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its middle (in *parnassiæ* it joins it about its middle); fimbria dull grey, quite dark.

Hab. Milwaukee, Wisconsin, July 24 (*Dr. S. Grænicher*).

Named after Mr. G. W. Peckham, in recognition of his work on the habits of Wisconsin Hymenoptera.

East Las Vegas, New Mexico, U.S.A.,

Dec. 13, 1901.

XXI.—*Investigations upon the Life-history of Salmon, and their Bearing on the Phenomena of Nuptial and Sexual Ornamentation and Development in the Animal Kingdom generally.* By G. E. H. BARRETT-HAMILTON, Capt. 5th Royal Irish Rifles.

THE coloration of animals, and especially that part of it which seems to have a connexion with sex, presents us with many problems of deep interest, and has formed the basis of a number of speculations, some of them examples of the best efforts of our strongest zoological thinkers. Many of these theories are of great ingenuity and have marked real stepping-stones in the progress of our knowledge. For this reason it would be in the highest degree ungrateful to attempt their downfall. Nor, indeed, would such an assault prove likely to be successful, so firmly established at the present day are the main lines of thought dealing with animal coloration.

Yet field-naturalists must often have felt dissatisfaction at the insufficiency of all known theories and have yearned for the discovery of some law which, embracing all the phenomena in its grasp, would place before their minds a comprehensive view of the whole question. At least that has been my own experience. While perfectly ready to admit that if some colours are procryptic, others aposematic, æsthetic, or even useful for purposes of mimicry, I have felt my attention more and more attracted to many examples of coloration which are inexplicable with reference to any one of the above-stated uses. Why, for instance, are the fauces of many birds so brilliantly tinted as to throw into the shade the glory of their plumage? * Why are the yolks of the eggs of some birds richly red, often in correspondence with a similar painting of legs, bill, and fauces? Why do † both sexes of so many animals belonging to almost all branches of the

* *E. g.* Kittiwake Gull (*Rissa tridactyla*).

† *E. g.* Chough (*Pyrrhocorax graculus*).

animal kingdom signalize the nuptial season by a special display of beauty? For these and numerous other questions there is as yet no sufficient answer.

A great defect in many of the current theories is their inability to explain the origin of the characters the modern uses of which they propound. If the Peahen's dinginess be protective, and her lord and master's splendour æsthetic, how did such a state of things first arise? Granted that there be under present conditions ample justification for such sexual diversity, is it credible that such a display had in its infancy the same meaning as it now has in its perfection? Can we really believe that a peacock with a slightly larger tail or more brilliant feathers was, in the early history of his race, preferable or in a better position than other less ornate fowl? Why are such beauties absent in youth? Why do they decay with age, and why does the old or diseased female partially assume them? The theory which will explain not only the origin but the present use of such developments must obviously be a broad one, based partially on physiological, partly on æsthetic or protective or other reasons.

Of late years a few writers * have attempted to probe the question from the physiological aspect, but the work of some of them has to my mind been frequently marred by an inability to take a sufficiently wide view of the question under consideration, leading them often to refuse due weight to the views of other thinkers.

Realizing the want of some such broad law, I had the good fortune to observe while in Kamchatka the spawning of the Salmonidæ of the genus *Oncorhynchus*. The phenomena displayed by these fish are very remarkable and have been more than once the subject of description and comment. They became for me the stimulus to much thought and deliberation on the subject of animal coloration. Unfortunately my stay in Kamchatka was brief, and it was not until after I had left the country that I realized what I believe to be the real significance of what I had seen.

In discussing the matter with friends my ideas were fortunately met with commendation, and, acting on the advice of Professor Newton, I brought the matter to the notice of the Cambridge Philosophical Society.

Briefly, what I had to say was as follows:—The spawning of the various species of *Oncorhynchus* is accompanied by striking changes of colour and shape, different in each species.

* *E. g.*, Wigglesworth, Newbigin, Cunningham, and others. Bateson has some most suggestive remarks in his discussion of the subject in the Introduction to his work 'Materials for the Study of Variation' (1894).

These might, and have, been mistaken for nuptial development, æsthetic and offensive. They are not so, however, but represent a pathological * condition in which the fish is manifestly out of condition, and, becoming continually more and more feeble, eventually succumbs.

What I wished to demonstrate was that the coloration and growth are due to a pathological † condition of uncertain nature. I suggested that "it may be a kind of piscine jaundice accompanied by the hypertrophy of certain organs, or it may be (and this I myself believe) that in the effort to produce as much spawn as possible the whole metabolism is so upset that the ordinary excretory organs are unable to do all the work demanded of them, and a last effort is made to get rid of the unduly increased quantity of poisonous products by depositing them in the skin."

Finally, I drew the conclusion that to such phenomena we may possibly look for a source and origin of many of the highly developed sexual characters met with in other animals. In these fish, gaudily coloured and changed in form, but all as the result of pathological conditions, we have several lines of development ready for the operation of sexual selection.

In the above-mentioned paper I had no intention of entering deeply into the work of others, but contented myself with referring to several important articles.

To one of these I now wish to refer at greater length, in

* My friend Dr. F. H. H. Guillemard, one of the Englishmen who have observed and described the phenomena in question (see the 'Cruise of the Marchesa,' vol. i. chapter 6), and to whom I sent a copy of my paper, writes me in a letter of 29th November, 1900, that, although he does not accept my explanation, "there can be no shadow of doubt that the changes in the fish are purely pathological."

Similarly Dr. Cunningham accepts the pathological condition, although he sees "no general or necessary connection between fecundity, or intense production of milt and eggs, and changes in the body, pathological or otherwise." On the contrary, he "would attribute the changes, the pathological condition, and the death of *Oncorhynchus* to the excitement and exertion and starvation which accompany the process of spawning" (*in lit.* of 28th Nov., 1900)—an opinion, after all, not very much at variance with my own.

† In the letter quoted above Dr. Cunningham cites the Conger as instance of a fish "which dies after spawning, and which before death shows a pathological condition. But in this case there are in the female no remarkable changes of colour and of structure. The Conger ceases to feed several months before spawning, and when ripe its bones have so much degenerated that they are as soft as cheese and the teeth all drop out. Here there is no excitement or struggle such as occurs among a crowd of salmon struggling with one another and ascending a river for miles from the sea. In the male Conger, which does not grow to more than 2½ feet in length, the eyes appear to become larger; but this may be merely due to the shrinking of the tissues of the head."

particular as it contains, as it seems to me, a most remarkable confirmation of my hypothesis. It is the 'Report of Investigations on the Life-History of Salmon,' published by the Fishery Board for Scotland in 1898. This report consists of a series of papers by several experts. There is hardly one of these which does not bear directly upon my hypothesis; in fact the support which they afford is, to my mind at all events, so obvious, that when quoting the more important passages I shall be saved from lengthy comments. Commencing with the "General Introduction" by Dr. D. Noel Paton, we find the statement that:—

"In the female the growth of these [the genital organs] is enormous. In April or May the ovaries constitute only about 1·2 per cent. of the weight of the fish, in November they are no less than 23·3 per cent. In a fish of 30 lbs. in the spring they weigh about 120 grms., in November they weigh about 2000 grms. The increase in the testes in the male is not so marked, but is sufficiently striking. In April or May these organs are about 0·15 per cent. of the weight of the fish, while in November they are 3·3 per cent." (pp. 1 & 2).

Surely then, if the above statement be true, here at the outset we have sufficient reason to suspect, as I suggested in my paper, that "in the effort to produce as much spawn as possible the whole metabolism is upset." Nothing would seem more likely than that such a concentration of energy upon the formation of milt and ova should cause the total unhinging of the normal processes of the fish's body.

Continuing, Dr. Noel Paton asks the question, "From what are these structures formed?" And before attempting an answer he points out that "as they [the genitalia] grow, the muscle, as is well known, undergoes marked and characteristic changes. Not only does it diminish in amount as the season advances, so that the fish which have been for some time in the river become smaller in the shoulder and back, but it loses its rich fatty character, while it becomes paler in colour" (p. 2).

Evidently then, so far at least as the muscles are concerned, the metabolism of the body is upset, and instead of being anabolic becomes markedly katabolic.

It is part of the duty of the various authors of the report to discuss the connexion, if any, between the changes in the muscles, the growth of the ovaries and testes, and the source of the energy used up by the salmon in fighting its way up stream, often up rapids and over falls. "Are the changes [it is asked] in the muscle connected with the performance of this work; and if so, to what extent are these changes con-

nected with the muscular work and to what extent with the growth of the genitalia?" (p. 2).

Such were some of the questions to the investigation of which the scientific officials of the Scotch Fishery Board devoted themselves. Briefly stated their conclusions, so far as they relate to my own paper, are:—

"That the genitalia of fish coming from the sea develop steadily from April on to the spawning-time, and that the genitalia of salmon in the earlier summer months develop more rapidly than those of grilse.

"That the proportion of the weight of genitalia to the weight of the fish is constant for all sizes of salmon" (p. 2).

Dr. Noel Paton and Dr. James C. Dunlop agree in confirming the conclusions arrived at by Mr. Archer* in a previous report, "that fish continue to feed in the sea at least till the end of August. The marked diminution in the amount of muscle in fish reaching the estuaries in October and November would seem to show that the supply of food is insufficient to yield the material necessary for the rapidly growing genital glands, and that therefore the solids of the muscle have to be drawn upon, or, at least, that accumulation of material in the muscles is prevented. The steady increase in weight per fish of standard length throughout the season seems to indicate that they continue to feed even after August and September, though, as will be shown later (p. 86), the flesh contains about 5 per cent. more water in October and November than in July and August, while the increase of weight is only 3·7 per cent.

"2nd. The fall in the amount of muscle from the early to the late part of the season in fish in the upper reaches supports the conclusions arrived at by Meischer Ruesch, and by Drs. Gulland and Gillespie, that the salmon does not feed in fresh water" (pp. 74–75).

If, then, as has already been shown, the salmon, leaving its marine feeding-ground, ascends the river and remains until the spawning-time, often for several months, without any supply of nourishment from without, during this period it must subsist upon the store of material in its body brought from the sea. It is to a study of "the progress of the changes which go on in the fish during its prolonged fast" and an attempt to explain "how the material for the growth of the genitalia and for the muscular energy required in the ascent of the stream is obtained" (p. 79) that a great portion of the

* See 'Annual Reports of the Fishery Board for Scotland,' part ii., 1895.

report is devoted, and especially to the verification of the investigation of Professor P. Meischer Ruesch*.

As a result of his investigations on this point Dr. Noel Paton finds that, as regards the muscles, the percentage of solids, although throughout the season markedly higher in the fish at the mouth than in the fish in the upper reaches of the river, remains unaltered in all until August. In October and November it falls markedly, but the weight of the muscle shows no diminution, being kept up by the addition of water (p. 86). The ovaries, on the contrary, increase in solids; and a balance of loss of muscle and gain of ovaries may be struck, from which it appears that "*the amount of solids lost by the muscle is not only amply sufficient to yield the solids gained by the ovary, but a large surplus is left*" (p. 87).

Similarly in a male fish the testes increase in size at the expense of the muscle, but they do not attain to anything like the same proportionate weight of the whole fish, as do the ovaries. Observations on male fish were more limited than those on female; but a balance and loss table was drawn up, from which the conclusion was drawn that "*the supply of solids, over that required for the construction of the testes, which is thus available for muscular energy, is considerably greater in the case of the male than of the female fish*" (pp. 88 & 91).

Passing on to a consideration of the various substances included in the term "solid," it is found that chemical observations show that "the fish leaves its marine feeding-ground with the muscle loaded with fat, and that this fat gradually diminishes in amount, being in part transmitted to the ovary and in part used up as a source of energy" (p. 106). The store of fat is, in fact, according to Dr. Paton, "*not only amply sufficient to yield all the fat required for the fat of the growing ovary, but also abundantly sufficient to yield energy for an enormous amount of muscular work*" (p. 98).

As regards the origin of this fat, it would appear that fat is drawn not only from the muscles, but from the intestines, and that "*this intestinal fat is the first to be drawn upon, and that it is used up more rapidly than the muscle-fat*" (p. 100). Further, "*the fats stored in the liver while the fish is feeding in the sea are to a great extent lost during the sojourn in fresh water*." As much as 20 grm. of fat per fish of standard length

* 'Statistische und biologische Beiträge zur Kenntniss von Lebendes Rheinlachs in Süsswasser.' A contribution to the literature of the Berlin Fisheries Exhibition of 1880. Published by Von Metzger and Wiltig, Leipzig. See also 'Histochemischen und physiologischen Arbeiten,' von Frederick Mierscher, Bd. ii. p. 116: Leipzig, 1897.

may be given off from the liver " (p. 101). It is shown that "*the accumulation of fat in the muscles is as great in the male as in the female, and that the fat is used up to quite as great an extent.*" On the other hand, the accumulation of fat in the testes is trifling in amount, and thus the conclusion is indicated that in the male the utilization of fat as a source of energy is much greater than in the female, and this is especially marked in the later months " (p. 104).

Similarly to the fat, the proteids of the muscles of salmon which have been in the river for some time "undergo a marked diminution, being in part transferred to the growing ovary and testes, and in part used as a source of muscular energy" (p. 112). The muscle of the kelt is very poor in soluble proteid (p. 118). Dr. James C. Dunlop finds that as regards the female fish examined in 1896 "the deficit of muscle proteid in upper-water fish is so large that, after allowing for the requirements of the ovaries, there remains a surplus loss. This surplus loss is available for the liberation of a large amount of energy" (p. 128).

As regards the male fish a very similar conclusion is formed, but in this case the "surplus loss is much greater than in female fish, and consequently a much larger amount is available for energy."

"The changes being exactly comparable to those observed in female salmon, it may be concluded that male salmon, like female salmon, have sufficient proteid stored in their muscles to meet all their requirements in fresh water, and that this proteid is called on to supply the want of the growing testes and for the liberation of energy" (p. 132).

Some important conclusions are reached by Dr. Paton during his consideration of the fats and proteids stored in the muscles as a source of muscular energy. Thus:—

"1. Of the fats lost from the muscle of female fish to August only a very small moiety—12 per cent.—goes to the ovaries. The remaining 88 per cent. is available as a source of energy. Taking the metabolism to November, 30 per cent. of the fats go to the ovary and 70 per cent. to energy.

"2. Of the proteids lost from the muscle to July and August in the female, 23 per cent. are transferred to the ovaries, 77 per cent. are available for energy; but later in the season the proteid lost from the muscle is almost entirely transferred to and built up in the growing ovaries, little or none being available for muscular energy.

"3. It thus follows that while in the earlier months the energy of muscular work is derived from the fats to the extent of 81 per cent., and from proteids to the extent of 19 per

cent., during the later months the fats are almost the sole source of energy.

"4. In the male, of the fat lost from the muscle to August 5 per cent. are accumulated in the testes, while 95 per cent. are available for energy. Of the proteids 14 per cent. go to the testes, leaving 86 per cent. as a source of energy.

"5. In the period to August, when male and female fish can be compared, the energy liberated per fish of standard length was in the female equivalent to 1,265,000 kgms.*, while in the male it was equivalent to 1,380,000 kgms. In the female, where fat accumulation in the ovaries is large, a greater proportion of energy appears to be derived from the proteids of the muscle than in the male, where the fish is comparatively poor in fats. Here the fats of muscle yield a larger proportion of energy than in the female. In the female to August of the total available energy about 20 per cent. is derived from the proteids, while in the male only 9 per cent. is obtained from this source" (p. 142).

Dr. Paton has constructed a table wherein it is attempted to show the work done by the female fish in ascending the rivers Dee and Spey as compared with the energy evolved from fats and proteids to August. An exact calculation is impossible, but it is shown that for the raising of the fish's body and the work of overcoming friction "an enormous surplus of energy is available from the combustion of the fat and proteids which disappear from the muscles throughout the sojourn of the fish in fresh water." It is also claimed by Dr. Paton that his "observations very clearly prove that *in a cold-blooded animal fats are a source of energy, and that they play a much more important part than the proteids*"—a conclusion adverse to that of Pflüger†, who has most strenuously maintained the view that the proteids are the great source of energy for muscular work (p. 142).

Turning to carbohydrates, we find that in the present investigations they have not been studied. Meischer Ruesch‡, however, found small amounts of sugar present in the blood and liver and glycogen in the muscles even when the salmon has been long in the river (p. 138).

As regards phosphorus and its compounds, the conclusion is drawn that a supply, "partly as inorganic phosphates, partly as lecithin, is stored in the muscles as these grow and become loaded with fat during the stay of the fish in the sea.

"* The kilogrammètre is the work done in lifting a kilogramme through one metre. It is equivalent to 7.24 foot-pounds."

† Arch. Bd. xlv.

‡ 'Histochemischen und physiologischen Arbeiten,' 1897, Bd. ii. p. 325.

"While the fish is in the river this stored phosphorus is transmitted from the muscle to the growing ovaries and testes, and in being transmitted undergoes changes in its chemical combinations. In the ovary the simple phosphates of the muscle are (a) combined with fatty acids and cholin to form the abundant supply of lecithin; (b) combined with proteids to form the pseudo- or para-nuclein-ichthulin—which is so abundant a constituent of the ovary; (c) in the testes, on the other hand, the phosphorus of the muscle-phosphates is elaborated with the more complex nucleic acid and combined with the characteristic base—protamin. . . .

"There is no evidence that the transference of phosphorus from the muscles to the genital organs is not direct. There is no evidence that the liver plays any intermediate part. In fact, all the evidence tells against any such idea. It is apparently in and by the active protoplasm of the growing ovaries and testes that these profound chemical changes are carried out" (p. 155).

"As to the source of the phosphorus stored in the muscle, there can be little doubt that it is in great measure derived from the phosphates in the bones of herrings and other fish upon which the salmon feeds" (p. 155).

In a female fish the balance between the phosphorus lost from the muscle and that gained by the ovaries is fairly close. "*The phosphorus lost from the muscle is just about sufficient to yield the phosphorus laid on by the ovaries, provided no phosphorus is excreted or used in other ways*" (p. 152).

"The liver cannot be regarded as the source of the phosphorus for the ovaries, and it is rather to the bones that we must look for any supply of this element over and above that yielded by the muscles which may be necessary for the growth of the ovaries" (p. 153).

Although the testes are particularly rich in phosphates, it would "appear that the store of phosphorus in the muscle is far more than sufficient to yield the phosphorus required in the constructive changes in the testes" (p. 155)—an interesting conclusion in view of the fact that "in the male during the summer months there is a great growth of bone in the snout, and it is highly probable that some of the phosphate stored in the muscles is utilized in this process" (p. 155).

Similarly Mr. E. D. W. Greig comes to the conclusion—" (1) that the quantity of iron in the ovary becomes distinctly increased during the development of that organ, (2) that a considerable amount of its iron is derived from the muscles, which become correspondingly poorer in iron, (3) that none of it is derived from the liver." A small quantity

unaccounted for may possibly be derived from the blood (p. 158).

The pigment of the salmon was investigated by Miss M. I. Newbigin. The nuptial colour-changes of the fish are well known. "When the fish comes from the sea the skin is of a clear bright silvery hue, while the flesh has the familiar strong pink colour. The small ovaries are of a yellow-brown colour. As the reproductive organs develop during the passage up the river certain definite colour-changes occur. The skin loses its bright silvery colour, and, more especially in the male, acquires a ruddy brown hue. At the same time the flesh becomes paler and paler, and in the female the rapidly growing ovaries acquire a fine orange-red colour. The testes in the male remain a creamy white.

"After spawning the skin tends in both sexes to lose its ruddy colour and to regain the bright silvery tint; the flesh, however, remains pale until the kelt has revisited the sea. In other words, the salmon comes from the sea with a store of pigment in the muscles. During its sojourn in the river this pigment disappears from the muscles, is apparently in the female for the most part transferred to the ovaries, and so to the ova, and in both sexes is to a smaller extent deposited in the skin, there to undergo further changes. The accumulation of pigment in the muscle is associated with the presence of a large amount of fat, and fat and pigment disappear *pari passu*" (p. 159).

A similar colour-change is observable, although in a lesser degree, in the Sea-Trout, and "even in certain varieties of brown trout, *e. g.* the Loch Leven trout"; and it is suggested that in the case of certain red-fleshed fish of other families, such as the Dawson Salmon of the Australians (*Osteoglossum Leichardti*) and the Australian mud-fish (*Ceratodus Forsteri*), the pigment is also associated with the presence of fat in the muscles.

Miss Newbigin's chemical investigations disclosed the presence, both in the flesh and in the mature ovaries, of two pigments. Of these "one is pink and gives the blue lipochrome reaction, while the other is yellow and does not give this reaction" (p. 161). The former "corresponds closely to the lipochrome pigment described in various animals, and notably in Crustacea, as tetronerythrin or zoonerythrin (by Moseley as crustaceorubrin)" (p. 161). The latter strongly resembles a pigment which may be obtained from the bright yellow fat of the cow. "It belongs to a group of pigments which are apparently exceedingly widely distributed in the animal kingdom, but which have been little investigated."

In the Salmon it "occurs in the muscle, the ovary, and in large amount in the liver," but "always in close association with fat," upon which its "solubility seems to depend" (p. 161).

As regards the significance of the pigment, Miss Newbigin finds that two pigments of "similar or perhaps identical nature occur in the lobster, and in all probability in other Crustacea." Hence Günther suggested that the Salmon derives its pigment directly from its food—a suggestion supported by the disappearance of the pigments while fasting, their reappearance when the animal begins to take food, and by their sporadic appearance in certain Brown Trout, as if they are dependent upon particular diet. The difficulty is that the Salmon does not feed directly upon Crustacea, but on haddock, herrings, and similar fish.

Miss Newbigin could find no trace of the red pigment either in the muscles or the viscera of the herring, and in her opinion "it hardly seems probable that the amount of pigment in the undigested food of the herring could be sufficient to supply all the colouring-matter of the salmon's muscle" (p. 161). Both muscle and viscera of herring, however, may be made to yield traces of a yellow pigment resembling that obtained from the liver of the salmon. Hence the suggestion that possibly "the salmon obtains the yellow pigment of its muscle from food in association with fat and that part of this pigment is modified to form the red"*, a process which the author compares to the transference of pigment to certain caterpillars from their food†, and to the frequent presence of yellow pigment, evidently thus derived, in the fat of sheep and cows.

This view brings with it another difficulty, viz. "that unless these three organisms can be shown to possess some physiological peculiarity, then we are forced to the conclusion that all yellow pigments in animals are derived from their food—a conclusion for which there seems little evidence." Further, if the presence of "pigment in the food is the only condition necessary to produce pigmented fat, it is difficult to understand why such coloured fat should not be universal in

* Poulton, Proc. Roy. Soc. London, liv. pp. 417-430; see also 'Natural Science,' vol. viii. pp. 98-100.

† Later investigations by Miss Newbigin have disclosed the presence in certain Copepoda of a red lipochrome, which exhibits the same general characters as the red pigment of salmon, and especially recalls the latter in its close association with fat. Unfortunately it was not obtained in quantity sufficient to allow of detailed investigations (see "Further Investigations on the Life-History of the Salmon in Fresh Water," in Proc. R. Soc. Edinburgh, Sess. 1899-1900).

herbivorous animals, for all green parts of plants contain also a certain amount of yellow pigment" (p. 163).

The difficulty is met by the conclusion "that the presence of pigment-containing fat in cattle, in caterpillars, and in the salmon is due in each case to the habit of ingesting coloured fatty food in an amount which is in excess of the immediate requirements, the consequence being that fat coloured with the pigment in a more or less modified condition is deposited in certain of the tissues. While the pigment so deposited is of no importance in cattle, in caterpillars it is important in producing the external coloration and in the salmon in colouring the ova. In the male salmon the pigment is probably eliminated as the fat is used up. The question is of some interest, because if the suggestion here made be correct, it shows that a characteristic pigmentation may be acquired, as it were, incidentally in the life-history of the individual under circumstances which render the question as to the inheritance of acquired character absolutely unimportant" * (p. 164).

In the general summary of results Dr. Noel Paton comes to the rather surprising conclusion that "it would thus seem to be the state of nutrition which is the factor determining migration towards the river; that when the salmon has accumulated the necessary supply of material it tends to return to its original habitat" (p. 170). This conclusion is based on the fact that the Salmonidæ are originally freshwater fish, the majority of which spend their whole life in fresh water. Others, like the Salmon, have apparently acquired the habit of quitting the fresh water in search of food, having accumulated a store of which in the body, the fish returns to its native element, and there performs its reproductive act.

"That the migration of the fish is not governed by the growth of the genitalia and by the *nisus generativus* † is," the author thinks, "shown by the fact that salmon are ascending rivers throughout the whole year with their genitalia in all

* I do not think it likely that either Miss Newhigin's conclusions as to the origin of the red pigment or Dr. Noel Paton's (see below) as to the cause of the return of the salmon to fresh water will be accepted without further discussion. Neither question, however, directly concerns the subject of this paper, and no good object would be obtained by devoting space to their treatment.

† Renewed investigations by Dr. Noel Paton and Miss Newhigin (Proc. R. Soc. Edinburgh, Sess. 1899-1900) lead them to strengthened opinions that "*the Salmon goes to the sea to feed and returns to the river when it has accumulated its full store of nourishment irrespective of the condition of the reproductive organs. The factor determining migration from sea to river is not the nisus generativus, but the state of nutrition.*"

stages of development" (p. 169). Further, although "a return to fresh water is essential for the completion of reproduction, for it has been shown that salt water prevents the development of the ova descent to the sea is not necessary for the development of the genitalia since experiments show that fish, when properly fed, may develop their genitalia without leaving fresh water" (p. 170).

As regards the fast of the salmon while in fresh water, the report is strong that not only does the salmon abstain from feeding while in fresh water, at least before spawning, but it cannot feed, since its alimentary canal is in a state of desquamative catarrh. The observations of Miescher Ruesch * are thus confirmed. Not only is food, as a rule, absent from the stomach-cavity, but the "slight acidity and small digestive power of the extracts of the gastric mucous membrane recorded lead to the conclusion that the fish both in the estuaries and in the rivers were in a fasting condition" (p. 32).

The assertion that the alimentary canal of the breeding salmon is in a state of acute desquamative catarrh, although directly denied by Dr. Alex. Brown †, afforded a very important support to my theory. It appears, however, that on this point alone the observations of the writer of the report are erroneous, and Dr. J. K. Barton ‡ has shown that the appearance of catarrh is due to the method of preparation of the specimens. This, however, does not affect the fact that the salmon while in fresh water is undergoing a physiological fast §, that its gastric juice is weak in peptogenic power and contains a decreased quantity of hydrochloric acid, and that consequently the number of bacteria in the digestive tract is increased. This disinclination or, it may be, inability to feed, accompanied as it is by discoloration and general failure of condition, may in fact be itself regarded as pathological, or, at all events, as reminiscent of a former pathological condition. Nor must it be forgotten that what is pathological in one animal may be normal in another, as I am reminded by Mr. Headley ||.

Such is a brief *résumé* of a most interesting series of papers.

* 'Fisherei-Ausstellung zu Berlin.' 1880.

† Zool. Anz. 1898, xxi. pp. 514, 517-521.

‡ Journ. Anat. & Phys., April 1900.

§ As Sir H. Maxwell says ('Memories of the Months,' 2nd series):—"Even a physiological fast is compatible with occasional irregular impulses of appetite, which exactly corresponds with the well-known capriciousness of salmon in taking any lure."

|| The connexion between disease and variation in general is, of course, not a new one. See Bateson, *op. cit.* p. 74.

The facts shown by the authors speak for themselves. I submit that they afford considerable support to my views if we regard the common Salmon as an instance of a species in which the pathological results of spawning and their fatal issue have undergone much modification. Whether, however, my views be accepted or not, it is of great importance and interest to have so clearly put before us the details of the exchange of material from one part of the body to the other under the influence of the generative organs.

The fact that the destination of much of the material thus lost from the muscles (70 per cent. in the case of fats, 77 per cent. in that of proteids, and a large proportion in that of phosphorus) is unknown is very significant. Some of it is, no doubt, used, as the authors suggest, as a source of energy; but I look to this surplus material for the formation of secondary sexual characters, as indeed is suggested in the case of the salmon's beak and in the deposition—apparently almost adventitiously—of some of the moving muscle-pigments in the fish's skin. There can, I think, be little doubt that given an animal wherein a considerable amount of surplus material and pigment is on the move, much of that material and pigment would, with an increased blood-supply, be at the service of and directed to, not only the genitalia, but to such other portions of the body as undergo special exertion or movement during courtship, an idea which I borrow gratefully from Dr. Cunningham.

It seems logical to presuppose that such a transference will be found to accompany the seasons of special sexual activity in other animals, and that upon the relative amount of surplus energy and material will depend the decoration or armature of the sexes. In animals whose sexual activity is permanent and not periodic it is probable that such a transference will be less marked, inasmuch as the permanent activity of the generative organs will prevent undue accumulation of fat and other surplus matter in the muscles, and will constantly, under the influence of heredity and natural selection, apply such surplus material to the parts where it is most urgently required.

Further, in the observation that the proportional use of proteids and fats "as a source of energy" is different in male and female salmon we have a most suggestive hint as to the origin of sexual dimorphism, whether seasonal or otherwise. We have in the Salmon a state of things which, if modified or accentuated by natural selection, might easily be the foundation of the numerous extraordinary instances of sexual dimorphism which the animal kingdom presents to us. My

suggestion that the capacity of each sex for the production of nuptial changes is equal is shown to be correct, but the disparity in the size and in the requirements of ova and testes accounts for the existence of a larger surplus of material in the male. This surplus may be used up partly as energy, partly in the production of the secondary characters—the growth of snout and discoloration of skin.

In my paper above alluded to I wrote of the deposition in the skin of some of the products of the disturbed metabolism, and I suggested that in the case of the females of dimorphic species the excess of pigment might be disposed of in several ways, as, for instance, in the pigmented eggs of birds. This is markedly confirmed by Miss Newbigin's statement that "in the river this pigment disappears from the muscles, is apparently in the female for the most part transferred to the ovaries, and so to the ova, and in both sexes is to a smaller extent deposited in the skin."

Lastly, it is important to note that while the transference is direct and unmarked by degeneration of the losing tissues, some of the matter transferred (*e. g.* the phosphorus) may be altered in the process—a fact which opens up enormous possibilities in the case of pigmentation, inasmuch as it is easy to imagine that the transference might in some cases be accompanied by unforeseen colour-changes or by the formation of pigment *de novo*.

Leeuwspruit, Orange River Colony,
South Africa.

24th August, 1901.

XXII.—*On some Questions of Malacological Nomenclature* *.

By O. v. MÖLLENDORFF, Ph.D.

MR. PILSBRY, who discussed my former paper on this subject †, is certainly right when he says that "controversy over names is a notoriously barren employment"; but it has been especially so in our case, because he does not apparently read German, and has in consequence misunderstood and misstated several of my views. In order to put the case fairly before the English-reading public, I may be permitted

* [Mr. Pilsbry's paper and Dr. von Möllendorff's reply having been placed before our readers, this discussion, so far as the 'Annals' is concerned, may now be considered to be closed.—EDS.]

† "The Nomenclature of European Helices," *Ann. & Mag. Nat. Hist.* (7) viii. pp. 325-329.