The Moulting and Growth-stages of Gammarus, with Descriptions of the Normals and Intersexes of *G. chevreuxi*.

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Ray Lankester Investigator for 1920.

With Plates I to XXI* and 4 Figures in the Text.

CONTENTS.

INTRODUCTION.

Many of the difficulties found in naming and classifying Crustacea are due to the extraordinary modifications caused by growth and sex, and the confusion arising from our lack of knowledge of these developmental stages has led to many errors. In the group Amphipoda, for example, the different growth-stages of a species may be, and often are, described

* The whole cost of producing the blocks from which the plates illustrating this paper have been printed has been met in part by the author and in part by special donations given for the purpose.—Ed.

as so many different species, or sometimes even as different genera. A striking instance of this is found in the widely distributed species *Jassa falcata*, which has more than thirty synonyms.

In the hope of throwing some light on the question of development which might be applicable to the group generally, the work described in this paper was commenced in 1909. If, as seemed practicable, the life-history of one species could be worked out, and some of the problems of development solved, the results could then be applied to the other members of the group and might even perhaps add a little to our knowledge of Crustacea as a whole. Much of the work described in this paper was done whilst holding the Ray Lankester Investigatorship, and my thanks are due to the Trustees for enabling me to carry it on.

When the work was begun nothing was known as to the length of life of an amphipod, its moulting periods, the length of time taken to reach maturity, the length of the breeding period, or the incubatory period of the eggs, nor at what stage of development the sexes could first be recognised. The last point is of special importance to systematists, because in species-work as a rule the distinctions are based on the secondary sexual characters, and though there is usually a marked difference between male and female at sexual maturity, yet in the young stages the sexes are often indistinguishable. I hoped to find characters by which the sexes could be distinguished on hatching, and also to be able to trace other characters common to the young as well as to the adult which could be used in establishing the specific identity at each stage of growth.

Quite recently this question has assumed a greater importance by reason of the appearance of the phenomenon of intersexuality in one of the species under observation. Both male and female intersexes were found, but were not recognised as such until nearly mature. Experiments were therefore started to find the early stages of the intersexes, to compare them with the growth of the normal animals and to see whether or not these differed in any degree from the normal.

It is impossible to study the different growth-stages directly from the living individual, for although an amphipod is a hardy creature and can be kept under the microscope without water for a short examination, the risk of injuring it by exposure to the air is too great, especially in its feeble condition after moulting. Apart from this danger, there is also the impossibility of getting clear definition of the detail, owing to the incessant jerking and wriggling movements of the struggles to escape from the transmitted light.

It soon appeared that the only way in which the problem could be studied was by examination of the moults or cast skins of the different growth-stages. The animals would have to be kept under observa-

tion and the moults collected when cast. In order to do this, it became necessary to find a species which would live in laboratory conditions.

The *Jassa falcata* just referred to was first chosen. It is very common all round Plymouth Sound on the buoys, and living near the surface of the water as it does, and making its "nests" at water-level it seemed as if it might be easy to accustom it to life in shallow water in the Laboratory. Various methods were tried, but it was found impossible to keep the Jassa alive for any length of time, and in the end the plan was adopted of picking out a number of animals at one stage of growth (judged by size and development), keeping each in a separate pot till it moulted, and then preserving each animal with its moult. The stage of growth attained would then be noted and a fresh supply of Jassa at this stage would be set out for the next moult. Several hundred moults were obtained by this method, but on examining them it was seen that the results would prove of small value, as it was not possible to judge whether the moults were from immature males or from immature females, nor could the limits of individual variation be traced and defined. It was evident that the only way to get accurate information was to obtain the complete series of moults from *one* animal, the male series from one male and the female from one female.

After many efforts to establish Jassa in the Laboratory it had to be given up, and more suitable species sought for. These were fortunately found in 1912 in dredgings from the ditches which drain Chelson Meadow, a salt marsh near Plymouth reclaimed from the tidal part of the Plym a little more than a century ago, and protected from the tide by an embankment, the accumulation of drainage water being emptied through sluice-gates into the river only at rare intervals. Three species of Gammarus were taken, *G. pulex* in the freshwater stream which runs in at the far end of the meadow, and two species in the brackish water of the ditches, *G. duebenii* and a new species, *G. chevreuxi*. With these the moulting experiments were commenced, and later, two other Gammarus were added, *G. locusta* and a littoral species not yet named. *G. duebenii* had to be given up because of its cannibal propensities, but good series of moults were obtained from the other four. *G. chevreuxi* soon developed a remarkable power of producing mutations especially in connection with the eye, its shape, colour, etc. Descriptions of some of these have been published, and because of the work already done, and the new mutations which are still arising, and also because of the appearance of intersexes amongst the normal males and females, this species is the one chosen to illustrate the moulting and growth of a Gammarus. The most striking mutation, the loss of one or of both eyes, will be described in a later paper.

The differences between the species studied are very marked, in the number of moults and the time taken to reach maturity, in the size and number of the eggs, in the time of incubation of the broods, and in the time between the hatching of the young and their extrusion.

In *G. locusta*, for example, the female lays a great number of very small eggs, as many as 143 being counted in one brood. In summer the eggs take from 9 to 10 days to hatch; the young, which are exceedingly small, are extruded from the pouch almost immediately, and the female moults and lays a fresh batch the same day. The young ones moult at short intervals till sexual maturity is reached, and then at longer periods. Eggs are laid after the twelfth moult. Fifty-two of the large brood above mentioned were placed together in a jar, through which a strong current of air was kept bubbling; of the 36 which survived to maturity the first male became mature at 35 days, and the first broods of eggs were laid on the 38th day. In order to obtain exact data of the moulting periods, 32 of the others were set out singly in finger-bowls, each with air-circulation gentle in this case so as not to injure the moults. Very few of these survived, 1, a male, moulted at intervals of 5, 3, 4, 3, 4, 3, 3, 4, 4, 5, 4, and 6 days, dying after the twelfth moult. Another, a female, moulted at intervals of 2, 4, 4, 3, 5, 5, 5, 5, 4, 4, and 5 days, and then after a period of 10 days moulted and laid eggs, no male being present.

The male *G. locusta* carries the female for one or two days before the young hatch. The female, as has just been shown, can, however, lay eggs without a male being present; in one such batch, 70 eggs were counted, but they were evidently infertile, and were thrown off later.

In *G. chevreuxi*, on the other hand, the female never lays eggs unless mated. The eggs are much larger and fewer in number than in *G. locusta*. Well-grown *G. chevreuxi* females have from 30 to 40 in a batch, the highest number recorded in these experiments being 63. They take longer between moults, lay eggs after the seventh moult, and keep the young at least 24 hours in the pouch before extrusion. The male carries the female for several days before the young hatch. Sometimes moulting takes place and a new batch is laid within a few hours of the extrusion, sometimes 2 or 3 days may elapse.

This species lives well in stagnant water; *G. locusta*, on the contrary, requires a continuous supply of air. *G. pulex* also will live in stagnant water, but does better when put under the "air-circulation."

G. pulex females, like the *G. chevreuxi* females, never deposit their eggs unless mated. The eggs are very large and few in number, usually from 12 to 18 in a batch, the highest number recorded in the experiments being 28. They take from 16 to 17 days to hatch in summer conditions. The young, which are large, are kept for about a day in the pouch after

hatching, and then extruded all together. The summer experiments were not successful in that none of the young survived to maturity. The early moults were at intervals of 5 to 7 days. The winter experiments, as was to be expected, gave much longer intervals between moults. One animal, a male, moulted at intervals of 12, 16, 14, 16, 18, 21, 14, and 16 days, another of the same brood, a female, at 13, 16, 12, 16, 18, 18, 16, 17, 17, and 23 days. Eggs are laid after the tenth moult.

In the littoral species (*Gammarus* sp.) the eggs are very large and few in number, only about 8 to 12 in a batch. The young hatch in about 12 to 14 days in the summer, but are kept in the pouch for several days, often having their first moult before being extruded. Sometimes the female will extrude them all together in about 4 or 5 days, sometimes she keeps them till they have all moulted and extrudes them and the moults together, or, and this is more usual, she will let them out one or two at a time, taking more than a week to do it. In one case the female kept some of the young for 13 days, and in another, one of the brood was retained for 17 days and had at least two moults before emerging. The incubation lasts for 12 to 14 or 15 days in summer, but the moulting period of the female is from 24 to 28 days. It will thus be seen that in this species the "incubatory periods," i.e. the periods from the time the eggs are laid to the time the young leave the egg (hatch), do not coincide with the "moulting periods," i.e. the periods between the laying of successive batches of eggs, which are always preceded by moulting. Indeed, it almost looks from the figures as if one moulting period in this species corresponds with two moulting periods in others, e.g. *G. chevreuxi*, the second of the two periods being occupied in protecting the already hatched young inside the brood pouch. The difference in habitat may account for this. These animals dwell on the shore fairly high up, under stones which are exposed for some hours between tides ; the other three species described live in the water, *G. pulex* in freshwater streams, *G. chevreuxi* in brackish water ditches, and *G. locusta*, a pelagic species, ranges from the water near the shore to the open ocean.

It is difficult to give the number of days to the first moult of the young in this littoral species of Gammarus. One kept for 5 days in the pouch, after emerging moulted at intervals of 8, 8, 9, 8, 10, and 12 days, and another at 8, 9, 10, 9, 9, and 9 days. None survived to maturity, owing to the difficulty of feeding them. They refused the rotted-leaf diet of the other species, and the minced shrimp with which they were fed often caused fouling of the water, pieces being carried off under the stones and so overlooked. The experiments could not be regulated easily as small stones had to be provided for shelter, and the pans had to be kept tilted to allow the animals to leave the water when they wished.

The number of moults to maturity varies with the species ; in

G. locusta eggs are laid after the twelfth moult, in *G. pulex* after the tenth, and in G. *chevreuxi* after the seventh. It is difficult to say precisely at which growth-stage the broodplates are first developed. The position of the broodplate (attached to the first joint of the leg, between the gill and the insertion of the second joint where the leg is pulled out in moulting) renders it very liable to injury during the act of moulting. This is especially so in the early stages, the cuticle being then too thin and delicate to retain its shape.

In *G. pulex*, where the cuticle is firmer and more substantial than in either *G. locusta* or *G. chevreuxi*, broodplates have been traced in four growth-stages preceding maturity. The development is as follows: in Moult 7 they appear as minute, rounded leaf-like plates, with margins entire; in Moult 8 they have lengthened, and increased to three times the size; in Moult 9 rudimentary hairs have developed on the margins (cf. broodplate in the upper figure of Text Fig. 4); in Moult 10 the broodplates are very large, the chitin is hard, the rudimentary hairs more numerous and more noticeable, showing under a high power as tiny conical excrescences. In the next stage sexual maturity is reached, and the broodplates are fully developed, with long fringing hairs. Three stages have been found in *G. locusta*, but in this species the cuticle is so thin in the young animals that it would be difficult to trace the earlier stages even if they were present. In Moult 10 the broodplates are very small and rounded, with margins entire; in Moult 11 rudimentary hairs appear on the margins; in Moult 12 the development is the same as in the tenth moult of *G. pulex*; and in the next stage sexual maturity is reached, and the broodplates are fully developed. Three stages have been traced in *G. chevreuxi* also. In this, the smallest of the three species, the broodplates are microscopic in Moult 5, round, with margins entire; much larger in Moult 6, with rudimentary hairs clearly indicated; in Moult 7 the hairs are seen as conical points on the margin, sometimes pushing out free of the cuticle, on the posterior margins. At the eighth growth-stage the animal is sexually mature, and the broodplates are fully developed. (See Plates III and IV, *Jour. Mar. Biol. Assoc.*, XII, 3, 1921.)

From the results set forth in this paper, it will be seen: (1) That the species sufficiently alike in structure to be included in one genus may yet differ widely *inter se* in many essential points connected with their reproduction; (2) that the bars to the interbreeding of even the most closely allied species would appear to be insuperable; and (3) that although different species may and do live together, and breed in the same place, their distinctive specific characters are preserved unchanged.

It seems important to emphasize these points, because of the help they may give in solving the difficulties systematists encounter in dealing

with collections of amphipods taken in the same locality. The genus Gammarus, with which we are concerned, is an instructive example of the confusion of species. Species which have been considered distinct by some observers are regarded as one "variable species" by others, and have been grouped together under one name as a "type" and its "varieties"; or again, two or more distinct species have been described as one species with various "intermediate forms" between the two extremes.

This confusion as to the proper determination of species has risen from lack of knowledge of the life-histories of the animals. On p. 377 I have dealt with a hitherto unsuspected but fruitful cause of much of the difficulty, viz. *the different breeding forms of the male*. So different, indeed, are they that an observer who did not know their life-history would be justified in separating them into distinct species (see figures of M.8 and M.10 of the male, Plates X and XII).

The intermediate forms referred to are probably only the several growth-stages of the various species, and not, as the authors appear to consider them, new forms produced by the intermating of these species.

DESCRIPTION OF A GAMMARUS.

It may be of service here to give a brief recapitulation of the structure of an amphipod of the genus Gammarus, using the terminology established by Stebbing (*Amphipoda*. Das Tierreich, Vol. XXI, 1906).

The body of a Gammarus (Text Fig. 1) is elongate and laterally compressed, and consists of head, peræon, and pleon. The *head* carries 2 pairs of antennæ, the eyes, and the mouth-organs; the *peræon* is divided into 7 segments, and the *pleon* into 6 segments and the telson. Each of the segments bears a pair of legs, those of the peræon 7-jointed with large expansions of the first joints called *sideplates*.

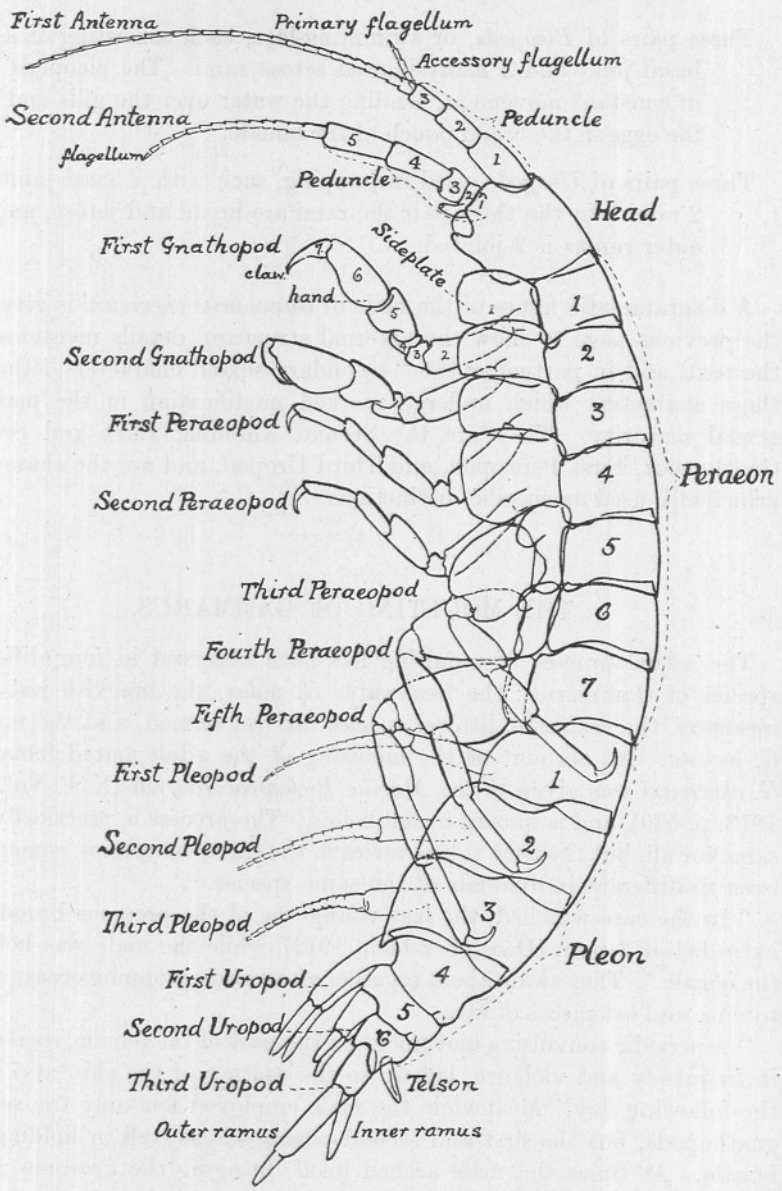
Taking the appendages in order, they are as follows :—

First Antenna, with a 3-jointed peduncle, and 2 flagella, a long many-jointed *primary*, and a much shorter *accessory*.

Second Antenna, shorter than Antenna 1, with a 5-jointed peduncle and 1 many-jointed flagellum.

Mouth-organs, *mandibles*, *maxillæ*, and *maxillipeds*, not dealt with in this paper.

First and Second Gnathopods, used as grasping organs, with expanded hands, much more developed in the male than in the female (see p. 360).



TEXT FIGURE 1.—Diagrammatic drawing of the male of *Gammarus chevreuxi*. ×10.

Five pairs of *Peræopods*, or walking-legs, the first two pairs bent forward at the third joint, the three hind pairs bent backward.

Three pairs of *Pleopods*, or swimming-legs, each consisting of a long basal joint and 2 many-jointed setose rami. The pleopods keep in constant movement, sending the water over the gills and over the eggs in the brood pouch of the female.

Three pairs of *Uropods*, used in jumping, each with a basal joint and 2 rami. In the third pair the rami are broad and setose, and the outer ramus is 2-jointed.

A diagrammatic figure of the male of *Gammarus chevreuxi* is given on the previous page to show the external structural details mentioned in the text, and in particular the "secondary sexual characters," that is, those characters which undergo marked modification in the male at sexual maturity. They are the Second Antenna, First and Second Gnathopods, First Peræopod, and Third Uropod, and are the characters principally used as specific distinctions.

THE MOULTING OF GAMMARUS.

The actual process of moulting has been observed in four different species of Gammarus: the freshwater *G. pulex*, the brackish water *G. chevreuxi*, the estuarine littoral species not yet named, and the marine *G. locusta*. An account of the moulting of the adult mated female of *G. chevreuxi* was given in the *Marine Biological Journal* (N.S., Vol. IX, 1913, p. 550), and is quoted in full below. The process is practically the same for all, but the time taken varies in the different species, sometimes even in different individuals of the same species.

"In the case watched, the last young one of the previous brood was extruded at 2 p.m. (December 14th, 1912), while the male was holding the female.* They swam about together afterwards, stopping occasionally to seize and eat pieces of ulva.

"A periodic convulsive movement on the part of the female, increasing in frequency and violence, led up to the casting of the skin at 7 p.m. the following day. Meanwhile the male employed not only the second gnathopods, but the first and second peræopods as well in holding the female. At times the male arched itself, bringing the urosome up to rest against the fifth peræon-segment of the female, and then suddenly

* The male usually carries the female with its second gnathopods, the claw of the right hand being inserted under the anterior edge of the tergum of the female's first peræon-segment, and the claw of the left hand under the posterior edge of the tergum of the fifth peræon-segment.

straightened out, rasping the uropods along the female's cuticle. During the whole time the male kept the lower antennæ bent over the head of the female, so touching both pairs of her antennæ. About two hours before the moult the female commenced a series of violent rapid jerks, bringing the head and urosome together, and then straightening suddenly, at intervals stiffening the body in the form of a comma, with the head bent downwards, and the body moving with a sort of convulsive tremor. Finally, the male ceased swimming, and they both lay quiet, while the female, helped by the male, freed the head from the old cuticle with the gnathopods. This process and the ensuing rest occupied not more than five minutes. Then the male suddenly arched the body as before and, in straightening again, pushed off the posterior portion of the moult with its uropods, assisted by the upward heaving of the female's body. It did not relinquish its hold for a moment. After moulting the female lay absolutely still, without even a movement of the pleopods, while the male kept up a steady current with his. In a few minutes they commenced to swim as before."

To this description a few more particulars may be added. It can nearly always be seen when a moult is imminent, especially in the young. The animal is very sluggish, keeping under the leaves out of the light, and not feeding much ; its colour becomes duller, and the whole body looks opaque. As the time of sloughing draws nearer, a thick secretion, probably lubricative in action, begins to ooze out between all the joints : in one very difficult case which was watched, the secretion was seen to ooze out of the pleon and hind peræopods first ; two hours later, out of the peræon and antennæ, by which time the body was drawn up inside, leaving the hindermost part of the cuticle empty and quite transparent. During moulting the animal lies on its side, moving spasmodically with a sort of convulsive tremor, every now and again bringing its head and tail together, and then straightening out suddenly with a jerk, apparently trying to loosen the old cuticle. It varies this by swimming rapidly in circles, with the dorsum inwards. At last the skin cracks just behind the head dorsally, the crack extending until the whole of the posterior margin of the head is free. The animal pulls vigorously at the cuticle covering its head, drawing the gnathopods down the antennæ, the body meanwhile pulsing and heaving against the dorsal crack, and so widening it. The cuticle then splits on each side along the length of the peræon at the junction of the sideplates. The final action in the very young is exceedingly rapid, taking barely a second to accomplish. The little animal gives a sudden heave, arches up its body, and squeezes out backwards through the dorsal crack, freeing the gnathopods last of all as it emerges.

In a good moult the skin comes off whole, with the appendages still in

place. The sideplate attached to the first joint of each peræopod splits down its internal face, a semicircular flap of skin opens at the place of insertion of the second joint, and the six free tapering joints are easily drawn out through this opening, leaving the old cuticle intact. The sloughing of the gnathopods, however, is much more difficult. In these the terminal joints are dilated distally, and having to be pulled out through narrow constricted openings the old cuticle generally gets badly torn. Even in a "good moult" the skin of the 2nd, 3rd, and 4th joints is ripped open lengthways and that of the 5th and 6th is split; but in difficult moults the old skin of the gnathopods is torn to pieces by the animal in its struggles, the mouth-organs often being used in the effort of stripping it off. The skin on the gills is much thinner and flimsier than on any other part of the body, and is always crumpled or torn in moulting. So also is the cuticle of the broodplates of the immature female, especially of the small ones found in Moults 5 and 6 of *G. chevreuxi*, which are often pulled out like the everted finger of a glove. The broodplates in the adult, on the contrary, are very stiff with a thick chitinous cuticle.

The moulting of the older animals takes a longer time, especially in the preparatory stage. The head-portion is pulled off first with the antennæ and mouth-organs attached, as well as the lining of the œsophagus, the foregut, and the stomach with its several chambers, fringing hairs and spines. Then the body with the peræopods is drawn out of the posterior part, and lastly, the gnathopods are pulled out.

Occasionally in a delicate or unhealthy animal a part of an antenna or one or two gills will be torn off in the struggle and will be found in the sloughed skin. The antennæ are always regenerated, but I do not think the gills are. I have occasionally found deformed gills or very tiny ones present in dead animals, probably due to disease, but it appears to be hopeless to try and find out anything about the gills from the cast skins, owing to their crumpled and torn condition.

It may be as well to refer here to the difficulties encountered in getting a series of moults from one animal. It has proved impossible to obtain a complete series of perfect moults from any one individual. Over 3000 moults were collected from *G. chevreuxi* alone, and incredible as it seems, out of that number there was not one single perfect series of either male or female. One reason is that the condition and substance of the chitin varies through the animal's life, probably with its health, some moults being fairly thick and easily sloughed off, while others may be so thin in texture that they are cast piecemeal in flakes, or crumpled out of all shape. Again, moulting is sometimes very difficult, perhaps owing to insufficiency of the lubricative secretion; in such cases the cuticle of the head and of the gnathopods, particularly of the latter, will be torn to

fragments by the animal in its efforts to get rid of it. But the chief cause of the difficulty lies in the fact that the *animals eat their moults* almost directly after ecdysis. Moulting, as far as my observation goes, takes place more often at night than in the daylight, and if it should happen early in the night, there will be very little, if any, of the sloughed cuticle left by the morning. The gnathopod cuticle, the last portion to be freed, is almost invariably eaten first. The males are more vigorous than the females, and more destructive of their moults, so naturally the series of male moults is more imperfect than that of the female ones.

Before passing on to describe the moults themselves, reference must be made to a picturesque legend which has grown up around *G. locusta*. It was originated by Spence Bate* in the days before the problems connected with the reproduction of amphipods were investigated, but that it still finds credence is shown by its being quoted in recent popular works on marine animals. The story which Spence Bate (l.c., p. 380) calls "one of the most interesting instances of maternal solicitude yet recorded among animals so low down in the scale of physical arrangement" is, briefly, that the mother Gammarus protects the young for some time after they are hatched until "as they grow older they obtain more confidence, and quitting, forget the anxious care that guarded them in their early hours"; that the young ones on hatching swim about keeping close to her as she moves slowly along; and that at the approach of danger, or at any alarm, *they rush back to the pouch* for shelter. The parent it was stated would then get excited and swim quickly about, and later when the threatened danger had passed, the young would emerge again and swim about as before.

Now, a moment's consideration of the structure of the pouch shows the impossibility of such a thing ever happening. The female Gammarus has 4 pairs of broodplates, 1 pair on each of the peræon-segments 2, 3, 4, and 5. The plates are fringed with long delicate hairs, which interlace and form a continuous pouch, open at both ends where the plates are separated by the width of the body. The young are very active when hatched, and can be seen moving about in the pouch, changing places, and endeavouring to push out when the mother relaxes the pressure on the broodplates. I have kept numerous amphipods of different genera under observation in the Laboratory, but I have never seen a young one re-enter the pouch after once getting clear of it. They will come partly out of the front opening, especially when the female is feeding, to share the food, but the lightest downward movement of her head sends them in again. They sometimes crawl on their sides out at the back end of the pouch on to the sternum of the 6th and 7th peræon-

* *A History of the British Sessile-eyed Crustacea*, by C. Spence Bate and J. O. Westwood. Vol. I, p. 380; Vol. II, p. xlv. London, 1863, 1868.

segments clinging tightly with their claws, but the first beat forward of the pleopods drives them back to safety inside. Should their clutch, however, not be sufficiently firm, they will be swept off in the swirling current made by the pleopods, and after that there is no return possible. The action of the pleopods alone would prevent it, and when it is remembered that the female casts the whole of the skin and fills the pouch again with eggs within a short time of hatching the brood, the impracticability of these young re-entering will be plainly seen. In *G. locusta*, the species mentioned by Spence Bate, the process (hatching, extruding, moulting, and laying) is speedier than in most of the species, and is usually completed in a day.

Summer and Winter Broods.

Amphipods breed long before they reach the maximum size of the species. The number of growth-stages from hatching to sexual maturity appears to be different not only in the different genera, but different even in the different species of any one genus.

In *Gammarus chevreuxi* the complete series to sexual maturity numbers 7, for both the normal male and the normal female. The animals mate after the sixth moult, and the eggs are laid and fertilised after the seventh moult. From sexual maturity onwards to the maximum of growth there is very little change in the moults of the normal female, except for the increase in size and in the number of the setæ. The normal male has *two more moults* before assuming the definitive "adult male" characters, but like the female after reaching this stage it does not change except for the increase in size and in the number of setæ and coiled hairs.

The actual number of moults before the sexual characters appear in the intersex is not known, but there are apparently more than in the normal. Of the hundreds of young from the Irregular Stock set out for moults only one intersex survived the fifth moult, and this one is figured, six stages in all. The stage of development reached was not nearly as advanced as that of the normal at the sixth stage.

As *G. chevreuxi* is a species which breeds all the year round, the broods laid in the summer have been compared detail for detail with those laid in the winter. The stages of growth were found to be identical, even to the number and position of the hairs; but, as might be expected, the summer broods reach maturity at a much quicker rate than the winter ones. They take, in fact, only about half the time, 34 to 40 days in the hot weather as compared with 74 to 99 in the cold months.

Broods kept in the Laboratory sometimes vary a good deal in the time taken to reach maturity. No two broods are alike in this respect, a later brood sometimes maturing before an earlier brood from the same parents, and kept as far as one can see under precisely similar conditions.

As a rule, all the individuals of any one brood will accomplish the first moult on the same day, and sometimes the second moults too will all occur together, but from the third moult when a great increase in activity can be noted, the strong ones go ahead and the weaker lag behind, although in the final result maturity is reached within a few days by all the members of the same brood.

The figures of the normal animals are taken chiefly from males and females of three summer broods of the F_2 generation from the Wild Stock first brought into the Laboratory. The normal female series is nearly perfect, but no complete series of any one male could be found out of all the moults of hundreds of animals which were examined. The first seven moults of the male series are from the summer broods ; but the three last are from the winter broods, and were taken from two males of nearly the same age. Unfortunately K.6, the male from which the figures of the eighth and ninth were drawn, had its tenth moult during the night, and had eaten part of it before the morning examination of the pots took place. Another male a day younger, which had been compared stage by stage with K.6 and which was due to moult that day, was killed in order to prevent the destruction of the moult of this stage and the figure of Moult 10 was drawn from it. It was compared with the moult fragments left by K.6 and was found identical in every point, even to the number of setæ.

The 3 *summer broods* mentioned above were : Brood A, extruded May 26, 1913, 26 young ; Brood B, extruded July 14, 1913, 17 young ; and Brood C, extruded July 13, 1913, 20 young.

Of these, Brood C matured in the shortest time, 3 females surviving to mate. One female, C.4, is figured in Plates I to V.* It moulted at intervals of 5, 5, 4, 5, 4, and 6 days. On the 33rd day a male was added, but as no mating took place, it was removed the next day, and another one put in the female's bowl. Mating followed at once, and on the 36th day the female moulted and laid 10 eggs (Plate V).

The second female, C.3, had a male added on the 33rd day, mated immediately and moulted and laid eggs the day after ; 16 young hatched and were extruded 10 days later, on August 26th. The pair mated again, but separated whilst the male moulted, mated once more, and on August 28th the female moulted and laid a fresh batch of eggs, the young being extruded 11 days after.

The third female, C.14, moulted at 6, 4, 4, 4, 3, and 5 days' intervals. The gonads were plainly visible on the 31st day ; a male was added on the 33rd day, mated at once, and on the next day the female moulted and laid eggs. The first young one was extruded 9 days later, 15 others on the following day.

* In these and in similar cases described in this paper the animals were examined and recorded only once in the twenty-four hours. If the *exact hour* of moulting had been known in each instance, it is not unlikely that there would have been less divergence between the different times recorded.

In Brood B, also, only 3 animals survived to maturity, 2 males and 1 female. One male, B.9, is figured in Plates VI to VIII. It became mature at the age of 40 days. The other male, B.3, lost through disease and regenerated, part of its antennæ, gnathopod 1, and the uropods. This disease is of common occurrence, and is found in the wild animals freshly brought in, as well as in the stock inbred for generations in the Laboratory. It manifests itself first as a brown mark or stain in a joint, and the joint so affected rots off In spite of the disease, B.3 matured at 38 days, and mated after this moult. It must be noted that its growth stages, except for the parts affected, were precisely the same as those figured for B.9, the normal male. This is of importance in view of the fact that an intersex appeared in this brood.

In intersexes, the growth-stages are very different from those of the normal animals, a much longer time is taken to reach maturity (that is until the distinguishing sexual characters appear), and the majority of intersexes seem to be incapable of breeding, or even of mating. The disease referred to above evidently does not delay maturity nor does it inhibit breeding.

The surviving female of this brood, B.5, had a male added on the 35th day, mated the following day, and moulted and laid eggs on the 38th day.

Brood A was not a vigorous brood, the animals were smaller than those of Broods B and C, and although more survived, the results are not of much value, owing to their propensity for eating their moults. One female, A.19, moulted at intervals of 4, 6, 7, 5, 7, 5, and 6 days. One male, A.20, is figured in Plates VII and IX. It moulted at intervals of 4 and 6 days, ate its third moult, and had the fourth on the 23rd day, then moulted at 6, 6, and 5 days. In 2 females, A.21 and A.23, the gonads were visible on the 37th and 39th days respectively.

The difference in the length of the moulting periods in winter can be shown in the *two winter broods** kept in an unheated room in which the temperature never rose above 10° C.

Brood 1, eggs laid October, 22, 1912, 34 young extruded on November 5. Six survivors reached maturity at 85, 88, 92, 93, 99, and 99 days respectively. Three moulted at intervals of 9, 13, 15, 12, 16, 17, and 17 days ; 11, 11, 14, 16, 11, 15, and 15 days ; and 10, 10, 14, 8, 11, and 14 days. One specimen, a male, moulted at the following intervals, 10, 10, 17, 10, 14, 16, 15, 17, 17, and 19 days. It reached its seventh moult, the moult at which these animals generally become mature, in 92 days, but being very small it was not seen to be a male until after its next moult, at the age of 108 days. Several females were tried with it, but it did not mate until it was 142 days old.

Brood 2, extruded on November 12, 1912, 39 in number. The 6 survivors reached maturity at 75, 81, 83, 85, 86, and 89 days respectively. The first to moult did so at intervals of 7, 9, 11, 8, 10, and 13 days ; the second at 8, 9, 11, 9, and 10 days ; another, a female, at 8, 10, 12, 12, 12, 16, 15, 14, and 17 days ; this was eaten by the male put into its bowl to test it.

The intersex, figured, C.N.397 f., is from the Irregular-eyed Stock, an F_1 from the Brood 269 in which male intersexes occurred. It was one of a brood of 10, extruded on July 30, 1921, and set out in finger bowls for observation. Only 3 of the 10 survived the third moult ; of these 2 were normals and grew quickly, the third was seen to be an intersex at the third moult, the difference in its size and swimming being very noticeable. It moulted at intervals of 6, 7, 7, 7, and 8 days, dying 14 days later from an overdue moult.

* See p. 554 *Jour. Mar. Biol. Assoc.*, Vol. IX, No. 4, 1913.

Although hundreds of young from this Stock have been set out in the hope of getting a complete series of intersex moults, this animal is the only one, so far, which has survived the fifth moult.

Method. It is not possible to mount the moults with any degree of success, the cuticle being too thin to bear the weight of a coverglass without collapsing out of all shape. The best results are obtained by mixing glycerine and alcohol in equal parts, adding a little eosin for staining purposes, and then using enough of this mixture to float the moult fragments into the required position under the microscope. A camel's-hair brush cut down to two hairs is useful in straightening out the parts in the stronger moults, but floating is always safer, when possible.

It only remains now, before dealing with the moults themselves, to describe those parts of the body most affected externally by the modifications of growth, viz. the antennæ, the outgrowths of the cuticle or sensory armature, and the gnathopods.

The Antennæ of *Gammarus chevreuxi*.

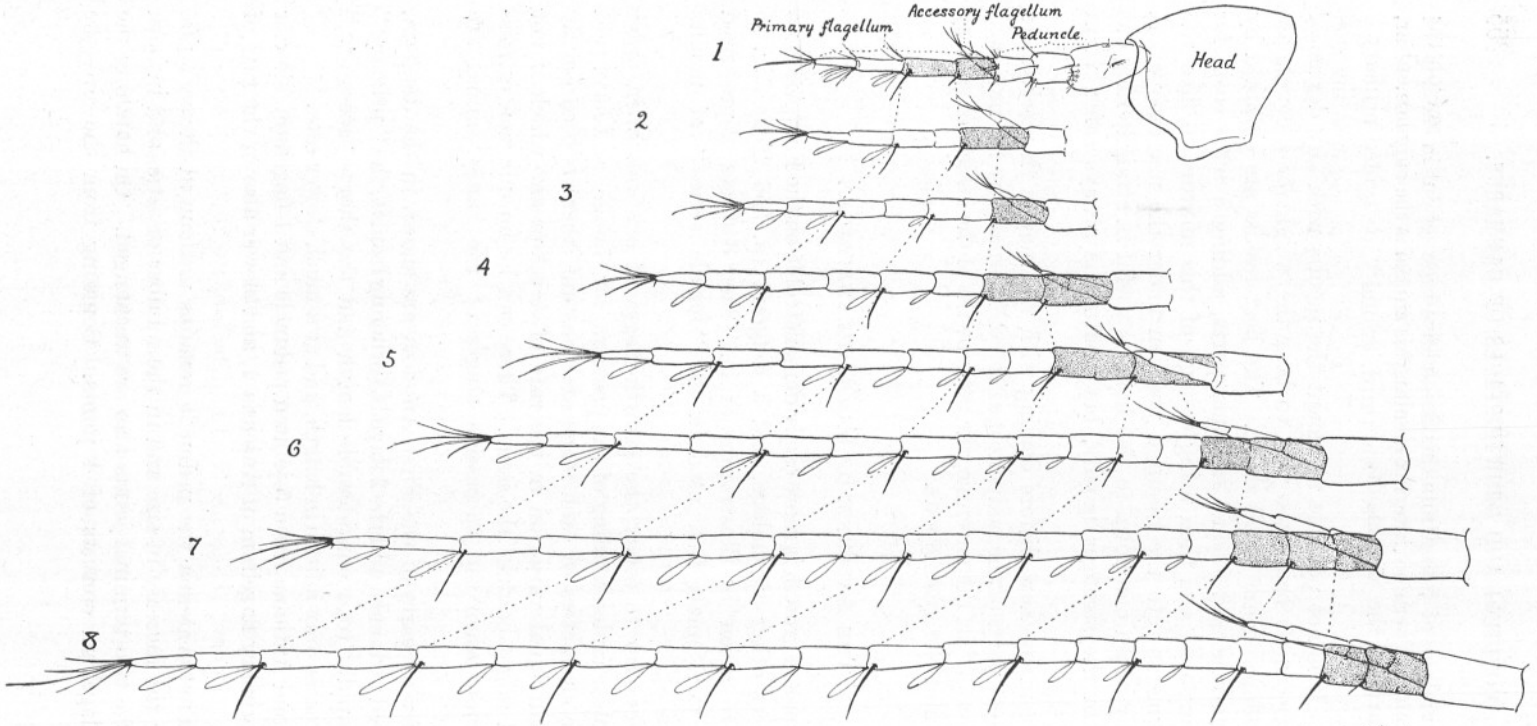
The process of growth is more easily demonstrable on the First Antenna than on any other appendage, and a diagram (p. 356, Text Fig. 2) is therefore given in illustration of it. The 8 stages represented are from the female C.4, used in the "female series" of moults (Figs. 1 to 8).

It is necessary to study the growth-stages of *one animal* in order to gain a clear understanding of the problem, for though, as I have said before, the characters of each stage are constant, there is occasionally a slight individual variation in the rate of development which if not recognised might confuse the issue. There can be no question of misinterpretation when the successive stages of the same animal are examined.

The different parts of the First Antenna are shown in the diagram, the 3-jointed peduncle, and the 2 flagella springing from it, the "primary" growing rapidly to a considerable length and the short "accessory," which increases only a little in length, and at a much slower rate.

The Second Antenna has a 5-jointed peduncle and 1 flagellum, shorter than the primary flagellum of Antenna 1, and slower also in the rate of growth.

In the First Antenna the peduncle remains unchanged through life, except for the increase in size and in the number of setæ, and in both antennæ the two terminal joints also are unchanged. On hatching the primary flagellum consists of 4 joints. Counting from the tip—the



TEXT FIGURE 2.—The progression of growth from birth to maturity as seen in the flagellum of the First Antenna. Stage 1 shows the head and First Antenna, with the 3-jointed peduncle, 4-jointed primary flagellum, and 2-jointed accessory flagellum. The dotted portion represents the growing-region or formative zone, and the new primary joints dividing off from it at successive stages. These joints subdivide later. In the Stages 2 to 8, only the outstanding bristles and sensory filaments are shown, the setæ being omitted. The 8 stages represented are all from the one animal, a female (C.4). The figures are taken from the Left Antenna, outer surface, with the exception of Fig. 5, which shows the Right Antenna, inner surface.

terminal joint; the second joint with 2 seta groups distally, one on the upper margin and one on the inner margin, with a sensory filament or æsthetasc inset in the middle; the third, a long "undivided primary" joint, carrying, in addition to the 2 seta-groups, a long outstanding stiff bristle behind the lower group on the outer side of the joint; and the fourth or proximal joint, also with an outstanding bristle.

The proximal joint is the growth-region, or formative zone of the flagellum. The process of growth is as follows:—

The proximal joint divides, usually into two portions, the distal one of which is a new joint which I have called the "*undivided primary joint.*" (Sometimes in the older animals more than one primary joint may be formed.) At the next moult this undivided primary joint elongates and itself divides into two portions, the distal part or *true primary* joint carrying the outstanding bristle in addition to the seta-groups, and the proximal portion, which may be called the *secondary joint*, developing the seta-groups, but never producing an outstanding bristle.

The process is repeated in each stage, the last-formed primary joint subdividing and giving rise to a secondary joint; the formative-zone dividing and giving off one or more undivided primary joints. In the diagram the formative zone and the undivided primary-joints are shaded.

The outstanding bristles occur only on the primary joints; the sensory filaments develop on all the joints *except the first-formed secondary joint* (see Growth-stage 2 in the diagram, Text Fig. 2).

The alternation in the armature of the joints is very characteristic in this species in both antennæ.

In the First Antenna the primary joints, easily distinguished by the outstanding bristle, carry 2 seta-groups, the upper group containing 3 setæ, 2 of which point outwards, and 1 inwards; the inner group with 4 setæ, 2 on either side of the sensory filament. The secondary joints also carry 2 seta-groups, but in the upper group the position of the setæ is reversed, 1 pointing outwards and 2 inwards, and the inner group has only 1 seta on either side of the filament. The alternation of the setæ (2, 1, 2, 1) is very striking when the antenna is viewed from the side.

In the first-formed secondary joint (joint 4 counting from the tip) the inner seta-group differs from those on the other joints, besides lacking a sensory filament. There are 3 setæ in each of its groups, in the upper group 1 seta points outwards and 2 inwards; in the inner group the position is reversed, 2 diverge outwards and 1 inwards. Sometimes, in an undivided primary joint, a seta of the secondary joint will appear at the point of division before that division takes place.

The Sensory Armature of *Gammarus chevreuxi*.

In this species the armature consists of sensory hairs, setæ, and strong spines, of which some remain unchanged throughout life whilst others, and these the important ones, are subject to extraordinary modification, involving even a complete change of form ; as, for example, the median serrulate-seta to a pointed-spine, and the pointed-spine in the male to a further development, the truncate-spine.

Some parts of the sensory equipment are common to the whole of the body, others again are peculiar to certain appendages ; for instance, the sensory filaments or æsthetascs (Fig. 25) are confined to the First Antenna, the serrated-hairs to the second joints of the gnathopods and the first two peræopods, the serrulate setæ and serrated-bristles to the gnathopods, and so on.

The armature of the body-cuticle consists of microscopic mobile hairs (Fig. 27) and spinules. These have not been figured, the scale at which the drawings were made not being large enough to admit of a proper representation. The hairs are scattered over the cuticle, inset sometimes singly each in a socket or pit in the skin, sometimes in rows of four to six, with the sockets coalesced and forming a small groove. Three series run down the length of the body, one along the median line and one on each side. The spinules are particularly numerous on the pleon, and are set so thickly together as to make the cuticle rasp-like to the touch ; they increase in number and size with age.

The sensory hairs, setæ, and spines may be divided into the following types, shown in Plate XV. Unfortunately the *texture* cannot be represented, nor the gradual hardening as the delicate setæ change to spines.

Hair (Fig. 26), long, thin, delicate in structure and very flexible. These develop as the animal approaches maturity, and are found generally on the under surface, e.g. on the gnathopod-hands, on the first and second joints of the peræopods of the hinder peræopods anteriorly, and in the mature female, on the margins of the broodplates.

Sensory-hair, thin, delicate, of varying lengths, with a small flagellum inserted at the tip. Found on the gnathopod-hands.

Plumose-hair (Fig. 27), short, very delicate and feathery, the flexible secondary hairs or barbs long and exceedingly fine. The shaft is slightly bulbous at the base, usually mobile and inset in a little socket. Found principally on the antennæ, the claws of the peræopods, and the telson.

Feathered-hair (Fig. 28), not as flexible as those just described, with a row of rather stiffer barbs on either side of the shaft. Found on the pleopods and third uropods.

Coiled-hair (Fig. 29), long, fine, and very flexible, the tip coiled when fully adult. Peculiar to the male and found only on the secondary

sexual characters, viz. the second antenna, first and second gnathopods, first peræopod, and third uropod. The coiled-hairs do not develop in the immature male until the sixth moult is reached, and then show as long fine hairs curving but not yet coiled. The most male of the female intersexes produce a few of these "immature-male" hairs distinctly curved on the second antennæ, nearly straight on the third uropods.

Serrated-hair (Fig. 30), very long and delicate, but stronger than the hairs previously described, with the terminal portion curved and serrated on either side of the shaft. Found only on the second joints of the gnathopods, and first and second peræopods.

Seta (Fig. 31), shorter than the hair, and stouter, tapering to a fine point. There are two kinds of setæ, not distinguishable at first, the one remaining unchanged through life, the other of different structure and modified with growth. The latter is slightly wider at the base and has the tip produced into a delicate hair-like point, or flagellum. It develops into the *slender-spine* (Fig. 32), with a very long slender shaft and a small hair-like flagellum at the tip. These "modifiable setæ" are found only on the hinder peræopods.

Sensory serrulate-seta (Fig. 33), midway between the seta and the spine, stiffer than a seta, but too delicate to be called a spine. It is found only in the angle-row of the hand in both gnathopods, and forms a very important character in distinguishing the sexes, and in distinguishing the normals from the intersexes (see p. 362). The serrulate-seta has a long, slender shaft, microscopically serrulate and ridged on the upper part with a flagellum inset at the tip of the shaft. The shaft appears to be hollow, and to have an outlet, opening at the tip of the flagellum. It develops into the pointed-spine.

The *marginal-seta* (Fig. 34) of the palm of the hand appears to be similar in structure to the serrulate-seta, but it is not easy to define the distinction between them. The marginal setæ are smaller, with the shaft smooth and shorter in proportion to the flagellum. They are not modifiable.

The *bent-seta* (Fig. 35) looks like a sensory hair, but has a stiffer shaft, lightly curved or bent in the middle. It is not modifiable. Found only on the hands of the gnathopods at the commencement of the "palmar-row."

Bristle, much longer and stouter than the seta, rigid and frequently curved.

Serrated-bristle (Fig. 36) and *dentate spine* (Fig. 37), with very stout bases, and strong curved shafts tapering to the flattened sensory tip, with the upper portion deeply serrated or toothed on either side. Found only on the posterior margins of the gnathopods.

Spine (Fig. 38), short and stout, with a fine flagellum near the tip. Found on the hinder peræopods, pleon, and uropods.

Slender-spine (Fig. 32), develops from the modifiable setæ on the hinder-peræopods.

Pointed-spine (Fig. 39), develops from the serrulate-seta. The shaft widens and curves over slightly, the conical tip being on the shorter straight side. The flagellum shows as a curved tubular process, apparently open at its free end, connected with the core of the shaft. Found only on the palms of the gnathopod-hands.

Truncate-spine (Fig. 40), peculiar to the adult male. It is the spine which undergoes most modification, developing from the first serrulate-seta of the angle-row, through the pointed-spine stage to a large broad flat-topped spine. The shaft decreases in length and increases greatly in width, so that the spine frequently becomes nearly as broad as it is long. The flagellum is gradually reduced and lost, and the tip becomes a flattened disc on which rows of spinulose ridges can be seen with a high power.

Curved-spine (Fig. 41), peculiar to the adult male, found at the palmar-angle.

The Modification of the Gnathopod-hands of *Gammarus chevreuxi*.

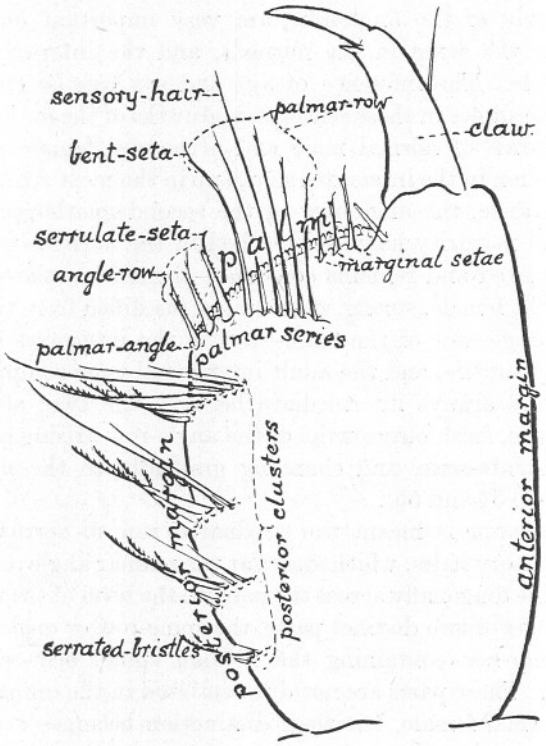
The hand is the name given to the expanded sixth joint of the gnathopods; the claw-like terminal joint closing down against the hand is often called the "finger," and these together form a powerful grasping-organ. The shape of the gnathopod hands, their size and sensory armature are of great importance in specific distinctions. Of all the parts of the body they are the most subject to modification by growth and sex, and the changes wrought are very striking, particularly in the male. As the male hands are the principal external characters used in separating the species of a genus, it follows that a correct reading of the changes undergone is of paramount importance to a clear understanding of taxonomic problems.

Figures are therefore given of the hands of both gnathopods at all the stages of growth from birth to sexual maturity, in order to show the extent of the modification up to that period (Plates XVI and XVII), whilst the fullest development attained by normal males and females, i.e. the maximum size for the species, is represented on Plates XVIII and XIX, and the development of the intersexes on Plates XIX and XX.

The principal features of the hand and the terms used in referring to them are shown in the accompanying diagram (Text Fig. 3).

The *palm* is the distal portion of the hand which extends from the insertion of the claw to the palmar angle. In the immature and the female the palm is transverse, but in the male, after sexual maturity is reached, it becomes indented and more and more oblique.

The *palmar-margin* is the crenulate distal edge of the palm. It is microscopically spinulose, and has on either side a row of the small marginal setæ running along its length and ending at the palmar-angle. In the immature and the female the palmar-margin remains unchanged,



TEXT FIGURE 3.

but in the mature male it begins to bend to the underside of the hand, more so in the first gnathopod than in the second, and this torsion grows more pronounced with age until eventually the palmar-angle with its two groups of spines is twisted completely underneath. The claw, which in the female is transverse and closes down against the transverse palmar-margin, bends in the male with, and to the same extent as the margin and comes at last to impinge against the under surface of the hand (see Figs. 50 and 51). In the intersexes this is reversed. The male intersex approximating to the female type has the transverse palm and

claw of the female, and the female intersex becoming increasingly male with age develops the torsion of the palm and claw (Figs. 52 and 53).

The *palmar-angle* is the angle formed by the junction of the palm with the lower or posterior margin of the hand. It is armed with two groups of setæ or spines one on either side ; the *angle-row* on the outer surface, the *angle-group* underneath. The claw closes down between these two groups.

The structure and modification of the sensory armature of the hand, and particularly of the angle-row, are very important characters for distinguishing the sexes in the normals, and the intersexes from the normal animals. The influence of age and sex can be clearly traced through all the stages in these sensory outgrowths of the cuticle, and once the typical forms of normal male and of normal female are realised, their combination in the intersexes shows up in the most striking manner. Take, for instance, the angle-row of the second gnathopod hand. As soon as sexual maturity has been reached in the normals the definitive adult type is fixed and remains constant—slender serrulate-setæ in the angle-row of the female, strong, stout spines (modified from the serrulate-setæ) in the angle-row of the male—but in the intersexes change continues throughout life, and the adult intersexual type as opposed to the normal types is always intermediate between the two, always mixed male and female, fresh outgrowths of the angle-row arising at each stage as *female* serrulate-setæ, and changing gradually to the *male* pointed spines (see Figs. 54 and 55).

By the *angle-row* is meant the graduated row of serrulate-setæ (or spines) and sensory hairs, which starts at the palmar angle and continues in a curving line diagonally across the palm to the level of the mid-margin. It really consists of two distinct parts, the spine-row or *angle-row* proper, and the *palmar-row* containing the median spine, bent-seta and the sensory hairs. These parts are not differentiated in the immature animal nor in the normal female, but their distinction becomes evident in the male as it approaches maturity, and in the most male of the female intersexes.

In Plate XVII the gradual separation of the palmar-row from the angle-row can be seen commencing at the seventh growth-stage. At the ninth stage the sensory hairs begin to draw together from a line into a cluster, and the complete development is shown in Moult 10, where the hairs are massed together in a dense cluster behind the truncate median spine.

The order in which the different spines and hairs appear and the modifications they undergo can be traced through the moults-series (Plates XVI and XVII).

Growth-stage 1. The first of the serrulate-setæ (the median-spine of the male) is developed at birth on the hands of both gnathopods in all the animals. In the normal female it remains unchanged through life in gnathopod 2 ; in gnathopod 1 it becomes gradually stouter and stronger, yet never loses its setiform character. It is this serrulate-seta which changes in the male at maturity to a pointed-spine and moves away from the spine-row at the angle to the middle of the palm, and then develops into the truncate-spine peculiar to the adult male.

Growth-stage 2. The bent-seta appears, arising above the median.

Growth-stage 3. The difference between the development of the normals and intersexes is first discernible. In the normals a second serrulate-seta appears *below* the first. This one, it is interesting to note, eventually becomes the largest spine of the angle-row, and its modification differs in the female in the two gnathopods. In the First Gnathopod in all, it changes to a strong pointed-spine ; so also in the Second Gnathopod in the male and intersexes, but in the female it remains unchanged through life. The first sensory-hair of the palmar-row appears *above* the bent-seta.

The new serrulate-setæ of the angle-row as they develop always arise on the lower side, and the new sensory-hairs on the upper side of the row and form a curving line across the palm.

In *Growth-stage* 6 sexual differentiation can be seen in the normal animals. The gnathopod hands, however, are still alike in the male and female ; development is not so far advanced in the intersex.

Growth-stage 7, the stage before sexual maturity. There is very little change in the female, but a considerable advance in the male. In the First Gnathopod the median-spine is seen diverging from the angle row towards the middle of the palm, whilst in the Second Gnathopod it has already diverged and is in its final position.

Growth-stage 8, sexual maturity attained. The adult characters of the female are now fixed, but the male passes through two more stages before assuming the definitive adult form. The median-spine is now of the " pointed " type.

Growth-stage 9 *of the male.* In the First Gnathopod the torsion of the palm is commencing. In the Second Gnathopod the spines in the angle-row are of the male type ; the median-spine is flattened at the tip, beginning the change to the truncate form ; and the sensory hairs are massed together in a cluster behind it.

Growth-stage 10 *of the male,* the fully adult form. In both gnathopods the typical male curved-spines are developed at the palmar angle ; the median-spine has completed the change, and is now a perfect truncate-spine.

In the female intersex there is a constant tendency to the male type.

In advanced forms (cf. Fig. 56) the median-seta not only diverges from the angle-row to the middle of the palm, but changes into a pointed spine like that of the young male in its first mature stage (Moult 8). The sensory hairs also diverge and form a cluster as in the young males. In two cases, Fig. 53 and CN 218b,* a further increase in maleness is shown in the torsion of the palm and claw of the First Gnathopod. The serrulate-setæ of the Second Gnathopod are modified into pointed-spines as in the male type, but though the change is towards increased maleness, the *intersexual type* as it may be called is always distinct, and remains intermediate between normal male and female. New additions to the angle-row arise as serrulate-setæ and change to pointed-spines, and in the typical intersex hand, either male or female, these two types will always be found together. In Plate XXI figures are given of a Female Intersex, CN. 229h., showing the hand of Gnathopod 2 at the age of 167 days and the same hand at the age of 367 days.

It will be seen that apart from size the character of the hands of the normals is practically unchanged from sexual maturity onwards, but that in the intersex a continuous modification takes place.

Description of the Moults of *Gammarus chevreuxi*.

The following account gives briefly the distinguishing characters of the successive growth-stages. These stages are clearly defined one from the other, and are *the same for winter as for summer broods*. The individual variation is very slight. There is sometimes a little difference in development between the two sides of an animal, one side, generally the right, developing at a rather quicker rate than the other. The sensory armature appears to be the same on both sides, but its distribution is occasionally slightly different, e.g. one joint of an appendage may have a spine or seta more than the corresponding joint on the other side, but when this occurs it very frequently happens also that another joint of the same appendage will carry a spine or seta less than the corresponding one on the other side.

The descriptions of the moults refer particularly to the individual specimens which have been figured, but in every instance the details have been confirmed by the examination of a great number of moults from other animals of the same stage and the essential constancy of the specific characters has thus been established. *Each stage* has proved to be remarkably constant, there being extremely little variation even in the numbers and positions of the individual setæ and spines.

The left side has been figured unless otherwise stated, and the mouth-

* *Journ. Mar. Biol. Assoc.*, Vol. XII, No. 3, p. 543, Fig. 112.

parts omitted where they would interfere with the detail of the gnathopods. The eyes are not shown in any of the figures of the moulted skins, as the cuticle extends uniformly over the cornea, and the eyes leave no impression visible in the moult.

Series I. The Normal Female.

Moult 1 (Female C.4, Fig. 1). The characters distinguishing Moult 1 are: primary flagella of both antennæ, 4-jointed; gnathopod-hands with 1 serrulate-seta at the palmar-angle; and third uropod with 3 spines distally on the first joint of the outer ramus.

On hatching, the young animal resembles the parents in that all the appendages are present. The difference in the proportion the various parts of the body bear to each other is, however, very marked, e.g. the head in the young is much larger in proportion, about a seventh of the total length of the body, measured dorsally, and the peræon and pleon are practically equal in length, whilst in the mature animal the head is an eleventh of the total length, and the peræon is a third as long again as the pleon.

The external characters of this stage are precisely the same in the normal male, and intersex, as in the female.

Head. The lateral and post-antennal corners are rounded; they become angular with growth.

First Antenna. On the upper side of the basal joint of the peduncle is a sensory groove with 1 delicate plumose hair inset. This groove is of great interest, as it appears to be analogous to the "auditory sac" found in many decapods (see p. 386 for description, and Fig. 27), but it has not hitherto been noted in the Amphipoda. The length of the groove and the number of the sensory hairs increase with age. On the outer side of the same joint and in a line with the groove is the group of 3 mobile plumose hairs, which is found unchanged through all the growth-stages.

The primary flagellum has 4 joints, the accessory flagellum 2.

The growth-region or formative zone in both First and Second Antennæ is at the proximal end of the flagella, the terminal joints remaining unchanged through life except for the addition of two or three setæ (see p. 355 for description and the diagram on p. 356).

Counting from the tip of the primary flagellum, the first joint has a cluster of 5 bristles, and 1 small sensory hair; the second joint carries on its inner surface a group of 4 setæ. with a long sensory-filament (*æsthetasc*, Fig. 25) inset in the middle; the third joint has a similar group of 2 setæ and a sensory filament, and in addition a strong stiff outstanding bristle behind the group; the fourth joint has a bristle of the same type, but not so far developed.

These outstanding bristles appear on alternate joints as the antennæ lengthen, and by their aid the method of growth can be traced through all the stages (see diagram).

The Second Antenna. The first of the bristle-groups of joints 4 and 5 of the peduncle is represented on each by 1 bristle at the lower distal angle. The flagellum is 4-jointed. Growth proceeds along the same lines as in the First Antenna, but not at the same rate.

First and Second Gnathopods. These form two of the principal distinguishing characters of the species, and undergo the most modification.

In both, the hands show the commencement of the angle-row, 1 large serrulate-seta (Fig. 33) being inset at the palmar-angle. This serrulate-seta develops in the male into the median truncate-spine. The angle-group of the under surface is represented by 2 very small sensory setæ.

The claw, in both gnathopods, is practically the same as at maturity, except, of course, in size; 2 stiff setæ are inset at its insertion, and it closes down between them against the crenulate palmar-margin. The fifth joint carries 2 large serrated-bristles (Fig. 36) on its posterior distal margin.

Uropod 3. Peduncle unarmed; 3 spines on the first joint of the outer ramus, 2 on the inner, and 1 on the outer distal margin; and 3 bristles, 1 long and 2 short, on the terminal joint; inner ramus only half the length of the first joint of the outer ramus, tipped with 1 long bristle.

Moult 2 (Female C.4, Fig. 2). The distinguishing characters are: flagellum of antennæ 1, 6-jointed; of antenna 2, 4-jointed; 1 serrulate-seta and the bent-seta in the palmar-series of the gnathopods 1 and 2; commencement of the first posterior-cluster on the hands, and of the sensory serrated-hair groups of the second joints of the gnathopods; and commencement of the spine-clusters of the third uropods.

Antenna 1. Basal joint with 2 sensory-hairs in the groove; primary flagellum with 6 joints, joint 4 (counting from the tip), the first of the new secondary-joints, never develops a sensory filament.

Antenna 2. No increase in the number of joints in the flagellum, but the proximal joint or formative zone has lengthened preparatory to division (see diagram, p. 356).

Gnathopods. On the hands in both gnathopods the bent-seta (Fig. 35), a long stiff seta with slightly bent shaft and flagellum at the tip, has now appeared on the anterior side of the serrulate-seta noted in Moult 1. This is the commencement of the "palmar row." One serrated-bristle of the first posterior cluster is found on the hands of gnathopod 2 in the female figured, C.4, but not in gnathopod 1. It is, however, present in the sister, C.14, and also in the male figured. On joint 2, in both gnathopods, the long sensory serrated-hairs (Fig. 30), peculiar to the gnathopods

and first two peræopods, have appeared, 1 each side in gnathopod 1, and 1 posteriorly in gnathopod 2 in this specimen ; (1 each side in gnathopod 2 in the sister, C.14, and in the male figured). These hairs are very long and flexile, curving round at the flattened tip in the older stages, and showing long delicate hyaline serrations on each side.

Peræopods. Peræopod 2 with 1 seta on the posterior margin of joint 2 : peræopods 4 and 5 with spines developed on the mid-margin of joint 6 ; peræopod 3 with a spine on the right side, but not on the left side (which is figured).

Uropod 3. Peduncle with 2 spines distally, one at each side : outer ramus with 4 spines on the distal margin, 2 on the outer side, and 2 and 1 seta on the inner side ; 1 spine about half-way on the outer margin, the commencement of the spine-clusters.

Moult 3 (from Female C.4, Fig. 3). The distinguishing characters are : gnathopod 1, the hand with 3 in the palmar-series ; gnathopod 2, the hand with 4 in the palmar-series ; posterior clusters on the fifth joints as well as on the hands ; and 1 sensory-hair on the under surface ; 2 spines on the anterior margins of the second joints in the hinder-peræopods.

Antenna 1. Basal joint with 3 sensory hairs in the groove ; primary flagellum 7-jointed, with 3 outstanding bristles, and 3 sensory-filaments in this specimen ; but in the male (and in other specimens) the division of the formative zone can be seen, and the armature of the new secondary-joint.

Antenna 2. One bristle developed on the lower margin of joint 4, the commencement of the second bristle-row ; flagellum with the same number of joints as in Moult 2, but with the proximal joint (formative zone) lengthened considerably.

Gnathopod 1. A second serrulate-seta has appeared posteriorly in the angle-row of the right hand, but not in the left ; on both hands the first of the serrated-bristle clusters is now represented ; and, on the inner surface, 1 hair of the first sensory-hair clusters can be seen, and 1 of the small sensory marginal-setæ which border the palm (Fig. 34).

Gnathopod 2. Both hands with a row of 4 at the palmar-angle, 2 serrulate-setæ posteriorly, the bent-seta, and 1 long delicate sensory-hair. A second serrated-bristle is found in the posterior cluster, and on the under surface, as in gnathopod 1, the first of the sensory-hair clusters, and the first of the marginal-setæ are represented. The second of the posterior bristle-clusters of joint 5 has appeared on gnathopod 2, but not in gnathopod 1 in this specimen, although it has developed in the male figured.

Both gnathopods now have 3 large curved serrated-bristles in the distal row on joint 5, and 3 long serrated-hairs on joint 2.

Peræopods. Peræopod 1, 1 seta posteriorly on joint 2, and 1 seta on the posterior mid-margin on joint 6; peræopod 2, the first of the long serrated-hairs on joint 2; peræopods 3 and 5 with 1 spine on the anterior margin of joint 2 above the distal one; peræopods 4 and 5 with 1 spine on the posterior mid-margin of joint 4; all 3 hinder peræopods with spines and setæ on both sides of joint 6.

Uropod 3. On the outer side, a second spine has developed in the peduncle distal cluster, and in the spine-cluster of the outer ramus.

Moult 4 (from Female C.4, gnathopod 1, peræopods 4 and 5 from sister female C.14, Fig. 4). The distinguishing characters are: flagellum of antenna 1, 8-jointed with the 2 proximal joints undivided and very long (or in some specimens 10-jointed with the proximal joints divided and short); antenna 2, flagellum 5-jointed; 2 bristle-rows represented on joints 4 and 5 of the peduncle; both gnathopods with 4 in the palmar-series of the hand, gnathopod 1 with 1 posterior bristle-cluster represented, gnathopod 2 with 2; peræopod 1 and peræopod 2 with 1 long serrated-hair on the second joint; hinder peræopods with joints 2, 4, and 6 carrying spines or setæ on both sides.

Antenna 1. Basal joint with 4 sensory-hairs in the "auditory" groove; primary flagellum 8-jointed, with 4 outstanding bristles, and 5 sensory filaments. The 2 proximal joints, i.e. the formative zone, and the undivided primary-joint, are long; in most of the other specimens male and female, these have divided, sometimes in both antennæ, sometimes in one only. The right antenna in this female (C.4) is rather more advanced than the left.

Antenna 2. Peduncle with 2 setæ on joint 3; on joint 5, 1 bristle of the second bristle-row has appeared, making 2 each on joints 4 and 5; the long proximal joint of the flagellum has divided into 2.

Gnathopod 1 missing in this specimen. The figure is taken from the sister, C.14. The palmar series numbers 4, 2 serrulate-setæ posteriorly, the stiff bent-seta, and 1 long slender hair; the posterior bristle-cluster now contains 2 serrated-bristles; joint 5 has 1 serrated-bristle of the second posterior cluster; and joint 2 a third long serrated-hair posteriorly.

Gnathopod 2. The hand with 4 in the palmar series; 1 of the slender flexible hairs has developed in the first posterior cluster, and 1 serrated-bristle of the second posterior cluster; also a second marginal-seta on the palm, outer side; on joint 5, 1 serrated-bristle of the second posterior cluster. On the under surface of the hand, the seta at the angle is now an almost perfect pointed spine. There are, in the adult animals, 2 rows of sensory-hairs underneath; the anterior one consisting of long curving hairs, and the posterior one longer and more slender; in this stage, the first hair of the first anterior group appears.

Peræopods. Peræopod 1, the first of the long sensory serrated-hairs present on joint 2 ; 1 seta on the mid-margin of joint 4, making 1 each side. Peræopod 2, 1 seta, mid-margin of joint 4 on the left side, not on the right, and 1 seta, mid-margin of joint 6, both sides. Peræopod 3, a second notch on the posterior margin of joint 2 ; 1 seta on the anterior mid-margin of joint 4. Peræopods 4 and 5 missing in specimen C.4, and drawn from the sister C.14. Both peræopods have 2 notches on the posterior margin of joint 2, peræopod 4 with 1 spine and peræopod 5 with 2 spines on the anterior margin above the distal group ; joint 4 in both is furnished with spines each side ; in peræopod 5 a spine has appeared on joint 5 mid-margin, and 2 of the long distal setæ in joint 6 have developed into the long slender spines (Fig. 32) peculiar to the hinder peræopods.

Uropod 3. One sensory-hair of the first sensory-cluster is present on the under surface of the first joint, outer ramus ; and 1 spine at the tip of the inner ramus.

Moult 5 (from Female C.4, Fig. 5). The gnathopods were missing from this specimen, and are therefore figured from the sister female C.14. The distinguishing characters are : Antenna 1, the flagellum either 10-jointed, with 2 long undivided proximal joints, or 12-jointed, with the 2 long joints divided into 4 short ones ; gnathopods with 5 in the palmar-series ; the hand of gnathopod 1 with 2 posterior-clusters, that of gnathopod 2, with 3 posterior-clusters ; uropod 3, with a spine midway on the peduncle ; 2 spines and 2 long bristles on the inner ramus.

This is the first moult in which the broodplates have been traced. They are microscopic in size, rounded, with no hairs yet developed on the margins, and are found on gnathopod 2 and the first three peræopods.

Antenna 1. The primary flagellum in C.4 is 10-jointed, the 2 proximal joints long, in C.14 12-jointed, the 4 proximal joints short. The growth is identical, the slight constrictions shown in the figures of C.4 (Fig. 5 in diagram) being continued across the joints as definite divisions in C.14. The latter was the more vigorous animal, and the slightly more advanced development is therefore to be expected. The armature is the same in both, 5 outstanding bristles and 7 sensory filaments. The accessory flagellum is 3-jointed in C.14, the same length in C.4 though only 2-jointed, but again the constriction is visible, which in C.14 has become a division.

Antenna 2. Peduncle with 2 bristle-clusters on joints 4 and 5 on left side, 3 on joint 4 of right side ; the flagellum is 6-jointed. In the sister C.14, there are 7 joints, the 4 proximal small ; in C.4 the proximal or formative zone is long, and the 2 next small, but the imminent division

of the long joint is shown by the appearance on it of the bristle of the new primary joint.

Gnathopod 1. Hand of C.14 ; 5 in the palmar-series, another long flexile hair having arisen at the anterior end of the row ; the serrulate-seta at the posterior end of the row is now a short, stout, almost perfect spine. Another marginal-seta has appeared near the insertion of the claw, and the first serrated-bristle of the second posterior-cluster. One hair of a second sensory group underneath, and 1 long seta on the outside of the hand, and 1 long seta on the outside of the fifth joint are also present.

Gnathopod 2. Hand of C.14 : 5 in the palmar-series ; 1 long seta on the outside of the hand as in gnathopod 1, and 1 serrated-bristle of the third posterior-cluster on joint 5 have appeared.

Peræopods. Peræopods 1 and 2, 1 seta in the mid-margin of joint 5 ; peræopods 3, 4, and 5 all with 2 spines on the anterior margin of joint 2, and spines in the mid-margin of joint 5. In all the peræopods of this stage the fourth, fifth, and sixth joints have spines and setæ in mid-margin, some on both sides, some on the posterior side only.

Uropod 3. One spine midway on the peduncle : setæ appearing in the spine-clusters of the outer ramus, and 1 feathered hair of the second sensory-cluster underneath, on the left side. There are 3 of these groups on the right side in specimen C.4 and on both sides in C.14. The inner ramus has 2 long bristles and 2 spines at the tip.

Telson with 2 spines at the tip, and, on the right side, 1 midway.

As this moult C.4 shows an unusual number of differences in the distribution of the sensory armature on the two sides of the animal, especially on the hinder peræopods, a list of these is given below.

Antenna 2. One bristle-cluster more on right side than on left side.

Peræopod 1. One seta less on joint 3, and 2 setæ less on the posterior margin of joint 4 on right side.

Peræopod 2. One serrated-hair on the posterior margin of joint 2, and 1 long seta of the distal group of joint 5 and the mid-marginal one less on right side.

Peræopod 3. One notch less on joint 2 on right side, but on joint 6 there are 2 spine-clusters and 2 seta-clusters on the margins represented on right side, only 1 each on left side.

Peræopod 4. One notch more on joint 2 on right side ; on anterior mid-margin on joint 4, 1 spine less on right side than on left side ; on joint 6, 1 spine more on right side.

Peræopod 5. On joint 6, 2 spine-clusters and 2 seta-clusters, represented on right side ; only 1 of each on left side.

Uropod 1. One spine midway on peduncle right side, none on left side.

Uropod 3. Two spines in inner side of peduncle right side, 1 on left side ; 3 feathered hairs on outer ramus right side, 2 on left side.

Telson. One spine midway on right side, not on left side ; 2 spines at the insertion of the telson right side, 1 on left side.

Moult 6 (from Female C.4, Fig. 6). Gnathopod 2 from the sister female C.14 and gnathopod 1 from A.19.

The character which distinguishes Moult 6 from all the other moults in the normal female is the presence of small oval broodplates with rudiments of the fringing hairs just indicated on the margins.

Head. Lateral corners well produced, post-antennal corner subacute.

Antenna 1. Basal joint with 4 sensory-hairs in the "auditory" groove, the distal one apart from the other three. Primary flagellum with 14 joints, 6 outstanding bristles, and 9 sensory-filaments. In C.14, the left antenna has 14 joints, the proximal or formative zone long and undivided ; the right antenna is 15-jointed, the proximal joint having divided. Accessory flagellum 3-jointed.

Antenna 2. Joints 4 and 5 of the peduncle each with 3 bristle-clusters represented ; flagellum 7-jointed, the formative zone lengthened, the next joint an undivided primary, showing the commencement of a division on the margin. In C.14, a more vigorous specimen, joint 4 of the peduncle has 4 bristle-clusters represented ; the flagellum on the right side has 8 joints, the formative zone long, and the next joint, a primary, divided, whilst in that of the left side the formative zone has also divided, and the joints therefore number 9.

Gnathopod 1. Missing in C.4, the figure is drawn from a smaller female, A.19, of Brood A. The palmar-series in C.14 consists of 6, 2 serrulate-setæ, the one at the angle now almost a spine, the stiff bent-seta, and 3 of the long flexile sensory-hairs : 1 serrated-bristle of the third posterior-cluster has appeared on the hand, and also on joint 5, but on the right side there are only 2 of the posterior-clusters on the hand as in A.19 ; 3 on joint 5. In the smaller specimen the development is not quite as advanced, but it will be seen that it is not possible to confuse either gnathopod 1 or gnathopod 2 with the previous stage, Moult 5.

Gnathopod 2. Left hand missing in specimen C.4, and figured from C.14 and A.19. In the right hand C.4, the palmar-series consists of 6, 2 serrulate-setæ at the angle, the bent-seta, and 3 of the flexile sensory-hairs ; in C.14 the right hand is the same as in C.4, with the addition of 1 serrated-bristle in the third posterior-cluster, but in the left hand there are 8 in the palmar-series, 3 serrulate-setæ, the bent-seta, 3 long flexile hairs in the row, and 1 crossing them in front. The fifth joint has 3 posterior-clusters in C.4 and A.19, 4 clusters in C.14. More marginal-setæ have developed, and 2 anterior and 3 posterior sensory-groups are present on the under surface. On the small *broodplates* developed on

this appendage and the three succeeding ones, rudiments of the fringing hairs can be seen, but the cuticle is too thin and crumpled in all the specimens to make sure of the exact number.

This is the first moult in which the broodplates are plainly evident.

Peræopods. A great increase in the number of setæ and spines ; joint 2 of peræopod 3, with 3 spines on the anterior margin, left side, 4 on the right ; C.14 has 4 on the left and 5 on the right : peræopod 4 with 3, and peræopod 5 with 4 on the anterior margin, and in C.14 also.

Uropod 3. Outer ramus, 3 feathered-hair clusters represented on the under surface left side, 4 on the right side ; 2 spine-clusters left side, 3 on the right side ; inner ramus, spine on margin and 1 feathered-hair. In C.14, outer ramus, 4 feathered-clusters, and 2 spine-clusters ; 2 feathered-hairs on inner ramus.

Telson. Spine midway on both sides.

Moult 7 (from Female C.4, Fig. 7). Gnathopods from the smaller female A.19. The principal characters distinguishing Moult 7 are the large broodplates, with numerous rudimentary or partially developed fringing hairs. The broodplates are graduated in size, the largest on gnathopod 2, and the smallest on peræopod 3.

Antenna 1. Flagellum 17-jointed, the formative zone divided into 2 short joints, the next and longer joint an "undivided primary" ; 12 sensory-filaments, 8 outstanding bristles ; accessory flagellum 3-jointed.

Antenna 2. Joint 4 of the peduncle with 3 bristle-clusters left side, 4 on right side ; flagellum 9-jointed, 4 outstanding bristles.

Gnathopods. Hands missing in C.4, figures drawn from the smaller specimen, A.19, for the sake of comparison with the figures of the male, A.20 taken from the same Brood A.

Gnathopod 1. 6 in the palmar-series, of the 2 serrulate-setæ in the angle-row the posterior one is now a stout, fully developed pointed-spine ; the seta at the angle on the under surface is also a fully developed spine, and on the right hand a second small spine has arisen beside it ; 2 posterior-clusters on the left hand, 3 on the right.

Gnathopod 2. Sideplate of joint 1 with 2 setæ inset at the anterior distal angle left side, 1 on right side ; palmar-series of 7, 3 graduated serrulate-setæ at the angle, the bent-seta, and 3 of the flexile sensory-hairs on the left side, 4 on the right, the fourth one in front inset across the others ; 3 posterior-clusters on the left hand, 4 on the right ; a great increase in the number of the serrated-bristles and sensory-hairs in these clusters. Broodplates large ; 8 tiny hairs developing, in the smaller female, A.19 ; in C.4 the broodplate is larger, with about 14 of these hairs.

Peræopods. C.4 ; peræopod 1, with 5 clusters of setæ on the posterior margin of joint 4 besides the distal one ; broodplate with 9 or 10 tiny

hairs : peræopod 2, broodplate smaller with about 6 hairs : peræopods 3 and 4 with 4 spines on the anterior margin of joint 2 ; peræopod 5 with 5 on the left side, the second proximal one very small, on the right there are 4, all large ; great increase in the number of spines and setæ on all the peræopods.

Uropod 2. Peduncle with 1 small spine midway on left side, absent on right side ; inner ramus with 1 spine midway on right side, absent on left side.

Uropod 3. Outer ramus, 3 spine-clusters on left side and 4 feathered clusters underneath, 5 on right side ; 2 more feathered hairs on the inner ramus.

Moult 8 (Fig. 8). This is the moult at which the female reaches sexual maturity. The specimen figured, C.4, laid 10 eggs.

The distinguishing characters are : the fully developed broodplates with long fringing hairs ; gnathopod 1 with 2 stout spines at the palmar-angle ; gnathopod 2 with a graduated row of 3 serrulate-setæ ; and the armature of the hinder peræopods, particularly of the second joints.

Antenna 1. Primary flagellum with 20 joints, the long formative zone showing the commencement of the line of division ; 10 outstanding bristles, and 15 sensory filaments ; accessory flagellum 4-jointed. C.14, the sister, has 21 joints in the primary flagellum and 4 in the accessory.

Antenna 2. Joint 4 of the peduncle with 3 bristle-clusters left side, joint 5 with 4 clusters ; flagellum 10-jointed, with 5 outstanding bristles.

Gnathopod 1. 8 in the palmar-series ; of the 3 serrulate-setæ of the angle-row the first is a little stouter, the other two are now perfectly developed strong pointed-spines ; the bent-seta and 4 sensory-hairs ; 2 spines on the under surface of the palmar-angle ; 2 posterior-clusters of serrated-bristles ; and, on the under surface of the hand, 3 anterior and 3 posterior sensory-groups ; on joint 5, 3 posterior-clusters. There is a great increase in the number of serrated-bristles, especially on joint 4, and in the number of long serrated-hairs on joint 2.

Gnathopod 2. Nine in the palmar-series, 3 graduated serrulate-setæ in the angle-row, the bent-seta, and 5 sensory-hairs, one in front crossing the others ; 2 spines on the angle, underneath ; 4 posterior-clusters with graduated serrated-bristles below, and long slender sensory-hairs above ; and on the under surface, 3 anterior and 4 posterior sensory-clusters. Broodplates very large and well developed, with 24 fringing hairs (Fig. 26) on each ; the posterior hairs, 6 on right side, 7 on left side, much shorter than the others.

Peræopod 1. Six clusters on posterior margin of joint 4. Broodplates about the same length as the gill, left side with 19 hairs, right side with 17.

Peræopod 2. Broodplates, 13 hairs left side, only 9 on right.

Peræopod 3. Four spines on the anterior margin left side, 5 on the

right, the proximal one very small ; 4 notches on posterior margin left side, 5 on the right. Broodplates the smallest of all, with 7 hairs.

Peræopods 4 *and* 5, with 4 and 5 spines on the anterior margins respectively.

Pleon segment 2. Three spines on the epimeron left side, 2 on the right. The cuticle of this segment and the following one is remarkably spinulose.

Uropod 3. Great increase of bristles and spines ; outer ramus with 3 spine-clusters, and 4 feathered clusters on left side ; terminal joint with 1 bristle, the commencement of a lateral cluster, on the inner side.

Series II. The Normal Male.

The males appear to be much more voracious than the females, cannibalism is frequent with them, whereas it is only rarely that the female turns to it. It has been found impossible to get a complete series of moults from one male, the difficulty being in the older stages, for as they grow older they devour their moults almost immediately after ecdysis. In order to get the complete series, I have had to draw certain stages from one male, fill in the missing stages from other males, and then compare this series with as many other male moults as could be obtained.

Moults 1, 2, 3, 4 are from the male B.9 ; it ate its fifth moult, and that stage was therefore figured from A.20 ; the sixth moult is from B.9 ; its seventh was nearly all eaten, and this stage also was figured from A.20 ; both B.9 and A.20 ate their eighth moults, and another male, K.6, was taken for Moult 8 and Moult 9. K.6 ate part of its tenth moult, and yet another male had to be taken, CN.444. This one, CN.444, had perfect moults of the stages 1, 2, 3, 4 ; the fifth moult was eaten ; the sixth moult was perfect, but there was such an unusually long period between the sixth and the seventh that I feared the animal might not be healthy, and therefore did not take it to illustrate the male series. It had the sixth, seventh, eighth, and ninth moults, and was then killed to make sure of getting the tenth stage. All its moults were afterwards examined point by point with the stages here figured as well as with many other males, and were found to agree in every detail.

The only difference ever found, and that an exceedingly slight one, is in the development, a strong and vigorous animal may be rather more advanced than the weaker ones.

Moult 1 (from the male B.9, Fig. 9). This moult is precisely the same in every detail as that of the female, already described.

Moult 2 (from the male B.9, Fig. 10). This moult is practically identical with that of the female.

Moult 3 (from the male B.9, Fig. 11). This moult also is practically identical with that of the female.

Antenna 1 has 3 sensory filaments on the right side, 4 on the left.

Peræopod 4. One spine present on the posterior margin of joint 4 right side, absent from left side.

Moult 4 (from the male B.9, Fig. 12). This moult of B.9 is exactly the same as in the female figured, except for a very slight increase in the sensory armature, due apparently to the fact that B.9 was the more vigorous animal of the two.

Antenna 1. Flagellum as in the female figured, except that the 2 long proximal joints of the latter are here divided into 4 short ones. In another male, A.20, the accessory flagellum of the left side is 3-jointed, the 2 proximal joints short, right side 2-jointed with the proximal joint long, not yet divided ; and in *Antenna* 2 it has one more bristle-cluster represented on joint 4 of the peduncle on the left side than in B.9, the specimen figured.

In B. 9, *peræopod* 1 has 1 of the long sensory serrated-hairs on each side of joint 2 ; *peræopod* 2, 1 seta each side on joint 4 ; *peræopods* 4 *and* 5 with 1 spine on joint 5 on both sides, *peræopod* 3 with this spine on the left side only.

Uropod 3. A second spine-cluster on the outer ramus, both sides.

Moult 5 (Fig. 13). As the male B.9 ate the whole of its fifth moult this growth-stage has been figured from another male, A.20.

This moult is practically identical with that of the normal female.

Antenna 1. Flagellum 10-jointed as in C.4 ; accessory flagellum on the right side 2-jointed with the proximal joint long and undivided, 3-jointed on the left side with the proximal joint divided.

Antenna 2. Flagellum with 5 joints in the male A.20, 6 and 7 joints respectively in the females C.4 and C.14, but all these animals are at the same growth-stage, as can be seen on examining the flagella. In A.20, the smallest of the three, the proximal joint (i.e. the formative zone) is lengthened preparatory to division, and the next joint, an " undivided primary," carries the seta of the new secondary joint (this seta frequently appearing before the division takes place). In C.4 also the proximal joint is lengthened, but the near division and the formation of a new primary is shown by an outstanding bristle being developed ; and the " undivided primary " has divided and formed a new secondary joint, thus making 6 joints in all. In C.14, the most vigorous of the animals, the division of both the proximal joint and the " undivided primary " has taken place, making 7 joints in all.

Moult 6 (from the male B.9, Fig. 14). Sexual differentiation is first seen in this moult. The distinguishing characters are : The presence of a few curving male hairs on Antenna 2 ; gnathopod hands like the female.

Antenna 1. Basal joint with 5 sensory-hairs in the groove ; flagellum the same length as in the female figured, 16-jointed, the 2 long proximal joints of the female (formative zone and "undivided primary") are divided in this animal, and show as 4 short joints.

Antenna 2, shows the first appearance of the sensory-coiled hairs characteristic of the male (Fig. 29). On the inner surface of joints 4 and 5 of the peduncle there are 4 rows of sensory hairs, and in the 3 distal rows one or two of the longest hairs have the tips curved inwards. In the mature male these hairs are also present on the two gnathopods, the first peræopods and the third uropods.

Gnathopods 1 *and* 2. The spines in the angle-row of the hand of gnathopod 1 are much stouter than in the female. In gnathopod 2 of the female the character of the angle-row does not change through life, the serrulate-setæ remaining serrulate-setæ through all the moults, but in the male these setæ gradually develop into stout spines, and the change can be clearly seen in this stage. The right hand of gnathopod 2 has a third serrulate-seta in the angle-row posterior to the other two. The hairs of the sensory clusters of the under surface are still short.

The rest of the moult is practically the same as in the female, except for the position and increase of a few spines or setæ.

Peræopod 3. With 4 spines on the anterior margin of joint 2 ; *peræopod* 4 with 3 ; and *peræopod* 5 with 4 on the left side, 3 on the right side.

Uropod 3. Outer ramus with 3 spine-clusters represented on the left side, 2 on the right side ; in the female figured there are 2 on the left and 3 on the right. Feathered-clusters in this specimen, 5 on the left, 4 on the right ; in the female 3 on the left, 4 on the right.

Telson. Another spine has appeared on the right side, near the tip.

Moult 7 (Plate IX). The principal distinguishing characters of this stage are : the coiling of the male hairs on the Second Antenna, and the commencement of the differentiation of the palmar-series of the gnathopod hands.

The male B.9 ate its seventh moult with the exception of peræopods 3 and 4 and the third uropods ; the figures have therefore been taken from another male, the A.20, figured in Moult 5.

Antenna 1. Flagellum 16-jointed, the formative zone lengthened, but not yet divided, 11 sensory-filaments, and 7 outstanding bristles ; accessory flagellum 3-jointed. In CN.444, a larger male, the formative zone has divided, and the "undivided primary" also.

Antenna 2. Flagellum as in the female figured ; 9-jointed, peduncle with 4 bristle-groups on joint 4, 3 on joint 5, with a good many more of the male hairs developed in the clusters underneath, more coiled than in the preceding moult. In CN.444, the flagellum has 10 joints, the long

proximal having divided; and one hair of another bristle-cluster is present on joint 5 of the peduncle.

Gnathopod 1. The change to the adult male type has commenced in the hands, more noticeably so in the right hand, where the differentiation of the palmar-series into palmar-row and angle-row is now clearly indicated. The second serrulate-seta of the angle-row is now a stout pointed-spine, the third and posterior one not so well developed. The first serrulate-seta has not yet been modified to a spine, but is stouter and stronger than in the last stage, and has diverged a little from the angle-row. The palmar-row in A.20 contains 4 of the long sensory-hairs in a line. In CN.444 there are 6 hairs, two very small.

Gnathopod 2 also shows the change towards the male type, more so on the right side than on the left. On the right side (see M.7 in Plate XVII) the differentiation is clearly seen; the palmar-row containing the first serrulate-seta and 5 long sensory-hairs has diverged a little from the angle-row towards the middle of the palm. The angle-row consists of the second and third serrulate-setæ (in order of development), the second and largest of the three being almost completely modified into a pointed-spine. The hand is larger in proportion than in the female, and has 4 posterior-clusters of serrated-bristles.

Peræopod 1. No coiled hairs have yet appeared; peræopod 4 in B.9 with a fifth spine on the anterior margin of joint 2, the right side as in the female C.4.

Uropod 3. The long sensory-hairs are much more numerous than in the female; in B.9 the uropods are damaged, but 5 rows can be seen on the right side, and more on the left with some of the hairs lightly coiled; some of these hairs have appeared on the inner ramus also.

Moult 8. Mature, first stage. From the male K.6 (Plate X).

This is the stage at which the males become sexually mature, but they undergo two more moults before they attain the definitive adult form.

The principal characters distinguishing Moult 8 of the male are: on gnathopods 1 and 2, the median-spine in the middle of the palmar-margin of both hands; a few coiled hairs on Antenna 2, and some lightly curved on uropod 3; those on peræopod 1 hardly noticeable.

Both the males, B.9 and A.20, figured for this series, destroyed their eighth moults; this stage and the two following have therefore been figured from K.6, a male from normal wild stock.

Antenna 1. Like that of the female; primary flagellum as in the female, 20-jointed on the right side, proximal-joint long showing the point of subdivision on the margin; on the left side this division has taken place, 21 joints being defined; 16 sensory-filaments on the right, 15 on the left, and 10 outstanding bristles in both as in the female (see diagram, Text Fig. 2), accessory flagellum 4-jointed.

Antenna 2. Peduncle, with 4 bristle-rows on joints 4 and 5, the bristles longer than in the female ; and 5 rows of sensory-hairs underneath, many of the male type coiled. The flagellum is 12-jointed, but it is at exactly the same stage as in the female. The 3 proximal joints in the female are : a long growing-piece and 2 "undivided primaries" ; in the male one of the primaries has divided, and the "long growing-piece" also shows a line of division. 6 outstanding bristles are present on the flagellum ; there are more setæ than in the female, and on the under surface of the proximal joints clusters of sensory male hairs are developing though not yet coiled.

Gnathopod 1. Hand much larger than in the female, with the differentiation of the palmar-series complete. The angle-row contains the 2 large, strong pointed-spines ; the median serrulate-seta is now transformed into a strong pointed-spine situated in the middle of the palmar-margin, with the palmar-row stretching out at an angle from it ; 6 long sensory-hairs in the row, one in front crossing the others. There are 3 posterior clusters of sensory hairs and serrated-bristles, with 3 hairs and 4 bristles ; 1 hair and 4 bristles ; and 2 bristles respectively. On the under surface there are 2 very stout spines at the angle, the smaller one beginning to assume the typical male form, the shaft curved, flagellum reduced, and tip flattened. Seven clusters of sensory hairs and setæ are present, 3 along the anterior margin, 3 on the posterior and the first of another series developing between this one and the posterior margin. The older hairs in the posterior series have lengthened, and are slightly coiled.

Gnathopod 2. As in gnathopod 1, the hand is much larger than in the female, with the palmar-series divided. On the left hand the serrulate-setæ of the angle-row (which do not change their character in the female) have developed into almost perfect pointed-spines. The median serrulate-seta has also changed to a spine, though it is not so far advanced as those of the angle-row. It is now situated in mid-margin with the palmar-row of 5 setting out at an angle from it. On the right hand the serrulate-setæ of the angle-row are not as well developed as on the left ; the median-seta, too, is less advanced, although it has commenced the change of form ; it has diverged from the angle-row, but not yet reached its final median position on the palmar margin. On the under side of the angle are 2 pointed-spines, the larger one perfectly modified, the smaller not quite as much developed. There is an increase of hairs in the sensory-clusters, some are coiled, but as they are still short they do not reach beyond the margin yet ; 4 posterior-clusters on the hand and on joint 5.

Peræopod 1. K.6 ; 1 slightly curved seta has appeared in each of the posterior clusters of joint 4.

Peræopod 3. Joint 2 with 3 spines on the anterior margin and 3

notches on the posterior left side, 4 spines and 4 notches on the right side.

Uropod 3. Both rami much more setose than in the female ; 8 clusters of sensory-hairs on the left side, several of the hairs slightly coiled ; on the terminal joint of the right side 1 bristle of a lateral cluster has appeared.

Moult 9. Mature male, second stage (Plate XI).

The characters distinguishing Moult 9 of the male are : The torsion of the palmar margin of gnathopod 1 ; the median spine with its flattened tip and small flagellum, and the group of long flexile hairs beside it, in both gnathopod hands ; and the coiled hairs on all the secondary sexual characters, antenna 2, gnathopods 1 and 2, peræopod 1, and uropod 3, most numerous on the antennæ and least numerous on gnathopod 1.

This moult is drawn from the same male K.6 as Moult 8.

Antenna 1. Primary flagellum 24-jointed, 19 sensory filaments ; accessory flagellum 5-jointed.

Antenna 2. Peduncle with a great increase in the number and length of the bristles and coiled hairs. Flagellum 12-jointed, the 3 proximal joints each with the distal hair of a new joint showing at the place of subdivision ; some coiled hairs have appeared on the inner surface of the 6 proximal joints.

Gnathopod 1. Hands much larger and more developed than in the last moult, the greatest change being in the palmar margin where the commencement of the torsion, so striking in the fully adult, can now be seen. The palmar-angle is bent in under the hand, the tip of the claw impinging against the under side. On the upper side of the angle are 2 strong pointed-spines, the smaller one of the curved-spine type characteristic of the fully adult male ; in this type the shaft is curved, the tip truncate, and the flagellum reduced or lost altogether. 2 of these small curved-spines are inset on the under side of the angle, with 1 long pointed one. The median-spine is large and stout, not tapering, the tip rather flattened and the flagellum small. The hairs in the palmar-row are now grouped in a dense cluster beside this spine, with 1 coiled hair present. The first of the 3 posterior groups also contains 2 coiled hairs. There are now 3 rows of the sensory-clusters underneath, but the hairs are still short.

Gnathopod 2. Three straight pointed-spines in the angle-row above, 2 below ; the median-spine and palmar-row have changed in the same way as those of gnathopod 1 ; 5 posterior clusters, the first containing 2 coiled hairs ; 2 rows of sensory-clusters underneath, the second one in the anterior row with 1 long coiled hair ; the first of the posterior row with 2 long coiled hairs, the second with 1.

Peræopods. Peræopod 1 with many coiled hairs developed in the

posterior clusters of joints 4 and 5. Hinder peræopods very spinose, with a great increase in the number and length of the spines.

Pleon segment 2. With 3 spines in a slanting line to the margin.

Pleon segment 3. With 3 spines on the inferior margin.

Uropods 1 *and* 2. With more spines developed on the margins of the peduncle and rami.

Uropod 3. Many coiled hairs on both rami ; 4 spine-clusters on the outer ramus ; 2 bristles in the lateral cluster of the terminal joint.

Telson. With 4 spines, 2 at the tip.

Moult 10. The definitive adult stage (Plate XII). The characters distinguishing Moult 10 of the male from all the preceding moults are : the great development of the coiled hairs on all the secondary sexual characters ; the pyriform hands of the first gnathopods ; the oblique deeply indented palm and the broad truncate median-spine of the palmar margin.

The male, K.6, from which the last 2 moults were taken, ate its tenth moult with the exception of the second antennæ, 1 second gnathopod hand, part of the pleon, and a few fragments of peræopods. The male CN.444 has been figured ; it was only one day younger than K.6, and was killed the day before the tenth moult was due to take place. The new cuticle is visible, showing that the moulting was very near, but, as these males rarely ever leave their moults untouched, commencing to eat them immediately the ecdysis is completed, it was thought better not to risk losing the record. K.6 had its eleventh moult 16 days after the other, and ate the most of that.

In this stage the adult characters are established and the normal male changes very little afterwards, except, of course, for the increase in size and in the sensory armature (see Plate XVIII).

The male at Moult 10 is quite easy to distinguish from the female with the naked eye, the large gnathopods and the long hairy third uropods giving it a very different form which is especially noticeable in swimming.

Antenna 1. Flagellum 28-jointed, 14 outstanding bristles and 23 sensory filaments ; accessory flagellum 5-jointed.

Antenna 2. Flagellum 14-jointed, the proximal joints not yet divided, showing the distal hairs of the new joints at the point of subdivision ; all, except the 2 terminal, with sensory-hairs on the inner surface. This under surface on joints 4 and 5 of the peduncle and on most of the flagellum is clothed with coiled hairs.

Gnathopods. Both hands are now of the " adult male " type, pyriform, with palm oblique, particularly in gnathopod 1, and indented.

Gnathopod 1. The palmar-angle is bent completely underneath, with 1 long pointed-spine and 2 small curved-spines on each side, but the second small curved-spine of the upper side does not show from above,

owing to the torsion of the margin. They are arranged in such a way that when the claw closes down there is a pair of spines (1 long and 1 short) on each side above the tip, and 1 small curved-spine each side at the tip. The median-spine is large and truncate, the flagellum reduced to nothing. Many of the bristles and long sensory setæ have developed into long coiled hairs; on joint 5 the anterior-cluster, and 2 of the posterior-clusters have some coiled hairs in them.

Gnathopod 2. The hand is broader than in gnathopod 1 and the palm is not quite so oblique, and but little bent in underneath at the angle; 3 stout pointed-spines, and coiled hairs as in gnathopod 1, but there are more serrated-bristles in the posterior-clusters.

Peræopod 1. With a large increase in the number of the coiled hairs on joints 4 and 5 posteriorly; and with some anteriorly on joint 4 at the distal angle.

Uropod 3 in K.6; with 4 spine-clusters and 1 seta-cluster on the outer ramus; and 2 lateral clusters on the terminal joint; 9 sensory rows on the under surface of the left side; and a large number of coiled hairs on both rami.

Series III. Intersex.

The 6 moults described below are taken from a specimen of the Irregular-eyed Stock, CN.397f., and compared with another intersex from normal stock. The two agree in practically every detail. At present these are the only two intersexes of which we have the early stages.

Moult 1 (Fig. 19).

Exactly like the normal animals.

Moult 2 (Fig. 20).

Except that it is smaller, this moult also is exactly like the normal animals.

Gnathopods. One long serrated-hair posteriorly on left side; 1 on each margin of joint 2, right side.

Peræopod 2. No seta on the posterior margin of joint 2; peræopod 3, no spine on joint 6.

Moult 3 (Fig. 21).

The distinction between the normal and the intersex can be clearly seen in this stage. In size, the intersex is much smaller, and in development it is intermediate between the second and third moults of the normal animals.

Antenna 1. Flagellum 6-jointed.

Antenna 2. Flagellum 4-jointed; no change in the armature from Moult 2.

Gnathopods 1 *and* 2. Joint 2 with 1 long serrated-hair on each side

as in normal Moult 2 ; hands like those figured for the normal male at the second growth-stage (2 in the palmar-series and 1 bristle in the posterior-cluster), but on the under surface they have 1 hair of the first sensory-cluster, which in the normal is not present in Moult 2, but appears in Moult 3. On the fifth joint, too, this intermediate condition is evident : Gnathopod 1 has 3 of the serrated-bristles in the first posterior-cluster, and gnathopod 2 has 3 serrated-bristles and 1 sensory-hair (as in the normal third moult) in this cluster, but has not yet developed the second posterior-cluster.

Peræopods. All are at the same stage as Moult 2 of the normal, except peræopod 3, which carries 1 spine on the anterior margin of joint 2 (a character of the normal third moult).

Uropods 3. Exactly like Moult 2 of the normal.

The characters distinguishing Moult 3, intersex : most of the characters are those of the earlier stage of the normals, Moult 2 ; but three of the characters of the third stage are present, viz. the commencement of the sensory-clusters on the under surface of the hand ; the number of serrated-bristles in the distal posterior-cluster of the gnathopods ; and the anterior marginal spine on joint 2 of peræopod 3, the first of the hinder peræopods.

Moult 4 (Fig. 22).

Antenna 1. Basal joint with 2 sensory-hairs in the groove ; as in the normal Moult 3, flagellum 7-jointed with 3 sensory-filaments and 3 outstanding bristles.

Antenna 2. One stage behind the normal in development.

Gnathopod 1. The hand is exactly like that of the normals in Moult 2, in development as well as in size (see Plate VI) ; it has the serrulate-seta at the angle, and the bent-seta ; and 1 bristle of the first posterior-cluster. The rest of the gnathopod is like the third normal stage.

Gnathopod 2. As in the normal Moult 3 for development, but in size it is no larger than Moult 2 ; hand as in the female figured (Moult 3) with the sensory-hair on the under surface ; 1 long serrated-hair less on joint 2 than in the normal.

Peræopod 1. As in the normal Moult 3, but with a long serrated-hair developed anteriorly on joint 2 : and without the spine on the distal angle of joint 5.

Peræopod 2. Like the male figured in the normal Moult 3, but without the serrated-hair on joint 2.

Hinder peræopods. These also are at the stage of the normal Moult 3 ; peræopod 4 has a spine in the mid-margin of joint 4 on the right side.

Uropod 3. Intermediate between the third and fourth stages of the normal, e.g. the spine at the tip of the inner ramus which appears in the normal Moult 4 is present, but the feathered hair of the outer ramus which develops at the same time in the normal animal has not appeared.

The characters distinguishing Moult 4 of the intersex are : most of the characters one stage behind the normal in development ; except gnathopod 1, in which the hand is 2 stages behind ; and uropod 3, which has the spine at the tip of the inner ramus, as in the normal Moult 4.

Moult 5 (Fig. 23).

Antenna 1. Flagellum 8-jointed ; 5 sensory-filaments, and 3 outstanding bristles ; it seems to be intermediate between the third and fourth stages of the normal, not quite as advanced in development as the latter : accessory flagellum 2-jointed, proximal joint long.

Antenna 2. Also intermediate between the third and fourth normal stages ; flagellum 4-jointed ; it has the proximal joint (formative zone) long and the armature as in the normal Moult 3, but with the distal outstanding bristle indicative of the new primary joint, showing at the point of division. This new joint appears in the normal Moult 4, but the armature in the normal fourth stage is more advanced. The peduncle is more developed than the flagellum ; it has the two posterior bristle-clusters of joints 4 and 5 represented by 1 bristle in each as in the normal Moult 4.

Gnathopod 1. The hand differs greatly from that of the normal animal of this stage ; it is about 2 stages behind in development resembling Moult 3 of the normal except in the palmar-series, which here consists of 4 (as in the normal Moult 4) ; the serrulate-seta on the under side of the angle has become an almost perfect pointed-spine, those of the upper side of the angle are much stouter also. It is like Moult 3 also in that only 1 serrated-bristle is present in the posterior-cluster on the outer side of the hand. The rest of the appendage as in the normal third stage, except that on joint 5 the second bristle-cluster is not represented.

Gnathopod 2 is practically the same as in the normal Moult 3, except that the posterior-clusters are a little more advanced, and the sensory armature of the under side of the hand is the same as in the normal fourth stage.

Perœopods. Perœopod 1 exactly as in the normal Moult 4 ; perœopod 2 not as advanced as perœopod 1, like the normal male of Moult 3 ; the hinder perœopods are very like those of the normal male of Moult 4, but not quite as far advanced in development, particularly in the second joints of perœopods 4 and 5.

Uropod 3 is about the normal fourth stage, almost exactly like that of the normal female figured.

The characters distinguishing Moult 5 of the intersex are : most of the characters intermediate between the third and fourth stages of the normal, except in gnathopod 1, which shows some of the characters of the second stage also. The spines are longer in proportion than in the

normal. The development appears to be further behind the normal than in the last moult.

Moult 6 (Fig. 24).

Antennæ. Exactly as in the normal fourth stage ; antenna 1, primary flagellum 10-jointed, 4 outstanding bristles, and 5 sensory-filaments ; antenna 2, flagellum 5-jointed.

Gnathopods. At the fourth stage of the normals in development, except the hand of gnathopod 2, in which the second posterior-cluster is not represented. The bristles and setæ are markedly longer in proportion than in the normal animals, and are more numerous in the posterior-clusters of the hand and of joint 5 of the second gnathopod.

Peræopods 1 *and* 2. As in the normal fourth stage ; peræopod 2 with 2 setæ inset on the posterior expansion of the sideplate (a character of the normal Moult 5), and with 1 seta less on joint 4 than in the normal Moult 4.

Hinder peræopods at the normal fifth stage, except the second joint of peræopods 4 and 5, which are not quite as far advanced.

Uropod 3. Left uropod damaged ; the right uropod, which is figured, was injured in Moult 2, and regenerated, but had not reached the same development as the left.

The characters distinguishing Moult 6 of the intersex are : most of the characters at the fourth stage of the normals in development, i.e. two stages behind, except the hand of gnathopod 2, which has the first bristle-cluster larger, and the second not represented ; peræopod 2 with 2 setæ on the posterior expansion of the sideplate, as in the fifth stage of the normals ; and the hinder peræopods, in which joints 3–7 are like those in the fifth stage of the normals. The bristles and setæ are much longer in proportion to the size of the animal.

This Moult 6 of the intersex has been compared in detail with the same moult in another specimen 1.B, from normal stock ; they agree in practically every particular, 1.B being slightly larger and carrying 2 or 3 more setæ.

The most important point about this moult is that the sexual differentiation which appears in the normal males and females at this stage is not shown, that is to say, neither the coiled hairs on the antennæ of the male nor the broodplates of the female are developed.

CONCLUSIONS AND SUMMARY.

The first point, perhaps, to strike an observer in examining an animal like *Gammarus chevreuxi* is the *constancy of the characters* of each successive stage of growth, i.e. the external characters of any number of individuals at any one stage of growth are practically identical to the

smallest detail. Changes of temperature, changes of habitat, of salinity, or of food, or of all combined do not appear to affect the form of the cuticle, or to alter a single hair of its outgrowths. The species has been kept under artificial conditions in the Laboratory for a period of twelve years, fed on a uniform diet, and inbred for generations, yet the animals have not differed in the slightest degree as regards the cuticle and sensory armature from the wild animals freshly brought in from the open.

Changes of temperature, it is true, can shorten or prolong a period of growth, but the moult at the end of the period lasting only 3 or 4 days, for example, is precisely the same as the moult sloughed off after a period of 18 to 20 days ; it is quite as large, and quite as fully developed. Adverse conditions, also, can and do affect the *texture* of the cuticle, although the outgrowths do not appear to be altered.

The next point of interest brought out by the investigation of the moults is the *progression of growth* traceable through succeeding stages. This is, of course, demonstrable on any of the appendages, but can be more easily followed on those parts which undergo the most modification, viz. the antennæ and the gnathopods.

For the progression of growth in the *Antennæ* see p. 355 and Text Fig. 2.

The progression of growth in the *gnathopods* is best demonstrated in the "hands" (see p. 360), and can be traced in the gradual change of the palmar-margin and armature through the immature stages to the stage at which the animals become sexually mature. The differentiation of the characters stops here in the female, but in the male it is continued through two more moults to the definitive "adult form." At this point the differentiation of characters stops in the male also, and the characters now assumed by both sexes are preserved unchanged through the rest of their lives, the only alteration afterwards being in the increase of size until the maximum growth of the species is attained, and in the increase in the number of spines and setæ in the groups.

In the intersexes, however, development proceeds on different lines. It is very much slower in the early stages, but both *growth in size* (in the female intersex) and *differentiation in the characters of both male and female intersexes persist to a much greater extent than in the normal males and females*, and continue throughout life. This important fact has, I think, been conclusively demonstrated in the course of these investigations. A series of the hands of the female intersex has been figured (Plate XXI) to show the change from the normal female type of palmar armature to the male type at the early mature stage. A remarkable development in both male and female intersexes is shown, one, a male intersex hand with two truncate median spines (Fig. 57) ; and two

others, female intersex hands, with two angle-rows of spines and setæ (Figs. 58 and 59).

The difference in size, too, is noteworthy ; the largest male measured 14·5 mm. in length at the age of 579 days, whilst the largest female-intersex, not much more than half its age, measured 17 mm. when 310 days old.

The progression of growth, as shown in the *setæ and spines*, is also of interest. The newly hatched animal starts life with certain setæ and spines already developed on all the appendages. Some of these setæ remain unchanged through all the succeeding growth-stages, others undergo modification into spines, some to an extraordinary extent. It may be noted here that *the setæ which undergo the most modification occur on those parts of the body which are most changed by growth and sex*, viz. the hands and in particular the palms of the First and Second Gnathopods, whilst the setæ which remain unaltered occur on those parts of the body which retain their characters practically unchanged through life. One point comes out clearly in connection with the unchanged setæ, and that is : *the proximal joint and the terminal joint in all the appendages are the same in the newly hatched as in the adult*, and the bristles, or setæ, or plumose hairs present on them at birth remain unaltered through life, except for size and the addition of 1 or 2 more setæ later.

The modifiable setæ and spines are of different types, each type confined to certain appendages, e.g. the serrulate-setæ and serrated-bristles occur only on the gnathopods ; the long sensory-hairs with the terminal portion serrated are found only on the second joints of the gnathopods, and the first two pairs of peræopods ; and the sensory setæ which develop into the long, very slender sensory spines occur only on the hinder peræopods. The spines which appear later on the uropods, on the epimera of the second and third pleon-segments, and on the second joints of the hinder peræopods are of a different type from the spines developed from setæ. They appear on the hinder peræopods in the third moult, as already-formed small, stout spines on the anterior margin of joint 2, when the modifiable setæ at the distal anterior angle of this same joint has just changed to a spine.

The *direction of growth* is the next point to be noted. Growth takes place at the proximal end of an organ and not at the distal, e.g. the new joints which arise on appendages such as the flagella of the antennæ are formed at the proximal end of the flagellum ; the new bristle-clusters of the gnathopods develop proximally, as do also the new marginal groups on the joints of the peræopods, and the spine-clusters of the third uropods.

The examination of the moults has revealed an interesting structural detail, too small to be easily detected in the living animal, viz. the *sensory groove* on the upper surface of the basal joints of the First Antenna. This

groove would appear to be analogous to the "auditory sac" found in *Anaspides* and in many of the Decapoda.* It lies longitudinally, is long, narrow, and shallow, lined with exceedingly thin and delicate chitin, and is inset with very fine mobile plumose hairs, each in a little socket. One of these hairs is present on hatching, others develop as the animal grows older (Fig. 27). The groove faces towards the inner side of the joint; on the outer side and in a line with it, is a group of 3 plumose mobile hairs, found unchanged in all the moults. This groove with the accompanying group of hairs I have found in many other amphipod genera, and it probably occurs in all.*

To summarise the results of the investigations :—

1. There is a constant change in the proportions of the body from birth to maturity, e.g. the peræon which is practically subequal to the pleon in length at birth, is a third as long again at maturity.

2. The early growth-stages of the male are externally indistinguishable from those of the female, and the secondary sexual characters are not recognised until the sixth stage.

3. The male takes longer than the female to reach the "definitive adult" stage and its secondary sexual characters undergo much greater modification. This fact, hitherto unknown, is probably the cause of much of the confusion in the taxonomy of the Amphipoda, the different breeding stages being described as different species.

Another cause of confusion may be the similarity of the young immature stages of the species of a genus. If, as in the case of *Gammarus*, several closely allied species inhabit the same locality, a dredging will contain the growth-stages of various species, with more young specimens than mature. In many instances these have been described as belonging to one single variable species, and the specific boundaries enlarged to admit of the so-called "varieties."

4. In the genus Gammarus the females of some of the species, e.g. *G. locusta*, lay eggs without a male being present, although the probability is that these eggs do not develop; certain others, e.g. *G. chevreuxi* and *G. pulex*, never deposit their eggs without a male.

5. It is shown that the differences between species, even the closely allied species of the same genus, are very marked; in the number of moults to maturity, and length of moulting period, in the size and number of the eggs, the length of the incubatory period, and the time of extrusion of the young. These differences probably form an insuperable bar to cross-breeding.

* Calman. 1911. *Life of Crustacea*, pp. 22–4. Geoffrey Smith. 1909. *Camb. Nat. Hist.*, Vol. IV, pp. 116 and 152.

6. It is at present not possible to establish specific characters which will hold good for both sexes at all stages of their growth, nor is it yet possible to distinguish the youngest stages of closely allied species by any structural character. At somewhat later stages when maturity is being approached definite differences can be seen, such e.g. as the shape of the broodplates in the immature females, or the sensory armature peculiar to the different species, though these differences have not yet been worked out in detail. The sideplates which may undergo less change than the other external parts, appear to be the most reliable characters for distinguishing the species of a genus, at least as far as *Gammarus* is concerned.

THE INTERSEXES OF *GAMMARUS CHEVREUXI*.

The appearance of intersexes in *Gammarus chevreuxi* has already been recorded (*Journ. Mar. Biol. Assoc.*, XII, 3, Sept., 1921), and a description given of the female intersexes.

These all occurred in the stock used in the Laboratory experiments, and many others have since appeared in the same stock. Male intersexes also have been recognised as such, and certain of these are now described and figured.

For the first time in the records of this species, intersexes have been found amongst the wild animals. A dredging was made in the ditches draining the salt marsh, Chelson Meadow, in February, 1922. Owing to the exceptionally dry season of 1921 the ditches were nearly empty, and the animals proved to be very scarce. After hours of work only 104 specimens were captured, but of these four were female intersexes.

I believe it will yet be found that intersexuality is not rare in the Amphipoda, and that the specimens hitherto recorded as "abnormal" in development will prove to be only abnormal in that they are intersexual and have developed some of the external characters of both male and female. Chilton, for instance, describes an ovigerous female of *Erichthonius brasiliensis* (*Dana*) with the second gnathopod of the young male,* and a female of *Corophium crassicorne* with the second antenna of the "immature male." †

A female intersex of *Tmetonyx similis* was described in *Journ. Mar. Biol. Assoc.*, Vol. XII, No. 3, 1921, p. 544.

The female intersexes previously described were characterised by having some of the characters of the male and some of the female ; they

* *Trans. N.Z. Inst.*, Vol. 54, p. 242, and figure. 1923.
† *Trans. N.Z. Inst.*, Vol. 53, p. 232. 1921.

resembled the male in general appearance, size, colour, and habit of swimming, but were provided with the broodplates of the female. The curved male hairs and the palmar-spines of the young male were present also in many of them. They appeared to vary in the degrees of intersexuality, and were divided into three groups according to the degree of development of the hairs on the broodplates, rudimentary, partially developed, or fully developed. There is probably a correlation between the development of the gonads and of the secondary sexual characters, but the exact extent of this correlation is not yet known.

The young stages had not then been observed in detail. The animals were not recognised as intersexes until they were mature, and the records previous to maturity referred chiefly to their slow development and small size.

The moult investigations have shown that the differentiation between normal and intersex becomes apparent in the second moult. The external characters on hatching are identical for normal male, normal female, and intersex. In the second moult the difference in size appears, which in the third moult is very marked. In the intersex series figured (Plates XIII and XIV) only the first 6 moults are represented, but in them it is easy to trace the difference in the rate of development as well as in size.

In the third moult the animal is intermediate between the second and third normal stages. In the fourth moult the characters are mostly one stage behind the normal with the hinder parts slightly more advanced in development. In the fifth moult the difference has become very marked, not only in size but in the rate of development which seems to be slower than before : most of the characters are now between the third and fourth normal stages.

In the sixth moult the intersex is about two stages behind the normal, but with certain distinctions which prevent the possibility of confusing it with the fourth normal stage. For example, it has the two indentations posteriorly on sideplate 4 (a character of the fifth normal moult), and parts of the hinder peræopods also are much more advanced than in the normal fourth moult. The most important point about this stage of the intersex is, that differentiation of secondary sexual characters is not yet indicated. In Moult 6, of the normal female, small broodplates are found ; and in the normal male a few of the coiled male hairs appear on the second antenna. At what stage in the intersex sexual differentiation can be traced is not yet known, but experiments are still proceeding to ascertain this point.

The most striking feature in the intersex, and one which distinguishes it from the normal, is the steady progression of growth (in size in the female intersexes) and of differentiation of the characters through the

whole of its life. In the normal animals sexual differentiation is complete at maturity; growth in size continues for some time longer, until the female reaches from 7 to 8 mm. in length, and the male from 11 to 13 mm.; then it practically ceases, the differences thereafter being hardly perceptible.

In the female intersex, on the other hand, not only does growth in size continue, but the differentiation of the characters in the "male" direction proceeds steadily on through life, although, apparently, the fully adult male characters are never reached.

In gnathopod 1 the female intersex hand develops almost exactly like that of the young male of the early mature stage (cf. the first gnathopod of CN.183m., Fig. 56, with the hand of the young male of Moult 9 in Plate XVI); the angle-row spines, the median pointed-spine divergent from the angle-row, and the extra spines on the under surface of the angle are all present.

It must be noted, however, that though in the female intersex the median-spine was modified into the pointed-spine of the young breeding male, the animal mated *as a female.*

In gnathopod 2 the development proceeds along the same lines as in the normal to a certain point. In the older female intersexes, as in the normal male, the serrulate-setæ of the angle-row change to pointed-spines, the first developed one of the row is modified into the median pointed-spine, and diverges from the angle-row to the middle of the palm, and even the claw moves its position and comes to impinge against the under surface of the hand as in the normal male, instead of closing down against the edge of the palmar margin as in the female. This point is the farthest towards maleness ever reached by the female intersexes, and even in these advanced specimens there is no mistaking the "intersexual type." This is best displayed perhaps in the angle-row. In the normal male the angle-row consists of spines and spines only, in the normal female of serrulate-setæ only, but in the older intersexes it is always mixed, serrulate-setæ and pointed-spines, and always changing, the serrulate-seta of one stage becoming the pointed-spine of the next.

In a specimen figured, CN.284a, the largest of the female intersexes, the various points towards maleness will be seen, the torsion of the palm, the divergence of the palmar-row, the extra spines developed on the under surface of the palmar-angle (Fig. 53), and the "intersexual type" angle-row (Fig. 49).

The hands of another female intersex, CN.229h, are also figured (Figs. 54 and 55), to show two stages of development, with six months' interval between.

The regular progression of the modification as well as the tendency always to develop more outgrowths than the normal, can be seen in

each moult, the older serrulate-setæ changing to spines, and new ones arising posteriorily at the angle. This is shown in the fullest development yet found in the intersexes in two specimens, CN.289a and CN.323a (Figs. 58 and 59).* In these, a *doubling* of the angle-row seems to be taking place, more plainly evident perhaps in CN.289a, where it is just commencing. The previous moult showed only one stout serrulate-seta below the angle-row; in the moult figured there are two.

In all these female intersexes the broodplates show an increase in the number of the fringing hairs with age as in the normal female, and the number continues to increase until it becomes larger than in the normal, although the size of the broodplate itself is much smaller (see p. 392, Text Fig. 4). This is true of the fringing hairs of all the specimens, rudimentary hairs increasing in number; partially developed hairs increasing also in length as well as number in later moults.

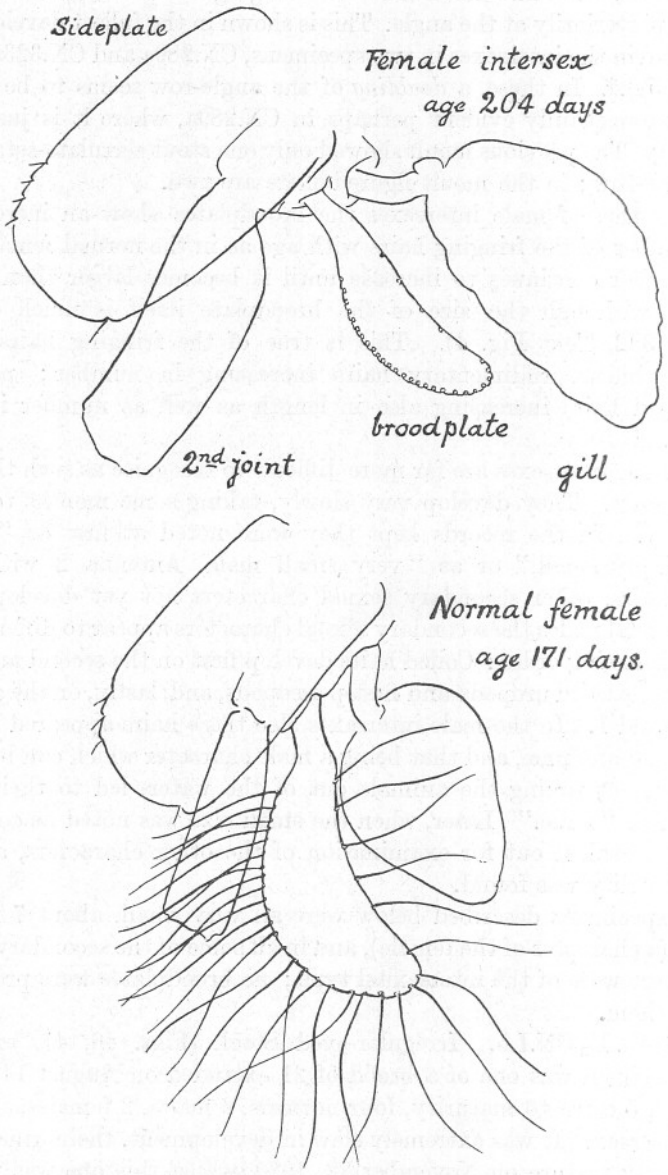
The male intersexes are far more difficult to recognise as such than the female ones. They develop very slowly, taking some months to reach maturity. In the records kept they were noted at first as "male ? exceedingly small," or as "very small male, Antenna 2 with male coiled hairs, other secondary sexual characters not yet developed."

In normal males the secondary sexual characters appear to differentiate in the following order: Coiled hairs develop first on the second antennæ, then on the third uropods and first peræopods, and, lastly, on the gnathopods 2 and 1. In the male intersexes also these hairs appeared first on the second antennæ, and that being a male character which can be easily seen without taking the animals out of the water, led to their being marked as "male." Later, when the small size was noted as constant, they were taken out for examination of the other characters, and the intersexuality was found.

The specimens described below were all very small, about 7 mm. in length (a character of the female), and in all some of the secondary sexual characters were of the intersexual type; no broodplates were present in any of them.

CN.314b. F_3 CN.I.b. Irregular-eyed Stock (Figs. 46, 47, and 52). This specimen was one of a brood of 21 extruded on August 14, 1920; of which 5 came to maturity, four normals, 2 males, 2 females, and this male intersex. It was extremely slow in development, the normal males being fully mature on November 22, 1920, whilst this one was marked "nearly mature, exceedingly small" on February 22, 1921. In the moult of December 3, 1920, male hairs were seen on the second antennæ, but the other secondary characters were not male. On March 12, 1921,

* The specimens 12 and 23 described in a previous paper, "Intersexes in *Gammarus chevreuxi*," Sexton and Huxley, *Journ. Mar. Biol. Assoc.*, Vol. XII, No. 3. 1921.



TEXT FIGURE 4.—Second gnathopod broodplates of two females from the same brood, CN.183, a normal and an intersex. The small size and rudimentary hairs of the intersex broodplate are characters of the immature normal female, but the number of the hairs is a character of the adult normal female. Drawn to the same magnification.

after a moult it was very feeble and as it was not likely to recover, it was preserved. It then measured only 7 mm.; age, 210 days.

In gnathopod 1 both hands had 3 spines in the angle-row, and the median pointed-spine and palmar-row as in the young normal male, the right hand, with 1 extra spine on the under side of the angle, not present in the left. Gnathopod 2 was of the typical "intersex" type; the palm transverse as in the female (cf. 314b gnath. 2 hand Fig. 47 with that of the female intersex 323a, Fig. 58), not, as in the normal male, oblique and deeply indented. The median pointed-spine was like that of the early mature stage of the normal male about as in Moult 8, not as advanced as Moult 9. The angle-row was typical "intersex," 1 pointed-spine and 4 serrulate-setæ in the row on the right hand; 2 spines and 2 serrulate-setæ on the left hand. On the under surface of the angle the right hand had only 1 spine; the left hand had 2, one not quite developed. Both gnathopod hands very setose, but there were only 5 posterior-clusters of serrated-bristles, i.e. at the age of 193 days the animal had no more clusters developed than the young mature male at the age of only 45 to 50 days.

The gills were very large, extending in peræopod 2 beyond the third joint.

The coiled hairs were present on the antennæ; but not on the first peræopods, nor on the gnathopods; on the third uropods a number of long fine sensory-hairs had developed, but none were coiled. The third uropods were of the intersex type, broad and spinose with about 10 sensory-clusters on the under surface of the outer ramus.

CN.289c. F_4 CN.I.b. Irregular-eyed Stock. This specimen was one of a brood of 13 black-eyed, extruded July 17, 1920, 5 of which came to maturity. None of them were normal; one, a female, had irregular eyes and no superior antennæ, mated and had young; another, a male, also irregular-eyed; the remaining three were intersexes, 2 females, one irregular-eyed, and 1 male. This specimen, also irregular-eyed, was noted as "very small" on September 8; on October 19 as "small male"; on November 24 as "exceedingly small for its age; too small to mate; antennæ with male hairs, but gnathopods appear to be of the intersex type." It died on December 3, 1920, age, 140 days; length, only 7 mm.

It is almost exactly like the male intersex just described; if anything very slightly more "male," as shown by the two or three coiled hairs on the first peræopod, and one or two more sensory-clusters on the third uropod.

The first antennæ were both broken; the second antennæ carried a few coiled hairs on both the peduncle and the flagellum.

In gnathopod 1 the hands were like those of CN.314b. (see Fig. 46). In

gnathopod 2 the angle-row, typically intersex, consisted of 2 pointed-spines and 2 serrulate-setæ on each hand; and on the under side of the angle 2 spines were present in each, one perfectly developed and one not quite fully modified; 6 serrated-bristle clusters on each hand. All the other details exactly as in CN.314b. No coiled hairs were found on the gnathopods, but 2 or 3 were present on the first peræopod, and the third uropod carried a number of the long sensory-hairs, curving but not coiled.

CN.269d. F_3 CN.I.b. Irregular-eyed Stock. One of a brood of 29 black-eyed, extruded June 21, 1920. Two were male intersexes, this one and the next to be described, CN.269b., both normal-eyed and spotted. This specimen was almost exactly the same as the two male intersexes previously described at its death at the age of 110 days. It was then 7 mm. in length.

Fragments of its moult, on September 16 at the age of 87 days, were found and examined. The stage of "male" development then reached was about the same as that of the normal male at its seventh moult. In both the gnathopod hands the median serrulate-seta had diverged from the angle-row; but, although broadened at the base, it was still a serrulate-seta, not a pointed-spine. Gnathopod 1 had 2 spines at the angle. Gnathopod 2 had in the right hand (the only one found) 3 serrulate-setæ in the angle-row, the first of them modified and almost a spine. By October 8, 3 spines had developed on each side of the angle on both hands of gnathopod 1. The hands of gnathopod 2 were then exactly like those figured for CN.314b. in size, shape, and armature (see Fig. 47).

This specimen, like the other two, CN.314b. and CN.289c., never developed the coiled hairs on the gnathopods. A few coiled hairs were present on the second antenna, and long fine sensory-hairs on the third uropod in the moult of September 16. At its death on October 8, coiled hairs were also found on the first peræopod; and a number of the sensory-hairs on the third uropod were lightly curved. It was far behind the normal male in development as well as in size. In the antennæ, for example, the stage reached was about the eighth stage of the normal, 22 joints in the right primary flagellum, 21 in the left of the First Antennæ, 4 joints in the accessory flagella, and 10 joints in the flagella of the Second Antennæ.

CN.269b., the second male intersex from the brood CN.269. This specimen was slightly larger than the three preceding ones, and more "male" in its development, as shown in the pyriform shape of the hand of the first gnathopod, and in the greater number of coiled hairs.

The development of the characters can be traced through several

moults. In the moult at the age of 138 days, a few coiled hairs were present on the second antenna and the first peræopod; 8 clusters of sensory-hairs, some lightly curved, on the third uropod; no coiled hairs on the gnathopods.

The hand of gnathopod 1 was more male than in the previous specimens described, pyriform, the palm oblique with the median spine just diverging from the angle-row. The hand of gnathopod 2 was of the intersex type, the median spine in mid-margin, and the angle-row composed of 3 slender spine-like serrulate-setæ.

In the moult at the age of 160 days, the number of the coiled hairs had increased on the second antenna, the first peræopod, and the third uropod; and a few had developed on both gnathopod hands.

The hand of gnathopod 1 was very like that of the young normal male of about 45 to 50 days old in the early mature stage, but not as large, the claw not much modified, and the coiled hairs and setæ much fewer. The hand of gnathopod 2 was intersexual in type, palm oblique, the serrulate-setæ of the angle-row modified into spines; only 5 posterior-clusters were present, and a very few coiled hairs.

It died on March 3, 1921, age 256 days. It had not increased perceptibly in size, nor altered much in character since attaining maturity, except that it became more intersexual rather than more male, although the number of the typical male coiled hairs had increased on the secondary sexual characters (cf. with this, the increase with age in the number of fringing hairs on the broodplates of the female intersex).

CN.199k. F_3 CN.I.b. (Fig. 57). Irregular-eyed Stock, one of a brood of 21 black-eyed, extruded April 5, 1920. Its eyes were very irregular on hatching; the right eye small, with 2 black and 1 red ommatidia, and with a long connecting thread-like white streak from the eye to a large spot over the stomach; the left eye was only a thin streak of white with 2 tiny specks of reddish black colour; it had a very large white patch on the left side over the stomach.

On June 30 it was marked as "male," but was then so small that it was considered unsafe to try and mate it, the smallest mature females being so much bigger that it was feared they would eat it if put into its bowl.

On July 1 a few coiled hairs were noted on the second antenna, 1 or 2 on the first peræopod, and the third uropod; none on the gnathopods. The hand of gnathopod 1 had 3 spines on each side of the angle; the median-spine slender, not long modified. The right hand of gnathopod 2 was the only one found in the moult; it had 1 spine and 2 serrulate-setæ in the angle-row; the palmar-row divergent, with the median-seta almost a pointed-spine; and midway between these two groups was a larger

spine with a blunt tip, carrying a flagellum; 5 clusters of serrulate-bristles on the posterior margin of the hand, and 5 sensory-clusters in the posterior row on the under surface. This appearance of a *second* spine, apart from the angle-row, in the palmar-series, is the only instance yet found of such an occurrence in the male intersexes. It is comparable with the *double* angle-row of specimens CN.323a. and CN.289a. female intersexes.

The eyes were examined on July 1, and were found to have changed considerably. The right eye had developed a fairly normal shape, and was almost a Black No-white. The left eye greatly increased in size, was very large and very irregular, with several ommatidia separate from the ommateum; almost No-white.

On July 26 a young fertile female was put into the bowl; mating took place, lasting till August 2. On August 5 the male intersex moulted. It mated again on August 9 for a day; the female moulted, but no eggs were laid. From August 20–24 another mating occurred, with the same result, the female moulted, no eggs laid. On August 31 it moulted once more, but did not mate again with any of the females. Its eyes remained unchanged till its death on September 16, 1920. It was only 7 mm. in length at the age of 164 days.

In the moult of August 5, gnathopod 1 had 1 median truncate-spine and 2 pointed-spines at the angle. In gnathopod 2, both hands had *two* truncate spines developed on the palmar margin, one the "median-seta" of July 1, with the cluster of sensory-hairs behind it, and the other half-way between this and the angle-row; 2 spines in the angle-row; and 7 serrated-bristle clusters. The figure given shows the hand of the second gnathopod on September 16 at the time of its death.

It will be seen that the intersexes described above begin life as males and then develop a certain degree of femaleness, or perhaps it would be better to say they are genetically males, but never attain to complete maleness, the immature (or female) characters persisting, and, in the case of the armature of the hands, combining with the partially developed male characters to produce the intersexual type. The small size reached is a female character, and so also is the shape of the gnathopod hands, and the absence of the male hairs from some of the secondary sexual characters. On the other hand, they never develop the most typical of the female characters, the broodplates, just as the female intersexes, however far advanced they may be towards maleness, never produce the typical male truncate-spines and coiled hairs.

My best thanks are due to the Director, Dr. E. J. Allen, for his help both during the course of the work and in the writing of this paper, and to Miss A. R. Clark for her assistance with the experiments.

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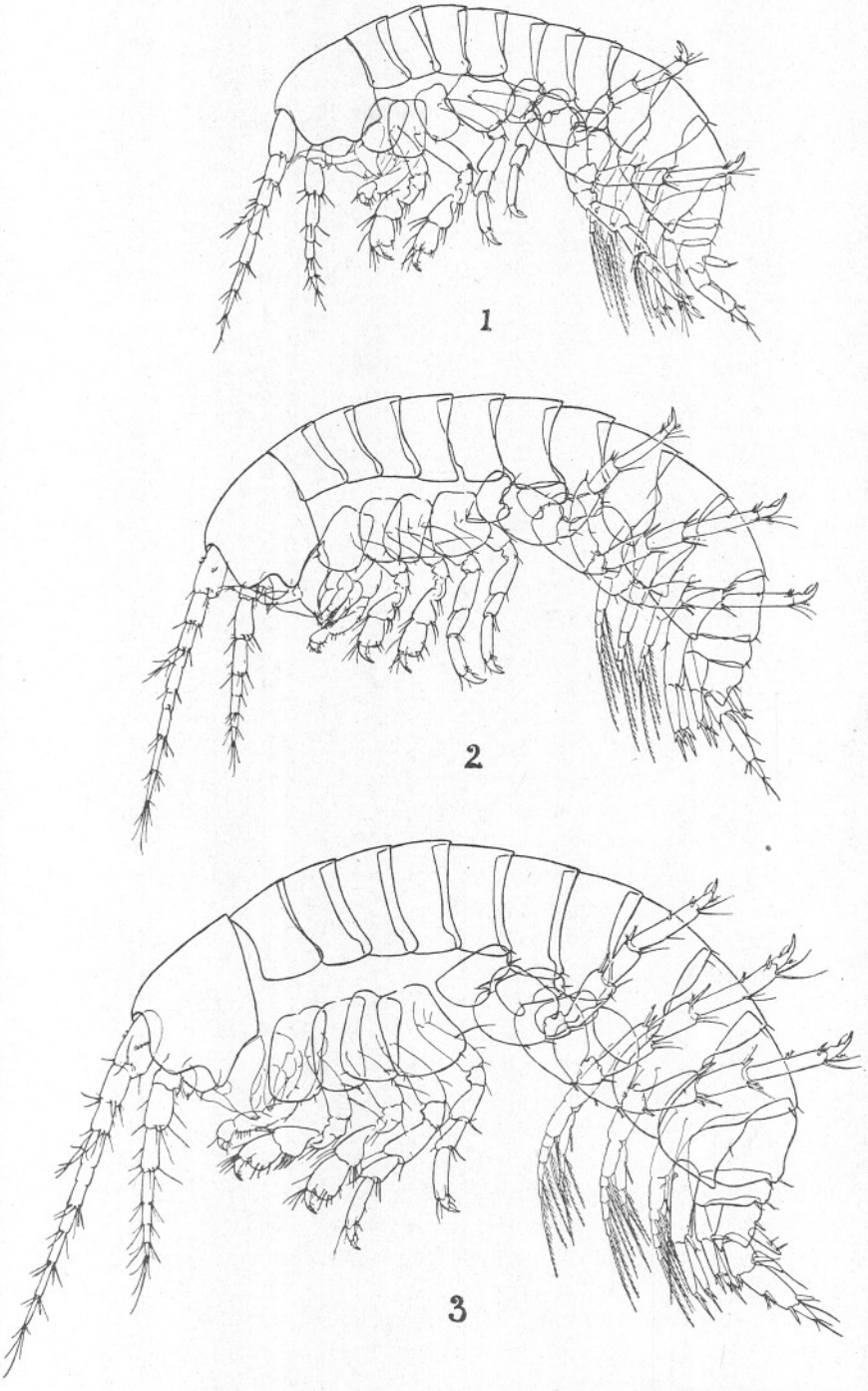

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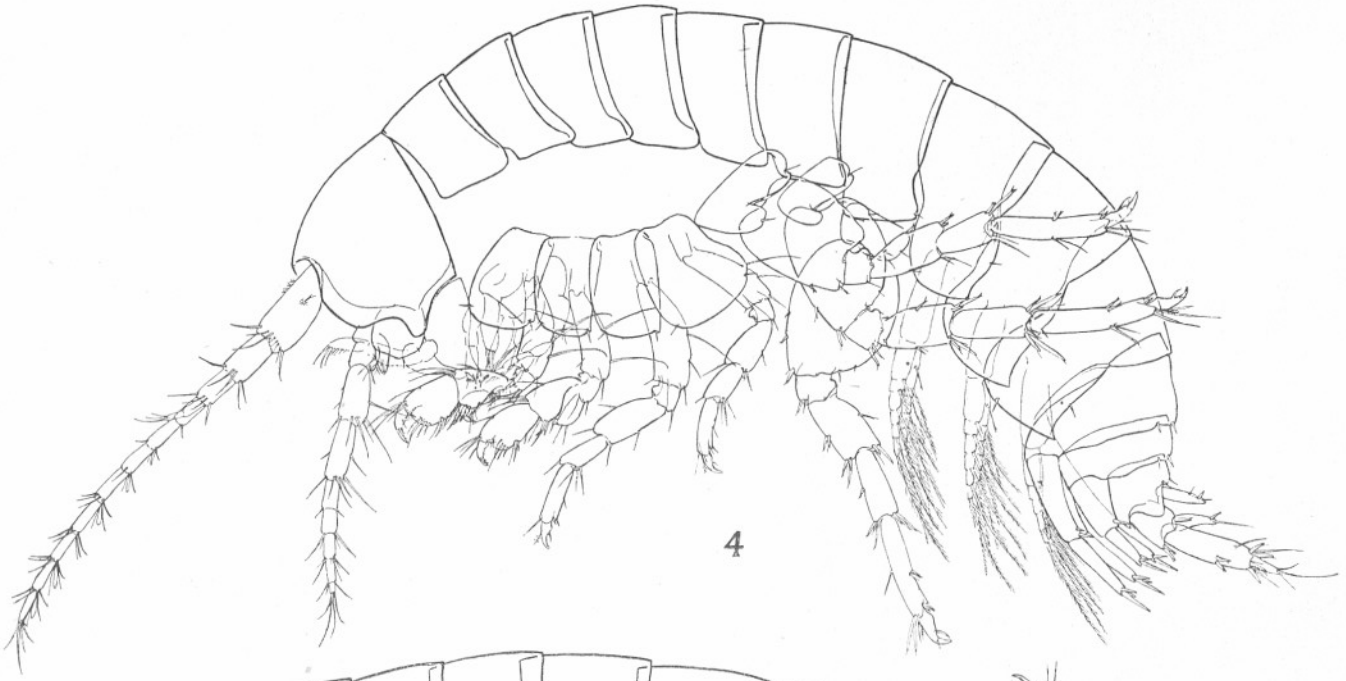
Normal Female. Moults 1, 2 and 3.



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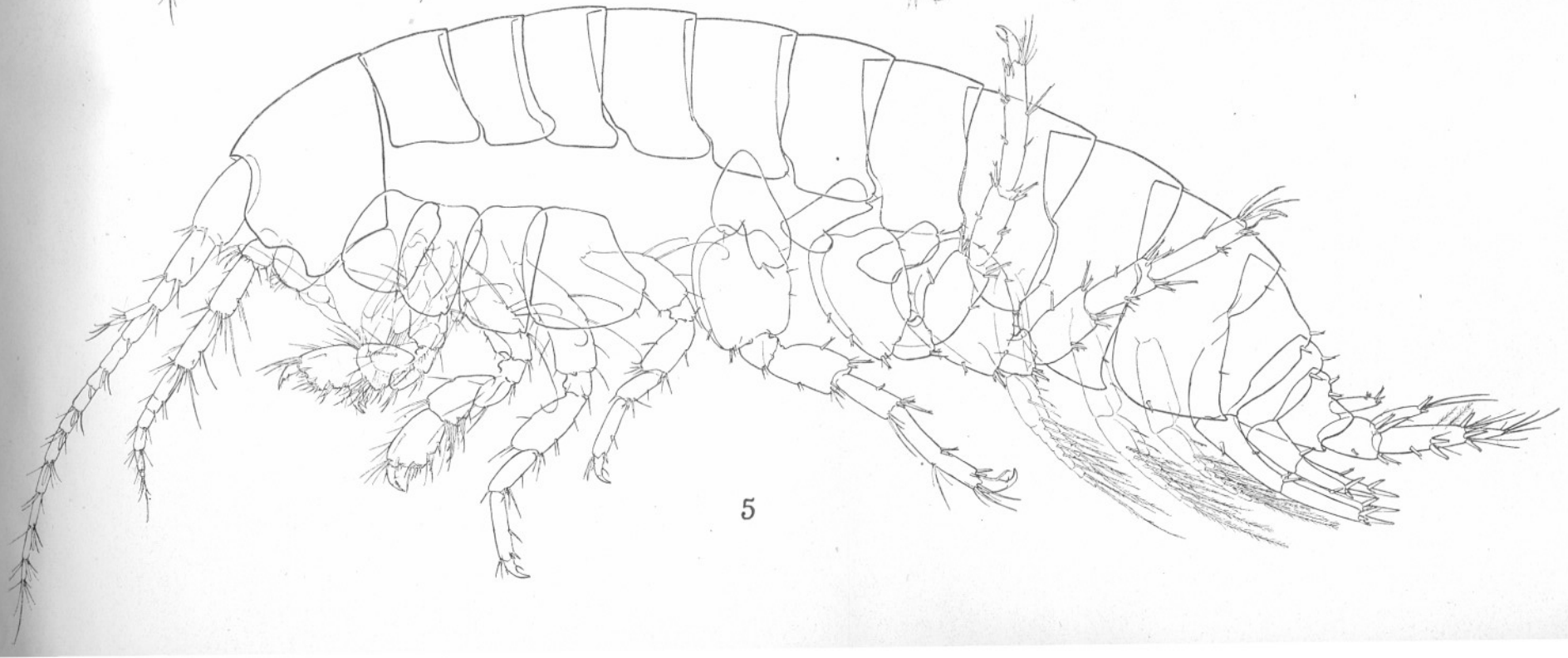

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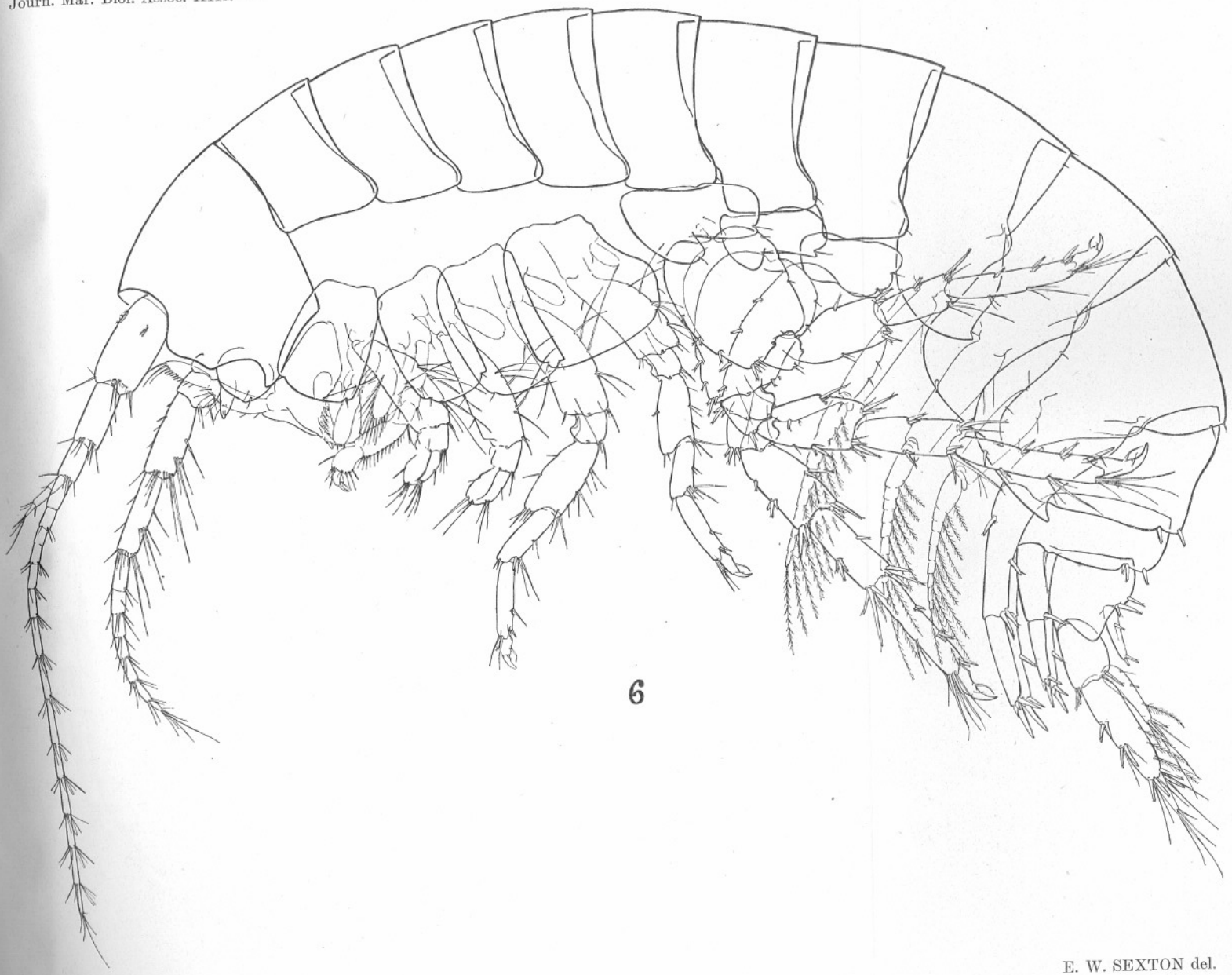

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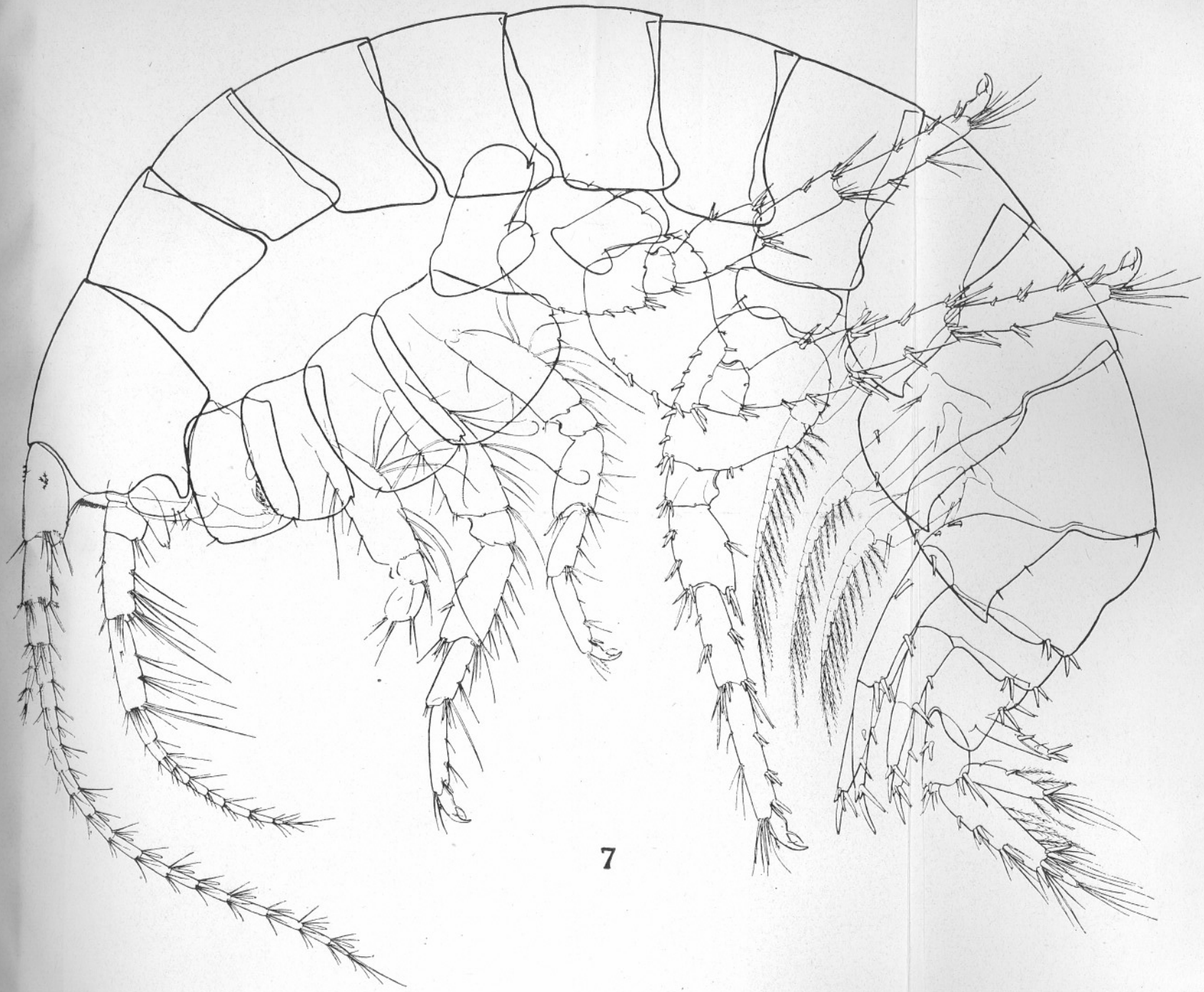

Normal Female. Moult 7.

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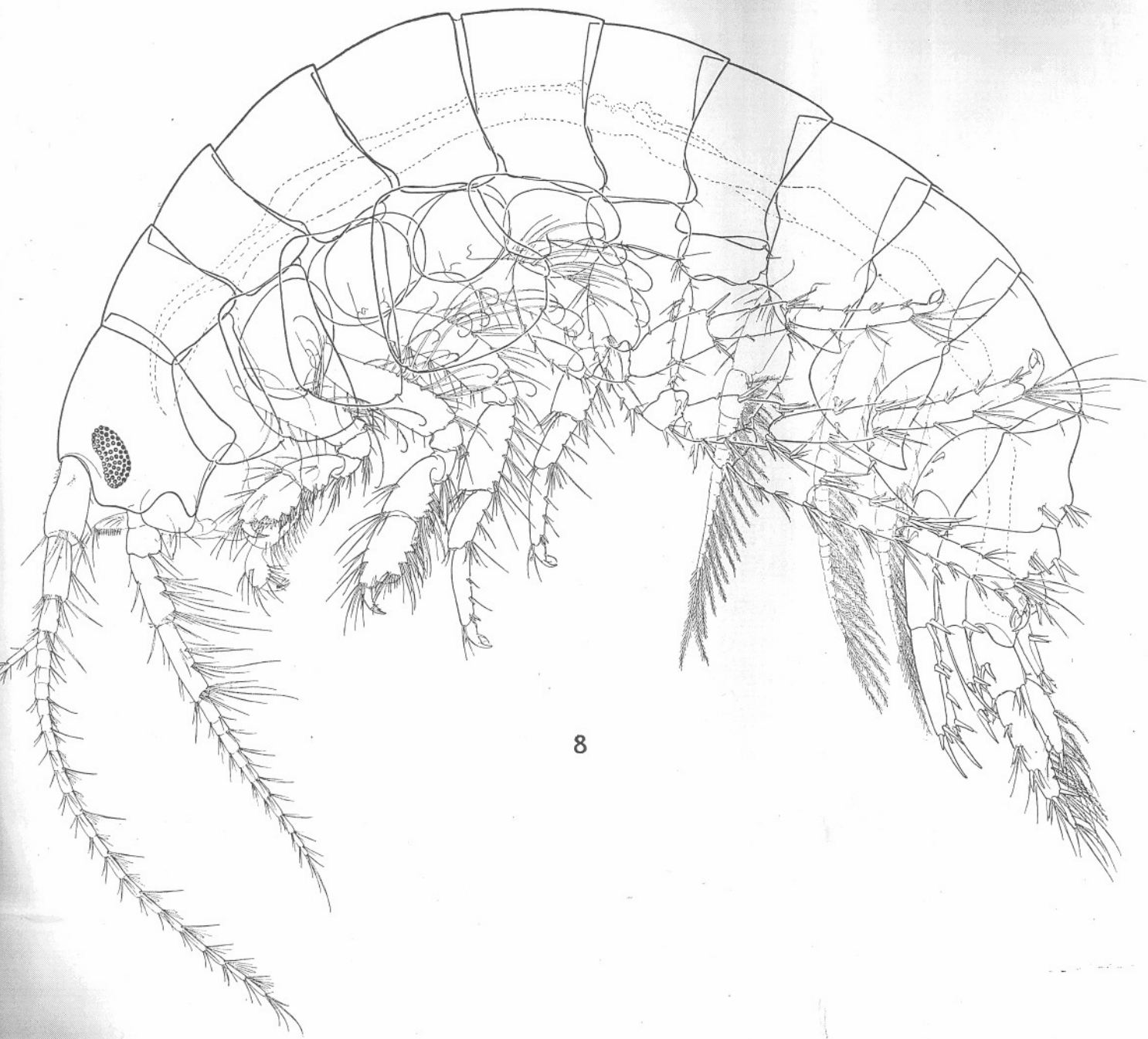

Normal Female. Moult 8.

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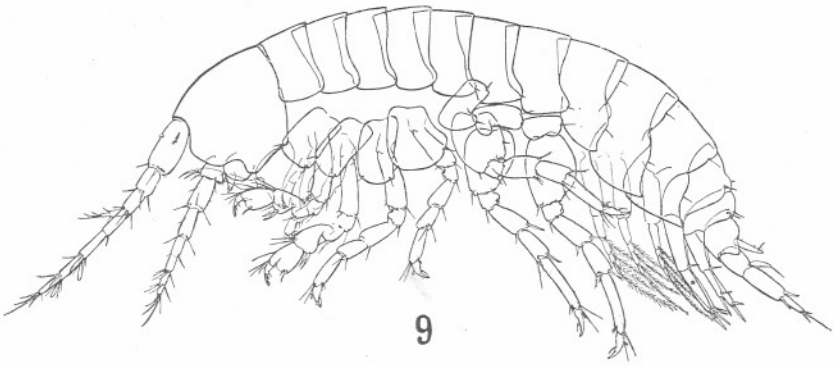

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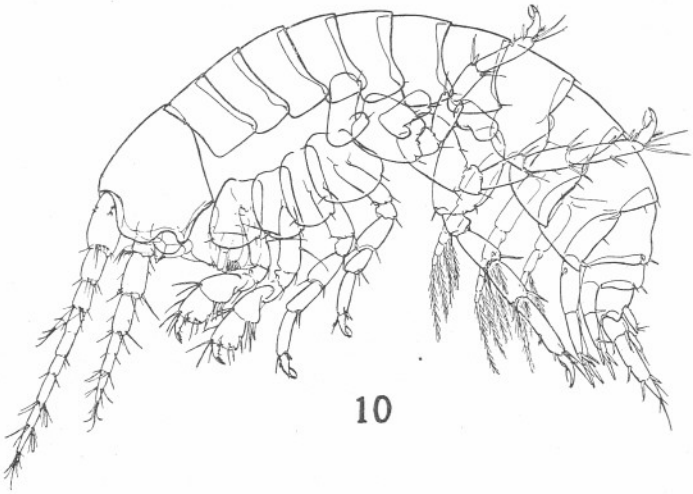

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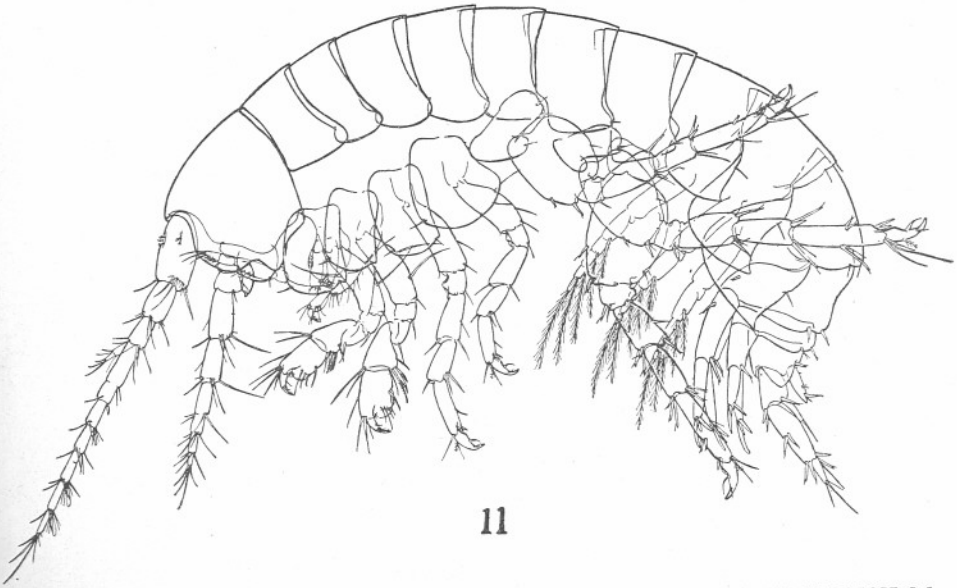

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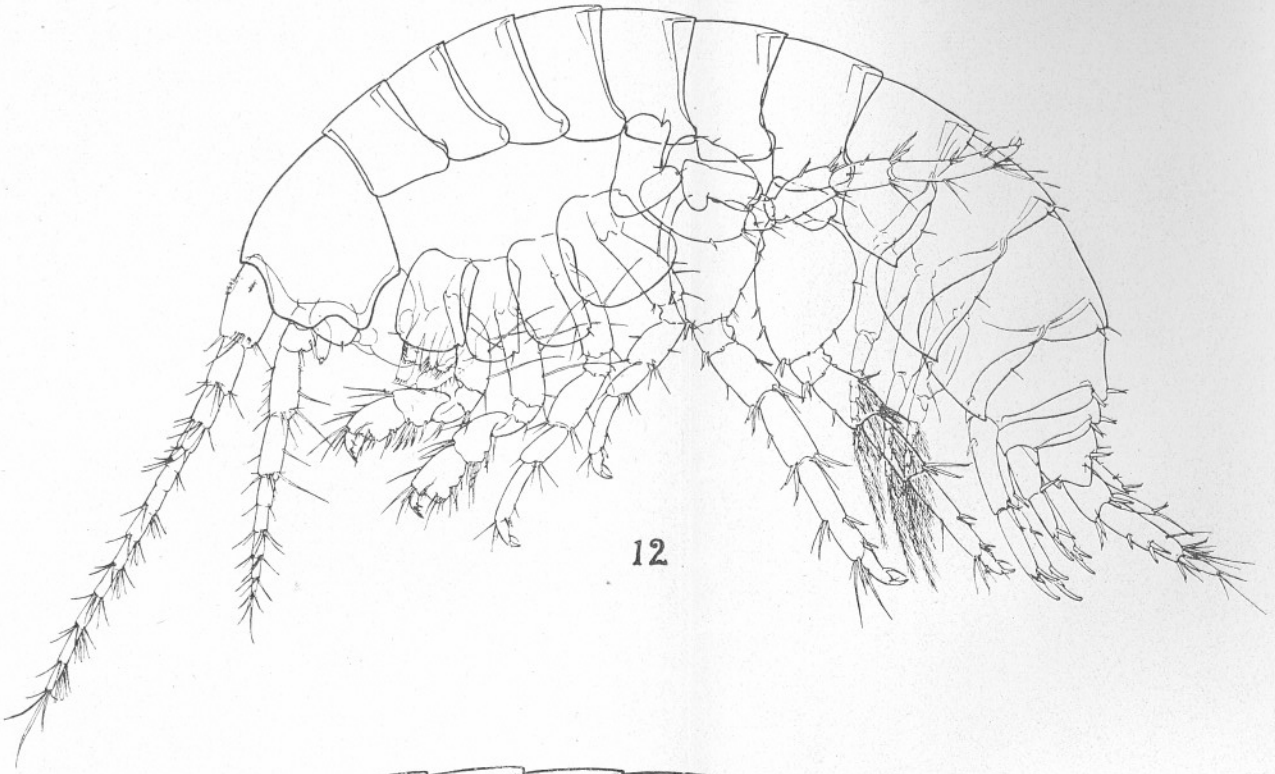
Normal Male. Moults 1, 2 and 3.



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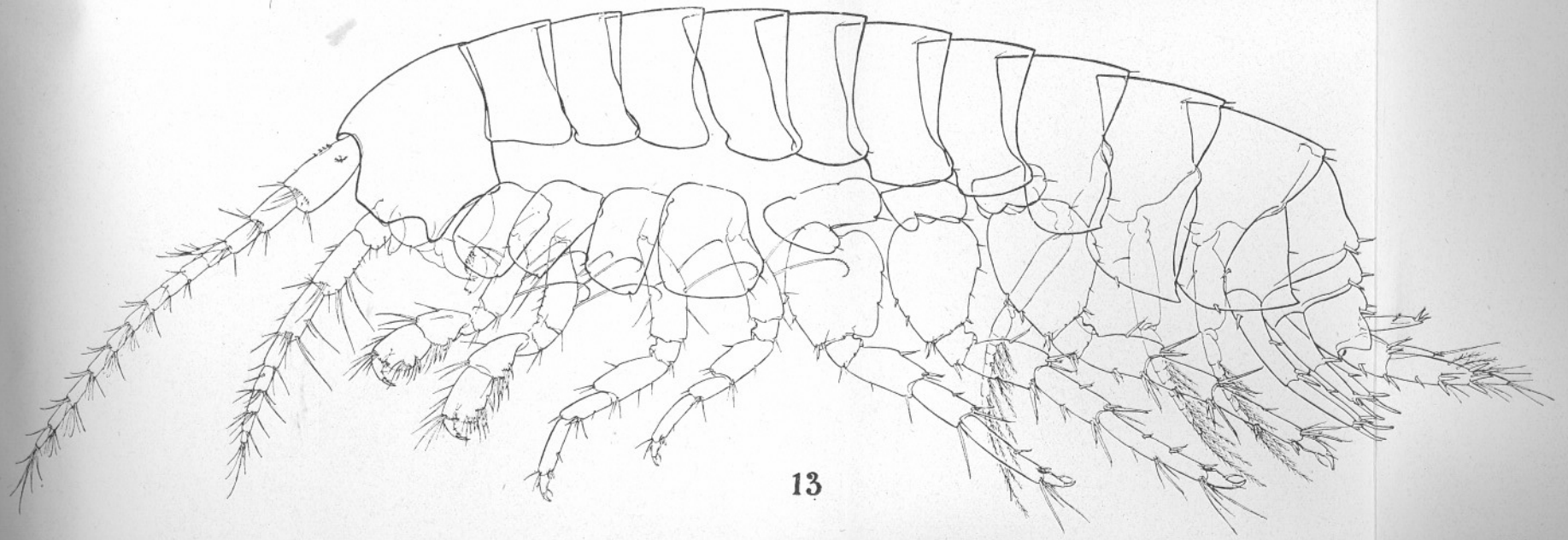

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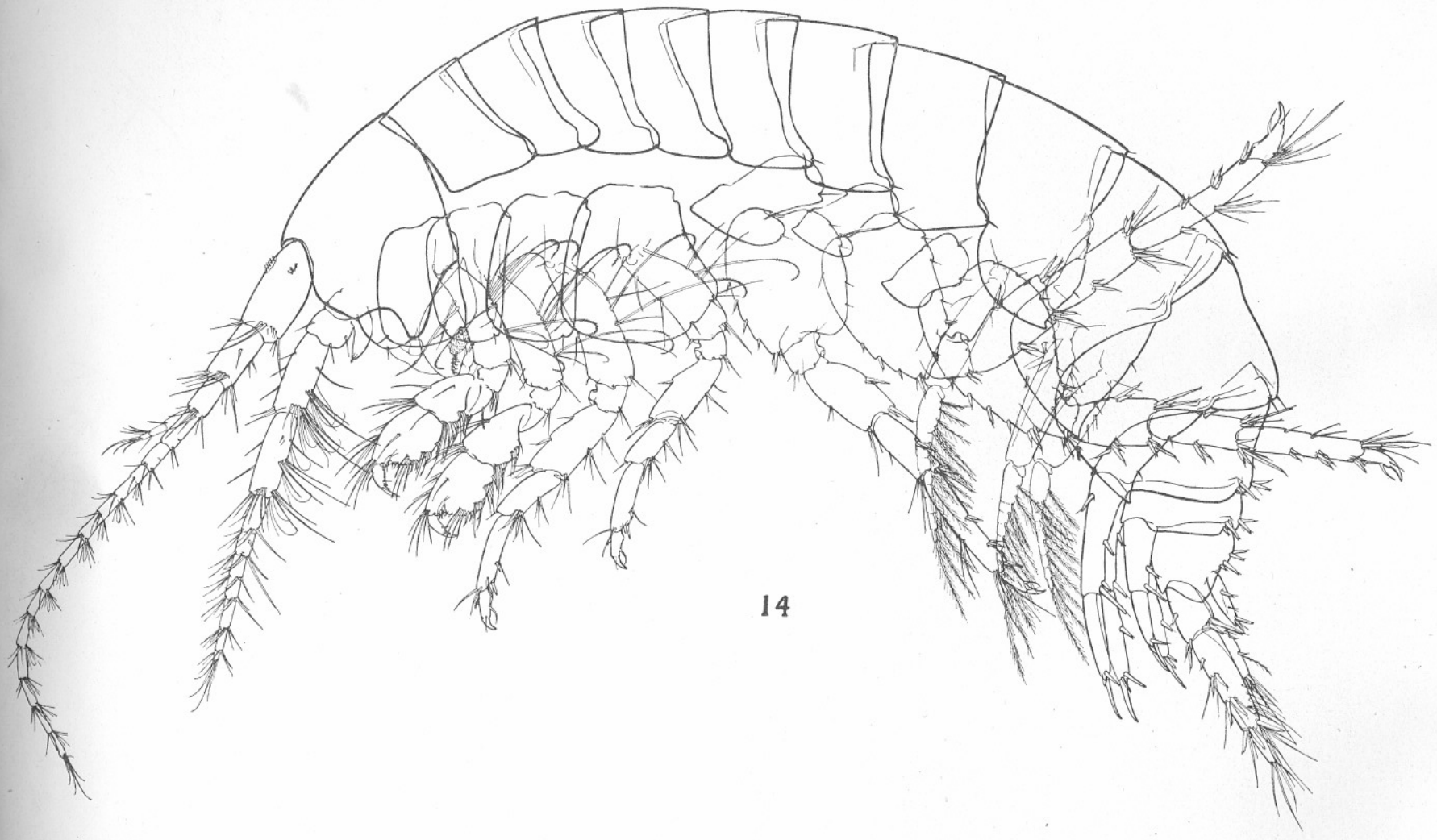

Normal Male. Moult 6.

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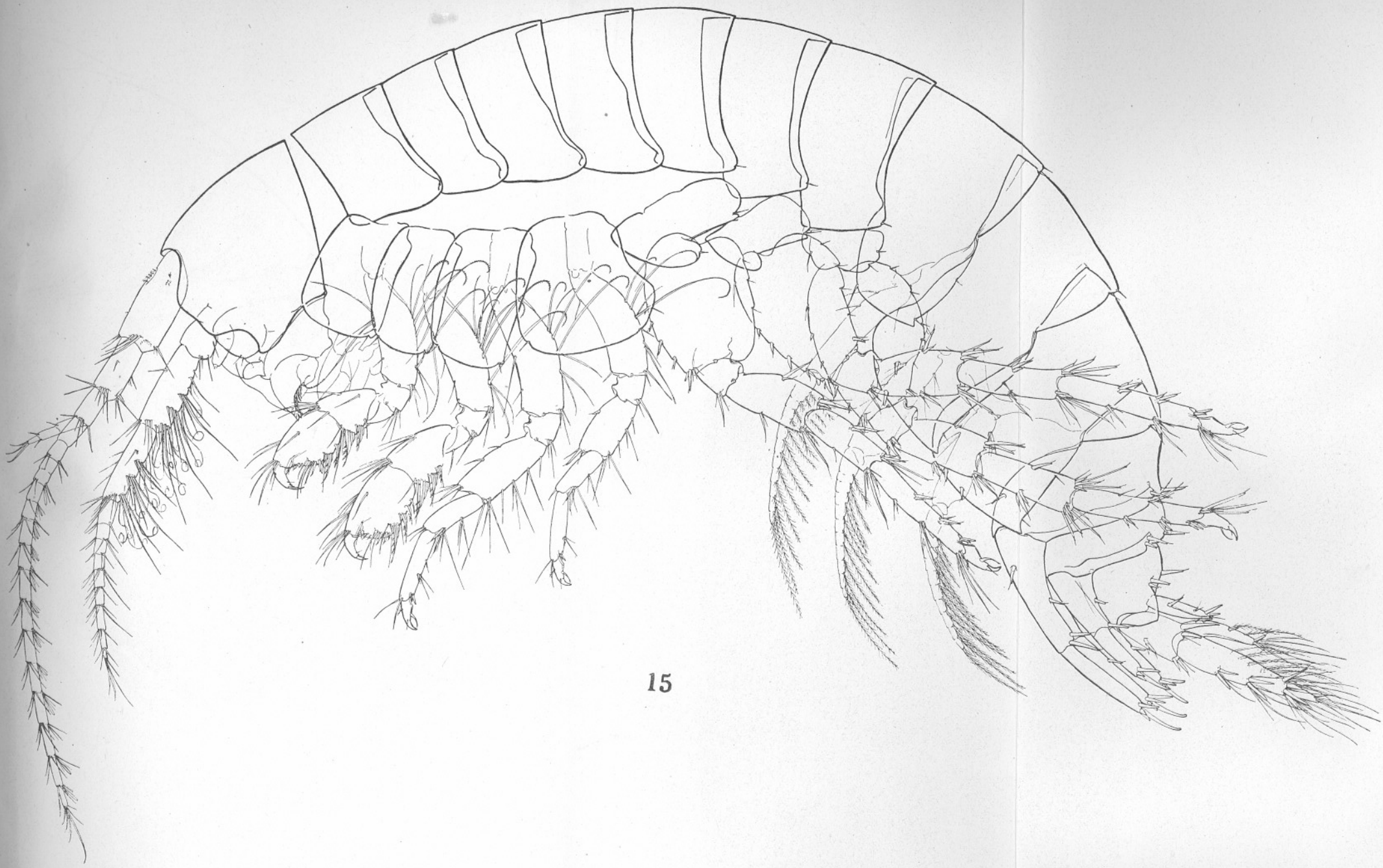

Normal Male. Moult 7.

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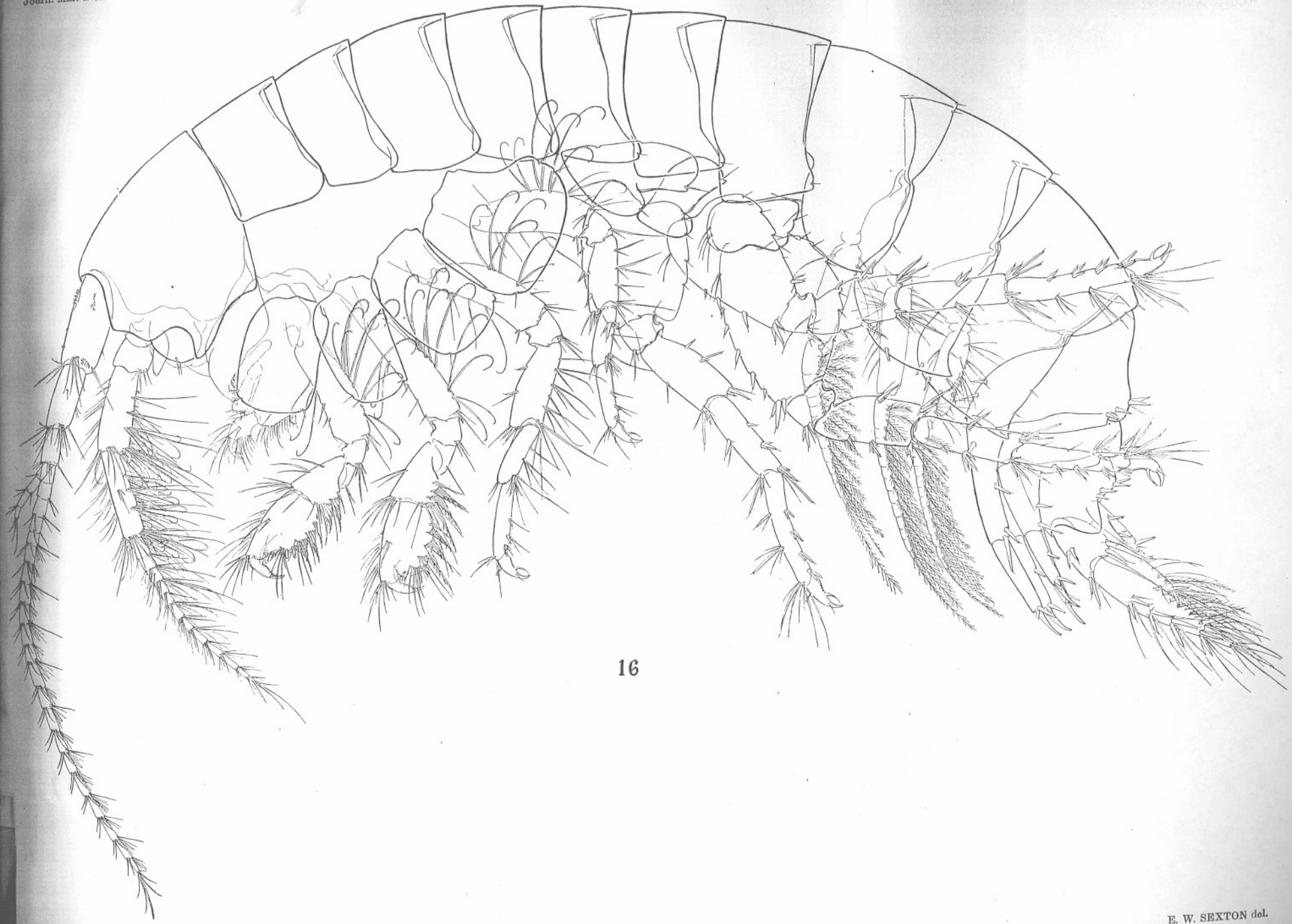

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Normal Male. Moult 8.

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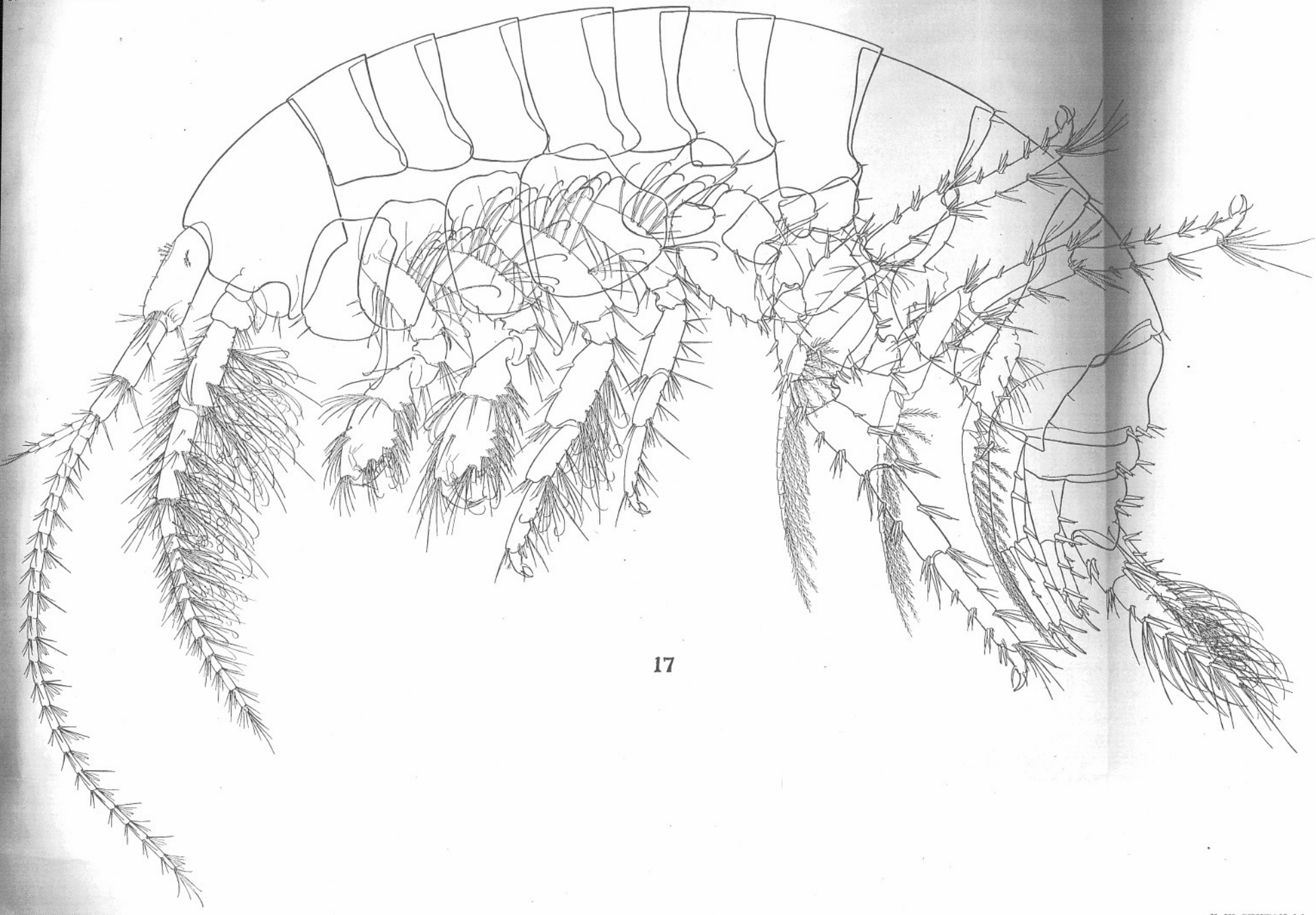

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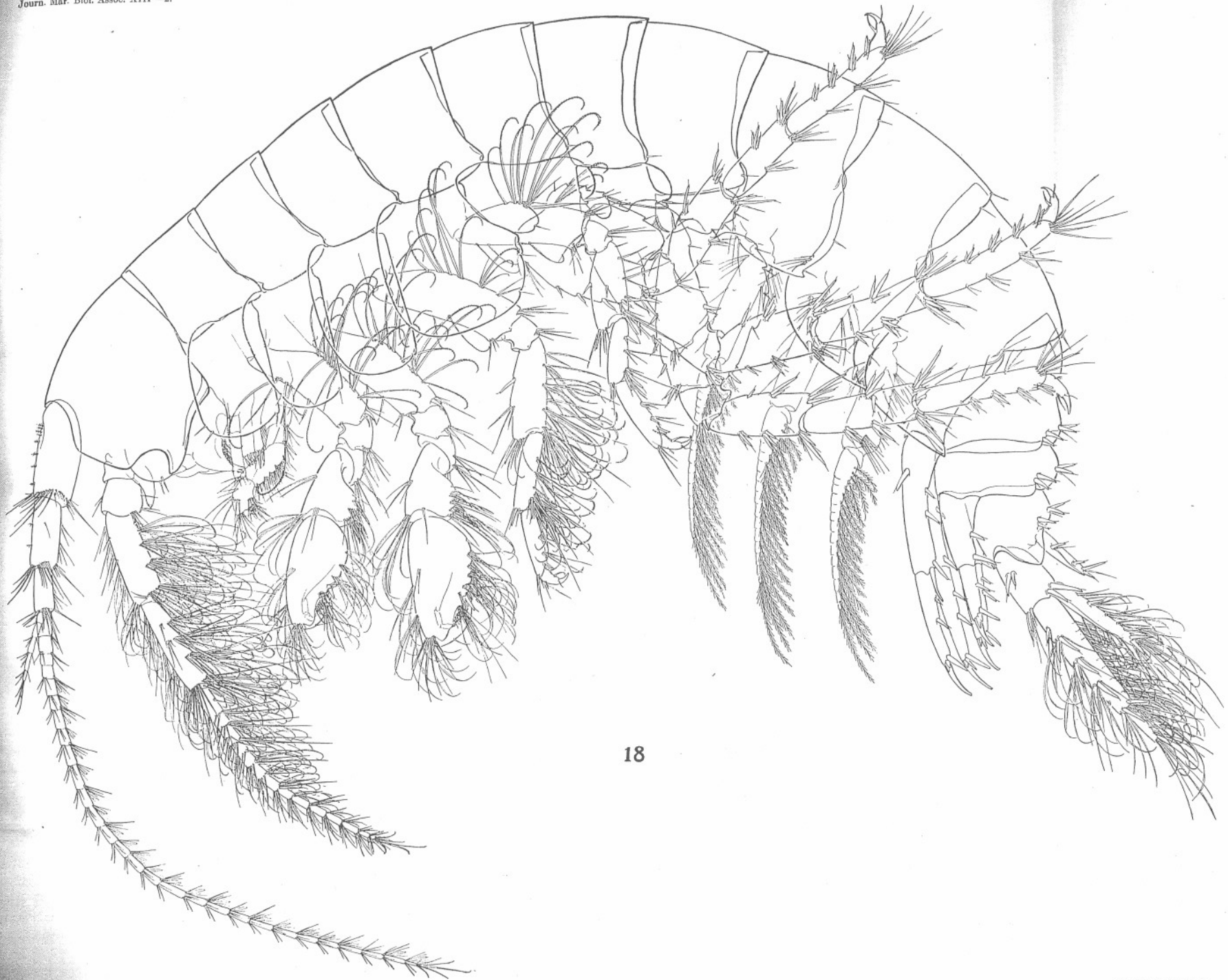

Normal Male. Moult 10.

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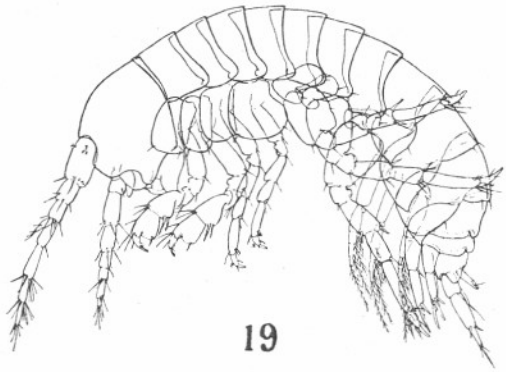
PLATE XIII.



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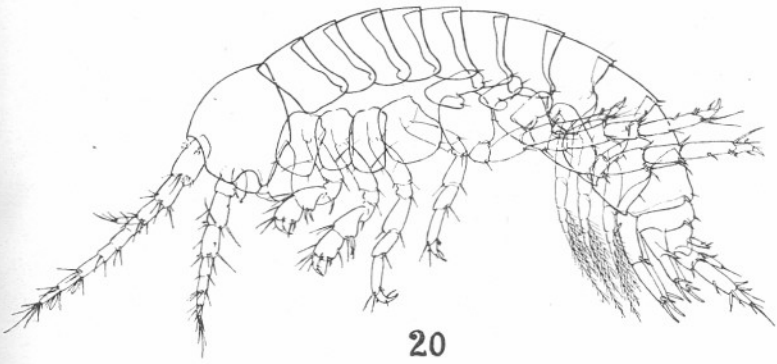

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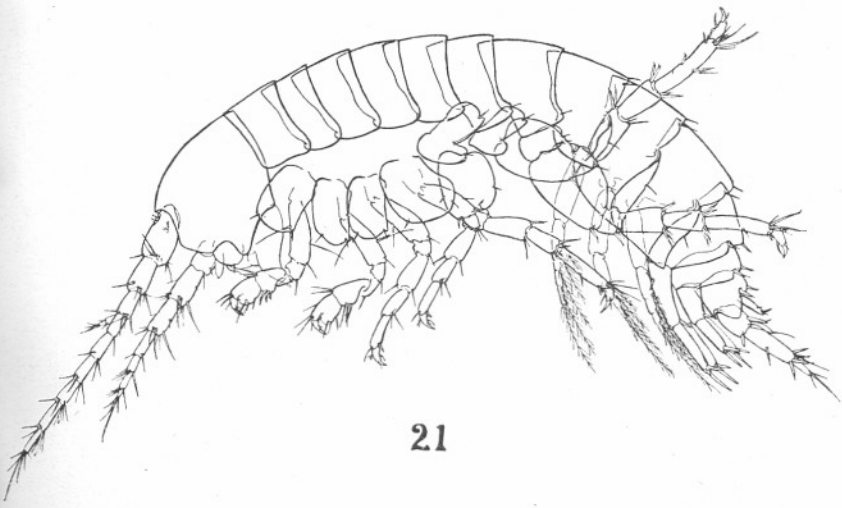
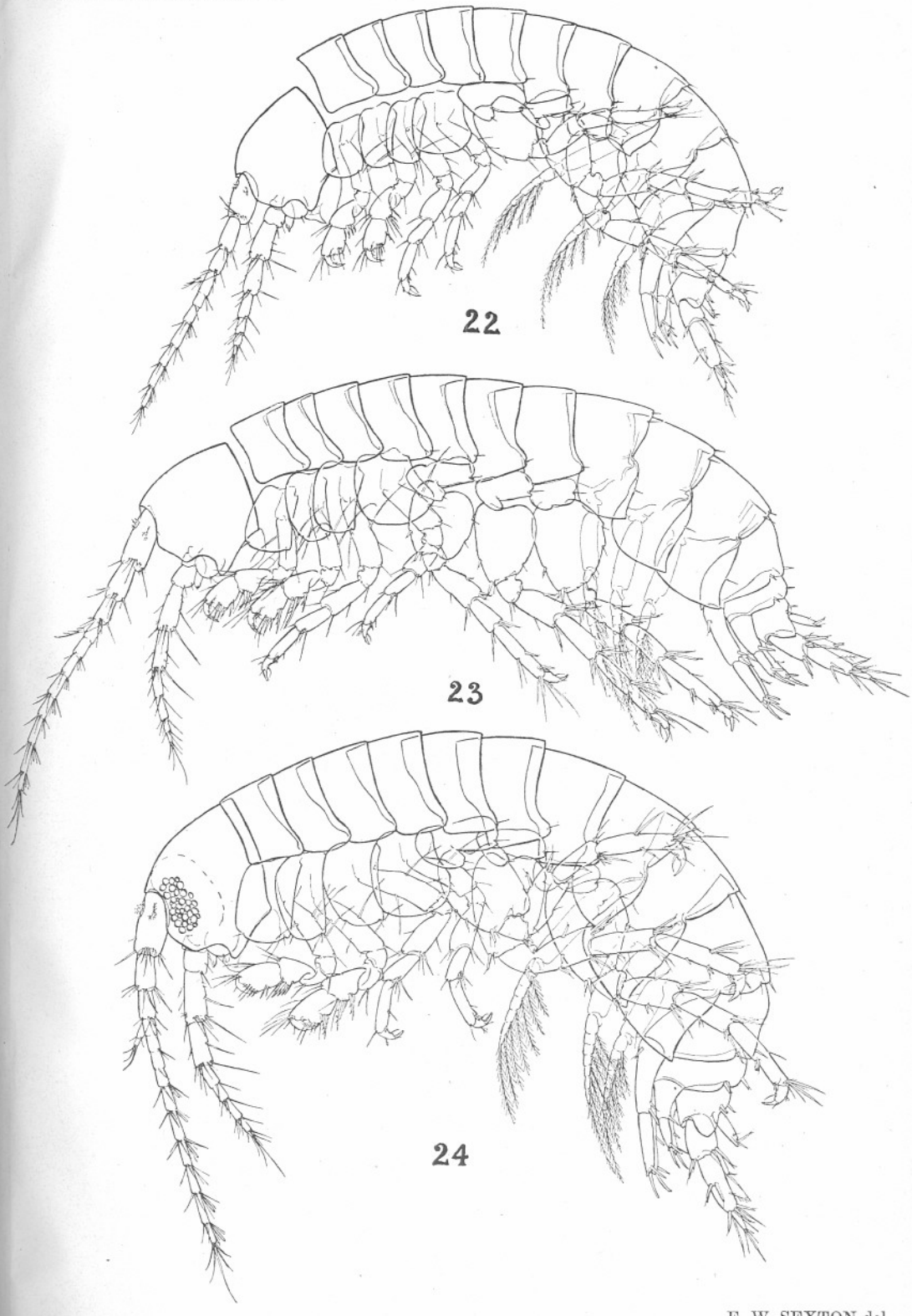


21

E. W. SEXTON del.

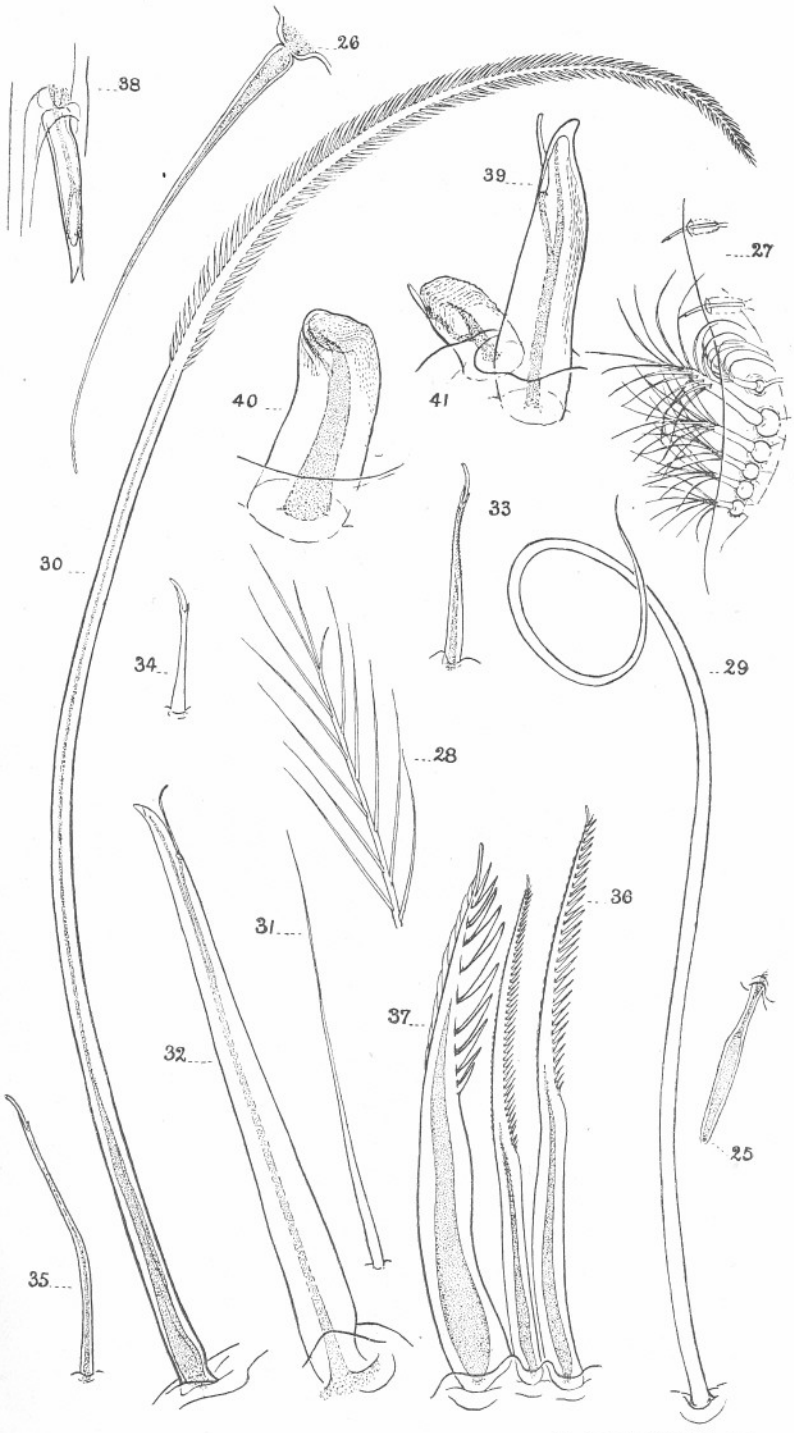
Intersex. ♂ Moults 1, 2 and 3.



E. W. SEXTON del.

Intersex. Moults 4, 5 and 6.

PLATE XV.



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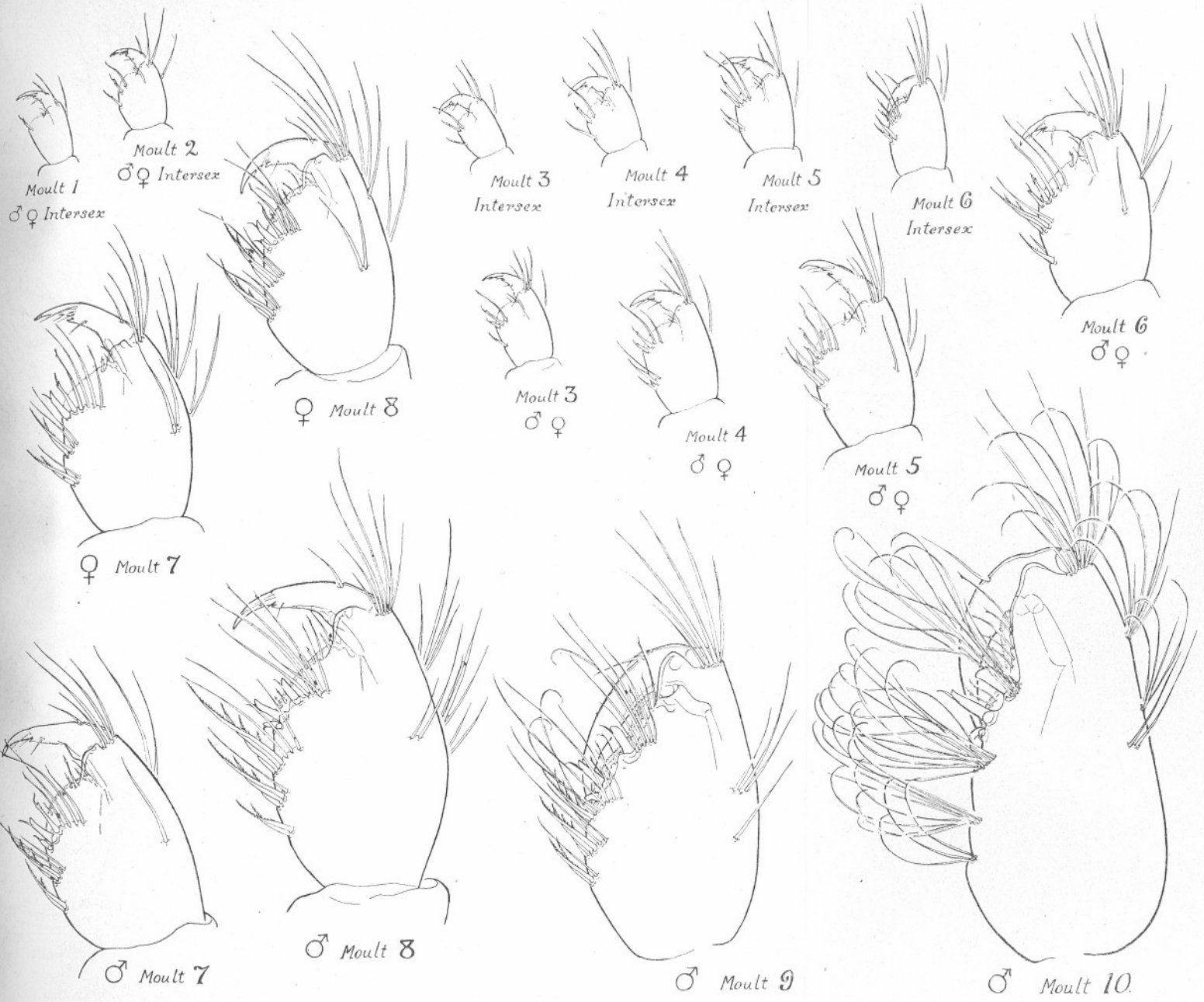
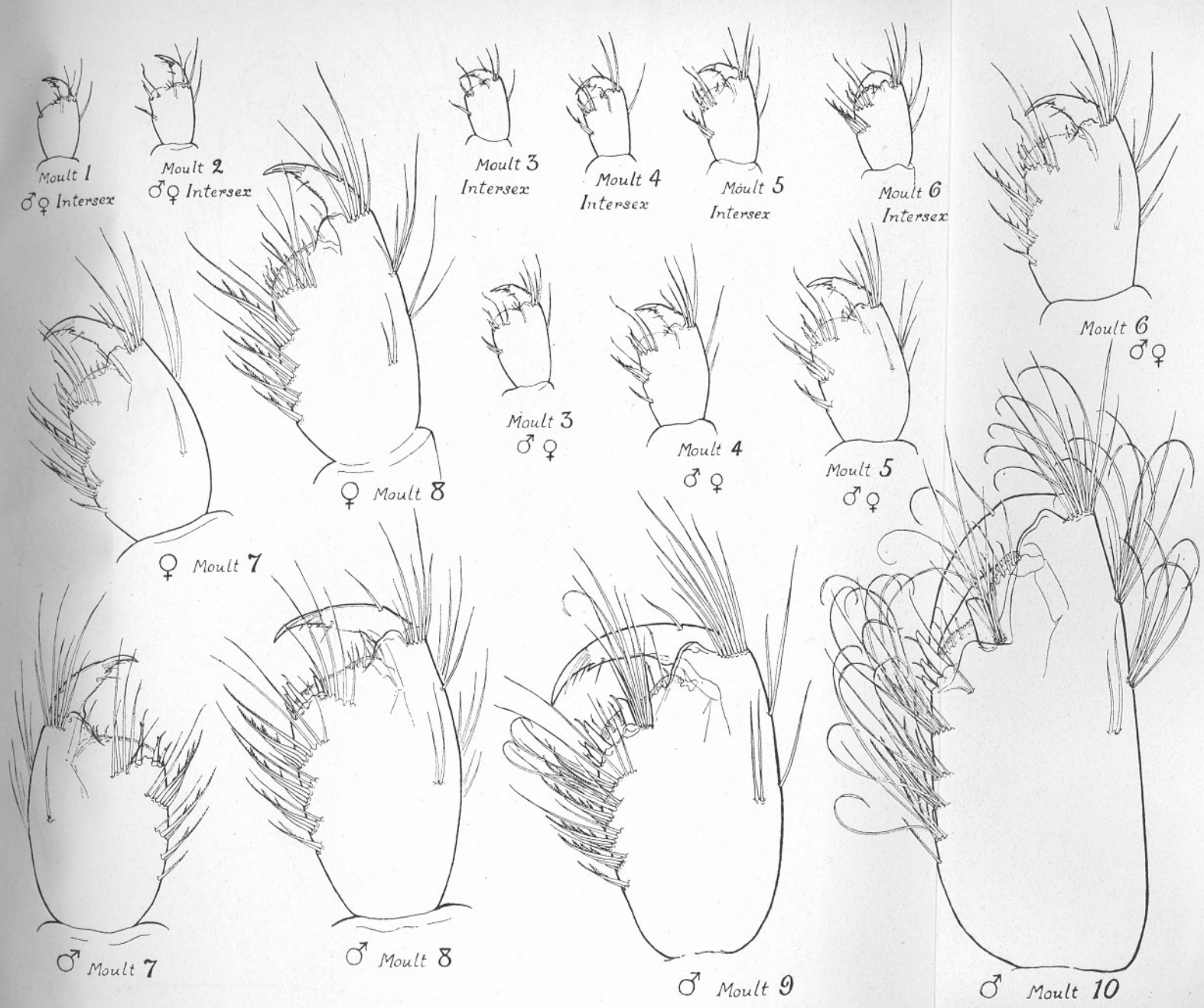


Hand. Gnathopod 1

E. W. SEXTON del.



Hand. Gnathopod 2.

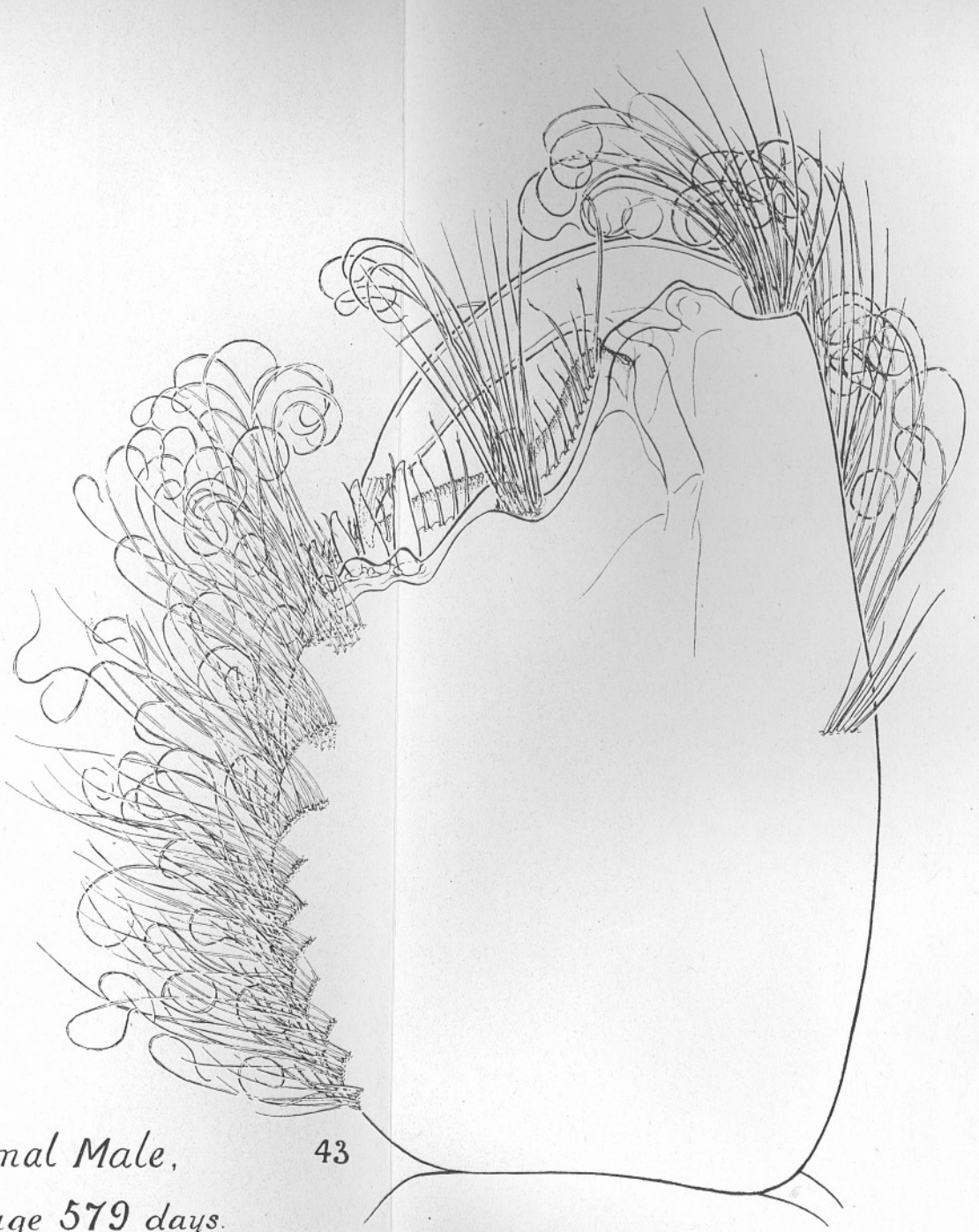
E. W. SEXTON del.

42

Hand. Gnathopod 1

Normal Male,

CN.22a, age 579 days.

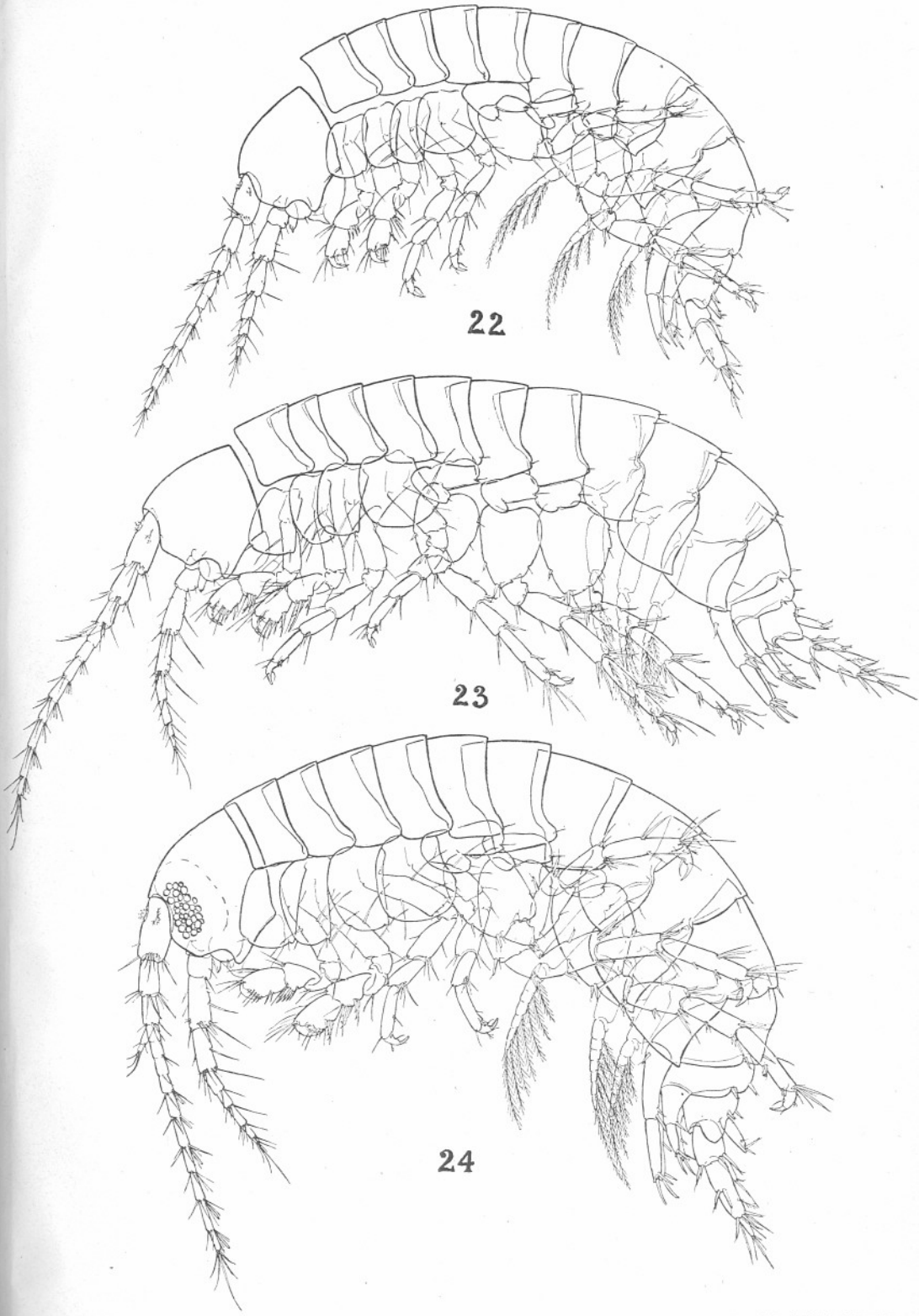


43

Hand. Gnathopod 2.

E. W. SEXTON del.

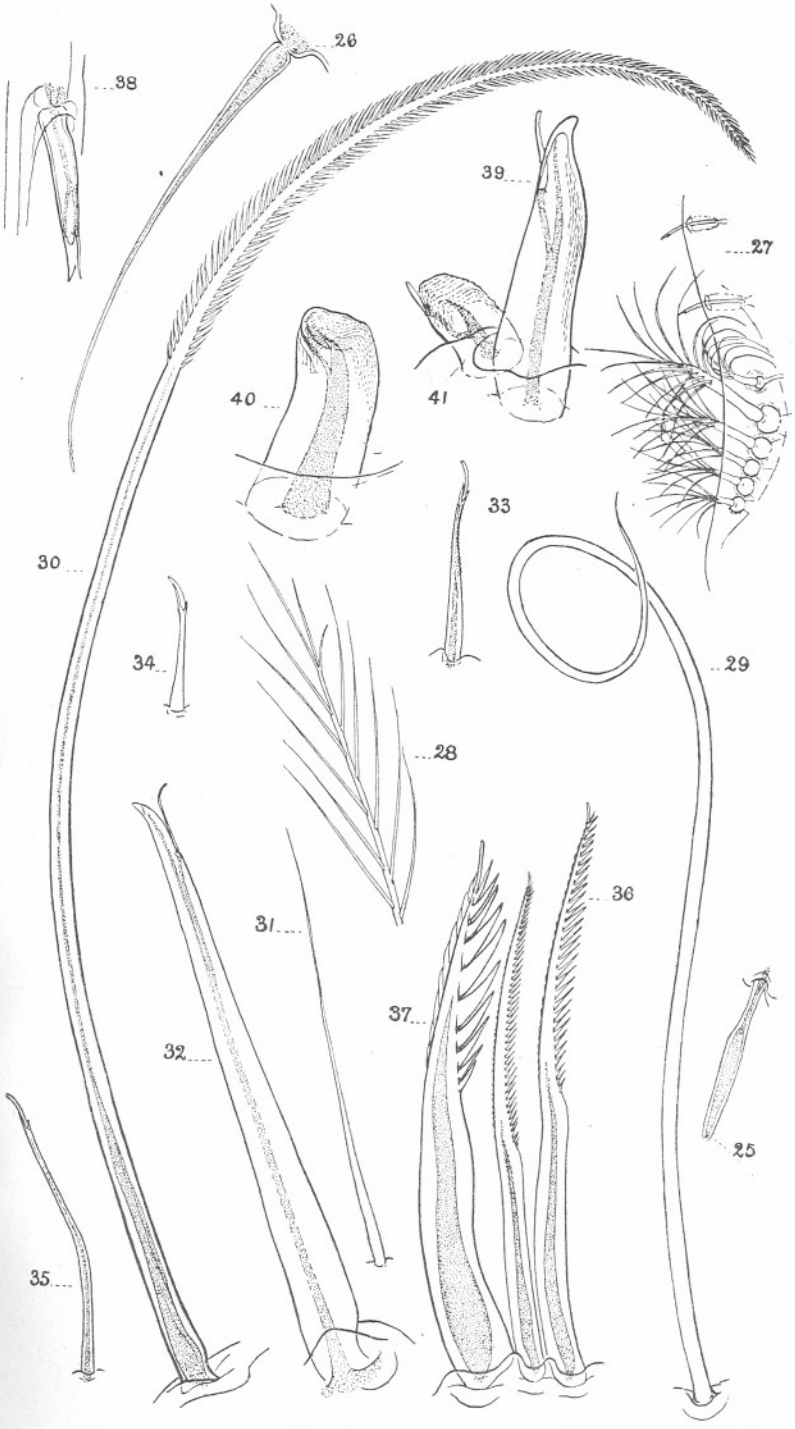
Journ. Mar. Biol. Assoc. XIII.—2



E. W. SEXTON del.

Intersex. Moults 4, 5 and 6.

PLATE XV.



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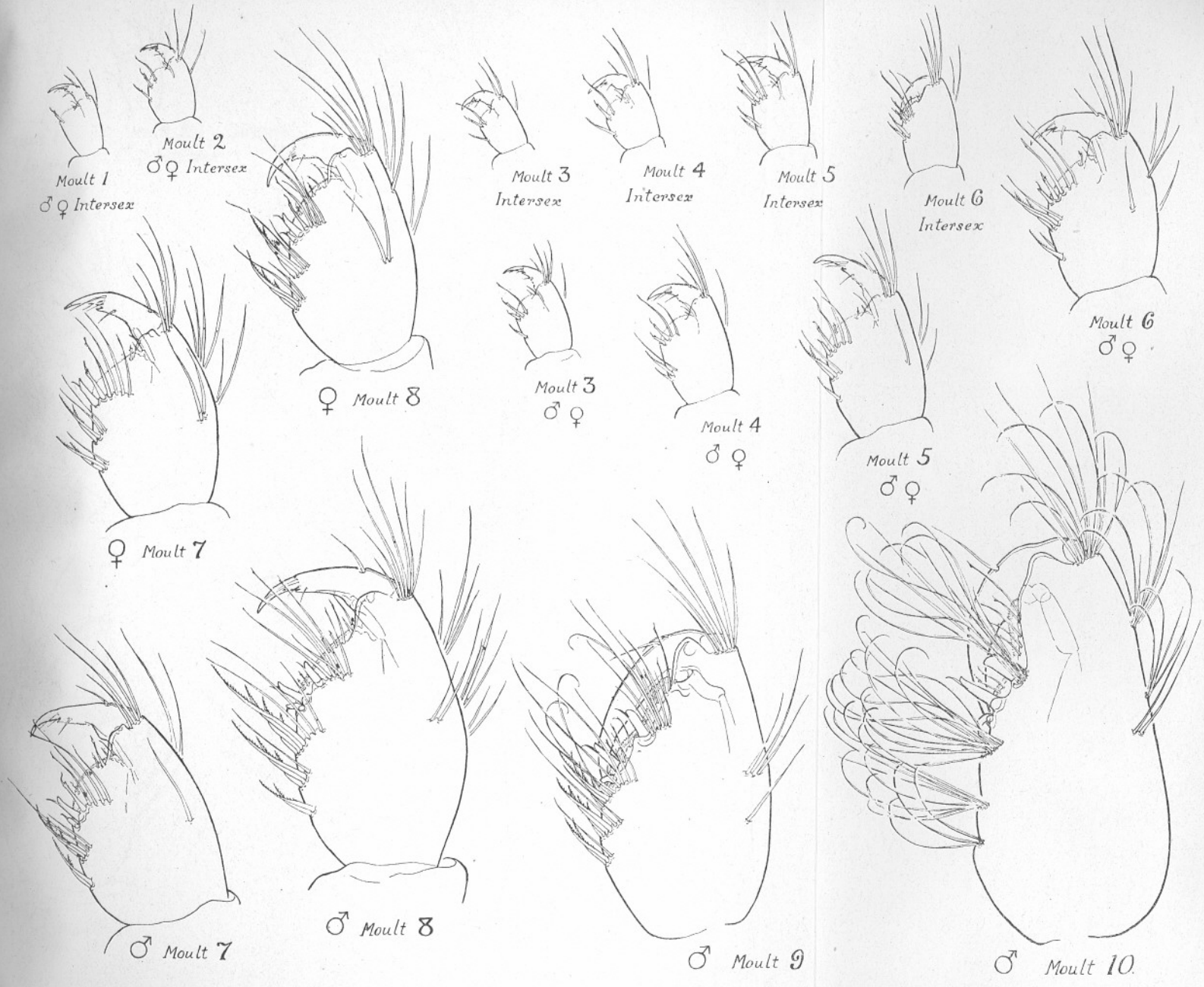
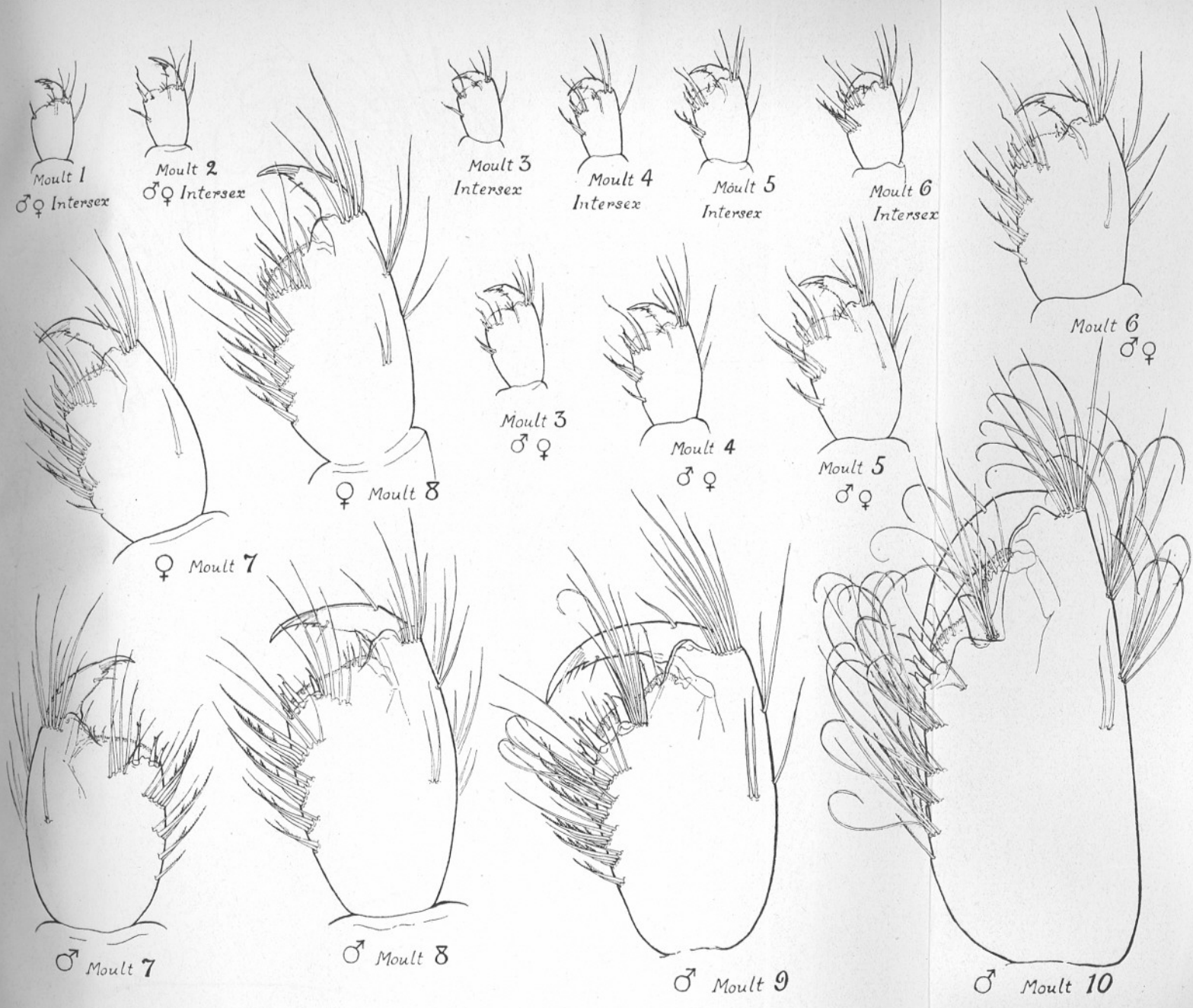


Hand. Gnathopod 1

E. W. SEXTON del.



Hand. Gnathopod 2.

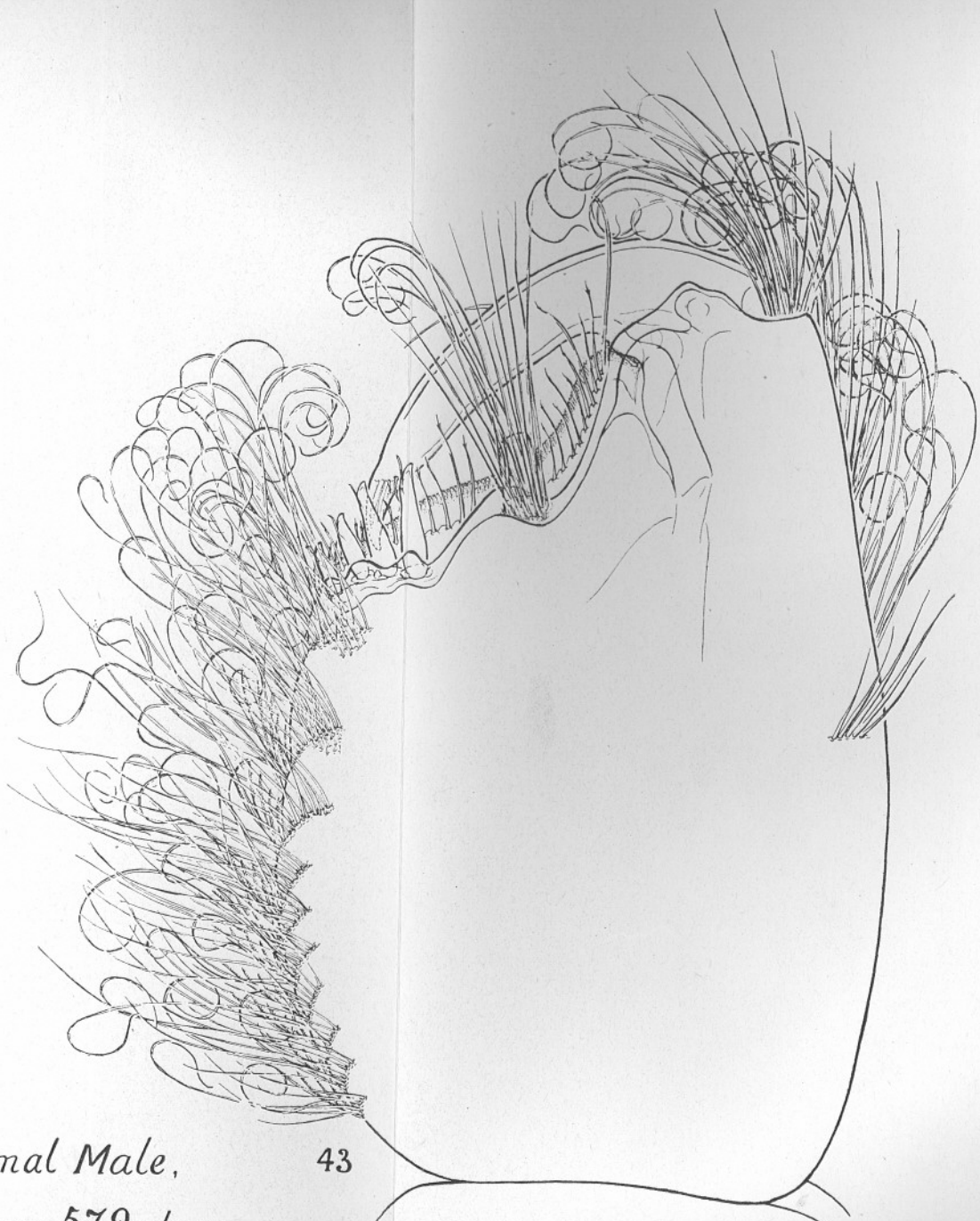
E. W. SEXTON del.

42

Hand. Gnathopod 1

Normal Male,

CN.22a, age 579 days.



43

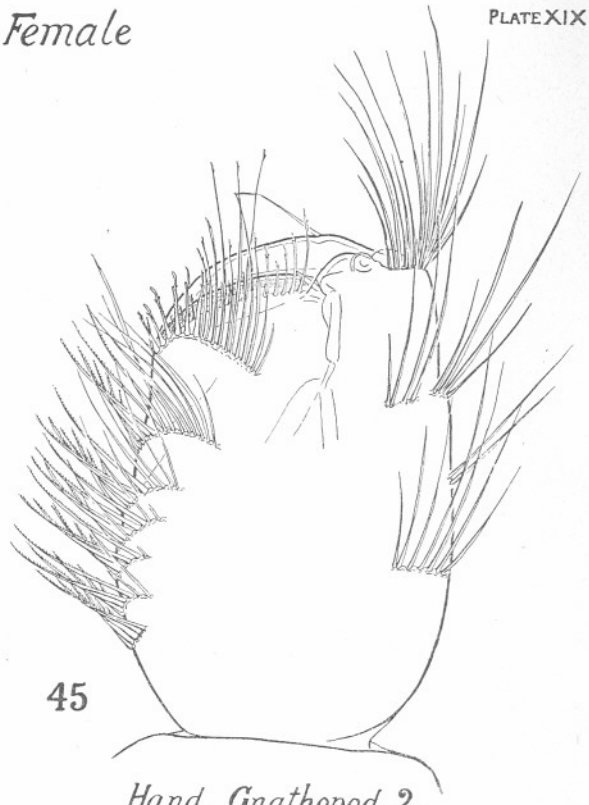
Hand. Gnathopod 2.

E. W. SEXTON del.

Normal Female

44

Hand. Gnathopod 1.



45

Hand. Gnathopod 2.

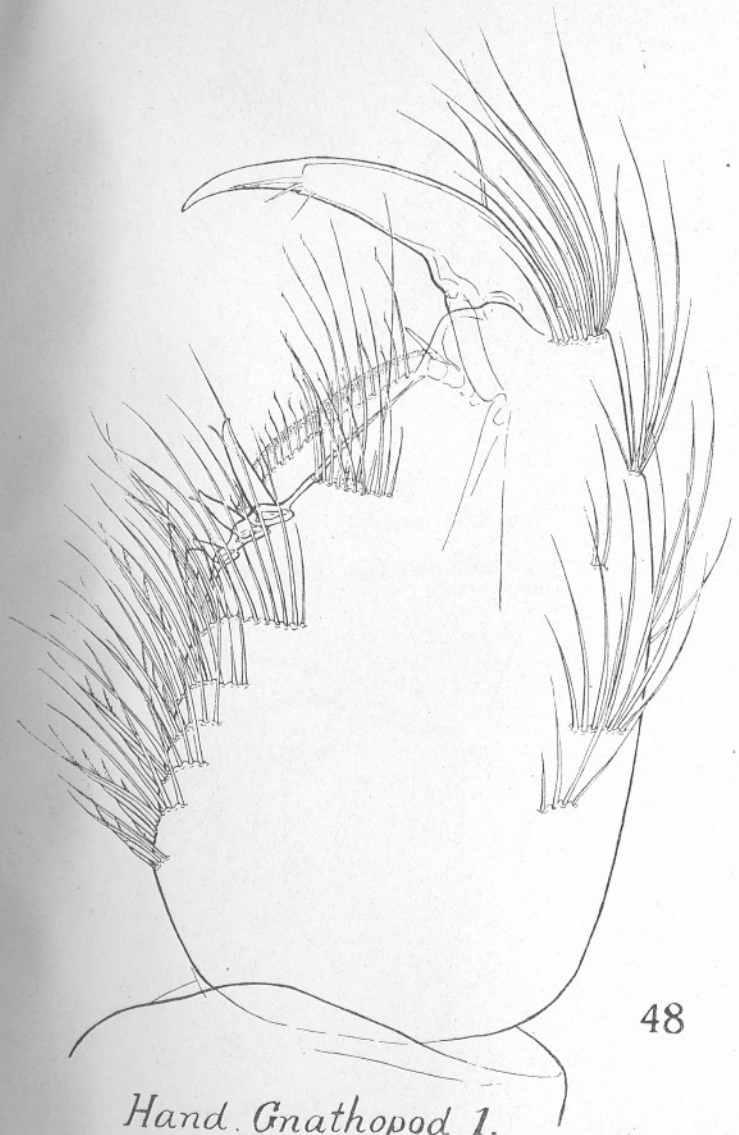
46

Hand Gnathopod 1

Male Intersex

47

Hand Gnathopod 2.



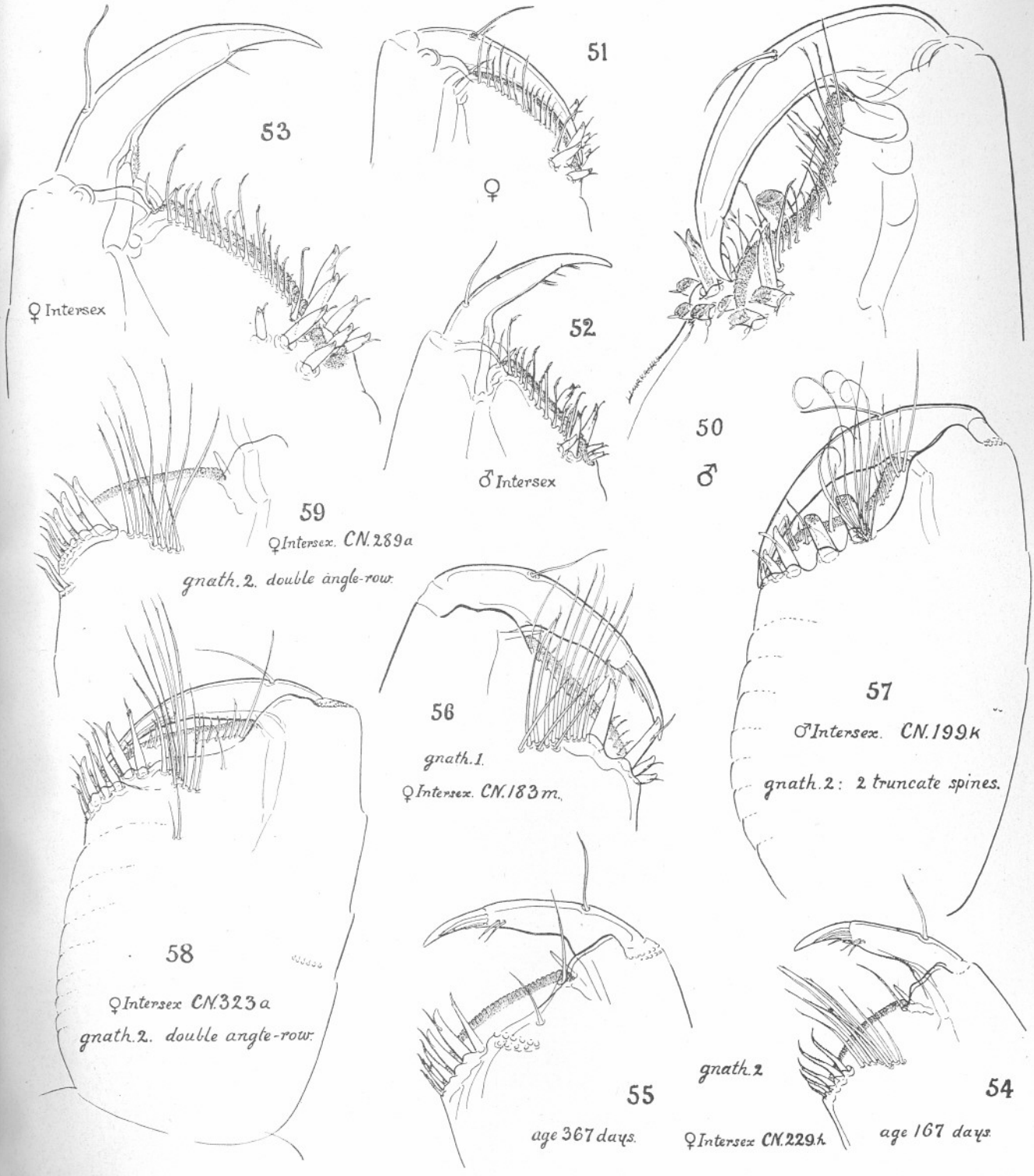
48

Hand. Gnathopod 1.

49

Hand. Gnathopod 2.

Female Intersex, CN284a, age 310 days.



E. W. SEXTON del.

DESCRIPTION OF THE PLATES

ALL the figures are taken from moults except Figs. 8 and 24, which are from the animals themselves. The gills are omitted from the drawings to avoid confusion of detail.

PLATE I.

FIG. 1. Moult 1 of the normal female, C.4, age 5 days, 18 July, 1913. ×39

,, 2. Moult 2. From the same female, age 10 days, 23 July, 1913. ×39

,, 3. Moult 3. From the same female, age 14 days, 27 July, 1913. ×39

PLATE II.

FIG. 4. Moult. 4. From the same female, age 19 days, 1 August, 1913. As the first six segments, gnathopod 1 and peræopods 4 and 5, were eaten by the female, these parts have been figured from the sister female, C.14. ×39

,, 5. Moult 5. From the female, C.4, age 23 days, August 5, 1913. Six joints of gnathopod 1 and the three terminal joints of gnathopod 2 were drawn from the sister female, C.14. The first antenna, left side, was eaten, and the right antenna is therefore figured *in situ*, with the inner surface showing. ×39

PLATE III.

FIG. 6. Moult 6. From the female, C.4, age 29 days, 11 August, 1913. The gnathopod hands were eaten. ×39

PLATE IV.

FIG. 7. Moult 7. From the female, C.4, age 36 days, 18 August, 1913. Six joints of gnathopod 1 and three of gnathopod 2 were eaten. The broodplates are not shown in this figure. ×39

PLATE V.

FIG. 8. Growth-stage 8 of the normal female. C.4, after moulting on August 18, 1913, laid 10 eggs. The animal was then preserved and figured. Broodplates not shown. ×39

PLATE VI.

FIG. 9. Moult 1 of the normal male, B.9, age 8 days, 22 July, 1913. ×39

,, 10. Moult 2 of the normal male, B.9, age 12 days, 26 July, 1913. ×39

11. Moult 3 of the normal male, B.9, age 17 days, 31 July, 1913. ×39

PLATE VII.

FIG. 12. Moult 4 of the normal male, B.9, age 21 days, 4 August, 1913. ×39

,, 13. Moult 5 of the normal male. Figured from another specimen, the male, A.20, age 29 days, 24 June, 1913. ×39

PLATE VIII.

FIG. 14. Moult 6 of the normal male, B.9, age 33 days, 16 August, 1913. (This male was mature at 40 days, but ate its moult.) ×39

PLATE IX.

FIG. 15. Moult 7 of the normal male. Figured from the male, A.20, at the age of 40 days, 5 July, 1913. ×39

PLATE X.

FIG. 16. First mature stage of the normal male, Moult 8. Owing to the difficulty of getting whole moults from the males of the summer broods, this stage and the two following were taken from winter broods. The structural details are exactly the same, but the time taken in development was naturally considerably longer. The male here figured, K.6, was 74 days old, 1 December, 1921. ×39

PLATE XI.

FIG. 17. Second mature stage of the normal male. Moult 9 from the winter male, K.6, age 92 days, 19 December, 1921. ×39

PLATE XII.

FIG. 18. Third stage, the "definitive adult" normal male. Moult 10 from the winter male, CN.444, age 110 days, 6 January, 1922. K.6 moulted on 6 January, but only the second gnathopod, the second antennae, pleon, uropods, and a few fragments of peræopods were found, the rest being eaten. These fragments were compared detail by detail with the male figured, and found to agree in all particulars. ×39

PLATE XIII.

FIG. 19. Moult 1 of the Intersex CN.397f., age 6 days, 5 August, 1921. ×39

„ 20. Moult 2 of the Intersex CN.397f., age 13 days, 12 August, 1921. ×39

„ 21. Moult 3 of the Intersex CN.397f., age 20 days, 19 August, 1921. ×39

PLATE XIV.

FIG. 22. Moult 4 of the Intersex CN.397f., age 27 days, 26 August, 1921. ×39

„ 23. Moult 5 of the Intersex CN.397f., age 35 days, 3 September, 1921. ×39

„ 24. Growth-stage 6 of the Intersex CN.397f., age 49 days. Dead on 17 September, 1921. ×39

PLATE XV.

FIG. 25. *Sensory filament* or aesthetasc from the First Antenna; normal female, CN.22a. ×290

„ 26. One of the shorter *hairs* from the posterior margin of the broodplate, second gnathopod; normal female, CN.22a. ×290

FIG. 27. *Plumose hairs* from the sensory groove on the basal joint of the peduncle of the First Antenna; female intersex, CN.284a. The normal female, CN.22a., has the same number The largest hair is the one first formed. Distally two of the "*skin-hairs*" are shown. ×290

,, 28. Tip of a *feathered hair* from the first pleopod; normal female, CN.22a. ×290

,, 29. *Coiled hair* from the palmar group, First Gnathopod; normal male, CN.22. ×290

,, 30. *Serrated-hair* from the posterior margin of the second joint, First Gnathopod; normal male, CN.22. ×290

,, 31. *Seta* from the second peræopod; normal female, CN.22a. ×290

,, 32. *Slender-spine* from the fifth joint of the fourth peræopod; normal female, CN.22a. ×290

,, 33. *Serrulate-seta* from the angle-row of the Second Gnathopod; normal female, CN.22a. ×290

,, 34. *Marginal-seta* from the palmar margin of the Second Gnathopod; female intersex, CN.284a. ×290

,, 35. *Bent seta* from the Second Gnathopod; normal female, CN.22a. ×290

,, 36. *Serrated-bristles*

,, 37. *Dentate-spine*, lateral view from the distal margin, under surface of the fifth joint, Second Gnathopod; female intersex, CN.284a. ×290

,, 38. *Spine* from the anterior margin of the second joint, fourth peræopod; normal female, CN.22a. ×290

,, 39. *Pointed-spine* from the upper side of the palmar-angle, First Gnathopod; normal male, CN.22. Seen from below. ×290

,, 40. *Truncate-spine* from the middle of the palm, First Gnathopod; normal male, CN.22. Seen from the under surface. ×290

,, 41. *Curved-spine* from the upper side of the palmar-angle, First Gnathopod; normal male, CN.22. Seen from below. ×290

PLATE XVI.

Illustrates the development of the hand of the First Gnathopod, from birth to sexual maturity in the normal male and female, and in the intersex to the sixth growth stage. The left hand is figured seen from the outer surface. ×97

PLATE XVII.

The development of the hand of the Second Gnathopod. The left hand is figured, except in the seventh moult of the male, where the right hand is shown. ×97

PLATE XVIII.

FIG. 42. The hand of the First Gnathopod (right side) of the male at its fullest development is figured for comparison with the hand at sexual maturity. The oldest normal male to die a natural death in the experiments, CN.22, was 579 days old. The figure shows the oblique palm, the male truncate-spine in mid-margin, and the pointed-spine and two male curved-spines at the palmar-angle. ×97

,, 43. The hand of the Second Gnathopod (left side) of the same male, CN.22, showing the indented palm, truncate-spine, the angle-row with 4 pointed-spines and 10 posterior-clusters. ×97

PLATE XIX.

FIG. 44. The hand of the First Gnathopod of the female at its fullest development. Taken from the oldest normal female, CN.22a., from the same brood as the male above, at the age of 679 days. The figure shows the unbroken palmar-series, and the small size characteristic of the female type. ×97

„ 45. The hand of the Second Gnathopod of the same female, showing the angle-row of 6 serrulate-setæ and the unbroken palmar-series. ×97

„ 46. The hand of the First Gnathopod of the Male Intersex, CN.314b., at the age of 210 days. The intermediate character of the palmar margin of the claw will be noted, the "female type" size, and the partial male development of the palmar-series. ×97

„ 47. The hand of the Second Gnathopod of the same specimen, showing the partial male development, and the small size and transverse palm of the "female type." ×97

PLATE XX.

FIG. 48. The hand of the First Gnathopod of the female intersex, CN.284a., at the age of 310 days, the largest specimen in this case, not the oldest. ×97

„ 49. The hand of the Second Gnathopod of the same specimen. In both the large size, a male character, is noticeable. Gnathopod 2 shows the intersexual type angle-row, mixed spines and serrulate-setæ, the transverse palm of the female, the separation of the palmar-row from the angle-row and the clustering of the hairs as in the male, the claw approaching the male type, and the large number of posterior-clusters. ×97

PLATE XXI.

FIGS. 50 to 53 illustrate the difference between the full-grown normal and intersexual types as shown in the undersurface of the palm in Gnathopod 1. The figure is taken from the oldest normal male, CN.22, and shows the oblique deeply-indented palm, the torsion of the palmar margin which brings both the spine-groups of the angle to the under surface, and the character of the male spines, the truncate in mid-margin and the curved at the palmar-angle with flattened spinulose tips. ×97

„ 51. The under surface of the palm, Gnathopod 1 of the oldest normal female, CN.22a., showing the transverse slightly rounded palm, with the claw closed down against the margin, the position of the spine-groups at the angle, one on the upper side and one on the under, and the character of the spines. ×97

, 52. The same view of the male intersex, CN.314b., showing the approach to the female type, the transverse palmar margin with the claw closing down against it, the small size and the female character of the spines in the under group at the palmar-angle. ×97

„ 53. The same view of the female intersex, CN.284a., showing the approach to the male type, the large size, the torsion of the palm, bringing the two spine-groups to the under surface, the claw, bent to the same degree as the palm, and the increase in the number of the spines developed at the angle. ×97

FIG. 54. The outer surface of the palm, Gnathopod 2, of the female intersex, CN.229h., at the age of 167 days. ×97

,, 55. The same hand at a later stage, 367 days old, illustrating the development of the intersexual type of angle-row. ×97

,, 56. The palm of the First Gnathopod, in the most male of all the female intersexes yet observed in the experiments. This specimen, CN.183m., had the pointed-spine in mid-margin, which is a character of the normal male in the first mature stage, and the palmar-series separated into palmar-row and angle-row. Cf. male intersex, CN.314b., figs. 46 and 47. ×97

,, 57. This figure and the two following illustrate a remarkable development in the sensory armature of the palm, viz. a duplication of spines in the angle-row. The specimen was a male intersex, CN.199k., age 164 days, with the small size of the female type, the Second Gnathopod with the indented palm of the male type, but with *two* truncate-spines in the palmar margin. ×97

,, 58. The second instance of the duplication was in a female intersex, CN.323, age 301 days. The figure shows *two* angle-rows developed on the palm of the Second Gnathopod. ×97

,, 59. The third specimen was a female intersex, CN.289a., 362 days old. The transverse palm of the Second Gnathopod shows the usual intersexual angle-row, with a *second* angle-row developing below it. The previous moult had only one stout setiform spine in this new row. ×97