SOME ABNORMALITIES AND REGENERATION OF PLEIOPODS IN CAMBARUS AND OTHER DECAPODA.[1]

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INTRODUCTION.

The two crayfishes whose abnormal appendages are described in this paper were found among a small number of specimens of *Cambarus virilis* Hagen, which were captured near the city of Chicago in the autumn of 1904. The discovery of these abnormal pleiopods led to an experimental study of the regeneration of the abdominal appendages in the crayfish, the results of which are given herein. The earlier experiments were unsuccessful owing to imperfect methods of handling the material, and to the use o mature animals in which the moults were infrequent. The later experiments, with improved methods of caring for the material, and with small immature specimens, have yielded satisfactory results.

These experiments were begun in the Hull Zoölogical Laboratory of the University of Chicago, continued in the Biological Laboratory of Transylvania University, and completed in the Marine Biological Laboratory of the Brooklyn Institute of Arts and Sciences at Cold Spring Harbor, Long Island. I wish to express my thanks to Dr. Davenport, director of the Marine Laboratory, who kindly placed the facilities necessary for the completion of the work at my disposal; also to Dr. A. E. Ortmann, of the Carnegie Museum, Pittsburgh, to whom I am indebted for identification of the species used in the experimental work; and to Dr. Faxon, of Harvard, and to Dr. Hans Przibram, of Vienna, for examining the abnormal specimens.

HISTORICAL SUMMARY.

The regeneration of the abdominal appendages of decapod crustaceans has been a subject of investigation for many years, but

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not until recently has a critical study of it been attempted. A review of the earlier literature relating to regeneration in the Decapoda has been given by Miss Steele, '04; it is necessary, therefore, to mention only a few of the later papers upon whose results my own observations have some bearing.

Morgan, '98, desiring to test Weismann's hypothesis, that regeneration is an adaptation, experimented with *Eupagurus longicarpus* to determine what relation, if any, existed between the power of regeneration and liability to injury. Because the hermit crab lives in shells where the abdominal appendages are protected from injury, whereas the thoracic appendages are not so protected, these two series of organs were chosen for this experiment. He came to the general conclusion that no such relation existed, and further supported this view by a second paper in 1900. The latter paper was based upon experiments in which the thoracic appendages were removed at unusual levels.

He found in the course of his experiments that the abdominal appendages of *Eupagurus* did not regenerate readily, although slight regenerative power existed. He suggested that this rarity of regeneration "may be connected in some way with the amount of food supply brought to the region from which they arise."

Miss Steele, '04, experimenting with *Cambarus virilis* and *C. gracilis* has obtained results similar to Morgan's. She says, speaking of the swimmerets: "I have found none to regenerate except the first pair in the male. . . . In the case of the other abdominal appendages except the sixth pair, regeneration, if it does take place, is very slow in beginning."

Emmel, '04, reported the observation of regeneration in the first appendages of the lobster. He experimented with the other appendages and says: "In experiments with the other four pairs of abdominal appendages or swimmerets, positive results were obtained in the second and third pairs, and it seems safe to say that all the swimmerets will regenerate."

Haseman, '07, mentions the regeneration of swimmerets in *C. propinquus*, giving figures showing the progress of differentiation, but he does not mention the fact that the regeneration of these appendages was considered doubtful.

A discussion of the results obtained by Morgan and Miss Steele will be found in connection with the discussion of my own observations in a later portion of this paper.

Abnormal Swimmerets.

Anomalous variations not of congenital origin are of little interest to the student of evolution; for it has never been definitely demonstrated that any acquired somatic variation is inherited. Moreover, no very important laws of variation are likely to be discovered by a study of teratological specimens. Nevertheless, it is advisable to place interesting cases of abnormal growth and regeneration on record, for we may finally acquire a knowledge of the physiology and mechanics of development sufficient at least to explain the origin of such anomalous variations.

The swimmeret shown in Fig. 1 is the right appendage of the second abdominal somite of a female *C. virilis*. The pleuron is much deformed, as is readily seen if compared with the normal pleuron of the opposite side of the same somite. The coxopodite of the abnormal appendage is much larger than normal. From this enlarged basal piece arise two appendages, one of which, near the posterior side of the coxopod, seems on casual observation to be a beautiful case of duplicity. The parts are perfectly doubled from the proximal portion of the basipodite outward. The two pleiopods thus united are normal in every particular beyond the point of union, the posterior member being somewhat larger than the anterior. From the anterior portion of the large coxopodite, completely separated in point of origin from the double pleiopod, arises another appendage which is uniramous, but of a size and structure typical of the endopodite of the second pleiopod.

It is an interesting circumstance that the first pleiopod lying immediately anterior to the one just described is also abnormal. This swimmeret is shown in Fig. 2. The lower portion of the appendage is much enlarged, and at the proximal end of the basipodite, there is a posterior projection set with stiff hairs, reminding one somewhat of the structure of the coxopodite of the pereiopods.

The third abnormal swimmeret is from a male *C. virilis* which was found to have three pairs of appendages instead of two, modified for sexual purposes. The right swimmeret of the pair is shown in Fig. 3, the left one being exactly like it. The character of the modification in this third pair is just the same as that of the second, except that the projection of the endopodite is smaller than on the second. The first and second pairs of appendages are perfectly normal. Moenkhaus, '03, has reported an exactly similar case in the same species, and so far as I know these are the only two cases on record.

The Problem, Materials, and Methods.

Being convinced that the abnormal swimmerets of the female *C. virilis* described herein were the result of regeneration after a somewhat extensive injury, and having before me the work of Morgan on *Eupagurus longicarpus*, and of Miss Steele on *C. virilis* and *C. gracilis*, I determined to perform a series of experiments with the crayfish in order to ascertain whether or not the abdominal swimmerets regenerate, and if so, under what conditions. These experiments were begun in 1905; and after two years of rather unsuccessful work the choice of material and the methods of handling it were so improved that gratifying results have been obtained.

At first attempts were made to keep the crayfishes in aquaria of running water. A large aquarium was divided by partitions of galvanized iron netting into a number of compartments, each about 30 cm. square. Each compartment was provided with gravel and flat stones, and fresh water from Lake Michigan was kept running constantly at a depth of about 5 cm.

The aquarium was cleaned frequently, and all precautions were taken to keep the animals in sanitary conditions; but in spite of the great care exercised, the crayfishes would die after several weeks of confinement. Since my first material was adult, and moulted therefore infrequently, death took place before any moults occurred. Many variations of these conditions were tried in an attempt to secure more favorable results, but without success.

During the last two years a method has been employed, which has obviated all difficulties, and has given entirely satisfactory results. Young specimens of *Cambarus* (*Bartonius*) *bartoni* Fabr., probably at the beginning of their second and third years were taken on March 24, 1907, from a small stream which crosses the Bryan Station pike about three fourths of a mile northeast from the city limits of Lexington, Ky. The specimens used are not like the typical *C. bartoni* of the eastern United States, but have a narrower areola, less spiny carpus, and a shorter but broader rostrum than the eastern form. Dr. Ortmann states that they agree with specimens described by W. P. Hay in the 20th Ann. Report of the Ind. Geol. Survey, 1895, after comparing the living specimens with those in the Carnegie Museum from Mitchell, Lawrence Co., Ind.

Each specimen was put into a tumbler with water not quite sufficient in amount to cover it. A small piece of mica schist coming not quite to the surface of the water, was placed in each tumbler so that the crayfishes could crawl upon it and expose themselves to the air at will. The tumblers were kept nearly covered by glass plates to prevent accidental desiccation. Care was taken not to cover the dishes entirely, as the air was found to become overcharged with carbon dioxide in a short time if so covered. The water was changed completely three or four times per day, and even oftener on very hot days; for crayfishes seem unable to endure warm water for any great length of time.

The water used in these experiments was supplied by the city water works of Lexington. This water is filtered through large Jewell filters before being pumped into the water mains, and is exceptionally pure. The complete change of such water every few hours rendered the multiplication of bacteria or growth of other fungous plants rather difficult, and tended to prevent the accumulation of any sediment.

When it appeared that any fungous growth was forming upon the appendages and about the thoracic region, each crayfish was treated for a few minutes with a bath of copper sulphate. The vessels and stones kept in them were occasionally treated with the same solution. The copper sulphate was used with a strength of one part to a million, when the animals could be left in it for some time. Solutions much stronger than this, one part in ten thousand, can be used for a few minutes at a time with entire success in destroying bacteria and fungi, and without injury to the crayfishes, provided they are washed thoroughly several times in plenty of pure water after the bath to cleanse their gills of the copper sulphate.

Young crayfishes are voracious creatures, and need to be fed frequently. I have fed them every day with entire success, but they soon tire of a uniform diet. Several kinds of food were used; and by rotation, so that they never received the same kind of food on successive days, their appetites were retained. Fresh raw beef was given them twice a week, and raw potatoes and pieces of *Myriophyllum*, which was kept growing in the laboratory, were used as vegetable foods. The *Myriophyllum* was covered with slime, which was found to contain unicellular algæ, rotifers, nematode worms, annelids, such as *Æolosoma hemprichii*, and other kinds of small animals. This slimy material was especially esteemed, and probably most nearly represents their normal diet. This food material was left in the glass with the animals for an hour or two, after which the remains were removed and fresh water placed in the vessels.

Using these methods, I have kept them alive for months in perfect health, with rapid growth during the moulting season. Occasionally a death would occur among them, but these fatalities were always obviously due to special causes, not to any general defects in the methods employed.

After ecdysis the cast off exoskeletons were used in the preparation of the drawings.

Experiments.

The experiments here described are a few typical ones selected from a series, all of which gave similar results. The numbers correspond to those used while recording notes on individual experiments.

No. 4. *C.* (*Bartonius*) *bartoni*, ♀. Fifth right abdominal appendage removed March 24, 1907. The appendage was cut off, leaving a short stump attached to the body (Fig. 4).

The first moult occurred in the afternoon of March 27, three days after the operation. No regeneration could be noticed, but the wound was perfectly healed (Fig. 5). The second moult occurred during the night following May 6, 1907. Between March 27 and May 6 no change could be detected even by use of the microscope. But that changes were taking place beneath the chitinous cuticle is evident from the expansion of the regenerating limb, which occurred immediately after this second ecdysis (see Fig. 6).

A third moult took place on June 19, 1907, at which time the appendage again expanded, reaching the size and condition shown in Fig. 7. The regenerated appendage measured at this time 3.3 mm. in length; the one on the opposite side of the same somite 4.8 mm. (Fig. 8). The regeneration was equal to nearly 69 per cent. of the normal size from March 24 to June 19, a rate which I consider by no means slow.

Owing to an unfortunate accident this crayfish was killed on the morning of July 5, 1907. Had it lived until after its fourth moult it would probably have shown a much more nearly complete regeneration of the appendage.

No. 7. *C.* (*Bartonius*) *bartoni*, ♀. Fourth left pleiopod removed March 24. The first moult after the operation took place the night of April 22, 1907. The amount of regeneration while not extensive was plainly visible. The second moult occurred May 25, 1907. The regenerating appendage expanded to nearly half the natural size, immediately after the exoskeleton was cast (Fig. 9).

No. 3. The same as No. 7 except that the fourth pleiopod was removed from the right side instead of the left. The first moult, on March 30, showed a small whitish papilla a little over one mm. in length, projecting from the base of the amputated limb. This projection increased slightly with age, but this individual was killed in July by the water in the vessel receiving direct sun-light through a partially open window blind, thus becoming much overheated. Fig. 10 reveals internal development. A later moult would probably have given results similar to No. 7. This specimen was probably a year, or perhaps even two years, older than No. 7, and consequently only one moult was recorded between March 24 and July 5, while some of the smaller, younger specimens moulted three times in a shorter period (cf. No. 4).

No. 2. *C. (Bartonius) bartoni*, ♂. The third right appendage was cut off March 24. On May 9, no moult having occurred, the stump of the appendage was cut longitudinally by means of sterilized scissors. The moult occurred on June 17, but no abnormal growth was noted. The appendage was perfect, and showed regeneration of more than 50 per cent. in size (Fig. 11).

No. 5. *C. (Bartonius) bartoni*, ♀. The second left appendage was removed March 24, 1907. The first moult occurred on May 8, 1907, and the regeneration amounted to about 30 per cent. The second moult took place on June 26, 1907, when the appendage showed about 65 per cent. of complete regeneration. Fig. 12 shows the point of amputation, and Fig. 13 the appendage after the second moult.

No. 6. *C. (Bartonius) bartoni*, ♂. Sixth right appendage was amputated just beyond the basal joint March 27, 1907, as shown in Fig. 14. It moulted the following day. A very narrow edge of white tissue was visible along the cut edges, but it is not probable that any regeneration had taken place. During the time preceding the next moult which occurred on May 27, the basal portions of the rami increased somewhat in size (Fig. 15), and after moulting the appendage was about one half natural size, and perfectly formed (Fig. 16).

A series of experiments on the pleiopods of *Palæmonetes vulgaris* was carried on at Cold Spring Harbor, and regeneration of all the abdominal swimmerets takes place rapidly in young specimens.

At present a series of experiments to test the regeneration of the antennæ from various levels and to compare the rate of regeneration of pleiopods and pereiopods in *C. (Bartonius) bartoni* is being carried on; but the data are insufficient as yet to permit a general statement regarding either phase of the series.

Discussion.

A. *The Abnormalities:* — As far as I have been able to ascertain, only one abnormal abdominal appendage has been recorded for any of the decapod crustaceans. In as much as all abnormal pleiopods described herein or elsewhere have been discovered accidentally, the rarity of such records is due in part, perhaps, to lack of careful observation; but the examinations which have been made show that they occur infrequently.

The abnormalities presented here are of interest for several reasons. The abnormal pleiopod is evidently the result of a regeneration after extensive injury in one instance, and just as evidently the result of undisturbed growth processes in the other instance. That is, the condition is congenital and may be considered as having arisen by mutation.

It would appear that the swimmerets shown in Figs. 1 and 2 probably resulted from an injury which removed part of the pleuron, and tore the first and second pleiopods near the base of each, as represented diagrammatically in Fig. 17. The coxopodite in Fig. 1 is abnormally large, which condition may possibly be explained by the fact that a large area was exposed when the mutilation occurred.

Very few genuine cases of duplicity have been described. Bateson mentions only four cases, all chelæ; Herrick has figured a double chela of a female lobster, and Zeleny has described a double chela of *Gelasimus pugilator* which regenerated instead of a normal single one during the course of his experiments.

Bateson states emphatically that "in arthropods and vertebrates such a phenomenon as the representation of one of the appendages by two identical appendages standing in succession is unknown. No right arm is ever succeeded on the same side of the body by another arm properly formed as right, and no crustacean has two right legs in succession where one should be."

While this supernumerary appendage may be regarded as a complementary image of the normal one, and therefore a left appendage instead of a right, there is nothing in the structure of either member to indicate that such a relation exists. The members are not imperfect, and are placed in succession, differing in these two respects from the cases admitted by Bateson.

At first appearance the coxopod of the abnormal first appendage is very much like that of the last pereiopod. And the anterior uniramous part of the second pleiopod is like the first pleiopod in being uniramous, but is a typical endopodite. There is a mere suggestion here of a shifting backward of the series of organs, a condition to which Bateson applied the term backward homœosis.

However if the injury actually took place as indicated in the diagram referred to above, the most plausible explanation which can be offered is in harmony with Bateson's statement. The regeneration should lead theoretically to triplication, that is, to the production of three appendages, two supernumerary ones on each cut appendage; and these on the right side of the body should stand as a left between two rights. The abnormal pleiopod shows defective regeneration only in the suppression of the exopodite of the anterior supernumerary appendage. The rounded projection of the first accessory pleiopod may be explained similarly as the fused basal portions of the two supernumeraries, whose tapering jointed ends have been completely suppressed.

The abnormalities have probably arisen after an injury caused by some force acting in the direction of the arrow in the diagram, Fig. 17, which produced two breaking surfaces, from which the new pleiopods arose, following the laws of symmetry for supernumerary appendages as stated by Bateson.

The abnormal appendage shown in Fig. 3, is a case of backward homœosis. It would be of interest to know the hereditary behavior of such unisexual characters if bred in confinement.

B. *Experiments.* — Few investigations of the regenerative power of the abdominal appendages of the Decapoda have been made, and the results obtained have not been entirely satisfactory. Morgan's experiments on *Eupagurus longicarpus* in 1898 showed that a slight power of regeneration existed in the appendages of two or three of the individuals he used; but his experiments extended over too brief a period of time to secure any marked regeneration. The first experiment was continued only twenty days, and the second for twenty-eight days. And the conditions under which the material was kept were possibly not the most sanitary, as the fact that over 40 per cent. of the individuals died during the twenty-eight days would seem to indicate. One would hardly expect regeneration to be rapid under conditions in which life itself could scarcely be maintained. My experience has shown that although regeneration may occur after an operation, and become visible without an intervening moult, it usually does not do so in the pleiopods. None of the individuals Morgan used was kept until a moult had occurred.

Miss Steele's experiments on *C. virilis* and *gracilis* were carried on for a sufficient length of time, but she found it difficult to provide the sanitary conditions necessary to such prolonged experimentation. The specimens used in her work were probably too old to give the best results. They measured not more than three inches in length, a size which would indicate that they were several years old at least. The younger the specimens used, the more frequently the moults take place. Those used in my experiments measured from one and six tenths to two and five tenths cm. in length, and were probably at the beginning of the second or third year. Two individuals measuring five cm. in length were also used. These did not yield as satisfactory results although some regeneration occurred. The difference was probably more in the frequency of moulting than in anything else. While one moult took place in these older ones, I could secure three in the younger. And to have kept the older individuals until the same number of moults occurred as in the younger ones, would have required two years instead of four or five months. The use of more nearly adult material, and the fact that slight attention was paid to the swimmerets may account for the slight regenerative power which Miss Steele was able to report.

My experiments show that the swimmerets of young specimens of *C.* (*Bartonius*) *bartoni* regenerate rapidly, and that the regeneration of any of the appendages may be practically completed in a single season of growth. The regeneration is not particularly slow in beginning, having become visible in one instance only six days after the operation was performed. It is usual, however, to find that the regeneration begins and takes place under the old exoskeleton, without showing any visible indications that the new parts are forming. For instance, No. 9 moulted on March 28, four days after the operation, and no regeneration could be noticed. The next moult took place April 30, but during that time no indication whatever that regeneration was occurring could be seen. Nevertheless, when the moult occurred it was evident that regeneration had taken place. If the experiment had been continued for only thirty days, the conclusion naturally drawn would have been that regeneration either did not occur, or was " very slow in beginning." As a matter of fact there is no way to tell how soon after March 28 the regeneration did begin, if indeed it had not already begun at that time.

To explain the slight regenerative power which he found in the abdominal appendages of *Eupagurus*, Morgan suggested that the food supply of these organs might be considerably less than that of the thoracic legs. It seems to me quite unnecessary to make this assumption, especially since I have shown that there is a rapid and complete regeneration of the swimmerets in young specimens of *C.* (*Bartonius*) *bartoni*. In this connection Emmel, '04, observed that swimmerets in the lobster will regenerate more rapidly than the pereiopods if the latter are cut "only a relatively short distance below the breaking plane." And he questions whether the supply of food material can explain the comparative difference in the regeneration of pereiopods and swimmerets. Moreover, if the limited food supply is responsible for lack of regenerative power how must we regard the regeneration of two supernumerary appendages in the abnormal swimmeret figured? It seems to me that some other explanation must be offered for the difference in regenerative power.

It has been a common experience with those who experiment with regenerative tissues, that the regeneration is always more rapid and complete in young individuals than in old ones. This fact is due probably to the greater plasticity, the more active and mobile condition of young tissues. They are more nearly embryonic in character, differentiation is not so complete, nor so fixed as in the older tissues. Emmel's ('08) recent work on the reversal of asymmetry in the lobster lends emphasis to this statement. He says: "In the first four stages of the lobster's development, a crusher may be produced on either the right or the left side of the body by the autotomous amputation of the chela on the opposite side — the regenerated chela becoming a nipper. During the fifth stage, although the chelæ are still symmetrical, the possibility for such experimental control disappears."

Since differentiation is known to proceed at different rates in different parts of the body, we may suppose that one part retains its primitive condition longer than another. If any portion of the adult regenerates less rapidly than another portion, may it not be an index of the comparative plasticity of the two parts? The more rapid regeneration of the thoracic appendages than of the swimmerets in the adult crayfish, may be due to a longer retention of the plastic embryonic condition of the cells in the region of the breaking joint by the former, certainly not to any proportionate difference in the food supply of the two series of organs.

The important point in Morgan's results which he properly emphasized, was that regeneration did take place, however slight it might be. While we cannot say that the abdominal appendages of crayfishes are never injured, yet injuries to them are rare in nature. Examination of hundreds of individuals has shown that there is a remarkable uniformity of size and structure in these organs, a condition which could not exist if mutilations were frequent. Yet these appendages possess as high a power of regeneration in youthful stages as any of the appendages which are so frequently torn away. My experiments strengthen very much the evidence in favor of Morgan's statement that there is no relation between power of regeneration and liability to injury.

Conclusions.

The following conclusions may be drawn from the study of abnormalities, and the results of the experiments described in this paper.

1. The abdominal swimmerets of *C.* (*Bartonius*) *bartoni* Fabr. all possess a high power of regeneration in immature specimens. Since regeneration of swimmerets has been noted in *Cambarus propinquus*, *Palæmonetes vulgarus*, *Homarus americanus* and *Eupagurus longicarpus*, it is probable that the decapods generally possess this power, especially in young individuals.

2. This regeneration usually cannot be seen till after one, and sometimes two, moults have occurred, due to masking of the regeneration by the exoskeleton.

3. Slow regenerative processes in the swimmerets of the older individuals are due probably to a lower degree of plasticity in the protoplasm rather than to insufficiency of the food supply.

4. Injuries may occur, but they are rare in swimmerets, and the power of regeneration and liability of the parts to injury are apparently independent.

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Explanation of Plate I.

All figures except Fig. 17 are $\times 5$.

Fig. 1. Second right pleiopod of *C. virilis* Hagen, ♀, showing two supernumerary appendages.

Fig. 2. First right pleiopod of the same specimen.

Fig. 3. Third right pleiopod of *C. virilis*, ♂, modified for sexual purposes.

Figs. 4–7. Successive steps in the regeneration of the fifth right pleiopod in *C.* (*Bartonius*) *bartoni*, ♀.

Fig. 8. Left pleiopod from same somite as Fig. 7, without regeneration, drawn to same scale.

Fig. 9. Fourth left pleiopod of young *C.* (*Bartonius*) *bartoni*, ♀, after two moults.

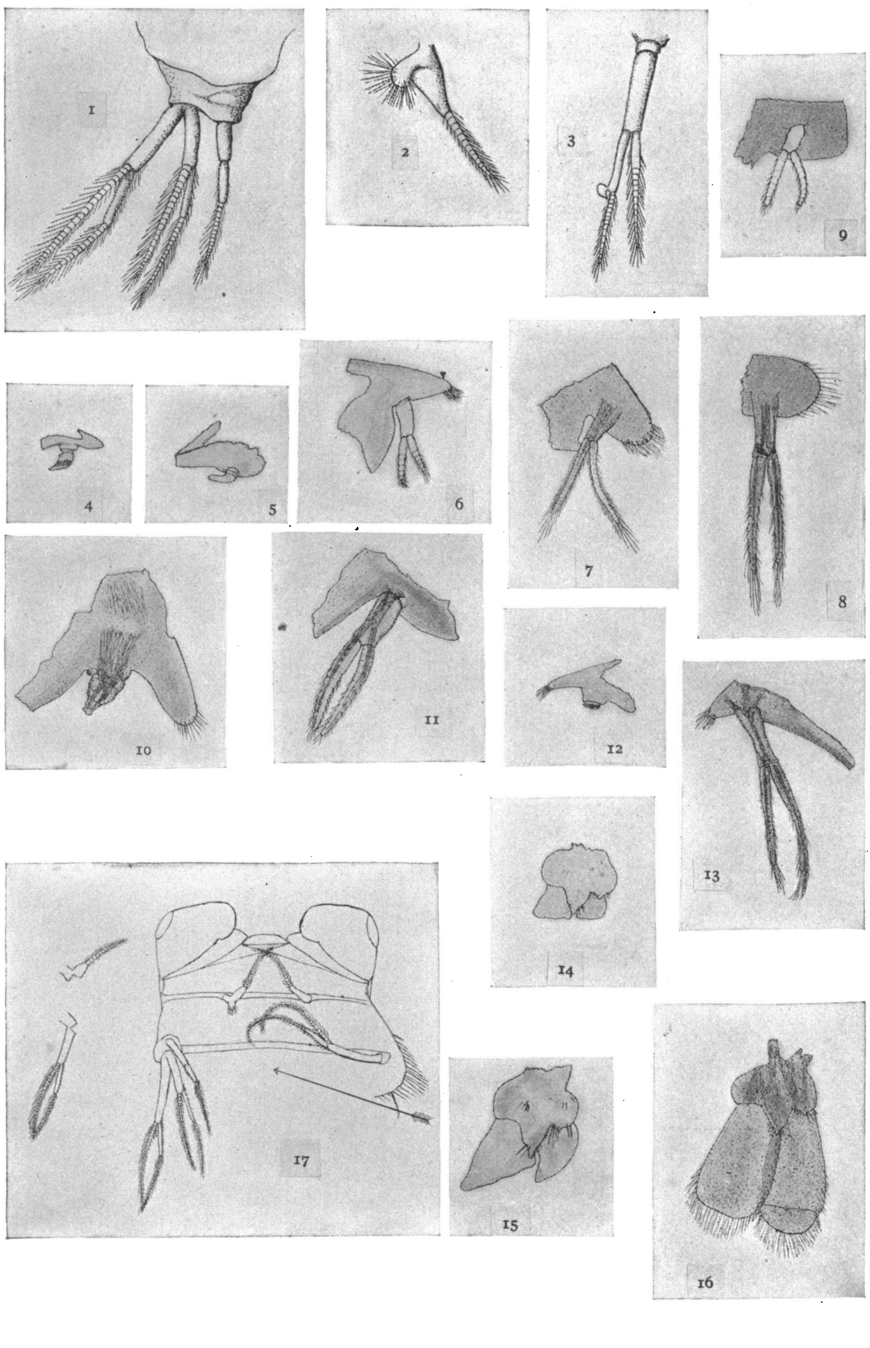
Fig. 10. Fourth left pleiopod of older *C.* (*Bartonius*) *bartoni*, ♀, after three and one half months.

Fig. 11. Third right pleiopod of *C.* (*Bartonius*) *bartoni*, ♂, after one moult.

Figs. 12–13. Second left pleiopod of *C.* (*Bartonius*) *bartoni*, ♀, condition immediately after amputation, and after the second moult.

Figs. 14–16. Right uropod of *C.* (*Bartonius*) *bartoni*, ♂, condition at amputation, before, and after, second ecdysis.

Fig. 17. Diagram illustrating the way in which the abnormal appendages shown in Figs. 1 and 2 may have been produced.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