INSTANCES OF HERMAPHRODITISM IN CRAYFISHES

By WILLIAM PERRY HAY

Howard University, Washington, D. C.

Hermaphroditism, that condition in which both sexes are combined in the same individual, is an interesting deviation from the normal line of animal development and as it affects not only the organs of reproduction but extends its effects to all the secondary sexual characters as well, it is worthy of the biologist's attention. Among certain of the lower animals the hermaphroditic condition seems to be the normal one just as in the great number of flowering plants the normal condition is to have both pistil and stamens developed in the same flower, but in the case of these animals as in the flowers mentioned there is usually some device by which self fertilization is prevented or made very difficult. Among those animals and plants in which distinct sexes have been developed hermaphroditism is very rare. In animals there is a period during which the embryo is non-sexual but its subsequent development is almost invariably along either the male or the female line.

In the case of the decapod Crustacea the only instance of undoubted hermaphroditism recorded is that of the lobster, *Homarus vulgaris,* described and figured by F. Nicholls in 1730.[1] The specimen externally showed the male sexual organs on the left side and the female organs on the right side. On being dissected the internal sexual organs were found to correspond; the right half of the body, therefore, was normally female while the left half was normally male.

Coming now to the crayfishes, the first recorded instances of abnormal development of sexual characters are by Rosseau and Desmarest.[2] In these cases females of *Astacus fluviatilis* were observed to possess two pairs of sexual orifices, one on the third, the other on the fourth pair of legs, which led by a branched oviduct to the ovary on each side of the body.

In 1870 Von Martens described three specimens of an Australian

[1] *Philosophical Transactions of the Royal Society of London,* vol. xxxvi, No. 413, p. 290.

[2] *Annales de la Societe Entomologique de France,* 2d Series, vi, pp. 479 and 481, pl. xiii, 1848.

crayfish, *Cheraps preissii*,[1] in which the normal openings of the oviducts on the third pair of legs co-existed with male orifices on the fifth pair of legs. The specimens had been preserved in alcohol for several years and their internal organs were doubtless badly preserved. No ovary was detected and no oviduct leading to the openings on the third pair of legs. A similar arrangement of openings was noticed in males of *Parastacus brasiliensis* and *P. pilimanus*.

In 1892 von Ihring[2] reported that in *Parastacus brasiliensis* he had found that two sets of apertures, one on the third and the other on the fifth pair of legs, coexisted in every individual of the "several dozen" examined by him and that on dissection they all proved to be males.

In 1898 Faxon[3] stated that not only *Parastacus brasiliensis* and *P. pilimanus*, but *P. saffordi, P. varicosus, P. defossus* and *P. hassleri*, as well, seemed invariably to possess two sets of genital orifices. No dissection of any of the specimens was described.

In 1898 Lönnberg[4] had an opportunity to examine a series of *Parastacus hassleri* and his observations form a most valuable contribution to the present discussion. He found that while the two pairs of genital orifices were present in every individual it was still possible by comparative measurements to separate his specimens into two lots, one of which from the broader abdomen, shorter antennae and weaker chelipeds he regarded as females, while the other, with an opposite set of characters, he took to be males. An examination of the internal anatomy proved the correctness of his theory. The males possessed only testes, the females only ovaries. The arrangement of sperm ducts and oviducts, however, was very remarkable. From each generative gland there were two ducts passing downward, one to the fifth and the other to the third pair of legs. In the females the anterior of these ducts alone was complete and functional, the posterior one ended blindly and could be of no use. In the males the reverse was the case, the anterior duct ended blindly while the posterior one was functional as a sperm duct. A more critical examination of the external genital apertures was now made and it was found that in each case there was actually only one pair of openings, those on the third pair of legs in the males and on the fifth pair of legs in the females being only shams.

[1] *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 18th Januar, p. 3, 1870.

[2] Congress International de Zoologie à Moscou, Aug., 1892.

[3] *Proceedings of the U. S. National Museum*, XX, p. 683, 1898.

[4] *Zoologischer Anzeiger*, XXI, pp. 334–335 and 345–352, 1898.

The ovaries were so filled with ova that there seemed to be no room for anything else but in the testes there were found, on microscopical examination, along with the usual elements of that organ, certain spherical bodies which Lönnberg thought might be young eggs. The summary of his investigation, therefore, was as follows:

"1. The supernumerary genital orifices on the third pair of legs of the male *Parastacus hassleri* and those on the fifth pair of legs of the female are closed.

"2. Both sexes can be distinguished on an examination of the outer parts.

"3. In both sexes a pair of supernumerary genital ducts (thus four in all) are present corresponding to those of the opposite sex.

"4. It seems at least possible that the male generative gland contains female elements (eggs) although I do not think it probable that these can be fully developed, still less be of propagative use.

"Thus it may be said that in *Parastacus hassleri* a partial hermaphroditism is prevailing, but male and female organs are not functionary in the same individual, neither are ripe elements of both sexes produced by the same specimen."

Lönnberg further states that his investigations of abnormal specimens of *Astacus astacus,* with first abdominal appendages resembling those of the male but with genital aperatures on the third pair of legs, show these to be invariably females with no trace of hermaphroditism in the internal organs, a conclusion which agrees with that of Bergendal.[1]

In the light of Lönnberg's conclusion that the condition of partial hermaphroditism in *P. hassleri* probably exemplifies the condition to be found in other species of the genus, an examination has been made of the specimens of *P. hassleri, P. defossus, P. saffordi* and *P. varicosus* in the collection of the U. S. National Museum. In the first three species there is found only one pair of actual openings, as Lönnberg has described above, but in *P. varicosus* there seem to be two pairs. It may be that in the latter case one pair only is natural and the other has been made by a needle in the hands of some investigator, but if so I am quite unable to distinguish which is the natural and which the artificial opening. It is very easy indeed to break through the shell at either of the points mentioned in any of the species, more easy perhaps in *P. defossus* and *P. saffordi* than in *P. hassleri,* as the apex of the tubercle on the fifth pair of legs is membranous only and the depressed operculum-like area on the third pair of legs is thin.

[1] *Bihang K. Sv. Vet. Akad. Handl.,* XIV, 1888, and XV, 1889.

From the evidence now before me I would say that undoubtedly a partial hermaphroditism as indicated by the two sets of ducts described by Lönnberg or a more complete hermaphroditism as shown by the two sets of genital orifices in *P. varicosus* is the normal condition in the species *P. brasiliensis, P. pilimanus, P. hassleri, P. defossus, P. saffordi* and *P. varicosus,* while contrasted to this group is *P. agassizi* which, so far as the dissection of one specimen will prove, does not possess more than a single pair of genital orifices or tubes.

In the genus *Cambarus* four specimens, two of *C. propinquus sanborni,* one of *C. diogenes* and one of *C. propinquus* have been described by Faxon[1] as showing to a greater or less degree a combination of sexual characters.

In the first specimen, *C. propinquus sanborni,* 60 mm. long, all the characters were those of the female, but the external openings of the generative organs were situated as in the male sex, upon a small papilla on the basal joint of each of the fifth pair of legs. The second specimen, belonging to the same species, 38 mm. long, was likewise a female in every way except that the first pair of abdominal appendages were like those of the male. The third specimen, *C. diogenes,* 84 mm. long, had all the external characters of the female except the first abdominal appendages which were curiously modified so as to resemble the same parts in the males of the genus *Astacus;* they were smaller in size and lacked the two large, recurved hooks of the normal *C. diogenes.* The fourth specimen, *C. propinquus,* 72 mm. long, agreed with the female in every respect except that the first pair of abdominal appendages were partly transformed into the condition which obtains in the male. The transformation was greater on the left side although on neither had it gone far enough to produce a perfect male appendage. A dissection of the first described specimen revealed the presence of many large ovarian eggs and Dr. Faxon's opinion was that the other three in all probability were females which had assumed some of the characters of the opposite sex.

To the list commented on above it is now possible to add four more. In the course of the examination of the extensive series of crayfish collected by the U. S. Fish Commission and by myself, all of which have been deposited in the U. S. National Museum, I have found two specimens of *C. spinosus,* one of *C. propinquus* and one of *C. affinis* which show evidences of hemaphroditism.

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[1] *Memoirs of the Museum of Comparative Zoology,* x, No. 4, p. 13, 1885.

The first two, *C. spinosus,* were collected from Clinch R., Tennessee, by Dr. B. W. Evermann, Oct. 12, 1893, and bear the U. S. National Museum number of 20,835. They are both 91 mm. in length and may be distinguished as number 1 and number 2.

In number 1 the general appearance is that of a young or second form male. The third pair of legs is hooked and the second pair of abdominal appendages is exactly as in the normal male. The first abdominal appendage of the right side is like that of the normal *C. spinosus* of the second form but is possibly a little short. The corresponding appendage of the left side is shorter, the outer ramus is fairly well formed but the inner is much stunted and bent strongly downward. The basal segment of the fifth pair of legs is imperforate although it bears a small papilla. There is a well developed annulus ventralis of the same structure but a little less prominent than in the normal female and the openings of the oviducts are perfectly formed and operculate and situated, as is usual, on the basal segments of the third pair of legs.

A dissection of this specimen fails to show any trace of male organs internally but there is a well developed ovary filled with nearly mature eggs.

In number 2 the general appearance is more like that of the female, the abdomen being broader and the chelipeds shorter than in number 1. Otherwise it corresponds perfectly with number 1 except that the first pair of abdominal appendages are short and blunt and are not provided with the long, slender tips characteristic of the males of this species. A dissection of this specimen shows it to correspond exactly with number 1.

The third specimen, *C. propinquus,* 53 mm. long, from near Sandusky, Ohio, is in general appearance a male of the second form but an examination of the ventral surface shows a striking lack of symmetry, the right side being more strongly feminine, while the left side is masculine. Thus on the right side, on the third pair of legs, there is a normally formed and operculate opening of an oviduct; this is not even indicated on the opposite side. On the other hand, the left leg of the third pair bears the usual small hook characteristic of the male, while the right leg shows no trace of it. The annulus ventralis, rather lower than usual, has the outline and sculpture characteristic of the species but the small conical elevation just behind it, on the sternum of the last thoracic segment, bears a pencil of hairs exactly as in the male. The first abdominal appendage of the left side is entirely similar to the usual second form appendage of the species and the basal segment of the contiguous fifth leg is

perforated by the opening of the sperm duct. The first abdominal appendage of the right side, while of the same pattern, is misshapen and only half as long as its fellow and the basal segment of the contiguous fifth leg is imperforate. The second abdominal appendage of the left side is developed as in the male while on the right side it is as in the female.

A careful dissection of this specimen has been attempted but it has been so poorly preserved that nothing can be determined. There is a large mass which is probably the ovary, but there is no trace of a spermary or sperm ducts and even the oviduct can not be identified with certainty.

The fourth specimen, *C. affinis,* 106 mm. long, from the Potomac River, near Washington, has all the external characters of a fully developed first form male except that on the basal segment of the third pair of legs there is, on each side, an orifice of an oviduct. These orifices are not operculate and in the living animal the white oviducts protruded conspicuously and first called my attention to the specimen. A careful examination shows no other female characters except that the basal segment of the fifth leg of the left side is not perforated by a sperm duct. The first pair of abdominal appendages are perfectly formed and the third pair of legs bear strong hooks. The internal organs of this specimen show a most astonishing reversal of conditions. There is a large ovary, a little more developed on the left side than on the right, well filled with nearly mature eggs. On each side a perfectly formed oviduct passes downward to the bases of the third legs. On the right side a short and not much coiled sperm duct leads upward from the base of the fifth leg to a rudimentary spermary which lies directly upon the ovarian mass and is partially imbedded in it. The diameter of the spermary is about four millimeters and its greatest thickness about two and a half millimeters. There is not the slightest trace of a spermary or sperm duct on the left side.

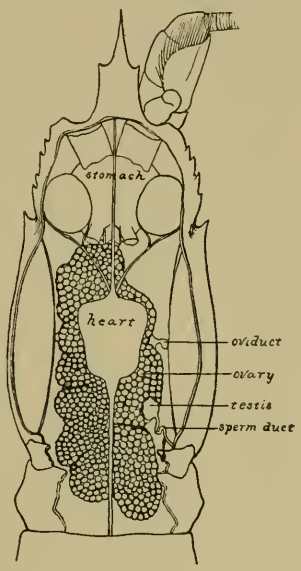

FIG. 27.—Dorsal view of an hermaphroditic individual of *Cambarus affinis.*

A microscopic examination of the spermary and the sperm duct have failed to show the presence of spermatozoa but there is a

thick epithelial layer which seems to be exactly like the spermatophoral cell layer of normal males. I therefore have little doubt that this specimen was capable of producing some spermatozoa. From the appearance of the ovaries it seems very probable that had the specimen been allowed to live, it would have produced a large number of perfectly normal eggs.

It might be added that during the time the specimen was kept alive it was seen in conjugation with a female of the same species and a little later was itself seized and held for a short time in the usual manner by a male. The latter, however, is a matter of little importance as I have several times observed the same thing in the case of two males neither of which was hermaphroditic.

It will be observed that of all the specimens belonging to the genus *Cambarus* described both by Dr. Faxon and myself only a single one, the individual of *C. affinis,* had perfectly developed external male characters. In all the other cases, with the possible exception of specimen number 1 of *C. spinosus,* the female characters were so strongly developed as to be unmistakable indices to the sex. Such dissection as was possible under the circumstances bore out perfectly the external indications and we may say without hesitation that the individuals were females. Even in the case of the specimen of *C. affinis* the internal organs pointed unmistakably to the conclusion that it too was functionally more a female than a male. It would therefore appear that in the genus *Cambarus* at least, hermaphroditic individuals are females which, owing to some ambiguity of the formative cells in the embryo, have developed to a greater or less degree the characters of the opposite sex. The condition is a very rare one and is usually shown in the external organs only. It has been observed by students of teratology that hermaphroditic individuals, in certain species, at least, as they grow older show masculine characters more and more strongly and it may be that something of the kind occurs in crayfishes. Most of the specimens of these animals which have been examined were small, the only fully adult one (*C. affinis*) had the most perfectly developed hermaphroditic characters and the inference is possible that this perfection of the male organs had been acquired with age.

In the genus *Astacus* indications of hemaphroditism appear to be quite as uncommon as in *Cambarus.* Among the Parastacidæ the condition of apparent hermaphroditism seems to be established in the genus *Parastacus* and may also be found to obtain in *Cheraps* but evidently is rare or altogether wanting in the other genera.