point out that they tend to disprove the assumption that there is a connection between sexual selection and sexual dimorphism, and also to point out that Professor Pearson has failed to show how the causes of sexual dimorphism are to be investigated by his mathematical methods.

If the theory I have formulated in my book on Sexual Dimorphism[1]) were true we should have a complete explanation of all the peculiarities of unisexual characters. That theory is founded on the truth that in a great number of the best known cases the special structures which constitute the unisexual characters are exposed in every generation to definite special stimulations produced by the behaviour of the animals in their sexual relations. The theory is merely that such stimulations cause excessive growth of the tissues affected, in other words, produce local hypertrophy, and that such processes of growth after a number of generations are inherited. The modifications of growth having been set up in mature individuals of only one sex during sexual maturity and activity, are inherited only in correlation with the same condition of the body. If the inherited process of development were thus a repetition more or less exact of the process set up by external stimulation, we should have an intelligible explanation of the well known and remarkable peculiarities in the development of secondary sexual characters. For the original process was limited to one sex, and was set up when the testes were functionally active, and when the nervous system was in a state of excitement which affected all the functions of the body. The hereditary repetition would therefore be similarly limited, whether the limitation was merely to one sex, or as in many cases restricted to one season of the year in that sex. Moreover as the original process of growth was associated with the functional activity of the testes, and the nervous excitement produced by that activity, the hereditary repetition would be wanting in an individual from which the testes had been removed, and thus we should have an explanation of the suppression of secondary characters in castrated males, otherwise one of the most inexplicable facts in all physiology.

Professor Meldola, in criticising my book[2]), declared that he could see no force in this argument. He stated that there was absolutely nothing in the Lamarckian explanation to account for the non-transmission of the male characters to the female. He asked why

1) Sexual Dimorphism in the Animal Kindom: London, A. & C. Black, 1900.
2) „Nature" Vol. 63, p. 197. Dec. 27, 1900.

should my view be supposed to account for the limitation of the male characters to the male, and the former view (Darwin's) to fail. He then repeated Wallace's suggestion that the female being in greater need of concealment had had any tendency to inherit the male characters eliminated by natural selection. These criticisms seem to me to show that my critic had failed to understand not only my theory but Darwin's. Darwin did not even attempt to explain the unisexual limitation, but pointed out that the variations must have been unisexually limited before they were selected. It is not a question of my explanation versus Darwin's but of mine versus none. Mine is a theory of the origin of certain variations, Darwin's a theory of their preservation. Professor Meldola does not show in what way or for what reason my hypothesis fails to explain the facts, he merely asserts that it fails. When in a correspondence in „Nature" I put forward some arguments in explanation of my position, Professor Meldola urged that my theory could not be true, because as I myself admitted, male characters were in certain cases developed also in the female as for instance in the Reindeer. My theory is intended to explain first and foremost secondary sexual characters of the most typical kind, which I defined as those which are affected by castration, which do not develop normally after removal of the generative organs. Whether such characters may ultimately be transferred to both sexes, or whether unisexual characters exist which are independent of the condition of the generative organs are secondary questions which do not necessarily invalidate my theory of the origin of the typical cases.

Professor Meldola at once attacked my definition, and stated that so far as he knew there was no single observation, with the exception perhaps of Stylopised bees, which would bring the sexual characters of fishes, reptiles, crustacea, insects etc., within its scope, and asked: „Is there any known case among these lower groups, where the removal of the generative organs leads to the appearance of the characters of one sex in individuals of the other sex?" Now from the facts collected by Darwin and those added by myself it is fully proved that in the lower classes to which Professor Meldola refers, unisexual characters as a general rule are not developed until the approach of sexual maturity, and the selfevident similarity of the phenomena in these lower animals with those seen in mammals and birds, justifies the conclusion that in the former also the development of the characters is physiologically correlated with the normal action of the reproductive organs. Professor Meldola's argument that my definition cancels at least half my own book would only be sound if he had proof that removal of the generative organs did not prevent the normal development of unisexual characters in fishes, reptiles, crustacea, etc.

Taking the words „removal of the generative organs“ literally, Professor Meldola's question may perhaps be answered in the negative; for although artificial castration has been attempted in fish, crayfish and even caterpillars, the effects of the operation on the unisexual characters do not appear to have been ascertained. It so happens, however, that there exists very remarkable evidence concerning the effects of a natural process of castration in one at least of the lower classes of animals, namely, the Crustacea. I refer to the remarkable observations which have been made principally by the eminent french zoologist, Alfred Giard, on what is known as parasitic castration. Professor Meldola, whose zoological studies have been chiefly devoted to insects, appears to be unacquainted with these important observations and they seem to me to afford strong support to my conclusions. One case which has been most carefully investigated is that of crabs infested by the parasite called Sacculina. The common shore crab *Carcinus moenas* is frequently attacked by one species of Sacculina. The parasite is a Cirripede, its early stages showing that it is allied to the barnacles. In its adult condition it forms a conspicuous bulbous structure attached by a thin peduncle to the lower surface of the abdomen, the so-called tail, of the crab. The peduncle is connected internally with a system of branching roots which ramify through nearly all the internal tissues of the crab. By means of these roots the parasite absorbs its nourishment from its host. Crabs infested with the parasite are almost invariably sterile. The generative organs, ovaries or testes, do not appear to be destroyed, but they are unable to become functionally active. The interesting fact in relation to my present subject is that male crabs infested by the Sacculina resemble the females externally, their secondary sexual characters being to a great extent suppressed, just as the antlers are suppressed in castrated stags. In the common shore crab the unisexual characters of the normal male are principally the enlargement of the pincher claws, and the different form and structure of the tail. In the normal male the tail is narrower than in the female, and of the seven segments of which it is composed the 3rd, 4th and 5th are firmly united, the joints between them being obliterated. In the infested male the tail is considerably broader and the lines of division between segments 3, 4 and 5 are quite distinct. According to Yves Delages who has made the most complete investigations of Sacculina, the crabs are infested when from three to four months old, and from four to twelve millimetres in diameter. Presumably at this time the special modifications of the male abdomen have not appeared, and the normal development of the testes being prevented by the presence of the Sacculina, at first entirely internal, the external or secondary modifications are also suppressed. It is possible, however, that even in the young

male crabs which are attacked by Sacculina the unisexual modifications have begun to appear, and that in subsequent development there is a regressive development of them. Another doubtful point is the history of both male and female crabs after the Sacculina has died. For the parasite does not kill the crab, it merely renders it incapable of reproduction. According to Delage the Sacculina lives a little more tha nthree years, and then dies a natural death, after having produced its eggs. After the death of the parasite the crab may recommence to moult and to grow, but the investigator does not say whether the crab recovers its fertility, nor has Giard discovered whether the suppressed secondary sexual characters of the male are recovered after the death of the parasite. Delage says he once met with a large crab which had no external Sacculina, or any trace of the scar where the peduncle had been attached, but around the intestine internally there were roots of a Sacculina in process of degeneration: he does not describe the sexual characters of this crab. Evidence therefore of the history of the crab after the death of the parasite is still to be obtained.

Other modifications of secondary sexual characters occur in both male and female shore crabs infested by Sacculina: in the normal male the first and second segments of the abdomen alone bear appendages which are modified as copulatory organs into stiff stylets: in the infested specimens these are more or less reduced in size. In the normal female the segments 2 to 5 bear four pairs of long appendages with two branches to which the eggs when laid are attached: these are reduced in size in the infested females.

In *Stenorhynchus phalangium* the sexual dimorphism is more pronounced than in *Carcinus maenas*, the difference between the sizes of the first pair of legs, the pincher claws, in the males and females being much greater. In male Stenorhynchus infested with Sacculina the pincher claws are no larger than in the female. In another form, *Inachus Scorpio*, the zoologist Fraisse was deceived by the effect of the parasite on the special characters of the males, and mistook them for females, so that he came to the conclusion that the males were never infested.

Another crustacean parasite belonging to a different order, namely, the Isopoda, lives in the branchial cavity of prawns and although it sends no processes into the interior of its host, but is entirely an external parasite, it nevertheless causes the host usually to be sterile. Giard does not say whether this is due to any special effect on the generative organs, but it appears to be due merely to the general effect on the nutrition of the host. However this may be, Giard has shown that the secondary sexual characters of the host are here also more or less completely suppressed. So much is this the case

that investigators previous to Giard's discovery had stated that only the females were attacked by the parasite, the truth being that the males infested were mistaken for females. The secondary sexual characters in the prawns are less marked than in crabs, they consist in modifications of the first two pairs of abdominal appendages for copulatory purposes, greater length of the thoracic chelae, and greater size of the olfactory branch of the first antennae.

It might perhaps be argued that the effect on the primary generative organs, ovaries or testes, being due to the disturbed nutrition of the host, the reduction of the secondary sexual characters was likewise simply due to diminished nutrition: the supply of nourishment being reduced the organs could not grow to their normal size. But it must be remembered that reduction in the supply of nourishment ought merely to reduce the size of the whole body, as starvation of a young animal is known to do, it does not necessarily reduce particular organs in comparison with others. The correct interpretation seems to be that the primary organs are not destroyed, but for want of nourishment are unable to produce generative products, and it is this functional development which is correlated with the development of the secondary characters.

The case of Stylopised bees to which Professor Meldola refers is precisely analogous with the cases of parasitic castration in Crustacea to which I have already referred. The facts in this case were carefully and successfully investigated by Professor Perez of Bordeaux in 1879. It was originally supposed that the bees carrying the parasite formed distinct species, but Perez found that they were individuals of other species modified by the effects of the parasite. The parasite Stylops is believed to belong to, or to be allied to, the Coleoptera or beetles. The minute active larva soon after it is hatched obtains entrance into the body of a larva of a solitary bee of the genus Andraena, and there changes into a footless maggot which lives at the expense of its host without killing it. The female stylopised Andraena has a head somewhat smaller than normal, the abdomen more globular, and more hairy: the most remarkable peculiarity is, however, that in the female the posterior legs are more slender, and their pollen brushes either much reduced or absent. The ovipositor is also reduced. The modifications of the male are of less degree, consisting chiefly in the loss of the coloration proper to the face. M. Perez found that in the female the development of the ovaries was completely arrested, and mature eggs were never produced, while in the male only the testicle of the side on which the parasite lies was affected, the other producing normal spermatozoa. In this case it is evident that the modifications of the hinder legs in the female bee are secondary sexual characters. It must be remembered

that the bees of the genus Andraena are solitary bees which provide food for their own young and do not produce neuter females or workers like the hive bees. According to my views therefore the hind legs in the female have been modified by the stimulations involved in collecting pollen for the young, and when the development of the ovaries is arrested the pollen brushes are imperfectly developed.

It may appear to be inconsistent with this interpretation that in the hive-bee the queen, a fully developed fertile female, is destitute of the pollen basket and pollen brush on the hind foot which are present in the worker. It might be argued that according to the above interpretation the sterility of the ovary in the worker ought to lead to the absence of modifications for nursing functions, and that these ought to be developed in the fertile queen. The explanation in this case is I believe that the ancestors of the hive bee possessed such modifications and that the queen has lost them through dis use. This effect of disuse has been correlated throughout the evolution with an increased fertility, and in the worker when the functional activity of the ovaries is suppressed the specialisations of the hind limb reappear. The ovary of the worker is not atrophied from the larval stage as in stylopised Andraena, it is merely prevented from attaining its perfect development. Possibly if the worker bee were stylopised its pollen collecting adaptations would be suppressed as in the solitary Andraena.

Although the last case and some others may offer special difficulties, I think the above facts indicate that there is at present no valid objection to the conclusion that in all cases throughout the animal kindom secondary differences between the two sexes of the same species depend for their perfect development on the presence and normal condition of the primary or essential generative organs, and I maintain that this dependence or correlation is explained on the hypothesis that external stimulations have been the determining causes of the secondary characters, but is not explained on the hypothesis that the said characters have been determined exclusively by the process of selection from variations arising in the germ and independent of external stimulations. [105]

Versuch einer Einteilung der nicht-nervösen Reflexe.

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(Fortsetzung.)

IV. Art der Reaktionen.

A. Vorbereitende Reaktionen oder Tonus. Jeder Organismus ist Zeit seines Lebens Sitz einer unausgesetzten Thätigkeit, von der jede Aeußerung eine Reaktion auf irgend einen Reiz darstellt. Die groben sinnfälligen Reaktionen, die einzigen, welche der Beobach-