THE LIFE-HISTORY OF A BRACKISH WATER AMPHIPOD GRANDIDIERELLA BONNIERI STEBBING*

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INTRODUCTION

Our knowledge of the life-history of amphipods is derived from the accounts given by Sexton and Mathews (1913) and Sexton (1924). Sexton (1924) has stated: "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." This is found very true in the case *Grandidierella bonnieri* Stebbing, for some stages of this species, referred to by Chilton (1921) as adult stages, were later pointed out by Barnard (1935) to be altogether of a different species. This shows that the confusion as to the proper determination of species has arisen from lack of our knowledge about the life-histories of the animals. This work was started in the hope that it might throw some light on such problems.

MATERIAL AND METHODS

*Grandidierella bonnieri* Stebbing, is a very common species, found in large numbers attached to green algae at Cooum and Adyar rivers which are shut off from the sea by a bar of sand for nearly eight months during the year. With the onset of the rainy season the bar is opened and there is a great lowering of the salinity of the water. These amphipods are able to withstand sudden changes of concentration as well as temperature of the medium. They are reared in the laboratory without any difficulty and fresh supplies are obtainable easily from the neighbourhood.

A feature of difference between the natural habitat and surroundings and that offered in the laboratory must be mentioned. In the natural surroundings, the amphipods when they moult, seek the shelter of floating weeds, debris and stones. In the laboratory, to facilitate observation, the organisms

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were left in clear glass bowls with water, in bright light with a few strands of algae intended more as food rather than as shelter. It is therefore probable that some of the observations on the incidence and duration of moulting may not be the same as what is obtained in nature. It was found much easier to study the moults rather than the live animals which soon after taken in a slide for microscopical examination gave violent jerks and tried to move away from the transmitted light. The study of the successive moulting stages was hence carried out by examining the moults, of the same individual as far as possible.

A collection of this species Grandidierella bonnieri was made on 6th December 1948 from the river Cooum and brought to the laboratory along with some algae. Three females with brood pouches in a fully developed condition were picked out by means of a pipette and each one was put in a separate finger bowl containing brackish water. One or two small strands of algae were also put in each bowl as food for the animals. These finger bowls were marked A, B and C.

**Mating and Bearing Eggs**

The female in finger bowl A when examined on the morning of 7th December 1948 was found to have its brood pouch empty having liberated twenty young ones which were moving in the bowl. The young ones were removed from the bowl. The next day the animal had moulted and the moult was taken out and a male was also added on to the same container and when observed on the morning of 9th December it was found that the brood pouch contained a fresh batch of eggs. The mating most probably must have occurred at night and as such was not observed. Daily observations continued as usual and on 14th December 16 young ones were liberated from the brood pouch. Three young ones, B1, B2 and B3 were taken and put in 3 different bowls for the study of the moulting stages (Table I).

The female in B also when examined on the morning of 7th December was found to have its brood pouch empty and 17 young ones were found moving in the bowl. The female was transferred to another bowl along with a male. The next day the female was found to have moulted and on 10th December it was found carrying a fresh batch of eggs in the brood pouch. 23 young ones were seen swimming about in the bowl on the 15th December. Three young ones, B1, B2 and B3 were taken and put in 3 different bowls for the study of the moulting stages (Table I).

On 8th December the female in bowl C was found to have liberated 14 young ones. They were all removed and a male was added and on 10th
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her projecting mouth parts and by lateral compression with her gnathopods and peraeopods. The young ones at times crawl on the back of the pouch, but the first beat of the pleopods forwards drives them back safely into the pouch.

**The Process of Moulting**

In *Grandidierella bonnieri* the process of moulting has been observed only in two instances. The head portion with the antennae and mouth organs attached is pulled off first. Then the body with the peraeopod is drawn out of the posterior part, and lastly the gnathopods are pulled out. In a good moult the skin comes off whole except for the break through which the body is pulled out. The side plate attached to the first joint of each peraeopod slips down its internal face. A semicircular flap of skin opens at the place of insertion of the second joint and six free tapering joints are easily drawn out through this opening, leaving the old cuticle intact. In difficult moults the old skin of the gnathopods is torn to pieces. Often the mouth organs are used in the act of stripping it off. Since the skin on the gills is much thinner and flimsier than on any other part of the body, it always gets crumpled or torn in moulting. This happens also in the brood plates in the immature female.

In this connection the difficulties in getting a series of moults from the same animal may be mentioned. Quite a large number of moults were taken but none of the series was complete. The amount of chitin deposited during the animals life varies with individuals, some moults therefore being fairly thick and easily sloughed off, while others thin in texture crumbling off when cast. The chief difficulty also lies in the fact that the animals eat their moults soon after they are cast. In most cases it was observed that the moulting took place at night, and if it had happened early in the night, there was very little chance of obtaining the moult.

**Developmental Stages**

The young animal soon after it is hatched out resembles the parents in having all the appendages present. The differences in the proportion of the various parts of the body is however, very marked.

*Stage 1* (Fig. 1).—The characters distinguishing this stage are: primary flagellum of antenna 1, 4 jointed; gnathopod 1, palm not well differentiated and uropod 3, with 2 spines at the distal end of the ramus.

The head is fairly large when compared to the body and is as long as the first 2 segments combined. Antenna 1, the peduncle slightly longer than the flagellum; flagellum 4 jointed; first joint of the peduncle stout, shorter
than the second with 2 or 3 small setae on the lower side; second joint with one small seta each at the distal end on either side; third joint shorter than the second with 2 or 3 setae at its distal end on either side and also a small accessory flagellum rather very small with 2 setae at its tip; first joint of the flagellum devoid of any setae at its distal end; second joint with one spine on either side at its distal end; third and fourth with a sensory filament each at its lower side in addition to the 2 or 3 setae present at the distal ends of the joints. At the tip of the fourth joint there arises another very short joint (which is not counted in any of these cases) with 2 or 3 setae. Antenna 2, flagellum shorter than the peduncle; flagellum 3 jointed; joints provided with small setae both on the inner and outer margins and the last joint of the flagellum with 4 to 6 short setae at its tip. Gnathopod 1, fifth joint as long as sixth; fifth joint with 4 spines on the inner margin and 2 at the distal end of the outer margin; sixth joint with 3 spines on the inner side and a single long spine at the middle of the joint at the outer side and 3 small setae at the distal end; seventh joint curved, inner side with 2 or 3 small spines. Gnathopod 2, fifth joint nearly as long as sixth; broader towards the base, 4–5 setae at the inner distal end 2 spines at the outer distal end; sixth joint, palm rather defined by a sharp angle and also provided with one spine.
at the defining angle; seventh joint curved reaching up to the end of the palm; inner side serrated. Peraeopods 1 and 2 almost the same; joints provided with one seta each at either side at the distal end of each joint; seventh joint long nearly as long as sixth. Uropod 1, peduncle slightly longer than the rami; rami provided with 4–6 small spines at its distal end; peduncle with a small spine at the upper distal end; both the rami devoid of any setae or spines on inner and outer margins. Uropod 2, very much like uropod 1, but much smaller. Uropod 3, uniramous; peduncle shorter than the ramus; rami with 2 spines one small and the other long; peduncle as well as the rami devoid of spines on both the margins. Length of the animal from front of the head to the end of uropods is about 1 mm.

Stage 2 (Fig. 2).—Head longer than the first two segments combined. Antenna 1, peduncle shorter than the flagellum; first joint of the peduncle with 2 small spines at the distal end; flagellum 6 jointed with sensory filaments on fifth and sixth joints. Antenna 2, flagellum short, 3 jointed; one curved spine at the distal end of second joint and two at the distal end of the third joint. Gnathopod 1, fifth joint smaller than sixth; lower margin with 6 spines; sixth joint with 5 spines at the inner margin. Gnathopod 2, fifth joint with lower margin slightly bulged out at the middle; sixth joint with 2 small spines at the middle of the outer margin and 3 spines at the outer distal end. Uropod 1, peduncle with a single spine at the distal end; rami equal; devoid of spines on the inner and outer margins; one long and 3 short spines at the tip. Uropod 2, like uropod 1, but smaller. Uropod 3, rami with a single long spine at the tip and a smaller one just behind it. Length of the animal is about 1.5 mm.

Stage 3 (Fig. 3).—Antenna 1, first joint of the peduncle with 2 small spines at the distal end; flagellum 8 jointed with sensory filaments on fifth, seventh and eighth joints. Gnathopod 1, second and third joints with a single spine each at the lower distal end; fifth joint slightly smaller than the sixth, lower margin with 4 or 5 setae and one or two spines; sixth joint with a stout spine at the middle of the lower margin. Gnathopod 2, second joint with 2 setae on the upper margin and one small spine at the inner distal end; fifth and sixth joints subequal; palm differentiated with a small spine at the angle; sixth joint widening distally. Peraeopods 1 and 2 alike; second joint with 3 small spines each on the upper and lower margins; fourth joint with a long slender spine at the anterior distal end and a short one at the middle; fifth joint with 2 small and 1 long spine at the lower margin; sixth joint slightly longer than fifth; seventh as long as the preceding joint. Uropod 1, peduncle longer than the rami, peduncle with 3 spines on the upper margin and one on the lower margin. Both inner and outer ramus with a single spine each
on the upper margin at the middle and the usual terminal spines at the end. Uropod 2, outer ramus without any spines on the margins and with 3 spines at the distal end. Inner ramus with a small spine on the upper margin. Uropod 3, both the margins of the ramus, devoid of any spines; distal end with 3 or 4 spines. Length of the animal is about 2 mm.

Stage 4 (Fig. 4).—Head nearly as long as the first 2 segments combined. Antenna 1, first joint of the flagellum with 5 spines at the lower margin; 4 or 5 small setae at the middle and 2–4 setae at the upper side; accessory flagellum rudimentary with 2 small setae at its tip; flagellum 10 jointed. Antenna 2, peduncle much longer than the flagellum; fourth and fifth joints of the peduncle subequal; flagellum smaller than the penultimate joint. Gnathopod 1, fifth joint longer than sixth; fifth with 7–8 spines at the lower margins; outer margin with one or two distal spines; sixth joint lower margin slightly bulged at the middle with a well-developed single spine and 4–6 small setae. Gnathodpod 2, fifth joint with 7–8 spines at the inner margin; sixth joint palm curved slightly with a few setae at the margins. Peropods 1 and 2 alike, second joint rather long; third joint slightly longer than fifth with the outer distal end produced; seventh joint tapering and slightly longer than the preceding joints. Uropod 1, peduncle with 2 spines on the upper side on both inner and outer margins; outer ramus with 2 spines on the outer margin and inner ramus with 1 spine on the inner margin. Uropod 2, with one spine each on the upper margins of each ramus. Uropod 3, with a single spine on the upper margin, at the middle and 4 spines at the distal end. Length of the animal is about 3–4 mm.

Stage 5 (Fig. 5).—The sexual differentiation is noticed at this stage. Antenna 1, the lower side of first joint of the peduncle with a single spine at the distal end and 2 short spines behind it; two more lateral spines on the lower side; second joint of the peduncle with 4–6 small setae on the lower side and 6–8 setae on the upper; flagellum 12 jointed with sensory filaments on seventh, ninth, eleventh and twelfth joints. Antenna 2, penultimate and antepenultimate joints of the flagellum subequal; flagellum 3 jointed. Gnathopod 1, second joint devoid of any spines on the upper margin; lower with a small spine at the distal end; fifth with 2 spines on the distal end on the upper margin and 14–16 slender spines on the inner margin. Gnathodpod 2, with 7 small spines on the upper margin and 4 on the lower margin; fifth joint with 15–20 slender spines on the inner margin. Uropod 1, peduncle with 2 small spines on the lower margin and a row of 4 spines on the upper; outer ramus with 2 spines on the upper margin and the inner with 3; both the rami devoid of spines on the lower margins. Uropod 2, peduncle with a small spine at the distal end on the upper side. Both the rami with 2 spines
each on the upper margins. Uropod 3, with a single spine on the upper margin and a group of about 5 spines at the distal end. Length of the animal is about 4-5 mm.

Stage 6 (Fig. 6).—The head shorter than the first two segments combined. Antenna 1 with a single spine rather thin pointing forwards on the lower side of the first joint of the peduncle at the distal end; behind it are 2 stout spines; three more lateral spines on the lower side; second joint of the peduncle rather elongated, with about 10 setae on the lower side and about 16 on the upper side; flagellum 15 jointed with sensory filaments on joints, tenth, twelfth, fourteenth and fifteenth. Antenna 2, peduncle much elongated; flagellum shorter than the last joint of the peduncle; flagellum 4 jointed; second and third joints with a curved spine at the middle of the segments. Gnathopod 1, fifth joint elongated; inner distal end rounded; lower margin with a large number of spines; sixth joint lower margin convex, a big spine at the middle and a smaller one behind. Gnathopod 2, fifth joint slightly convex at the lower side with a number of spines; sixth joint elongated, widening distally, both margins provided with
spines and setae. Uropod 1, peduncle longer than rami; peduncle with 6 short spines on the upper margin and 3 on the lower; outer ramus and inner ramus each with 4 spines on the upper margins; both rami provided with the usual terminal spines. Uropod 2, smaller than uropod 1; outer ramus shorter than the inner; outer with 3 lateral spines on the upper side and 4 spines on the outer side in addition to the usual terminal spines. Uropod 3, peduncle short; rami with 2 spines at the upper margin and 5 spines at the distal end. Length of the animal is about 5–6 mm.

Stage 7 (Fig. 7).—Antenna 1, peduncle shorter than flagellum; first joint of the peduncle with 6–8 small setae on the upper margin and with 2 or 3 slender spines at the anterior distal end; third joint of the peduncle about \( \frac{1}{2} \) the length of the second; flagellum 17 jointed with sensory filaments on tenth, twelfth, fourteenth, sixteenth and seventeenth joints. Antenna 2, third joint of the peduncle with a pair of stout spines on the upper margin and 2 or 3 lateral spines on the lower margin; penultimate and antepenultimate joints of the peduncle are subequal; flagellum 4 jointed, joints provided with setae and curved spines. Gnathopod 1, fifth joint with a large number of spines on the lower side; 4 or 5 thin spines on the upper margin and about 3–4 at the anterior distal end; sixth joint with one stout spine at the middle on the lower margin and 3 in a row just behind it; seventh joint well developed and serrated in the inner margin. Gnathopod 2, fifth joint with a large number of slender spines on the lower margin and 3 or 4 on the upper margin; sixth joint with a row of 3 small spines on the lower margin and a slightly longer one at the posterior distal end. Peraeopods 1 and 2 alike; sixth joint longer and tapering towards the distal end; seventh joint about as long as the sixth. Uropod 1, peduncle with 5 spines on the upper margin and 3 on the lower margin; outer ramus and inner ramus with 4 spines each on the upper margins. Uropod 2, like uropod 1, but much smaller. Uropod 3, ramus with 4–5 spines on the margin. Length of the animal is about 6–7 mm.

Stage 8 (Fig. 8).—Antenna 1, first joint of the peduncle more than half as long as second, lower side with 3 lateral spines and a small thin one at the distal end and 2 pairs of spines just behind it. Flagellum 19 jointed with sensory filaments on tenth, twelfth, fourteenth, sixteenth, eighteenth and nineteenth joints. Antenna 2, peduncle rather very well developed; flagellum subequal to the last joint of the peduncle; flagellum 5 jointed. Gnathopod 1, fifth joint longer than the sixth; lower margin with a large number of spines; sixth joint with 4 stout blunt spines at the lower end; seventh joint well developed, curved. Gnathopod 2, fifth joint with a few spines on the
upper margin, lower margin with numerous long spines; sixth joint with 7 short lateral spines on the inner margin; palm differentiated. Pereopod 1 and 2 alike, fifth joint with 4 long and 3 short spines on the lower margin and a long and a short spine at the outer distal end and 3 short spines on the margin; sixth joint long and elongate. Uropod 1, peduncle with 6 lateral spines on the outer margin; outer ramus with 5 spines on the outer margin and 3 spines on the inner margin in addition to the usual terminal spines. Inner ramus with 2 spines on the outer margin and 5 spines on the inner margin. Uropod 2, rami unequal; outer ramus with 4 spines on the outer margin, inner ramus with 3 spines on the outer side and 5 on the inner side besides the usual terminal spines (4–5). Uropod 3, with 6 lateral spines, on the upper margin. Length of the animal is about 6–7 mm.

**Differentiation of Features of Antenna 1 during the Growth**

In antenna 1, the process of growth could be demonstrated better than in any other appendage. This process has been illustrated here with the aid of the drawings (Figs. 9–16), made from the successive moult stages from a female amphipod. The successive growth stages of the same animal were examined, throughout, to avoid the slight individual variation in the rate of development of different animals.

The young one, extruded from the brood pouch on 14th December 1948 had a peduncle which was 3 jointed and a short flagellum which was 4 jointed. The peduncle remained unchanged throughout its life, except for the fact that it increased in length and a few more spines and setae were added on to it. The accessory flagellum was so small and was rather rudimentary with a few setae at the tip of it. The first joint of the flagellum was devoid of any setae at its distal end and the second joint with one spine on either side at its distal end. The third and fourth joints were provided with a sensory filament each at its lower side in addition to the 2 or 3 setae present at the distal ends of the joints. At the tip of the fourth joint there appeared another very short joint, which was not counted, with 2 or 3 setae at its tip. The first moult took place on 17th December 1948 and the antenna 1 of the moult was examined and found identical with the description given above. In two drys time (19th December) 2 more joints were added on to it and the sensory filaments were seen on fifth, seventh and eighth joints (counting it from the base of the flagellum). In the fourth moult stage (24th December), it was found to have the antenna 1 to be 10 jointed, but no more sensory filaments were added. This was followed by the fifth moult stage (28th December) where the antenna 1 was found to have 13 joints. In this stage the sensory filaments were found on segments 8, 10, 12 and 13. It passed on
Figs. 9–16. Differentiation of features of antenna I during the growth from birth to maturity. Only the sensory filaments are shown, the setae being omitted.
Life-history of Amphipod Grandidierella bonnieri Stebbing

to the sixth stage (5th January) and the antenna 1 in this stage was found to have 15 joints and had five sensory filaments on segments sixth, tenth, twelfth, fourteenth and fifteenth. In another six days time (11th January), it reached the seventh moult stage. In this stage the antenna 1 was found to have 17 joints. It reached the last and the final stage in another 7 days time (18th January) wherein the antenna 1 was found to have 19 joints. The sensory filaments were found on segments tenth, twelfth, fourteenth, sixteenth, eighteenth and nineteenth. In all these cases the sensory filaments were present in the penultimate and antepenultimate joints. The preceding joint was devoid of a sensory filament and the one below had a sensory one. Thus it could be seen that the growth takes place not at the distal end but at the proximal end of the flagellum.

SUMMARY

The life-history of a brackish water amphipod, Grandidierella bonnieri Stebbing, is described from the successive moult stages. The actual process of moulting is described. The changes that takes place in antenna 1, the gnathopods, the uropods and the peraeopods, which have a very high taxonomic value, have been described in detail. The differentiation of features of antenna 1 during the growth has been illustrated and fully described.

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