VIII. *On the Feeding Mechanism of the* Branchiopoda.

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With an Appendix on *The Mouth Parts of the* Branchiopoda.

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(*Communicated by* E. W. MACBRIDE, *F.R.S.*)

(Received June 16, 1932.)

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INTRODUCTION.

In LANKESTER's classical essay (1881) on the appendages of Apus he defines the proximal endite of the trunk limb as a " gnathobase," stating that " it is a jaw process " and " clearly has the function of assisting, by means of apposition to its fellow of the opposite side, in seizing and moving particles which may be introduced into the mouth " (p. 348). Since then, various authors have discussed the homologies of the parts of the Branchiopod phyllopodium always referring to the basal endite as the gnathobase, and further, those workers who have investigated the feeding mechanisms of the Branchiopoda, LUNDBLAD (1920), NAUMANN (1921) STORCH (1924), and ERIKSSON (1928), have taken for granted that the basal endites move the food particles towards the mouth.

[Published June 20, 1933.

In 1927 Miss Manton and I pointed out that in the Anostraca the proximal setæ of the basal endite are covered over medially by setæ from the limb in front so that they cannot transport food towards the mouth and certainly do not work in apposition to their fellows on the opposite side.

The word "gnathobase" was obviously coined as a functional and not merely a topographical term, and it thus seemed to me desirable that a functional study should be made of this structure in the Branchiopoda. I have therefore made a comparative study of the feeding mechanisms of the more generalised Branchiopods with special reference to the significance of the basal endite.

The conclusions of this paper are largely based on the observations on *Chirocephalus diaphanus*, a general description of which I have already published (1928 *a*), and it is perhaps unnecessary to add that, as the Anostraca form such an homogeneous group, the observations made on *Chirocephalus* can be taken safely as applying to all other Anostraca.

The deductions I have drawn from the study of this form are essential for the proper understanding of my views on other Branchiopoda, and so the first part of this paper is a detailed account of my present views on the feeding of the Anostraca.

Chirocephalus is a large form, easily obtained, and since it is without a carapace, it lends itself to direct observation better than other Branchiopoda. I found it possible to demonstrate the feeding currents experimentally by injecting a coloured fluid between successive limbs (1928, p. 811). In other forms such experiments are difficult, if not impossible. The limbs are closely covered by a carapace, and any attempt to interfere with this upsets the rhythmical movements of the limbs, or, more often, causes them to stop moving. The removal of the carapace is impossible as it is a vascular structure attached to the body in the region of the pericardium. Any attempt to cut it off allows so much blood to escape that the animal collapses almost at once, presumably because the limbs are extremely thin-walled, and, for their movement, require a certain blood pressure.

Again, it is not possible to use the iron saccharate feeding-method which has been used with success in filtratory Malacostraca. In these forms the filter limb is the maxilla, and here the food, and also iron saccharate, is deposited before it is scraped off by other limbs into the mouth. It is therefore possible to identify the filtered residue in sections of specially preserved material. Now, in the Branchiopoda usually all the trunk limbs are filters, but at the same time, they are self-cleaners, that is, they are always provided with some mechanism whereby they scrape off the residue as fast as it is deposited. Obviously then, any attempt to test the filtratory power of a limb by causing it to filter off iron saccharate will be unsuccessful.

A method often used in such a study as this is that of injecting near the living animal a suspension of carmine particles. I have used this method, but consider that it is of little use and may be misleading. Carmine particles are of various sizes, and their first effect on touching a Branchiopod limb is to adhere and clog the filters. Coloured starch grains (CANNON and MANTON, 1927, p. 220), are much better for this purpose, but here again they only demonstrate the major currents which can always be observed directly by watching the natural particles floating round the animal under observation.

With the exception of the experiment on *Chirocephalus*, and a somewhat similar experiment on *Daphnia* (p. 303), I have done nothing which may be termed experimental in the sense in which that word is now used. My method has been, when observing a living animal, to observe the major currents round it and the type of rhythmical movement of the limbs. Then I have studied the homologies and structure of the limbs, and more particularly the arrangement and movement of the parts of the limbs. From this, considering the limb as a solid object moving through an aqueous medium, I have deduced the various minor currents through and between the limbs which cannot be observed directly, but which always include those currents which lead directly to the collection of food and its transference to the mouth.

In those forms where I have been unable to study the type of limb movement, as for example, in the fossil form *Lepidocaris*, I have deduced this from the forms I have studied alive, on the principle that evolution of function is as continuous as that of structure.

I have thus, apart from the cases mentioned, avoided experimental work. Such work in connection with a subject of this type would lead at best to a mass of inferential results. I have preferred to attack the problem to a large extent theoretically and consider that this leads to more satisfactory results. The conclusions at which I have arrived are certainly inferential, but as they are based on simple mechanical principles, I maintain that the probability of their correctness is greater than those which involved the consideration of the effects of experimental conditions.

With regard to actual technique, I have used no other methods than those of fine dissection and microtome dissection as described in my paper on *Nebalia* (1927, p. 355).

I have to thank the following gentlemen for gifts of material :—

Professor J. H. ASHWORTH, F.R.S. ; L. C. BEADLE, Esq. ; Dr. W. T. CALMAN, F.R.S. ; Dr. G. S. CARTER ; Professor D. FEDOTOV ; Dr. R. GURNEY ; D. J. SCOURFIELD, Esq., I.S.O. ; and The " Discovery " Committee.

ANOSTRACA.

" *Chirocephalus* feeds on minute suspended particles that it separates from water currents produced by its trunk limbs. Water is sucked into the mid-ventral space between the limbs mainly from in front and from above, the animal normally swimming on its back. It passes out laterally between the limbs and is swept backwards in two powerful lateral swimming currents." (CANNON, 1928, p. 821 and text-figs. 1 and 2, pp. 808–9). The food particles carried by the water currents remain in the median space.

The feeding process may be divided into three main parts : (1) the production of the swimming-feeding currents ; (2) the abstraction of food particles from those currents ; and (3) the transference of the food so collected to the mouth.

Current Production.

The account of the mechanism of current production in *Chirocephalus*, which I have already published (1928 *a*, p. 808) agrees with, and extends, that of LUNDBLAD (1920, p. 36) for *Tanymastix stagnalis*.

The trunk limbs are phyllopodia, armed on the inner edge with a series of backwardly projecting endites of which the proximal is very large. On the outer edge there is a bract (gill) and a series of exites, the distal being the exopodite, which similarly project backwards, fig. 3. The distal portion of the limb, the endopodite, is hinged on the basal portion and is also directed posteriorly (fig. 4 and also CANNON, 1928 *a*, text-fig. 3, p. 810). Thus between any two successive limbs there is a space, the " inter-limb space," of which the front and hind walls are formed by the corms of the two limbs. The endites, exites and endopodite of the anterior of the two limbs form respectively the inner wall, the outer wall and the roof of the space, while its floor is formed by the body wall.

At the end of the backstroke the limbs slope backwards at an acute angle to the axis of the body, fig. 1, limb 5, close against each other, so that the inter-limb spaces are at their minimum volume. As any two successive limbs move forwards their inter-limb space is enlarged and water is sucked in, fig. 1, limbs 6–10. This suction causes the endopodites and exites of the front limb to flap back against the hinder limb and act as valves, closing the lateral and upper entrance to the inter-limb space. The only entrance, during this phase, is thus from the median space through the fringe of long filter setæ on the edge of the endites, fig. 2A. Therefore water passes from the mid-ventral space into the inter-limb spaces and, to replace it, water is drawn from the surrounding regions.

As the limbs commence their backstroke they extend as rigid plates, thus opening up free exits from the inter-limb spaces, and water from the latter is thrown out backwards, fig. 1, limbs 1–5, producing the swimming stream.

A constant supply of water is thus being drawn from the surrounding regions into the median space between the two rows of limbs, sucked into the lateral inter-limb spaces and then thrown out backwards. Put in other words, the median space is being continually emptied and, to replace this, water is drawn from the surrounding region. Its only entrance is between the distal ends of the limbs, but the median space extends right up to the ventral body wall at the proximal end of the limbs. Now suction occurs throughout this length, and in fact, as I shall show later (p. 275), is at a maximum near the body wall. Hence, of the water entering the median space, some will be sucked into the inter-limb spaces at once near the distal ends of the limbs fig. 1, inter-limb space 10–11, but the bulk will pass towards the ventral body wall before being sucked away, fig. 1, inter-limb space 6–7. There is thus in the median space a definite movement of water towards the mid-ventral line. Also, since the region of suction is continually passing forwards (see below), the water, on entering the median space will be subjected to two forces, one drawing it towards the body and the other anteriorly, and it will pass, on the whole, obliquely forwards to the mid-ventral line. This is what NAUMANN described as the "vertikale Transportströme."

The trunk limbs exhibit a marked metachronial rhythm in their oscillations, text-fig. 1. "Every limb commences its backstroke just before the limb immediately anterior to it, or the oscillation phase of any limb is slightly in advance of the limb immediately preceding it." (CANNON, 1928 *a*, p. 816.) The phase difference between any pair of successive limbs I quoted (1928, p. 808) for *Chirocephalus* as about one-sixth of a complete oscillation.*

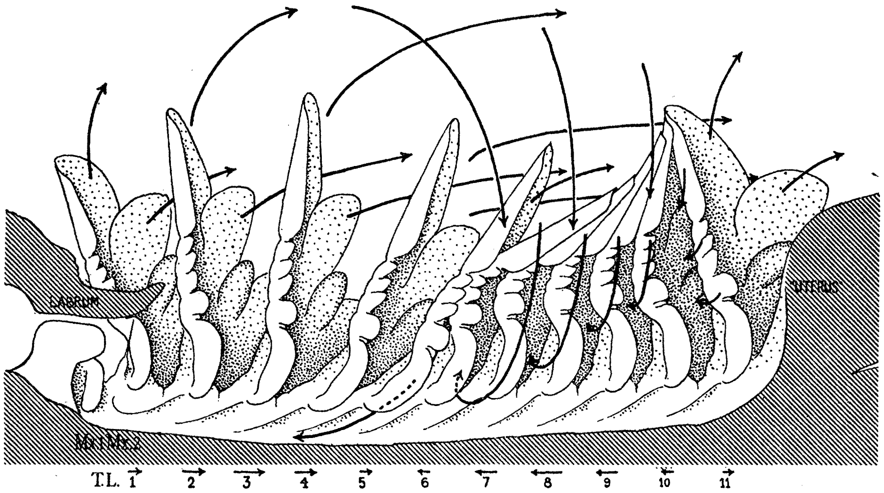

FIG. 1.—Outline sketch of left half of an Anostracan (based on *Branchinella australiensis*) to show swimming and feeding currents. The arrows below the trunk limbs indicate their relative movements. All setæ have been omitted.†

The important result of this rhythm is that the limbs appear to move in waves which pass forwards and that, between the crests of two waves there must always be two successive limbs, one of which, the anterior, is still moving backwards, while the other, the posterior, has just commenced to move forwards, fig. 1, limbs 5 and 6. The latter flexes at about the level of its second to third endites, its endopodite and exites flapping

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* STORCH (1929, p. 58) disputes this on the strength of a photograph of a living *Branchipus stagnalis* (Plate IV) which shows a phase difference between successive limbs of $\frac{1}{22}$ of a complete oscillation. It would indeed be strange if all Anostraca moved their limbs with an identical rhythm. I have recently reared two other fresh water Anostraca, one from South Africa and one from South America, and found that they showed a rhythm of limb movements precisely the same as that of *Chirocephalus*. In all three forms the limbs moved in such a way that there always appeared to be two waves of limb movement passing forwards. Hence, I cannot agree with STORCH when he states that to the naked eye no difference can be seen between the speed of limb movement—he presumably means rhythm—of *Chirocephalus* and *Branchipus*.

† Throughout this paper whole limbs and gnathobases have been figured as if the animal were on its back, with its head to the left.

back against the limb behind. Moving forward it comes into contact with the limb in front and this results in the proximal part of the inter-limb space being nearly obliterated so that the water in it is suddenly expelled.

To understand this process the shape of the inter-limb space and of the median food groove must be considered. In most Anostraca this is extremely difficult to study. It can be made out from sections, but allowance has to be made for the distortion that results from embedding such thin walled limbs. I have, however, one specimen of the large Anostracan *Branchinella australiensis* which I found possible to dissect so that the walls of the food groove and the shape of the inter-limb space could be studied under a binocular microscope. In this form the endites and the inner portion of the endopodite are very sharply marked off from the rest of the limb, and owing to its size, it is possible to cut off this series and so open up to view the inter-limb space, fig. 2, A. From this dissection and from a series of frontal sections of beautifully preserved *Branchinecta gaini*, fig. 3, it is clear that the main corm is thicker from back to front just median to its main axis than it is towards the endite series. Considering now the two limbs which are moving towards each other, it will be these thickened parts which will come into contact first. This will effectively divide the inter-limb space into two, a lateral chamber open to the exterior between the exites and a medial chamber, fig. 3. This medial chamber is of critical importance in the feeding mechanism. Until the two approaching limbs are in contact it is merely the medial part of the inter-limb space, but directly they touch, it is converted into a chamber with only one exit. Anteriorly, posteriorly and laterally the two limbs form its walls, fig. 1, inter-limb space 5 and 6, while medially, it is closed by the proximal endites of the anterior of the two limbs. Distally it is closed by the points of flexure of the limbs coming into contact, and it can be seen from fig. 2, A, that the anterior edge of the posterior limb at the level of the second endite fits into a depression in the hinder wall of the front limb. Proximally, however, it has an exit opening into a gutter in the wall of the food groove which slopes towards the mouth, fig. 2, A.

The food-groove is a mid-ventral channel about as deep as wide and approximately square in section, fig. 4, A, the limbs being attached to the body on the tops of its walls. The proximal setæ from the basal endites project towards the floor of the groove close against its walls, fig. 2, B. From the proximal limit of the basal endite, in *Branchinella australiensis*, there is a marked ridge which slopes forwards towards the floor of the groove and becomes merged into its walls. In this way, each pair of successive ridges marks off a subsidiary groove—the exit groove—leading directly from the inter-limb space into the food groove, text-fig. 1 and 2, A. I first found this system of ridges in *Branchinecta gaini* and confirmed it in transverse sections. I then found the same system in *Chirocephalus diaphanus*, but in neither of these forms is it so obvious as in the form I have figured.

Considering again the two successive limbs which are approaching each other. Directly they touch, the median chamber of the inter-limb space is formed. For a short time afterwards they will continue to approach each other. Now the chitin of the limbs is excessively thin, especially that of the corm, so that the limbs will press on each other with the result that the median chamber of the inter-limb space will be squeezed. Its contained water will be forced out *via* its only exit, the exit groove, and so forwards along the food groove. Thus along the latter there will occur a series of spurts of water passing forwards from those inter-limb spaces in which the anterior limb is finishing its backstroke and the posterior has just commenced to move forwards. But during the rhythmical movement of the limbs as a whole, this set of conditions continually passes forwards and hence the spurts in the food groove will also pass from behind forwards.

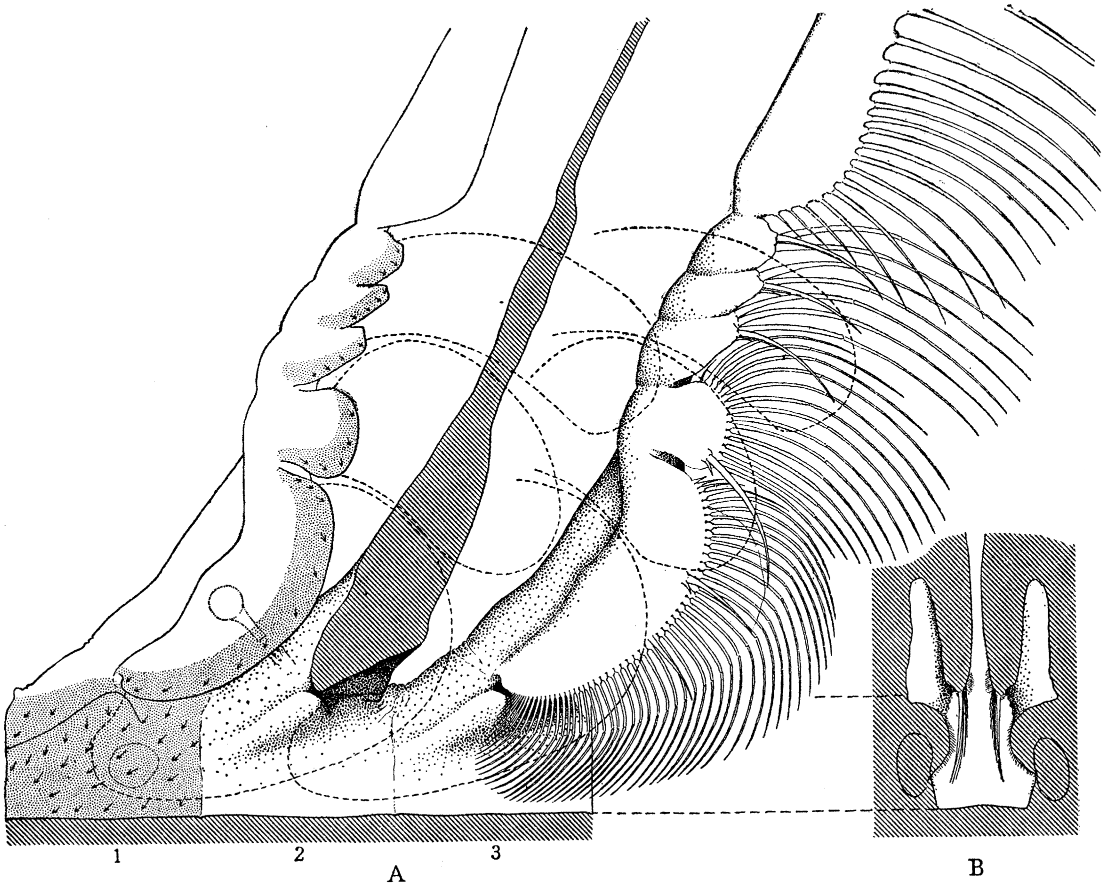

Fig. 2.—A. Median view of three consecutive trunk limbs of *Branchinella australiensis*. Only the median parts of the limbs are shown. Limb 1.—The setæ are omitted. The setules on the edges of the endites and on the wall of the food groove are indicated by machine stippling, their direction being shown by arrows. Limb 2.—The endites have been cut away to show the shape of the inter-limb space behind and its exit channel. Limb 3.—The endites complete with setæ are figured.

The extent of the setæ on limbs 1 and 2 is indicated by dotted lines.

B.—Posterior view of lower edge of basal endites of a pair of trunk limbs of *Branchinecta gaini*, showing the exit grooves opening into the food groove between the filter setæ and the main axis of the limb.

The presence of this food stream has been briefly described by LUNDBLAD and others, but they describe it merely as an anteriorly directed food current, while I demonstrated (1928, *a*, p. 821) it conclusively by experiment. I injected an aqueous solution of methyl blue* so as to fill completely one of the inter-limb spaces of a captive *Chirocephalus*, and was then able to demonstrate that at the *end* of the backstroke of the limb forming the anterior wall of this inter-limb, a spurt of the blue solution was forced forwards along the food groove. I also found that, unless the inter-limb space was completely filled " down to the base of the limb, this forward current cannot be seen " (1928, *a*, p. 811). It is obvious from what I have already described that, unless this is done, the median chamber will not be filled with the dye, and hence no coloured anterior current will be visible.

Abstraction of Food Particles from Water Currents.

All workers agree that the long setæ on the edges of the basal endites of the trunk limbs constitute the retaining wall that keeps the food particles in the median space and further, that the food so retained is transferred to the mid-ventral food groove *en route* for the mouth, but there are different views as to how this takes place.

In my paper on *Chirocephalus*, I suggested (1928, *a*, p. 815) that the food particles were sucked on to the basal endite setæ on the fore stroke (suction phase) of the limb " and immediately blown off again by the more powerful backstroke and at once sucked into the food groove " by the vertical streams. Hence I could not admit that the endites were filtratory in the ordinary sense of the word. As I had previously argued, such a mechanism can accurately be called " filtratory " only if the particles are deposited as a residue on the setæ and remain to be scraped off by some other structure. Such a scouring structure LUNDBLAD (1920, p. 43) finds in EKMAN's setæ, and the strip of setules on the median face of the endites close to the bases of the filter setæ, fig. 2, A, limb 1.

My present view is a combination of LUNDBLAD's explanation and the views I have previously put forward. For the sake of simplicity, I shall refer to the limbs and the endites as filtratory and indicate, where necessary, those processes in which true filtration occurs and those in which food particles are merely retained in certain definite channels.

Throughout this paper I use the term " filtratory setæ." By this I mean a very definite type of seta. Such setæ are always arranged approximately parallel to each other in a plane. Each seta is armed on either side with a row of regularly and closely spaced fine setules. These project towards and often slightly beyond one surface of the plate formed by the filtratory setæ and are of such a length that they touch the setules from the neighbouring seta. The filter setæ thus form a mat with all the setules

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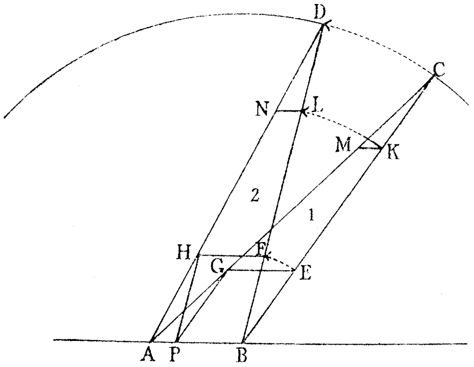
* STORCH (1929, p. 54) misquotes me as having stated that I used methylene blue. This is important for anyone attempting to repeat my experiment, as this dye is useless for the purpose, since it diffuses so rapidly that the water in the dish is coloured blue before the pipette can be brought near the animal. Methyl blue, on the other hand, is much less soluble and several injections can be made before the water becomes so blue as to obscure the experiment.

slightly projecting from one surface. If water is caused to pass from this surface, through the setæ, then any particle carried on the water stream is retained by the setules. On the other hand, water passing in the opposite direction would not be filtered. This type of seta has been found to occur wherever minute suspended matter is retained by a limb, *e.g.*, the 3rd and 4th trunk limb of *Daphnia* (STORCH 1924) on the maxilla of *Hemimysis*, and *Paranaspides* (CANNON and MANTON 1927 and 1929) on the maxilla of *Calanus* and *Diaptomus* (CANNON 1928 *b*) on the trunk limb of *Nebalia* (CANNON 1927), and on the maxillule of *Asterope* (CANNON, *unpublished*).

Consider now any two successive limbs moving forwards. Owing to the metachronial rhythm of the limb movement, the hinder limb commences moving forwards just before the front. The latter thus appears at first, to be pushed forwards, the two limbs touching at the point of flexure of the hind limb. The inter-limb space is consequently triangular in section, the base being the body wall and the apex the point where the two limbs touch. As the limbs move forwards, this triangle, commencing at an acute angle to the body swings towards the normal to the body axis. It can easily be shown geometrically that a triangle swinging in this way through the arc of a circle increases in area at a maximum rate towards its base.* But the area of this triangle is a measure of the volume of the inter-limb space. Hence, during the first part of the forward stroke there will be maximum increase in volume and thus maximum suction at the bases of the limbs close against the body wall, fig. 1, inter-limb space 6–7.

* The lines BC and AC represent the proximal portions of two successive limbs, AB representing the ventral body wall between their bases, and C being the point where they touch during the first part of the forward stroke. The triangle ACB clearly represents a parasagittal section of the inter-limb spaces, and hence is a measure, of the volume of this space. As the limbs swing forward they come to occupy the position BD and AD, the triangle ADB now representing the volume of the inter-limb space. As triangle ADB has the same base as triangle ACB but has a greater height, it is greater in area than triangle ACB. Hence there has been an increase in the total volume of the inter-limb space as the limbs swing forward.



Draw a line MK parallel to the base AB and another line GE also parallel to AB and the same distance above AB as MK is below C. This cuts off two imaginary slices of the inter-limb space of equal thickness, one at its apex and the other against the body wall, the volume of these slices being represented by triangle CMK and the quadrangle AGEB respectively. As the limbs swing forward the triangle CMK changes to the triangle DNL, and the quadrangle AGEB to AHFB. From G and H, draw lines parallel to CB and DB respectively. These will meet on the line AB at P. Now the increase in the slice AGEB as the limbs swing forward from position 1 to position 2 = the increase in the triangle APG + the increase in the parallelogram BEGP. But triangle APG is congruent with triangle CMK which represents the volume of the imaginary slice at the apex of the inter-limb space. That is, the increase in the slice near the body wall (AGEB) = the increase in the slice at the apex (CMK) plus something more, or, in other words, the increase in volume is greater at the base than at the apex.

Towards the end of the forward movement, the hinder limb will straighten out and swing backwards, so that the limbs will cease touching at the point of flexure but will be in contact at the tips of the endopodites, fig. 1, inter-limb space 10–11. This will open up the whole of the inter-limb space and suction will be general throughout its length during the short interval until the anterior of the two limbs also commences its backstroke.

It is this fact of maximum suction towards the bases of the limbs during the greater part of their forward stroke that is responsible for the marked movement of water between the two rows of limbs in a vertical direction towards the mid-ventral groove—NAUMANN'S "vertikale Transportströme." There would, of course, be a movement of this type if the limbs swung forwards parallel to each other and suction were consequently uniform throughout their length. The maximum suction at the base of the limbs simply enhances this water movement.

The filter setæ on the edge of the second endite and on the distal part of the basal endite project posteriorly but, as the edge of the latter curves forwards at the base of the limb, so the setæ come to point first downwards into the food groove and then slightly anteriorly, fig. 2, A. The setæ can thus be divided into two groups: the distal, which project backwards and lie close against the median face of the basal endites of the limb behind, and the proximal, which project towards the body close against the walls of the food groove, fig. 2, B. Now, considering again the forward movement of any two successive limbs. At the commencement, the hinder limb will touch the front limb at about the level of the second endite. The distal group of setæ of the front limb will thus lie close against, and, in fact, will be sucked against the flat surface of the basal endite of the hinder of the two limbs. They cannot, therefore, act to any great extent as filters, but on the other hand, the proximal group of setæ project downwards across an open space and merely separate the median space from the lateral inter-limb space, fig. 2, A. There is nothing to hinder water passing through them and hence it is through them that maximum filtration must occur.

At the commencement of the suction phase, therefore, filtration is confined to a small area at the base of the limbs; all the water entering the inter-limb space must

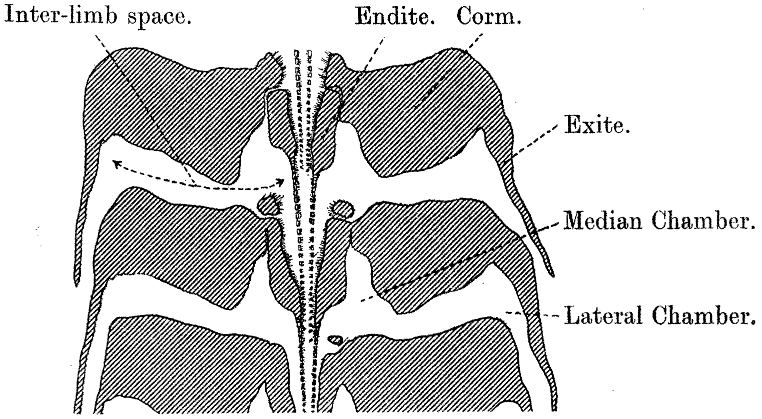


FIG. 3.—Frontal section through three consecutive pairs of trunk limbs of *Branchinecta gaini* to show the shape of the inter-limb spaces and the valvular arrangement of the exite series.

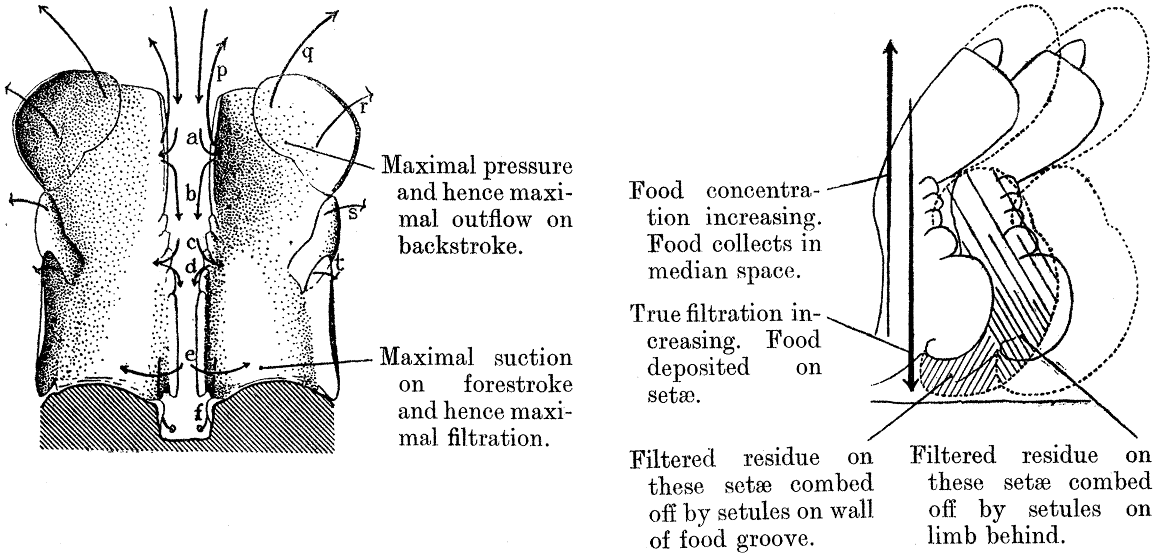
pass through the small zone of proximal setæ, fig. 1, inter-limb space 6–7, and hence the filtration must be powerful.

Later, as the limbs continue to move forward, the basal endite of the front limb will slide anteriorly from its position close against the limb behind and allow its distal setæ to act as filters, so that filtration is spread over a greater area and on the whole will not be so powerful as in the preceding phase, fig. 1, inter-limb space 7–8, 8–9, 9–10. However, as I have already explained, even in this phase filtration will be most effective nearest to the body wall.

Finally, at the end of the forestroke the hinder of the two limbs straightens out and commences to move backwards allowing the whole of the setæ of the front limb to act as filters, and filtration is general along the length of the inner edge of the limb, fig. 1, inter-limb space 10–11.

Thus, from a consideration of the shape and movement of the endites, it is clear that effective filtration diminishes as the forestroke proceeds, and the arrangement of the setæ on the endites also supports this. At the commencement, the basal parts only of the proximal setæ are exposed to the suction current into the inter-limb chamber. These are robust and beset with typical filtratory setules on their median faces and any particle sucked against them must be firmly held. As the forestroke proceeds, the whole of the filtratory setæ become exposed to the suction current, that is, their tips as well as their basal portions, but the tips, feathered with setules, are extremely thin, and, while they will retain the larger particles, they will not offer such resistance to the passage of water as the basal parts, so that the greater part of the water will pass through them, together with the finer particles and filtration will not be so effective.

On the backstroke of the limbs, the water from the inter-limb spaces is thrown out posteriorly, figs. 1 and 4, A. The pressure which produces this result will depend



Maximal pressure and hence maximal outflow on backstroke.

Maximal suction on forestroke and hence maximal filtration.

Food concentration increasing. Food collects in median space.

True filtration increasing. Food deposited on setæ.

Filtered residue on these setæ combed off by setules on wall of food groove.

Filtered residue on these setæ combed off by setules on limb behind.

Fig. 4.—A. Posterior view of a pair of trunk limbs of an Anostracan to show swimming and feeding currents. B.—Outline sketch of median view of two consecutive trunk limbs of an Anostracan to show region of food concentration and of true filtration. Both figures based on *Branchinecta gaini*.

on the rate of movement of the surfaces of the limb pressing backwards against the water. Clearly, the distal parts of the limbs are moving fastest, the proximal hardly at all, and hence the greatest pressure will be produced towards the tips of the limbs, while the pressure at the base will scarcely increase, fig. 4, A, *p* . . . *t*.

This pressure will act in all directions and so, in addition to producing the swimming current, will tend to force water from the inter-limb spaces back into the median space through the filter setæ, fig. 4, A, *b* and *d*. As a result, where the pressure is sufficiently great, that is, on the distal parts of the limbs, the particles retained on the filter setæ during the forestroke will be blown off again into the median space, while on the proximal setæ there will be no such tendency and the filtered residue will remain to be removed in some other way, fig. 4, B.

To summarise, the metachronial rhythm of the limbs together with the arrangement and constitution of the basal endites and their setæ result in maximum filtration taking place at the base of the limbs. Moreover, this is true filtration ; the food particles being collected on the setæ of the basal endites, while on the more distal parts of the limb the setæ act as retaining setæ, concentrating the food particles in the median space, but not filtering them in the ordinary sense of the word.

Transport of Food to Mouth.

In considering the transport of food to the mouth, obviously distinction must be made between the two portions of collected food ; the food concentrated towards the tips of the limbs is free in the food stream, that filtered at the bases is held on the setæ so that different mechanisms must come into play.

The concentrated food, of course, may be thrown out into the swimming stream on the next backstroke, fig. 4, A, *p*. If, however, it succeeds in remaining in the median space, it will be sucked towards the body, fig. 4, A, *b*, by the next suction phase which is moving forward. It will then again be sucked on to the filter setæ, fig. 4, A, *c*, but this time more proximally and will now become part of the filtered residue.

The filtered residue is combed off the setæ by an armature of setules which have been described by SPANGENBERG (1875, p. 22) and later by LUNDBLAD (1920, p. 46). Close against the bases of the filter setæ of all the endites on their median faces there occurs a strip of exceedingly fine setules which together form a feltwork. The setules are too fine and numerous to figure without exaggeration and so, in fig. 2, A, I have indicated their distribution by stippling, the arrows marking the direction in which they point. In addition, the walls of the food groove are covered with a similar feltwork and these have been figured in the same way. A maximum concentration is to be found along the lower edge of the basal endite and in the wall of the exit groove leading from the inter-limb space.

Consider now any two successive limbs loaded with their filtered residue which are commencing to move forwards. The suction thus produced will cause the setæ of the front limb to be sucked, distally, against the endites of the limb behind and, proximally, against the wall of the food groove, so that the setules will project between the filtratory setæ. As a result, during the forward movement, the filtered residue of the front limb will be combed off by the setules behind.

Of this filtered residue, that combed off more distally will be either swept free into the median space, or will be blown there on the next backstroke, fig. 4, A, *d*. It will then be sucked towards the food groove as the next succeeding suction phase passes forward to meet it and again sucked on to the filter setæ, fig. 4, A, *e*, but this time on to the proximal setæ of the basal endite.

In the last two paragraphs, in order to make the processes clear, I have considered the filtration and scouring of the setæ as two separate processes, but it must be remembered that they go on simultaneously. That is, as a limb moves forward the residue which remains on it from its previous forward movement is scraped off and at the same time, a new deposit is sucked on to it.

The residue on the most proximal setæ forms the ultimate food. It is combed off by the setules, not on the limb behind, but those arming the exit groove leading from the inter-limb space, and is now blown forwards to the mouth along the food groove by the anteriorly directed oral currents, figs. 1 and 4, A, *f*.

"The food particles . . . . are arrested in the maxillary region by the entangling secretion of the labral glands, and the viscid mass pushed into the mouth by the maxillules" (CANNON, 1928, p. 813). In addition, it is probable that the food is mixed with a mucus-like secretion as soon as it is combed on to the walls of the food groove. In the middle of each exit groove there is a conspicuous bun-shaped gland, fig. 2, A and B, which most likely exudes a viscid material on the collected mass. Also, on the outer face of the basal endite near its proximal margin, there is a pear-shaped gland with a conspicuous opening, fig. 2, A; whatever secretion this produces passes into the entrance of the exit groove and so must be squirted into the food groove with each spurt of the oral stream.*

In the remaining forms dealt with in this paper, the trunk limbs differ from those of the Anostraca in that the proximal endite is a "gnathobase." But the arrangement of the exite series as a whole, and of the endopodites of the limbs is the same as in this group.

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* In a text-book on 'The Invertebrata' (BORRADAILE, EASTHAM, POTTS and SAUNDERS, 1932, p. 321), BORRADAILE publishes a figure of *Chirocephalus* swimming on its back "Partly after CANNON." The anterior food current is figured as a continuous stream, which it is not. In my original figure it was shown as in fig. 1 of this paper. In his description of the feeding mechanism he states (p. 320) that on the forestroke of the limbs the exite series and large distal endites are pressed back by the resistance of the water till they reach the limb behind. While the viscous resistance of the water must assist this process its main cause is the suction in the inter-limb space. He also states (p. 320) that "particles which are retained in the median gully fall (the animal being on its back) dorsalwards into a median food groove of the ventral surface." The particles on which *Chirocephalus* feeds are floating particles, that is, they either do not fall at all or else fall extremely slowly. Also *Chirocephalus* often gathers food from the bottom while swimming dorsal side uppermost.

The method of limb movement I have observed in the Cladocera—*Sida, Moina,* and various other Daphnids,—the Conchostracan *Estheria* and the Notostracan *Lepidurus,* and in each case it is the same as in the *Chirocephalus diaphanus.* I have previously suggested that this type of limb movement is an inheritance from the Annelid ancestor of the Crustacea (CANNON, 1928, p. 816), and so I deduce that it is characteristic of the whole of the Branchiopoda.

From what I have already written in regard to *Chirocephalus,* I have tried to establish that the water currents are a necessary result of the type of limb movement and the valvular apparatus of the limbs. In other words, if the limbs move in the way I have described, then, since their exite series and endopodites are arranged as valves, the water currents are a necessary result. No other currents than those described are possible.

LIPOSTRACA.

The Devonian Crustacean, *Lepidocaris rhyniensis,* described in such splendid detail by SCOURFIELD (1926), resembles a minute Anostracan, but its trunk limbs are of two very distinct types. The posterior are flat biramous paddles without any marked endites and with the exopodite placed terminally side by side with the endopodite. The first three to five limbs, however, can be considered as phyllopodia comparable with those of modern Branchiopoda. In the first three, at least, the exopodite has swung round laterally, the endopodite now forming the termination of the limb. No bracts have been described, but these may not have been preserved in fossil form or special branchiæ may have been unnecessary in such a minute form. Also there are no exites proximal to the exopodites, but there are large scales projecting downwards from the side of the body at the bases of the limbs. BORRADAILE (1927, p. 17), has suggested that these may represent proepipodites, but I consider that, together with the exopodites, they complete the lateral valve to the inter-limb space. The endopodite slopes slightly backwards on to the limb behind and so forms the ventral valve. The valvular arrangement thus occurs on these anterior limbs similar to that of *Chirocephalus,* and on the assumption that they moved in a similar manner to those of the latter, it must be deduced that they functioned in a similar manner.

I think it doubtful whether the posterior limbs moved in the same rhythm as the anterior. *Lepidocaris* possessed large swimming antennæ—like a Daphnid—and it is possible that these were the sole swimming organs when the animal was feeding. The position of the posterior limbs in all the specimens I have seen is the same. They slope forwards in a bunch and show such a marked resemblance to the thoracic limbs of *Calanus* that it seems to me at least possible that they were used in the same manner. That is, in ordinary slow swimming they were kept motionless and were only used for sudden very rapid movements. The first five pairs of trunk limbs, at least, each carried a well-defined gnathobase which represents the first of a series of six endites. All except the gnathobase are armed with a double row of setæ, both rows pointing postero-medially, the hinder row extending backwards more than the front. In this way the anterior row of the second limb project through the posterior row of the first limb, a condition similar to that of *Estheria* and *Apus*. These setæ are described by SCOURFIELD, but are longer than those shown in his figures. They are long tapering setæ, armed irregularly on the more distal parts with setules. Between the two rows on each endite there is a very strong spine or claw.

Each gnathobase is quadrangular, slightly narrower distally than towards the body. The posterior edge carries setæ which are in series with the posterior row on the more distal endites, fig. 5, limb 1, and on the lower edge these are continued forwards to the anterior edge of the gnathobase as a single row so closely set that the setæ touch at their bases, fig. 5, limb 2. They project towards the body and then curve forwards towards the mouth, and since they arise from the most proximal endite and extend towards the body, there must have been a space to accommodate them. That is, there must have been a mid-ventral groove between the two rows of limbs—at least in the region of the first five pairs—and the limbs must have arisen from the tops of the walls of this groove. Again I find these gnathobasic setæ considerably longer than those shown in SCOURFIELD's figures.

FIG. 5.—Oblique frontal view of the mouth parts and anterior trunk limbs of *Lepidocaris rhyniensis*. The chip of chert has been ground down and the ground surface is indicated by stippling. The mouth is at the bottom left-hand corner. The unground chip was discovered by Mr. D. J. SCOURFIELD.*

On the median face of the gnathobase on the lower margin there is a well-marked

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* The pieces of chert referred to were found in the "further search for animal remains in the Rhynie Chert" for which a grant was made by the Royal Society from the Government Grant Fund.

ridge which bears a powerful claw posteriorly, fig. 5, limb 1. The ridge is of considerable thickness as can be seen from the drawing of a fortunate chip which shows the gnathobase as viewed from the body wall, fig. 6. The claws point definitely posteriorly. Fig. 7 shows a chip sent to me by Mr. SCOURFIELD, in which nine of the ten gnathobases are present, and it can be seen that the claws all point backwards.

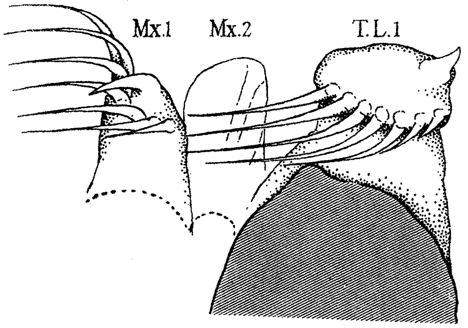

FIG. 6.—Maxillule, maxilla and gnathobase of first trunk limb of *Lepidocaris rhyniensis* viewed from ventral surface of the body to show the claw-bearing ridge on the gnathobase.

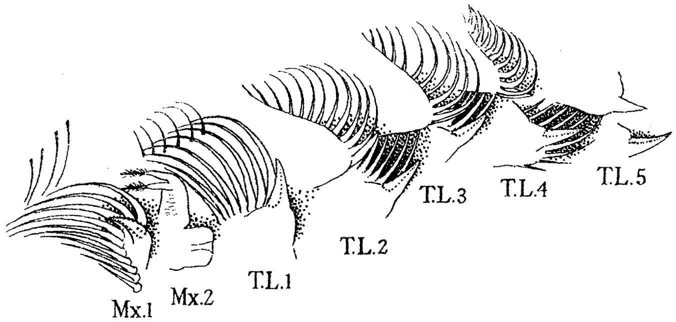

FIG. 7.—Oblique frontal view of the gnathobases of *Lepidocaris rhyniensis*. This figure and fig. 5 show the complete maxilla of *Lepidocaris*. See appendix p. 348.

The whole of the median face of the gnathobase is covered with closely set setules (SCOURFIELD, 1926, p. 166).

The structure of the gnathobase of *Lepidocaris* is of great importance as it represents a constitution from which the gnathobases of all other adult Branchiopoda, with the exception of the Notostraca, can be directly derived. In support of this derivation, I have figured a comparison of the larval gnathobase of *Estheria* with those of a young and an adult *Lepidocaris*, fig. 8. The gnathobase of an adult *Estheria* is exceedingly complex, fig. 22, but in the larval form it passes through stages which closely resemble those of *Lepidocaris*. In fact, the only real difference is that the gnathobase of *Estheria* has two claws instead of one. However, the fact that there is only one claw in *Lepidocaris* is, I think, of little significance. From a study of the adult gnathobases of other Branchiopoda, especially those of the Cladocera I think the important fact is that there is a ridge capable of bearing claws or spines, at least on its posterior part.

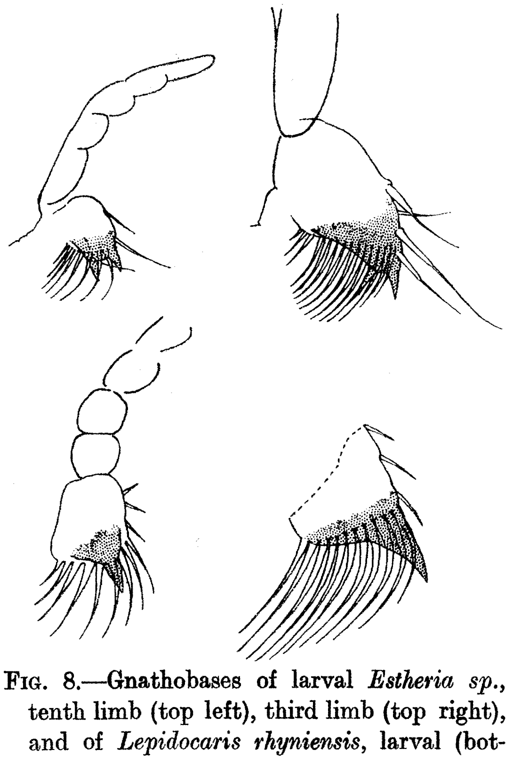

FIG. 8.—Gnathobases of larval *Estheria sp.*, tenth limb (top left), third limb (top right), and of *Lepidocaris rhyniensis*, larval (bottom left) and adult (bottom right).

With regard to the probable functioning of the gnathobases of *Lepidocaris*, it will be more convenient to return to this in the discussion after the feeding mechanism of *Sida* has been described.

CLADOCERA.

In this order I have dealt only with the sub-order Calyptomera and omit any reference to the aberrant Gymnomera such as *Leptodora*, *Evadne* and *Podon*. The Calyptomera are divided into two tribes, the Ctenopoda and the Anomopoda. Of the former I have studied *Sida cristallina* alive, and preparations of various other forms, while among the Anomopoda I have studied *Daphnia* and *Simocephalus* alive besides the primitive Daphniid *Moina* and preparations of others.

CTENOPODA.

The feeding mechanism of *Sida* has been studied recently by STORCH (1929), using an elaborate high speed cinematograph. His photographs show that the type of limb movement is the same as that which I have described for *Chirocephalus* (1928, *a*) and have outlined further in the present paper. The limbs of *Sida*, however, move comparatively slowly and it is possible to analyse the type of movement directly.*

The details of the limbs cannot be made out with exactness in the living animal either directly or by photographs, as, like all the Calyptomera, they are enveloped in a carapace. Also the lower parts of the limbs project into the deep food groove on either side of which are the ventral body muscles and the gonads. Hence, in side view, these obscure the gnathobases and it is difficult to make out any detail in this most important position.

The detailed structure of the limbs of *Sida*, as far as I am aware, has never yet been properly figured. The figures used by STORCH (1929) are those published by BEHNING (1912) in a purely systematic account of the limbs of the Branchiopoda, and are drawings on a very small scale of the limbs after they have been removed from the body and flattened under a cover slip. In fig. 9 I have drawn the more median parts of an undisturbed third trunk limb of *Sida* as seen from the median plane, while fig. 10 is an outline drawing of a sagittal half of *Sida*, in which all the setæ have been omitted to show the relationship of the valvular exopodite and bract to the rest of the limb. This diagram was obtained by first drawing a preparation of an undisturbed sagittal half. Outlines of the limbs were then re-arranged in accordance with the data supplied by STORCH (1929) of his photograph No. 69 in his fig. 5 (p. 23).

The first trunk limbs differ from the succeeding four pairs in various details, but chiefly in the gnathobase which I shall describe later (p. 286). The second to fifth limbs are closely similar but diminish in size posteriorly. This reduction in size,

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* STORCH (1929, fig. 5, p. 23) gives a table of data referring to a strip of his film. The photographs on either side of his No. 68 show a speed of limb movement of 600 beats per minute, those about No. 83 a speed of 540, while in the text, p. 22, he several times quotes a speed of 450.

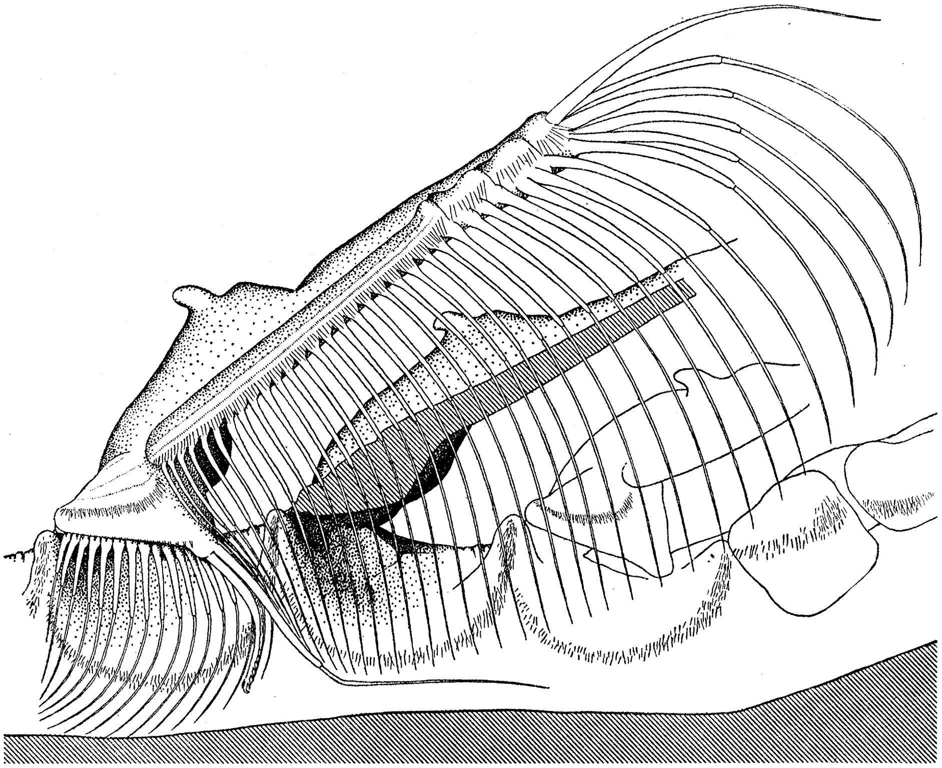


Fig. 9.—Median view of third to sixth limb of *Sida crystallina*. Only the median parts of the limbs are shown. The setules on the endites and food groove wall are figured individually. Limb 3.—The endites and gnathobase complete with setæ are figured. Limb 4.—The endites and gnathobase have been omitted to show the shape of the inter-limb space behind and its exit channel. Limbs 5 and 6.—The setæ are omitted.

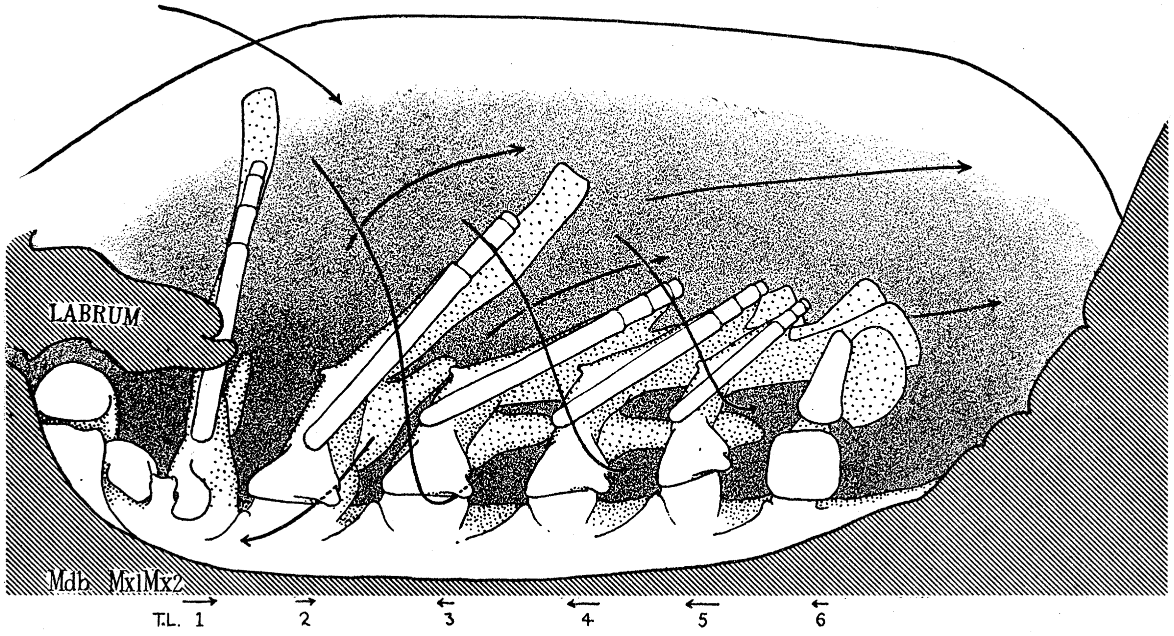


Fig. 10.—Outline sketch of left half of *Sida crystallina* to show swimming and feeding currents. The arrows below the trunk limbs indicate their relative movements. All setæ have been omitted.

however, does not affect the gnathobase, which is as large on the fifth limb as on the second.

In these four limbs the gnathobase is a triangular plate hanging down into the mid-ventral groove flat against its walls. The base of the triangle is parallel to the floor of the groove and the apex is merged into the attachment of the gnathobase to the limb. On the lateral face of the gnathobase, that is, towards the limb, the lower edge bears a row of perfect filter setæ. The anterior of these are shorter than the rest and point directly towards the body. The more posterior curve forwards towards the mouth. Each seta is beset on either side with an extremely fine set of setules pointing obliquely towards the median plane. The row of setæ must therefore offer an efficient filtratory surface to water passing from the median space into the inter-limb space. On the median face of the gnathobase along the lower edge there is a well-defined but small ridge which extends posteriorly to a conspicuous prominence from which arise two long setæ. The anterior is a powerful claw which projects in a curve towards the body and then turns towards the median plane, its distal half being serrated with very short lateral claws. The posterior seta slopes backwards to the floor of the mid-ventral groove at an angle of about 45° and then, tapering, runs along the floor as far as the gnathobase next but one behind. This distal thinner portion is armed with stout setules which slope away from the body, set comparatively far apart in two rows, a median and a lateral. Commencing at the anterior end of the claw-bearing ridge and extending backwards is a row of very short, stout spines which project medianly and towards the body. These spines occur on the ridge anteriorly, but posteriorly they arise from points just above it; they stop short at the claw-bearing prominence. In addition, the median face of the gnathobase is armed with several rows of minute setules which converge towards the second endite, fig. 9.

The distal part of the limb shows a very large second endite, a third, a fourth, and a fifth which are small and diminish somewhat distally, and beyond this the endite series is obscure. The second to fifth form a straight line, the divisions between them being indicated by minute folds in the chitin. From the study of preparations I do not think there is any movement between the endites. In the oscillation of the limbs the series must move as one rigid structure. STORCH's photographs, I think, support this view, although the endites cannot be made out with any certainty.

From the edge of the endites a row of filter setæ project backwards and slope towards the body. These are beset with filtratory setules but not so closely as the filtratory setæ of the gnathobase. They are so long that the more proximal reach to the floor of the mid-ventral groove, completely covering the gnathobase of the limb behind, while those situated about the middle of the length of the limb reach so far as to overlap the endite series of the limb but one behind. All the setæ on the second, third and fourth endites are in one parasagittal plane, and the more distal curve over so as to form a hood covering the corresponding setæ of the shorter limb behind.

Along the edge of the endites close against the bases of the filter setæ, there is a row of setules approximately in alignment with the setæ when viewed from the median aspect but projecting obliquely towards the median plane. They are thus comb setules projecting through the filter setæ of the limb in front. They are longer than the spines in the corresponding position on the gnathobase but are not so stout. Close behind this is another row which are smaller and more closely set, and behind them is a third row even smaller.

The first trunk limb, apart from the different gnathobase, differs in its arrangement of comb setules. These have dwindled to a few irregularly scattered setules, but beyond this, there is a row of peculiar setæ or spines which curve postero-medially. They are arranged in groups of four at the base of the second endite, diminishing to two at the other end, and then isolated spines on the more distal endites. In addition, towards the upper end of the second endite, there is a single isolated seta.

The sixth trunk limb differs markedly from the others. Its gnathobase consists of a large squarish setose lobe which projects close against the corresponding structure on the other side. That this is actually the gnathobase can be seen in a very young *Sida* where it is in alignment with the more anterior gnathobases and is approximately of the same shape. It does not, however, carry filter setæ, but is well armed with a row of comb setules, fig. 9. The endites in place of filter setæ, carry a few extremely thick soft setæ armed on either side with a flat plate of fine setules and project postero-medially.

Comparing the trunk limb of *Sida* with that of the Anostraca it is clear that the second and more distal endites function in the same manner as those of *Chirocephalus* forming a wall of setæ which retain the food particles in the space between the limb rows. Considering only these endites on the forward stroke of the limbs, fig. 10, limbs 3–6, particles carried on the water and sucked into the inter-limb spaces will be filtered off by the filter setæ. On the backstroke, fig. 10, limbs 1 and 2, the particles so retained on the more distal setæ will be blown off again into the middle space. Particles not dislodged in this way, that is, the residue carried on the more proximal setæ, and any stray particles remaining adherent to the more distal setæ will be combed off by the armature of comb setules. For the setæ distal to about the middle point of the second endite, the corresponding comb setules occur on the second and following endites of the limb behind. For the setæ of the proximal half of the second endite the comb setules are represented by the row of stout setules on the claw ridge of the gnathobase behind. That this is the method of functioning of these setules is supported by the fact that on the first trunk limb, which is, of course, not overlapped by filter setæ, the comb setules have practically disappeared (see above, para. 2). The comb setules for the fifth trunk limb occur as a row of stout setules on the gnathobase of the sixth limb and as a mat of finer setules which extends up the endite lobe.

The food particles having been retained from the water-currents in this manner will be sucked towards the mid-ventral groove. Here again, as in *Chirocephalus,* is the region where true filtration occurs and where food particles are ultimately deposited before being transferred to the mouth. Now this is the region occupied by the gnathobase, and I have already described that the setæ it bears, far from being stout setæ for pushing food forward or for acting as jaws, are typical filtratory setæ (see above, p. 285). They occupy a position on the limb functionally analogous to the most proximal setæ of the endites of *Chirocephalus* which I have shown form the real filtratory portion of the limb, and I therefore maintain that in *Sida* the gnathobase functions in the same manner as a true filtratory organ.

I have previously argued that if it is maintained that an organ is a true filter, then at the same time it must be demonstrated that there is a mechanism for scouring the residue off the filter. In *Sida* such an apparatus occurs and shows a remarkably close adaptation to the filter itself. As in *Chirocephalus*, there is a well-marked ridge in the wall of the mid-ventral groove commencing at a prominence at the base of the limb, which curves anteriorly towards the body and merges into the wall. Running in a semicircle from one prominence to the next behind, there is a strip of comb setules. These setules span *exactly* that area that must be covered by the gnathobase in its movements backwards and forwards. They project in between the filtratory setules of the gnathobase and point approximately along their length.

This exact correspondence between the setules and the overlying gnathobasic setæ in itself is sufficient evidence on which to label the former comb setules, but there is additional evidence to be obtained from the sixth limb. Here there are no filter setæ but there is an armature of setules which I have already described. These I maintain comb the particles off the filter setæ of the distal endites of the fifth limb. Now they are continuous forwards with the semicircles of setules corresponding to the gnathobases, fig. 9, and if they function as comb setules on the sixth limb, it is safe to deduce that the same series acts in a similar manner further forwards.

From what I have described so far, the functioning of the limb is closely similar to that of *Chirocephalus*. Food is concentrated in the median space by the more distal filter setæ, but that these are not the ultimate filters is indicated by the fact that they are comparatively wide apart, and further that the setules do not completely span the gaps between them. The food particles so concentrated are sucked towards the mid-ventral groove and finally on to the filter setæ of the gnathobase. From this position they are combed off by the comb setules on the walls of the food groove on the next forward movement of the limb, and are finally blown forwards by the spurts of water from the inter-limb spaces at the end of the next backstroke. The anteriorly directed exit grooves from the inter-limb spaces which I have described in Anostraca are here very well defined by the ridges running from the base of each limb, fig. 9. I thus maintain that there is a forwardly directed current in the food groove produced in exactly the same way as by *Chirocephalus*.

The function of the two long posterior setæ on the claw-bearing ridge of the gnathobase is, I think, clear in the case of the posterior, but to understand this the movements of the limb as a whole must be considered. On the anterior edge of the first five limbs, there is a marked knob of thickened chitin, fig. 9. This is not very prominent on the first but extremely clear on the others. It is the point of attachment of the main muscles which pull the limb forwards. From a region just distal to this knob, muscles run to the exopodite, but there is very little musculature in the endite series. This arrangement, I believe, indicates that in the forward movement of the limb the basal portion up to the anterior knob swings through an arc of a circle, the more distal parts being dragged forward, and it is on this assumption that I have drawn fig. 10. That is, the distal part of the endite series flaps down on the limb behind. This will cause the tips of the filter setæ of these endites to approach the floor of the food groove. On the other hand, as the limb moves forwards, the gnathobase pivots upwards about its anterior corner so that its hinder corner is raised away from the floor of the food groove and from this point arises the long posterior seta of the claw ridge. Thus, at the forward position of the limb, fig. 10, limb 5, this long seta is in a position lying across the median face of the filter setæ of the second endite. From the posterior corner of the gnathobase is a muscle which runs horizontally through the limb to attach to the antero-lateral cuticle. If this muscle contracts while the limb is in its forward position, it must press the long posterior seta against the filter setæ on the second endite. Now when the limb commences its backstroke it immediately straightens out, and so drags the filter setæ across the long posterior seta. This must result in any food particles which have been deposited on these setæ being swept off. During the backstroke the long posterior seta is beaten down into the food groove and carries with it any food particles it has gathered. Here they are blown forwards by the anteriorly directed food stream.

The function of the peculiar anterior claw on the claw-bearing ridge is not at all clear. ERIKSSON (1928, p. 107) suggests that it acts as an obstruction to any large particle and prevents it entering the food groove. It is, however, possible that its function is to assist the muscle attached to the gnathobase in holding in the hinder part of the gnathobase when the limb is at the end of the backstroke. This is the position of the limb when the water from the inter-limb space behind it is being forced out through the exit channel. There will be high pressure in the inter-limb space, and this will press on the hinder part of the gnathobase and tend to force it medially, and if this should happen the water could escape posteriorly. Now at this instant the anterior claw of the claw-bearing ridge will be pressed down on to the floor of the food groove; its terminal portion projects directly towards the median plane, that is, it lies across the floor and its lateral serrations would thus cause it to hold firm against any lateral pressure.

The only other suggestion I can make is that, since it has a small forwards movement it may be used in pushing forwards any large particle that may be accidentally drawn into the median space so that it can be thrown out by the caudal furca. I suggest that in the Conchostraca (p. 317) a similar claw, which, however, has a much greater forwards movement, may be used in pushing forwards the compact mass of filtered and triturated food, but this cannot be so in *Sida*. The food groove of *Sida* is normally free from any solid mass of food as in the case of *Chirocephalus*.

The conclusion I have arrived at, that the gnathobase of *Sida* is the main filtratory part of the limb is, I consider, sufficiently established from the anatomy of the limb and associated structures. Even more convincing evidence can be obtained from a comparison of the trunk limbs of *Sida* with those of the related forms *Holopedium* and *Diaphanosoma.* The gnathobases of the second to fifth trunk limbs of *Holopedium gibberum* are very similar to those of *Sida*, but while in the latter the posterior corner projects directly backwards, the lower edge of the gnathobase being parallel to the floor of the food groove, in *Holopedium* the posterior corner points distinctly away from the body, the lower edge forming an angle of about 45° with the floor of the food groove, fig. 11 ; that is, the posterior corner is swinging up towards the more distal endites.

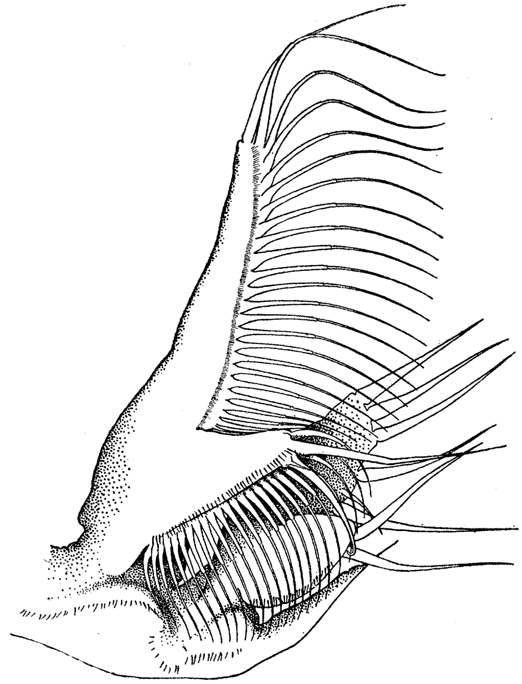


FIG. 11.—Median view of fifth and sixth trunk limbs of *Holopedium gibberum*. Only the median parts of the limbs are shown.

In *Diaphanosoma* the process which is seen commencing in *Holopedium* is almost complete. The gnathobases of the second to fifth trunk limbs have swung up so that their posterior corners nearly reach the edge of the second endite, fig. 12. In fact, in a median view of the limbs it is difficult to tell at first sight where the gnathobase ends and where the second endite begins. This point, however, is clearly marked by the claw-bearing ridge which carries the same two spines, a very long posterior one with a curved claw in front of it. The setæ of the distal endites thus form an almost unbroken series with those of the gnathobase. I do not think that any worker has denied that the distal setæ are filter setæ. That being so, it cannot be maintained that the gnathobasic setæ with which they are continuous are other than filter setæ.

The limb of *Diaphanosoma* must work in almost the same manner as the Anostracan limb. There can be very little movement of the gnathobase relative to the more distal endites. The entire limb, including the gnathobase, must move forwards as a whole. The only difference is the addition of the long posteriorly directed seta from the claw-bearing ridge which, as in *Sida*, must sweep the residue collected into the food groove where it will be blown forwards to the mouth.

This merging of the gnathobase into the distal endite series cannot be seen from limbs isolated from the body and flattened under a cover slip. Such preparations distort the limb and the posterior corner of the gnathobase is pressed away from the second endite so that apparently there is a clearly separated gnathobase.

These two forms show other interesting points which fit in with my deductions from

Sida. In *Holopedium* the comb setules on the second and more distal endites are very fine, while those on the gnathobase are much stouter. This I consider, supports my view that the true filtration occurs on the gnathobasic setæ

The gnathobase of the first trunk limb of *Holopedium* in size and shape is similar to that of the second, fig. 16, unlike *Sida* and *Diaphanosoma*, where it is much smaller and of a different shape. It is armed with a row of comb setules in the typical position. The half of this row nearest the posterior corner must serve to comb the most proximal filter setæ of the second endite of this same limb and these point in the normal direction.

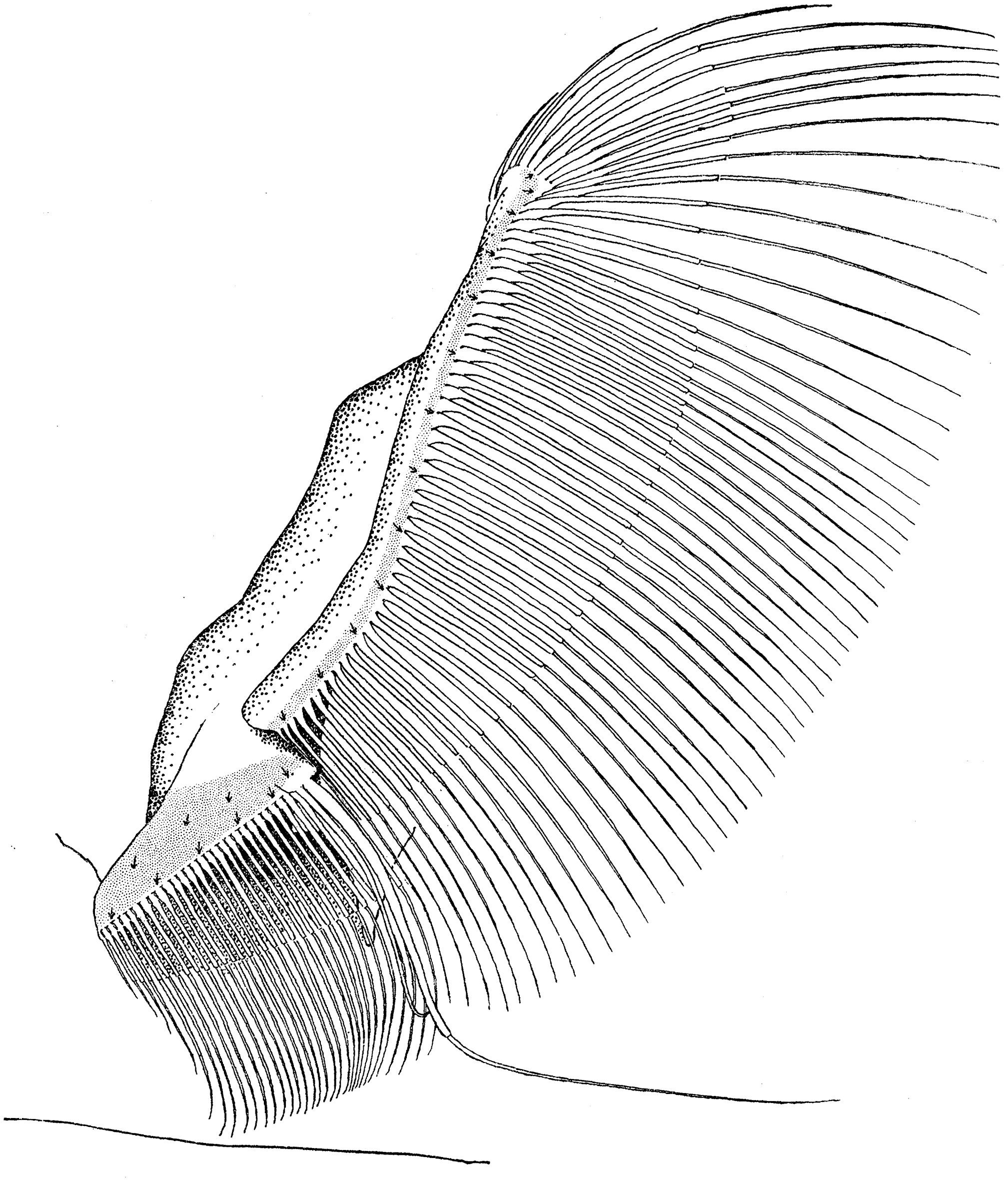


Fig. 12.—Median view of third trunk limb of *Diaphanosoma brachyurum*. Only the median parts of the limbs are shown. The setules on endites and gnathobase are indicated by machine stippling, their direction being shown by arrows.

The anterior half has no filter setæ to comb and the setules have turned forwards and fit closely against the hind wall of the maxillule, and presumably they scour this surface clean. Similarly the comb setules of the second endite are, towards the base, stout and long, and they project obliquely forwards, fig. 16. From their position they must comb the lateral surfaces of the labrum.

The sixth trunk limb, fig. 11, supports my contention that the peculiar squarish lobe occurring at the base of the corresponding limb of *Sida* is really the gnathobase. For in *Holopedium* this structure is an elongated oval mass projecting upwards from the base of the limb just as does the gnathobase of the limb in front. The comb setules extend up the inner margin of this lobe and must comb the posterior filter setæ of the fifth gnathobase, and further, the comb setules on the wall of the food groove stop short just below the first setule on the sixth gnathobase so that there is no filter seta left without its comb setules and at the same time, there are no superfluous setules.

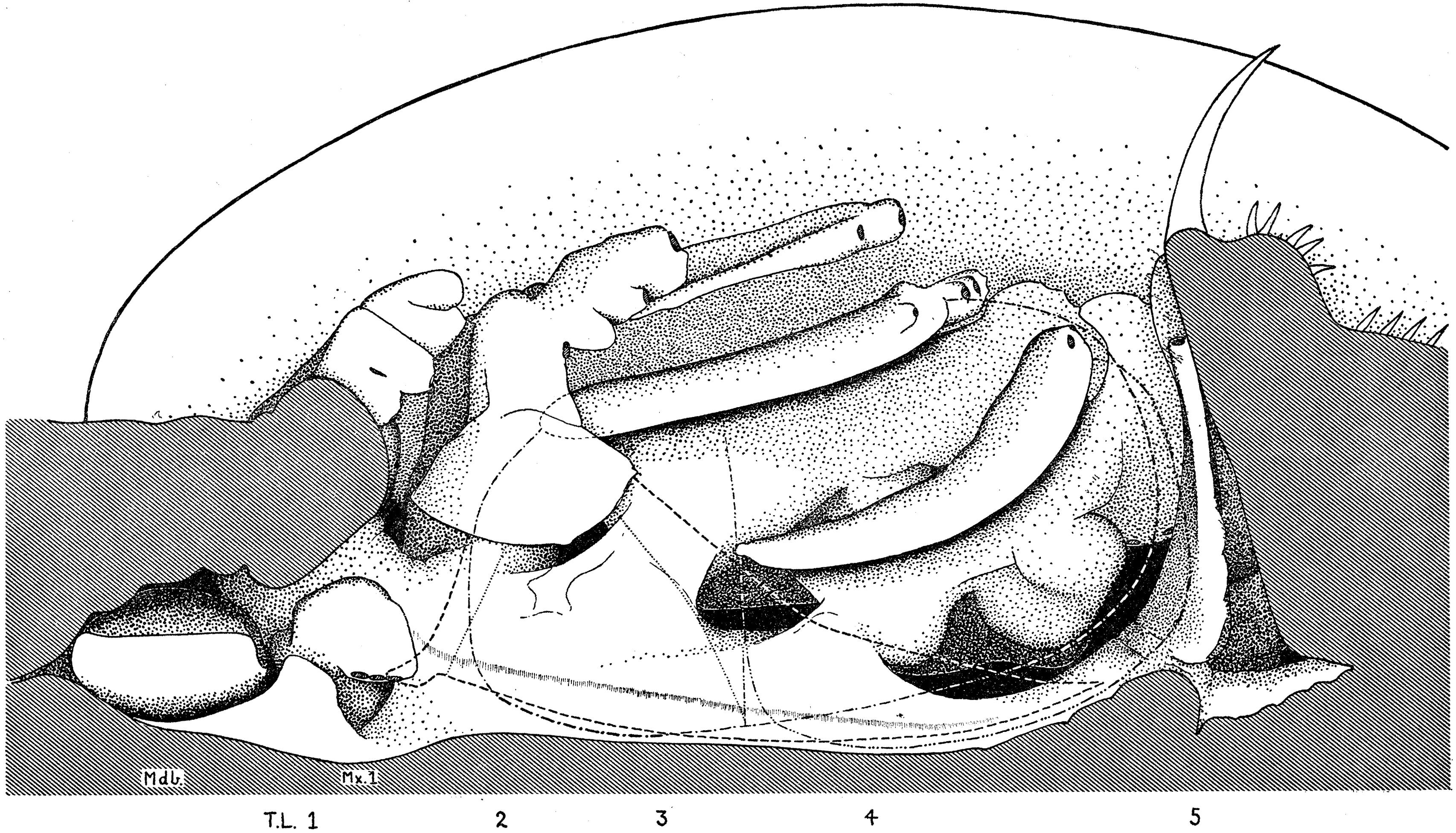
In *Diaphanosoma* comb setules occur on the endites in the same position as in *Sida*, but they are much too fine to figure individually, fig. 12. Those on the food groove wall can only be made out with an oil immersion lens; they form a more or less straight row along each wall, and such an arrangement would be expected since the gnathobases have become merged into the endite series.

I have referred to the long setæ on the gnathobases and endites of *Diaphanosoma* as "filter setæ," but I must admit that, even with an oil immersion lens and excellent illumination, I have been unable to see any lateral setules on them except for a few on the tips of each seta. I think this is undoubtedly due to their minute size. My preparations are all in glycerine and perhaps in another mounting medium they would be visible. It is extremely unlikely that a limb so similar in other respects to that of *Holopedium* should differ from it in such an important detail.

ANOMOPODA (*Daphniidæ*).

The tribe Anomopoda includes the true Daphnids of the family Daphniidæ—forms whose feeding mechanism is by far the most elaborate in the whole of the Branchiopoda. The feeding mechanism of *Daphnia* has been dealt with in great detail (STORCH, 1924), but with very unsatisfactory results, the reason for which is, I think, two-fold. Firstly, the shape of the limbs as they occur on the body and their relation to the food groove have not yet been fully studied. As far as I know, the limbs of *Daphnia* have never been figured from the median plane. STORCH (1924, fig. 12, p. 176) gives a diagram of the third and fourth trunk limbs but their attachments to the body are omitted, and as I shall show this is of critical importance. LILLJEBORG (1900) also figured the third trunk limb but the dotted line which presumably indicates the attachment to the body is incorrect. And secondly, the only attempts to establish the homologies of the parts of the limbs have led to very conflicting results.

In text-fig. 13, I have drawn a sagittal half of *Daphnia magna* in which the limbs are treated as solid objects and show the shape of the limbs and their relation to the food



— — — outline of setæ from gnathobasic lobe T.L.2.
— · — · — · — outline of filter setæ from gnathobase of T.L.3.
— ··· — ··· — outline of filter setæ from gnathobase of T.L.4.
.... anterior and posterior limit of middle group of modified filter setæ on gnathobasic lobe of T.L.2.
—— ·· —— anterior limit of modified filter setæ on gnathobase of T.L.3, which brush gnathobase of T.L.4.

Fig. 13.—Outline sketch of left half of *Daphnia magna*. All setæ have been omitted but the extent of those on the second, third and fourth trunk limbs is indicated by distinctive dotted lines.

groove. The filter setæ are omitted but their extent is indicated by dotted lines, and in addition, fig. 14 shows the complete individual limbs drawn from the same specimen.

The homologies of the first trunk limb are doubtful. It is not a valvular limb, and the exopodite, if it occurs at all, is merged into the main axis of the limb. The endite series is obscure and does not carry filter setæ but large feather paddle setæ similar to those on the distal endites of the second trunk limb, while the gnathobase has probably disappeared or dwindled and become merged into the second endite. My reasons for suggesting this are that in *Sida*, and more especially, in *Diaphanosoma*, the gnathobase of the first trunk limb is very small compared with those more posterior. In these two forms, however, the first gnathobase, although small, is modified so that in addition to its filtratory function it can push the collected food mass on to the maxillules. In the Daphniidæ, I believe, this modification arose similarly on the second gnathobase which ultimately took over this function completely and the first gnathobase disappeared. This reasoning will be more clear after the consideration of the second trunk limb.

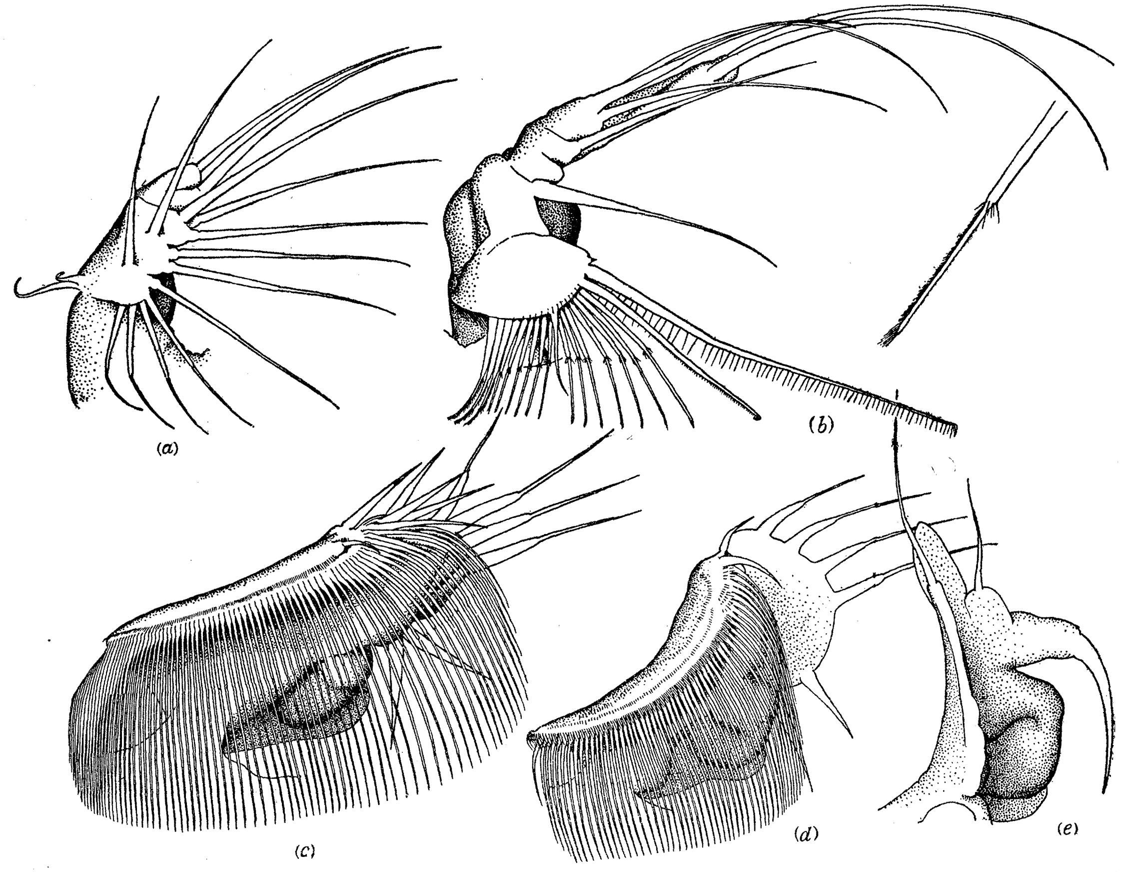


FIG. 14.—Median view of left trunk limbs of *Daphnia magna*, $a - e =$ first to fifth trunk limbs respectively. A seta of the middle group of gnathobasic lobe is shown on the right of trunk limb 2.

On the second trunk limb there is a structure which in shape and position is so like the gnathobase of *Sida* that there seems good reason to believe that it is a gnathobase. I cannot agree with BORRADAILE's suggestion (1926, p. 119) that since it arises at some distance from the body wall the true gnathobase must have disappeared. Actually, it is no further from the attachment of the limb to the body than is the gnathobase of *Sida*. It is a long way from the floor of the food groove because the latter happens to be deep at this point, but even so, the setæ which it bears on its lower edge reach to the bottom, as in all the gnathobases I have described. Also the stretching away from the body of the gnathobases can be seen in *Holopedium*, figs. 11 and 16.

STORCH (1924, p. 138 and pp. 182–188) gives a lengthy account of this part of the second trunk limb which he calls the "Maxillarfortsatz" (= Maxillärprozesz, LILLJEBORG'S and BEHNING'S). He gives a figure (1924, fig. 13, p. 183), but this is incorrect in one critical point. As he rightly describes there are at the hind end two long posteriorly directed spines, while at the anterior end there is a group of three which curve forwards to the maxillules. In between there is a row of radiating straight setæ which vary in number—thirteen in the specimen I have figured, fig. 14, *b*. The point omitted by STORCH is that at the base of this middle group on the median side, there is a minute but distinct ridge which bears a single spine about the middle of its length. This ridge at once suggested the claw-bearing ridge of *Sida* or *Lepidocaris*. That it is actually this can be seen from the form which is considered by systematists as the most primitive of the Daphniidæ, namely, *Moina*. I have studied *Moina rectirostris* and *Moina macrocarpa* and in both these forms the gnathobasic lobe of the second limb has a very marked ridge which ends anteriorly in the three curved spines pointing towards the maxillules, fig. 15. But, more important, these three spines are not completely anterior to the setæ of the middle group but overlie medially the first four of the latter, and I suggest from this alone that the three anterior spines are posterior spines of the claw-bearing ridge which in *Daphnia* have migrated forwards and come secondarily into line with the more lateral primitive filter setæ of the gnathobase. The migration suggested can be seen taking place in the limbs of *Holopedium* and *Sida* on the first trunk limb gnathobase, and I have already stated that I consider that the second trunk limb in the Daphniidæ copied the first in the modification of its gnathobase.

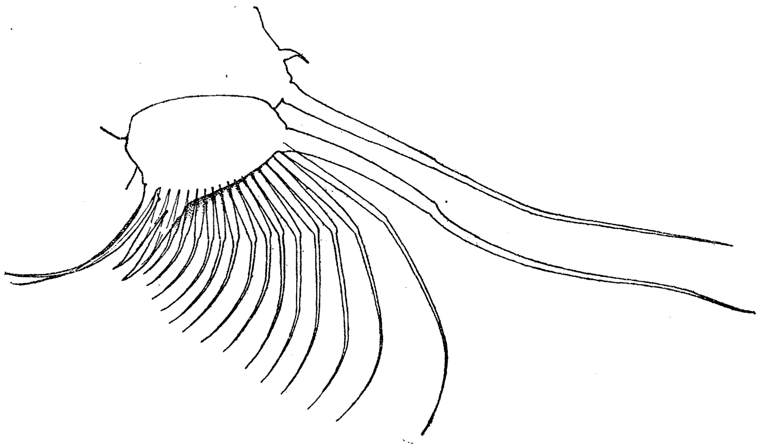


FIG. 15.—Median view of gnathobasic lobe of second trunk limb of *Moina rectirostris*.

In *Holopedium* the second to fifth gnathobases carry, posteriorly on the claw-bearing ridge, one long posteriorly directed spine, immediately in front of which is a powerful curved claw similar to that of *Sida*. At the base of this claw and in front of it is a minute spine, fig. 16. On the first gnathobase the long posterior spine is the same as on the other limbs while the curved claw is much more powerful, and curves forwards, reaching almost to the anterior limit of the filter setæ. In the backstroke of the limb this claw must push forwards on to the maxillules and so functionally correspond to the three anterior spines of the gnathobasic lobe of the second trunk limb of *Daphnia* or *Moina*. The change in this claw, however, is not merely a change in direction. It is actually shifting forwards at its base as the minute spine, which in the more posterior limbs is the anterior member of the three on the claw-bearing ridge, in this limb arises between the other two.

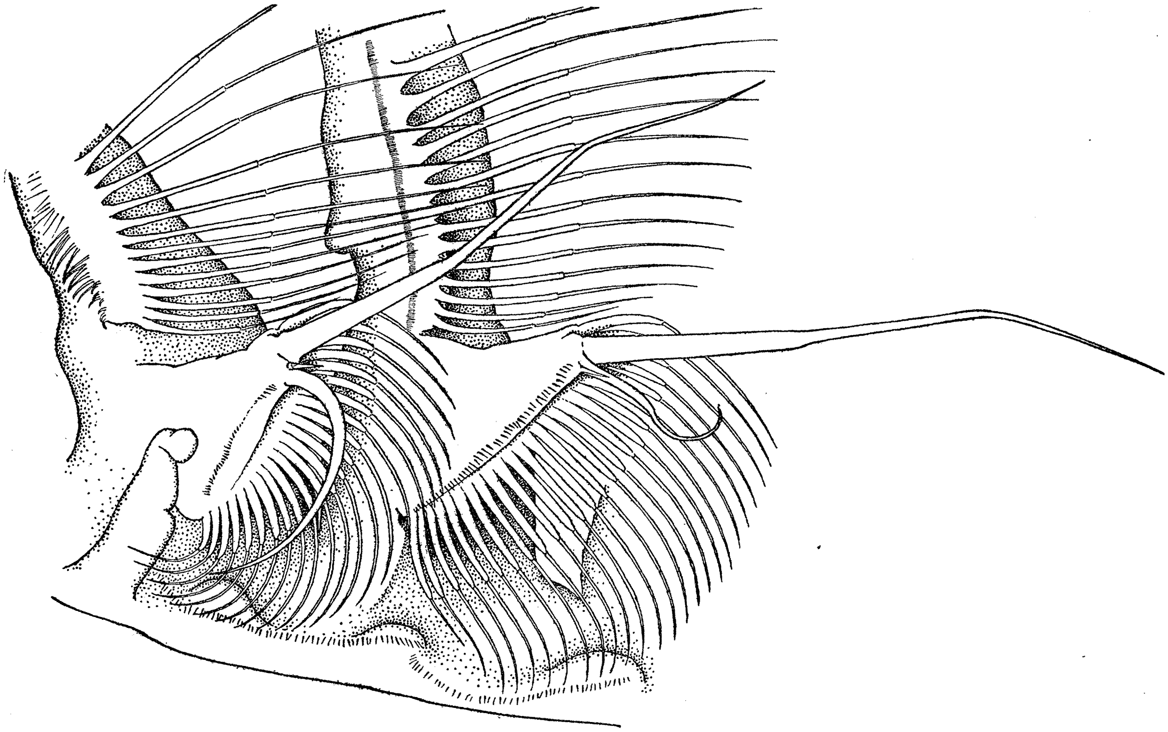


FIG. 16.—Median view of gnathobases of first and second trunk limbs of *Holopedium gibberum*. This figure shows in outline the maxilla of *Holopedium*. It is an extremely small transparent lobe covered with long setules.

In *Sida* the gnathobase of the first trunk limb differs from those more posterior in that in place of the curved claw there is a group of three very stout spines, the anterior two of which curve forwards, fig. 17. There does not appear to have been any forward migration of spines as the posterior of the three touches the long posteriorly directed seta. The claw-bearing ridge has simply developed a row of three spines instead of one.

Thus, on purely morphological grounds, I consider that in the evolution of the gnathobasic lobe of the second trunk limb of *Daphnia* a group of spines were developed on the claw-bearing ridge in front of the posterior claw. These curved forwards (*Sida*) and then migrated forwards (*Moina*) and finally came to rest in front of, and in alignment with, the filter setæ of the gnathobase (*Daphnia*).

On the hind end of the gnathobasic lobe of *Daphnia* are two posteriorly directed setæ, but these do not correspond to the two setæ in a similar position in *Sida*. The anterior of the two is homologous with the posterior seta of *Sida*. The curved claw of *Sida* may have migrated forwards to form one of the three curved claws on the anterior limb of the gnathobasic lobe, but, more probably, it is represented by the isolated seta on the middle of the claw-bearing ridge. I think this is probable from the arrangement of the first gnathobase of *Sida*. Here there is the long posteriorly directed seta and immediately in front of it, that is, in the position of the curved claw, is a stout tapering seta which still points backwards, fig. 17, and in shape and direction this spine is similar to the isolated spine of *Daphnia*.

The hinder of the posterior spines of *Daphnia* does not belong to the gnathobase, but to the second endite. This can be seen from *Moina*, fig. 15. Here the gnathobase proper carries one long posteriorly directed seta and is separated from the second endite by a distinct jointing in the cuticle. This second endite carries similarly one long posteriorly directed spine which, however, is shorter, and immediately above its base is a small tubercle ending in a minute spine. Now in *Daphnia* immediately above the hindmost of the two posteriorly directed setæ is a similar minute tubercle, showing that the gnathobasic lobe in *Daphnia* consists of the gnathobase fused with, at least, the second endite.

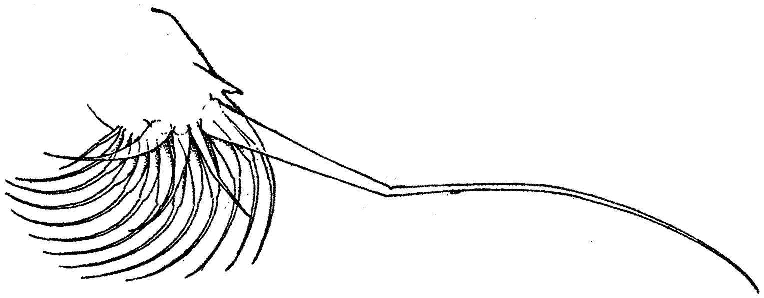


FIG. 17.—Median view of gnathobase of first trunk limb of *Sida crystallina*.

I do not think it is possible to say much about the homologies of the remaining endites, as they are not armed with filter setæ and the number of joints varies in different genera. On the inner margin of the limb there are a varying number of long thick setæ armed variously, but for the most part, armed on either side with a sheet of fine setules, so that each seta offers a good paddle surface. The lateral half of the limb is important in that it is not arranged as a valve, that is, the exopodite does not fall back on the limb behind, but rather overlies its distal parts. The exopodite terminates in long feathered paddle setæ similar to those on the distal endites.

The third and fourth trunk limbs of *Daphnia*, fig. 14, *c* and *d*, can be considered together, as they are constitutionally the same. In these limbs, according to BORRADAILE (1926, p. 119), " there is no gnathobase but an elongate lobe which starts at some distance from the base of the limb, bears the long fine fringe, and appears to represent the second to fourth endites." Again, I do not accept this view, but consider, on the contrary, that the greater part of the long fringe of setæ—if not all—represents the gnathobase itself.

In a median view of the third trunk limb of *Daphnia*, close above the bases of the fringe of filter setæ and well towards the posterior end, is a ridge, which looks like a tubercle, carrying a short slightly curved seta. This ridge can only be seen in an undisturbed preparation. On flattening the limb under a cover-slip the seta can be found only with difficulty and then it appears merely as one of the group of spines with which the endite series terminates ; in fact, it is so inconspicuous that LILLJEBORG omitted it from his figure of the undisturbed limb. A similar spine can be seen in *Simocephalus*. It represents the posterior spine of the claw-bearing ridge of the gnathobase and that this is so can again be seen from the more primitive form *Moina*.

In *Moina* these parts of the third and fourth trunk limbs, certainly in the case of the fourth limb, *look* like gnathobases as they are not very much larger than the gnathobase of the second limb and they have comparatively few setæ and not the enormous number as in the case of *Daphnia*. But in place of the small isolated spine of *Daphnia*, the third trunk limb of *Moina* bears a long spine curving backwards which is proportionately as long as the posteriorly directed spine on the gnathobase of *Sida*. I take this spine to be a land-mark indicating the hinder end of the gnathobase.

In *Sida*, in *Chirocephalus* and also in *Estheria* (fig. 22), the food groove wall is marked by a prominence immediately below the gnathobase (see above, p. 272 and p. 287), from which the ridges run marking off the exit grooves from the inter-limb spaces. Such a prominence thus marks the anterior limit of the gnathobase and can be seen very distinctly at the anterior end of the filter plate of the third trunk limb of *Moina* and *Simocephalus*.

Thus again on morphological grounds and quite apart from the functional evidence, I deduce that the main part at least of the filter comb of the third limb represents its gnathobase. From the close similarity of the fourth limb to the third it is legitimate to apply the same reasoning to this limb.

The distal part of the third trunk limb of *Moina* is obscurely segmented, but in *Daphnia* it is possible to make out a definite segmentation. The filter comb of setæ appears at first sight as a single row of regularly spaced setæ, and so they are at their tips, but at the distal end of the comb row it can be seen that there is a row of four setæ, which at their bases are not in a line with those in front, and behind them a row of two setæ. It is possible that these represent the much diminished second and third endites. This would mean that the filter comb really represents three endites. Beyond this is a group of four paddle setæ arising from three indistinct joints. If these represent endites, this would give a total of six.

The anatomy of the fifth trunk limb can best be seen from fig. 14, *e*. Its chief characteristics are the absence of endites, and an exopodite consisting of a process terminating in a long thick spine which curves round the outside of the epipodite towards the body and is armed on either side with a sheet of fine setules. This limb has been described at length by STORCH (1924, p. 168, fig. 7).

Daphnid Feeding Mechanism.

I take for granted that the Daphniidæ evolved from some Ctenopod-like ancestor. This being so, it follows from the morphology of the trunk limbs of *Daphnia* that only the second, third and fourth of the series could possibly retain the primitive filtering mechanism, for only in these limbs is the gnathobase retained. However, the filter setæ of the gnathobasic lobe of the second limb are armed with setules in such a way that the lobe cannot act as a filter (see p. 306), so that only the third and fourth trunk limbs are to be looked upon as filters.

The arrangement of the parts of the filter limbs of *Daphnia* is directly comparable with that of *Sida.* According to the old homologies it would be stated that they differ from those of *Sida* in sloping backwards so as to become almost parallel to the body, while according to the homologies I have put forward, it can be stated that the gnathobase of *Daphnia* occupies the same position as it does in *Sida*; but while it has increased in size, the distal parts of the limb have dwindled and have given up partly—or completely—participating in the filtration process. It is this dwindling of the distal parts which has brought the exite series downwards towards the body, so that they lie at an acute angle to the body axis.

This sloping back of the third and fourth trunk limbs has involved a slight modification of their valvular action. The exopodites and exites flap back against the limb behind in their more distal parts and must act just as do the corresponding structures in *Sida*, but the more proximal parts flap back against the body wall, fig. 13, and as a correlation, the body wall from the third limb backwards has developed a projecting ridge against which the pro-epipodites of the filter limbs fit closely on their forward stroke. This ridge has been figured diagrammatically by STORCH (1924, figs. 18, *a* and *b*, pp. 198 and 199).

The fourth limb I have stated flaps back against the fifth, its exopodite resting over the peculiar recurved exopodite spine of the latter during the greater part of its forestroke. The fifth limb, however, does not strictly move backwards and forwards. Its inner margin remains stationary close against the sides of the front edge of the caudal furca, and its outer parts swing backwards and forwards about this margin just as a door swings about its hinges. During the greater part of the suction stroke of the fourth limb, the fifth limb rotates forwards so that it closes the inter-limb space between the two limbs from behind, and conversely during the greater part of the backstroke, it swings backwards and so allows the outflow of water from this inter-limb space.

The relative movements of the limbs of *Daphnia* are difficult to follow and, as far as I am aware, have never been fully described. It is possible, however, to observe accurately certain facts which can be plotted in the form of curves and from this the type of rhythm of the limb movements can be deduced.

The fifth, fourth and third limb appear to move forwards almost together, that is, there is a very small phase difference between them. There is a difference, however, and it is very important. The fifth limb swings forwards and is followed almost immediately by the forward suction stroke of the fourth and then the third limb.

The phase difference between the third and second limb is greater, but the second limb does not move much in a backwards and forwards direction. Its movement is mainly lateral, though the third limb appears to push it forwards at the end of its forestroke.

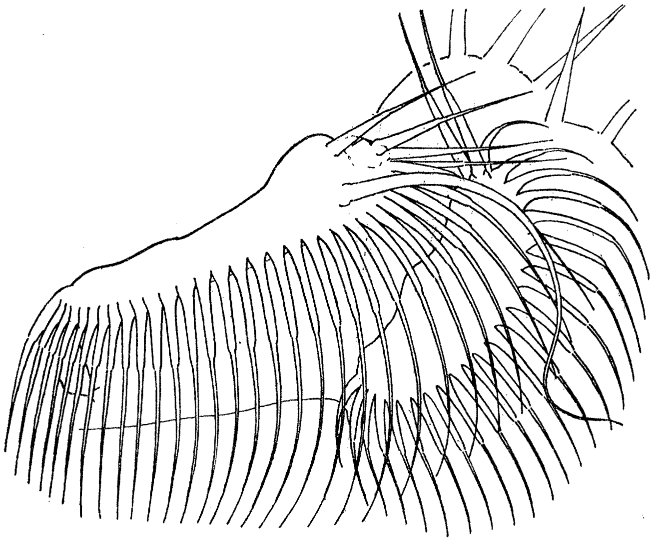


FIG. 18.—Median view of gnathobases of third and fourth trunk limbs of *Moina macrocarpa*.

The phase difference between the second and first limb is large, and, as the second appears to move forwards very little, the fact which is most easy to observe is that the first and third limbs move almost in opposite phase. Under low power it is possible to watch the first and fifth limbs together and then it can be seen that these two limbs move even more nearly in opposite phase.

These observations are recorded in fig. 19. It will be seen that, although there is not true metachronial rhythm, yet the phases of limb movement appear to move forwards.*

Now *Moina* possesses limbs of the same type arranged in the same manner as those of *Daphnia*, and on morphological grounds it is considered as one of the most

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* The meaning of the term "metachronial" or "metachronal" rhythm is not clearly defined and its derivation does not help. I am assuming that, strictly, in a series of structures moving with metachronial rhythm the phase difference is constant between any consecutive pair.

primitive of the Daphniidæ. It would be expected then that its limbs would move in a rhythm more nearly metachronial than those of *Daphnia*, and this is actually the case. *Moina* is a beautifully transparent form and it is possible to see the details of the limbs with considerable accuracy. I found that it moved its limbs in the same typical metachronial rhythm as *Sida*. The only difference I could observe was that there appeared to be a somewhat greater phase difference between the fifth and fourth limbs than between the others, that is, the fifth limb swung forwards precociously.

I have plotted these results together with the corresponding curves for *Sida*, in the latter case not taken from my own observation but based on STORCH's photographs. From a comparison of these curves it is clear that the specialisation which has taken place in the evolution of *Daphnia* from a Ctenopod has involved a modification of the original metachronial rhythm just as much as a structural modification of the limbs, and this mechanical change I consider just as important as the morphological alterations.

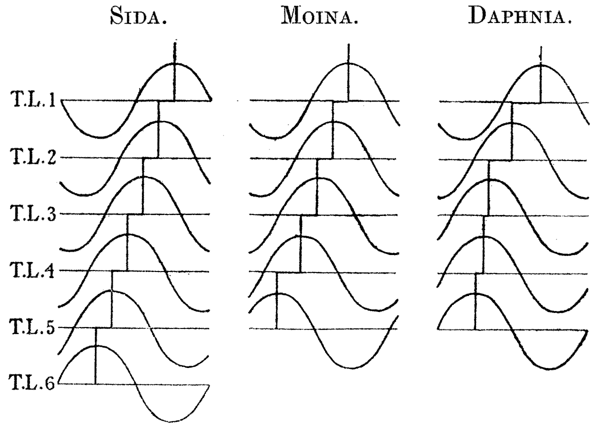

FIG. 19.—Curves illustrating the metachronial rhythm of the limb movements of *Sida*, *Moina* and *Daphnia*. The horizontal depth of the steps joining the curves indicates the phase difference between consecutive limbs.

In order to illustrate the movements of the individual limbs of *Daphnia* I have drawn an outline diagram, fig. 20, based on fig. 13, showing the position of the limbs when the third and fourth trunk limbs are nearing the end of their forestroke (above) and their backstroke (below). It is not possible to draw these figures accurately as the third and fourth trunk limbs do not end their strokes together, but the figure illustrates sufficiently the relative movements of the limbs.

The two outlines have been drawn on numbered co-ordinates so that it is possible to see the change in position of any part of the limb (seen from the median aspect) during its complete stroke.

During the forestroke of the fourth limb its gnathobase swings upwards and away from the body and moves slightly forwards. As already stated, its exite series flaps against the limb behind which rotates forwards and so closes the inter-limb space from behind (see p. 298). The upward swing of the hind end of the gnathobase thus increases the volume of the inter-limb space and so water must be sucked in and its only entrance is through the filter setæ on the gnathobase (current 1). This is the typical suction action such as occurs in *Sida* or the Anostraca, but with the difference that, as the hind end of the gnathobase moves away from the body, the front end moves slightly towards it.

On the backstroke of the fourth limb the hind end of the gnathobase comes down against the stationary inner edge of the fifth limb, while the front tilts slightly upwards. The limb bends at about the level of the end of the gnathobase, the exopodite flapping away from the body, so that water in the distal part of the inter-limb space is thrown out

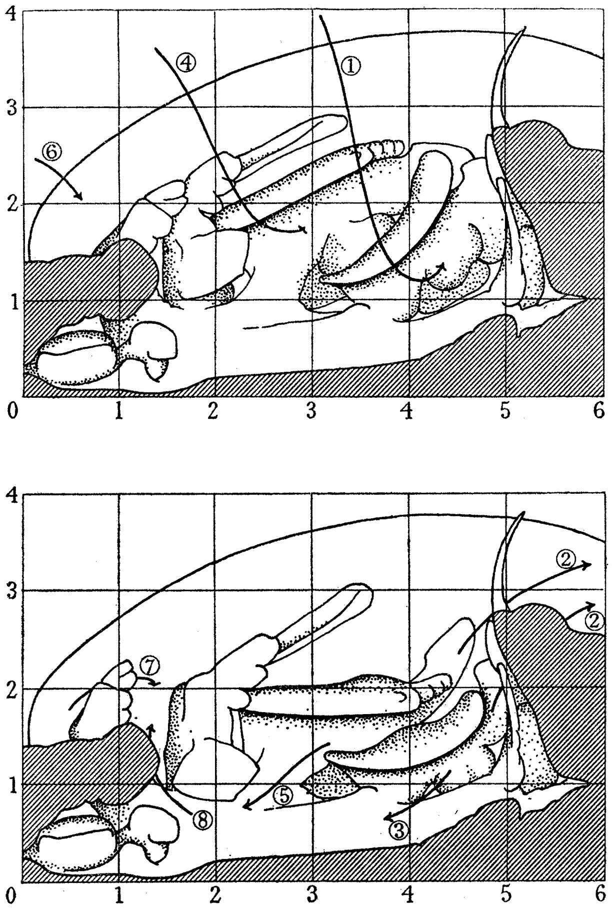

FIG. 20.—Outline sketches of left half of *Daphnia magna*, based on text-fig. 13 to show movements of limbs and feeding currents. Above, the third and fourth trunk limbs are approximately at the end of their forestroke and below, at the end of their backstroke. A co-ordinate frame has been traced over the figures so that the movements of the limbs can be seen.

backwards (current 2). The inter-limb space nearer the body, as in the Anostraca (see above, p. 272), is divided into an inner median and an outer lateral chamber by the thickness of the corm of the limb. The water in the lateral chamber is thrown out backwards, but that in the median chamber is forced forwards into the median food groove (current 3). This forward spurt is enhanced by the upward tilt of the front end of the gnathobase as the hind end beats down towards the body, but a much more important factor is the rapid forward swing of the fifth limb just as the fourth limb is finishing its backstroke. Thus the fourth limb beats backwards until its gnathobase touches the limb behind, then the lateral parts of the fifth limb swing forwards as a door pressing on the water in the inter-limb space. The water in the median chamber has only one way out for, distally, the gnathobase touches the limb behind, while laterally, the thick corm of the limb forms a barrier ; hence it must be directly pushed forwards by the moving fifth limb.

The movement of the third limb is similar to that of the fourth but its amplitude is greater. During the forestroke the gnathobase moves as a whole away from the body and forwards, thus increasing the volume of the inter-limb space and the exite series act in a typical manner as valves, so that water is sucked in through the filter setæ (current 4). The front end of the gnathobase approaches the body as the hind end moves away, as in the action of the fourth limb, but to a greater degree.

During the backstroke the end of the gnathobase approaches the gnathobase of the fourth limb about the middle of its length. As in the inter-limb space 4–5, the distal water is thrown out backwards (current 2), but the water in the median chamber is forced forwards along the food groove (current 5) ; the fourth limb commences to move forwards just as the third limb is finishing its backstroke. From the diagram it can be seen that the fourth limb has a marked hump about the middle of its gnathobase ; this must press against the thick corm of the third limb directly it commences to move forwards and so effectively close this exit from the inter-limb space.

The pivoting action of the gnathobase of both third and fourth limbs, however, must be equally effective in producing this forward current. As the hind end of the gnathobase moves towards the body it presses on the water, but at the same time the front end very markedly moves away and this must suck on the water. Now the front end of the gnathobase projects forwards considerably beyond the main axis of the limb especially on the third limb. In both it is connected to the corm by a very thin membrane (gnathobasic membrane). This membrane must act as a barrier cutting off the effect of suction from the inter-limb space in front and confining it to a suction from the hinder part of the inter-limb space forwards.

This mechanism of the production of the anteriorly directed stream in the food groove is simply a specialisation of that of *Sida* or *Chirocephalus*. In *Daphnia*, however, there is another effect which is of great importance, namely, the movement of the first trunk limb. From what I have described and from fig. 20, it can be seen that as the third and fourth trunk limbs are moving backwards, the first is moving forwards and increasing markedly the inter-limb space 1–2 ; a suction is thus produced in this region.

When the first limb moves backwards it moves away from the front edges of the carapace and thus sucks water into the space so formed (current 6), while on the forward stroke suction is produced behind the limb. The water in front of the limb will be sucked round the first limb and will take the line of least resistance, namely, round the outside of the limb in the distal parts of the inter-limb space 1–2 (current 7).

No doubt some will pass round the median side and be sucked into the space through the endite setæ, fig. 14, *a*. These setæ usually remain remarkably clean but sometimes particles adhere to them, which means that some water must have passed through them from the median side. When this happens the limbs are very soon pushed backwards and cleaned by the gnathobasic lobe of the second trunk limb. However, the water from this region in front of the first limb will not pass into the proximal part of the inter-limb space 1–2, for on the outside the passage is blocked by the large gill, and on the median side by the labrum. Yet from the shape of the limb, there must be a marked suction in this region, fig. 20 ; there is only one place from which water can come to supply this proximal suction and that is the food groove (current 8).

Now from the diagram it can be seen that as the third and fourth trunk limbs are ending their backstroke, that is, when they are themselves producing spurts of water forwards from the hind end of the food groove, the first trunk limb is sucking water out of the anterior end. Thus there must occur an intermittent food current towards the mouth produced by pressure from behind and suction in front.

The demonstration of this anterior food current is not difficult. It can be observed directly in *Simocephalus*. This form, as is well known, will remain for a long time upside down in a watch-glass so that it is possible to look directly into the food groove. Particles are often seen sucked into the hind end of the median space by the fourth trunk limb, when they are *suddenly* blown forwards to the mouth. They do not move gradually forwards. There is no possibility of their being swept forwards by setæ as there are no setæ which move forwards to such a degree. More particularly the setæ of the gnathobasic lobe of the second trunk limb cannot possibly sweep them forwards as, in the hind end of the food groove, the only setæ from this lobe are the posteriorly directed setæ and these move towards the body and not towards the mouth.

A more difficult way of demonstrating this current is to inject a coloured solution by a very fine pipette near a *Daphnia* lying on its side in a compressorium. Methyl blue is a convenient solution as it does not diffuse into the water too rapidly. The solution is drawn towards the body, and if it is drawn as a fine stream, as sometimes happens, and if again it enters the shell towards the hind end of the body, it may be seen sucked into the inter-limb space 4–5. In this case a spurt of blue solution can be seen immediately afterwards passing along the food groove. This is an experiment that only succeeds now and again as the solution usually enters in such a large stream that the whole of the shell cavity becomes immediately blue. Another difficulty in looking for this food stream from the lateral aspect is to know exactly where the food groove occurs. The anterior part of the food groove is very deep, fig. 13, so that in side view it occurs considerably below the attachment of the limbs to the body. It is obscured by the ventral longitudinal muscles which lie directly over it as the animal lies on its side, so that it is quite impossible to see isolated particles from this view. If, however, the microscope field is flooded with bright light it is then possible to see the coloured solution through the musculature.

To summarise the current production in *Daphnia,* water is sucked into the shell cavity mainly by the action of the third and fourth trunk limbs. It passes through the filter combs, into inter-limb spaces 3–4 and 4–5. On the backstroke of the third and fourth limbs, some of this water is forced out backwards and finds an exit on either side of the caudal furca. A considerable part of water, however, is forced forwards by the pivotting action of the gnathobases along the food groove towards the mouth, while, at the same time, water is sucked out of the food groove by the forward stroke of the first trunk limb into inter-limb space 1–2. This water is then forced backwards on the next backstroke of the first limb along the outside of the more posterior limbs and passes out at the hind end of the shell.

The primitive method of scraping the residue off the filter setæ of the gnathobases which I call the first method, is that seen in *Sida* where a row of comb setules occurs on the wall of the food groove corresponding exactly to the position and length of the gnathobase, fig. 9. Now, if the gnathobase enlarges disproportionately to the rest of the limb, then unless the space between the limbs enlarges to a similar degree, the gnathobase will extend backwards beyond its corresponding strip of comb setules. This has happened in *Holopedium,* fig. 16. As a result, while the front part of the gnathobase is combed in the same manner as in *Sida,* the hind part is combed by the row of comb setules on the claw ridge of the gnathobase behind. This I call the second method.

In the Daphniidæ we should expect to find both methods of collecting the filtered residue as, in this family, the gnathobases have enlarged to a greater extent than in any other.

In *Moina* the walls of the food groove are armed irregularly with comb setules as far back as the fifth limb. They are not arranged in localised strips as in *Sida.* In *Daphnia* the walls appear almost devoid of setules but with an oil immersion lens it is just possible to see a strip of fine setules very close together and regularly spaced, extending from the maxillules to the fifth trunk limb. They appear more as a striation than as distinct setules, and in fig. 13, they have necessarily been exaggerated in thickness. STORCH mentions them (1924, p. 188) and for some reason not stated, suggests that they represent the missing maxilla. From their size it is obvious that they cannot effect much scouring of the filter setæ and hence the second method of collecting the residue from the filter setæ must be present.

In *Daphnia* from the arrangement of the limbs it is obvious that it is only on the hinder part of the third trunk limb that the second method of scouring can obtain, for only here are there two overlapping gnathobases. Thus on trunk limb four at the bases of the filter setæ there occurs a strip of long setules which correspond exactly with the setules in the homologous position on the gnathobase of *Sida* or *Holopedium,* fig. 14, *d.* They project obliquely towards the body through the posterior filter setæ of the third limb which lie over them medially. In addition, there are other rows of much smaller setules arranged behind which correspond to the subsidiary setules on the gnathobase of *Sida*, fig. 9. As the third limb moves away from the body to a much greater degree than the fourth, their gnathobases must exhibit considerable relative motion; thus as the third limb moves over the fourth its filtered residue on its posterior setæ will be combed off by the comb setules on the fourth limb.

Trunk limb 3 carries a similar row of setules at the base of its filter setæ, fig. 14, *c*. but these are very short. There are no filter setæ for them to comb as the limb in front has given up its filtratory function and I presume they are functionless, just as are the comb setules on the distal endites of the first limb of *Sida*. They are simply characteristics of a gnathobase.

This leaves the front part of the filter comb of the third limb and the whole of the filter comb of the fourth limb from which the filtered residue has to be removed in some other way. It is simplest to consider the fourth limb first and then return to the anterior part of the third.

The residue on the fourth limb is combed off entirely by the third limb; this is a completely new development. In all the forms I have described the filtered residue on any limb is combed off either by setules on the gnathobase behind, or at least, by setules posterior to it on the food groove wall, while here it is the reverse, as the residue is combed off by the limb in front. The filter setæ on the third limb show a very interesting modification for this purpose. The tips of these filter setæ on the anterior part of the gnathobase taper to fine points, fig. 21, *a*, just as do ordinary filter setæ, their setules being arranged on either side of the seta right down to the tip. Those on the posterior

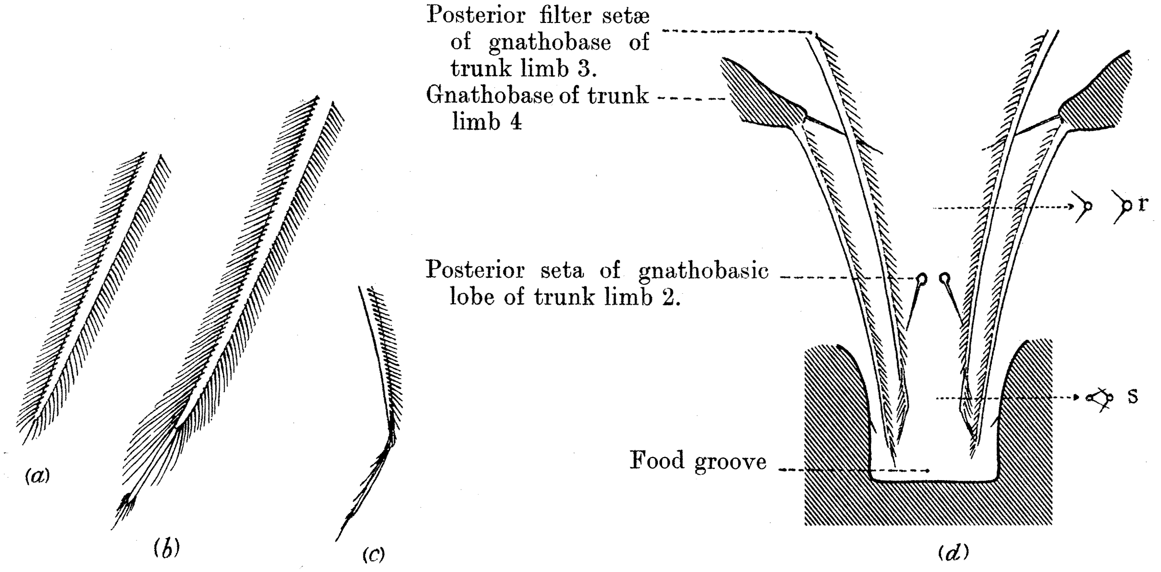

FIG. 21.—(*a*) Median view of end of filter seta on anterior part of gnathobase of third trunk limb of *Daphnia magna*: (*b*) Median view of end of filter seta on posterior part of gnathobase of third trunk limb of *Daphnia magna*: (*c*) Conjectured anterior view of same seta as figured in (*b*); (*d*) Diagram of transverse section through gnathobases of third and fourth trunk limbs to show the reciprocal combing action between the two. At *r* and *s* are figured frontal sections through the filter setæ of the gnathobases near the bases and tips respectively.

part, however, that is, those which overlie the filter setæ of the fourth limbs, are modified at their tips, fig. 21, *b*. The setules in this region reverse so as to point laterally instead of medially, fig. 21, *c*, and they are longer than the normal. In addition, there appears to be a new outgrowth from the tip of the seta, set at an angle to it. This outgrowth is so fine and transparent that it can only be made out, and then with difficulty, under an oil immersion lens in a caustic potash preparation cleared in glycerine. The tips of these posterior filter setæ are thus modified as brushes pointing outwards against the third limb filter setæ, and it is these brushes that must comb off the residue collected on this limb. This is indicated diagrammatically in fig. 21, *d*.

The anterior part of the third limb filter comb is scoured by the gnathobasic lobe of the second trunk limb. The setæ on this lobe consist of three distinct groups, functionally as well as morphologically. The middle group represents the primitive filter setæ of the gnathobase and I have already stated that these setæ are armed with setules in such a way that they cannot act as filters. STORCH (1924, p. 186 and fig. 15, p. 185), has described and figured them and shown that the setules occur on the outer face of the setæ, so that they cannot act as a filter to a current passing laterally from the median space. STORCH's figure shows the setules regularly arranged and similar to those on the typical filter setæ of the third limb, but this is not so. The setules have not only reversed but have become slightly longer and are irregularly arranged, which is unlike any filter seta. Filtratory setules are always regularly arranged and are stiff.

In addition, the tips of the setæ of this middle group are bent laterally and are armed with long setules, the seta thus forming a brush along its whole length which terminates in an enlargement, fig. 14, *b*. In the movement up and down of the gnathobasic lobe, the setæ of this middle group will thus brush the filtered residue off the anterior setæ of the third limb into the food groove.

The posterior part of the filter plate of the third limb is thus combed from the outside by setules on the fourth limb, while the anterior part is brushed on the inside by the modified filter setæ on the gnathobasic lobe. The division between these two parts should be marked by that seta which passes over the anterior end of the gnathobase of the fourth trunk limb. I traced this in fig. 13, and found that it corresponded *exactly* with the hinder limit reached by the posterior modified filter seta of the gnathobasic lobe of the second limb.

The movement of the greater part of the second limb is small. The main axis of the limb up to its point of flexure rotates slightly backwards and forwards and at the same time, inwards and outwards, fig. 20, while the distal part appears to move simply backwards and forwards. The gnathobasic lobe, however, exhibits a very marked movement. As the whole limb moves forwards and outwards the hinder corner of the gnathobasic lobe swings upwards away from the body so that the long posterior seta, fig. 14, *b*, comes to lie almost parallel to the edge of the third trunk limb. During this phase the gnathobasic membrane becomes stretched to the utmost. On the backstroke of the limb the gnathobase swings forwards so that its posterior seta swings downwards into the food groove, and at the same time its most anterior brush setæ move directly on to the maxillules.

The arrangement of setules on the two posterior setæ is shown in fig. 14, *b*. Those on the hindmost of the two are long, coarse and widely separated, while those on the other are very fine, short, and closely set. In the figure is shown a row of setules which project obliquely outwards, but there is another row projecting directly outwards which is hidden by the thickness of the seta.

Fig. 20 shows that the posterior setæ are being beaten down towards the food groove while the third and fourth trunk limbs are beating backwards. Now, during this phase the filtered particles in addition to being combed off by the comb setules, will be partly blown off by pressure in the inter-limb spaces acting through the filter setæ exactly as in the Anostraca, etc. (see p. 278). Such particles blown free into the median space will be beaten down into the food groove by the posterior setæ of the gnathobasic lobe.

So far, I have described how the residue is filtered, combed off and then partly blown and partly sucked forwards along the food groove. In the region of the second limb it meets the down-thrust into the food groove of the gnathobasic lobe. The modified filter setæ of this lobe are each armed about the middle of their length with a circlet of fairly stout setules, fig. 14, *b*. These I consider must serve to push the residue towards the floor of the food groove. This action places the food particles in a position where they can be directly passed on to the mouth parts, but more especially, it sweeps the food particles out of the main water stream. The median groove is very deep in the region of the second limb and it is blocked anteriorly by the maxillules and labrum. Water is streaming forwards and passing out into the inter-limb spaces 1–2. The entrance to these is high up on the top of the walls of the median groove and hence water must pass upwards from the floor of the food groove to enter these spaces. Thus the region in the lower part of the food groove just behind the maxillules must be a region of comparative quiet and it is into this region that the gnathobasic lobe of the second limb beats the particles.

In this region I do not think that the filtered particles are to be considered as free for here are extruded the secretions of the labral glands, the functions of which, I have previously suggested (1922, p. 229), is to entangle the food particles. The residue must thus be considered as a viscid mass which is swept downwards by the modified filter setæ, and then pushed forwards by the three anterior brush setæ of the gnathobasic lobe on to the maxillules.

The food collected in this way is passed forwards by the maxillules at irregular intervals on to the mandibles. The maxillules each bear three setæ which curve forwards towards the mouth. They are heavily armed with setules pointing forwards on their median faces; they have been described and figured by STORCH (1924, p. 188, fig. 17).

The feeding mechanism of *Moina* shows differences from that of *Daphnia* which can be correlated with (1) the more primitive rhythm of limb movement, and (2) the more primitive nature of the gnathobases.

I have already described the rhythm (p. 300). The limbs move with the same rhythm as those of *Sida* with the exception of the fifth. This limb is similar in structure to that of *Daphnia* and moves in the same way, but its forward swing comes soon after the middle of the backstroke of the limb in front, a process which is very marked and easy to observe. The water from the inter-limb spaces 4–5 must thus be shot forwards with considerable force.

The fourth and third limb gnathobases move in the primitive manner in that their anterior end marks the point about which they pivot, so that there is no suction caused by the raising of the anterior end away from the body. The forcing forwards of water from the inter-limb spaces 3–4 must depend solely on the metachronial rhythm of the limbs as in *Sida*.

The second limb moves backwards and forwards in a normal manner. Now since the phase difference between the first four limbs is approximately the same there must be a suction phase into the inter-limb spaces 2–3, just as there is into inter-limb spaces 3–4, and the gnathobase of the second limb in a more primitive form would offer a filtratory surface to this inflow. In *Moina*, however, this gnathobase, like that of *Daphnia*, has given up its filtratory function and become an organ brushing the residue off the limb behind. The setules on its filter setæ have reversed, but not to such a marked degree as those of *Daphnia*. Thus water passing through it into the inter-limb spaces 2–3, would not be filtered. To compensate for this the gnathobase of the third limb extends forwards and covers the entrance to this space. Thus the third limb filters water passing into both inter-limb spaces before and behind it.

The same reasoning would apply to *Daphnia* but there is very little suction into the inter-limb space 2–3 as the second limb moves forwards scarcely at all, and, as I have stated, appears to be pushed forwards at the end of the forestroke of the third limb.

The first limb has lost its gnathobase and hence the entrance into inter-limb space 1–2 is unguarded. Water is thus sucked unhindered from the food groove as the first limb moves forwards just as in *Daphnia*.

The filter setæ on the limbs of *Sida* are cleaned partly (laterally) by setules on the food groove wall and on the limb behind, and partly (medially) by the posterior setæ from the claw-bearing ridge of the gnathobase of the same limb (p. 288). In *Diaphanosoma*, fig. 12, this posterior seta combs the residue off the filter setæ of the next limb behind. In *Moina* the filter setæ of the fourth trunk limb are cleaned from the outside by irregular setules on the food groove wall. Medially, however, they are cleaned by the long posterior seta arising from the claw-bearing ridge of the third limb gnathobase.

The reason for the dwindling of this seta in *Daphnia* can be understood by comparing the outlines of the third and fourth limbs of *Daphnia*, figs. 13 and 14, *c* and *d*, with those of *Moina*, fig. 18. In *Daphnia* the third limb gnathobase has enlarged to such an extent as completely to cover the fourth gnathobase. Its posterior seta is thus cut off from the latter and so cannot function as in more primitive forms. Hence, it has dwindled and as a compensation the tips of the filter setæ of the hinder part of the third gnathobase have become modified as brushes and have taken over its function.

CONCHOSTRACA.

Estheria naturally cannot be studied in the living state with the same ease as *Chirocephalus* owing to the presence of the large bivalve carapace enveloping the limbs. But, although the details of limb structure cannot be seen, the type of limb movement can be observed accurately and it is found to be the same as that of the Anostraca. The limbs in their forestroke appear to push forward the limb immediately in front and the phases of limb movement appear to move forward in waves. It can therefore, be deduced that, since the arrangement of the endites and exites is the same in *Estheria* as in *Chirocephalus*, the general suction of water through the limbs is the same in the two forms, and, more especially, the maximum suction into the inter-limb spaces will occur at the base of the limb in the region of the basal endites (gnathobases).

The limbs of *Estheria* are much closer together than those of the Anostraca. This has two results; first, the inter-limb spaces will be practically obliterated when the limbs are at the end of their backstroke and hence the suction on the forestroke must be relatively powerful, and second, the volume of the inter-limb spaces is small so that the amount of water which passes through them is also relatively small. This difference may be accounted for by the different habits of the two groups. The Anostraca use the momentum of the filtered water for propelling them forwards and hence the greater the amount of water which can be thrown out posteriorly, the greater will be their ability to swim rapidly. *Estheria*, on the other hand, lives in mud, and when it is necessary to swim, uses its antennæ for this purpose. The water drawn between the limbs is used entirely for feeding and so, while it can be relatively smaller in volume, the suction and hence filtration, must be powerful.

In another respect, *Estheria* differs from the Anostraca. Its limbs show a transition as the series is followed posteriorly. The first fifteen limbs are similar, differing only in size and in the numbers of setæ on the various parts. Behind the fifteenth limb there are very marked changes in structure which are dealt with later (p. 316). The first part of this section applies only to the anterior limbs.

By propping the animal upside down between two strips of thick glass it is possible to look directly into the mid-ventral groove, but the space between the two rows of limbs is relatively so narrow and deep that little can be seen distinctly. A forward movement of particles along the mid-ventral line can be observed in certain circumstances, and LUNDBLAD (1916, p. 267) has ascribed this to an orally directed current.

That there is actually a marked oral current in the anterior part of the food groove can be established by comparing the walls of the food groove with those of the Anostraca.

For while in the latter, the exit grooves leading from the inter-limb spaces are distinct, in *Estheria* they are much more so, but they are very hard to see. In a sagittal half they can be made out, but with difficulty, as the underlying musculature obscures them. Fig. 22 was based on a microtome-cut sagittal half which was subsequently cleared in caustic potash. The shape of the grooves was then mapped out by focussing at various levels and plotting the contours, and subsequently confirmed by a series of parasagittal sections.

The presence of these exit grooves in itself does not prove the existence of an oral current. But the type of limb arrangement and movement being the same in *Estheria* as in *Chirocephalus*, and since it can be proved experimentally that an oral food current exists in the latter form, it can be deduced that, the exit grooves being more definite in *Estheria*, there will *a fortiori* be an oral current in this form.

The retaining wall of setæ which keeps the food particles in the mid-ventral space occurs on all the endites and is not confined, as in the Anostraca, mainly to the basal endites. It is convenient to commence with a consideration of the first twelve pairs of trunk limbs and of these to consider the second endite to the sixth (endopodite), and then the first (gnathobase).

The endites are armed on their inner edges with two rows of setæ, fig. 22, limb 3. The hind row consists of very long setæ which point directly backward and so lie close against the endites of the more posterior limbs, extending as far as the limb but one behind. These setæ are thin and run parallel to each other. They are set close together and the intervening spaces are spanned by dense rows of filtratory setules, so that they are typical filter-setæ.

The front row projects postero-medially. Its setæ are stout and comparatively short and radiate from the edge of the endite. This row must thus project in between the hind rows of the next two limbs in front. In this way the mid-ventral space is walled on either side by a zig-zag of setæ which closely recalls the condition in *Nebalia* (Cannon, 1927). In the latter however, the setæ all point forwards against the food current, and are hooked together at their tips.

In addition to these filtratory setæ the margin of the second to sixth endite is clothed with a dense mat of setules, fig. 22, limb 2, which correspond in position to the similar setules in the Anostraca.

Beyond this strip of setules along the line where the endites curve round and merge into the corm of the limb, there is a row of stout and very short setæ which project only a short distance from the surface of the endites and curve inwards and backwards, fig. 22, limb 3. Their function is uncertain, but it is possible that they act by dislodging any particle that by chance penetrates the filtratory setæ and becomes attached to the hinder surfaces of the limbs in the inter-limb spaces.

The functioning of the filtratory setæ must be, in general, the same as that of the more distal setæ on the basal endites of the Anostracan limb, the hind row of setæ forming the filtratory surface. Particles will be sucked on to them on the forestroke of the limb and combed off by the front row setæ and at once sucked towards the food groove.

The strip of setules will also comb particles from the filtratory setæ, but it is possible that in addition, they act as a barrier preventing the passage of water into the inter-limb spaces by damping down the suction in the region where they occur and so causing the suction to take place to a larger extent at the bases of the limb. Thus, the limbs of

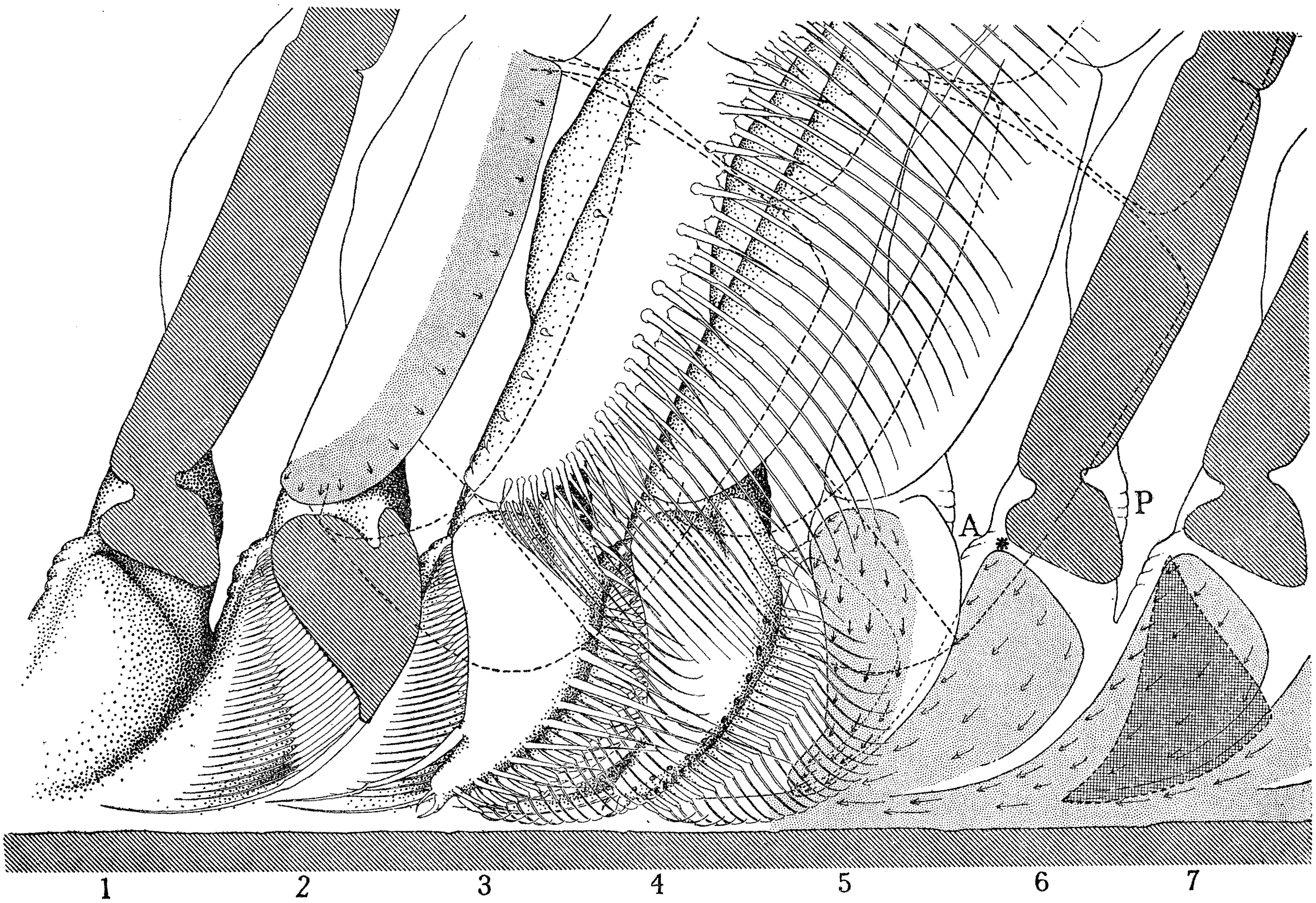

Fig. 22.—Median view of seven consecutive trunk limbs of *Estheria siberica*. Only the median parts of the limbs are shown. For the sake of simplicity the same limb has been drawn seven times over. Actually the limbs diminish in size from before backwards. Limb 1.—The endites and gnathobase have been removed to show the shape of the inter-limb space behind and its exit channel. Limb 2.—The median part of the gnathobase has been removed to show the line of attachment of the filter setæ. The setæ of the endites are omitted, but their extent is indicated by dotted lines. The setules at the edge of the endites are indicated by machine stippling, their direction being shown by arrows. Limb 3.—The endites, and gnathobase complete with setæ are figured. Limb 4.—The collecting setæ have been omitted to expose the brush setæ. The endites as in limb 2. Limbs 5, 6 and 7.—The setules on the median face of the gnathobase and the wall of the food groove are indicated by machine stippling, their direction being shown by arrows. On limb 6 is an asterisk marking the axis of rotation of the limb. On limb 7 the dotted triangle marks the boundaries of the filter setæ of this limb and indicates their relationship to the exit channel from the inter-limb space behind.

Estheria are comparatively close together, and for the main part of the forestroke the endites we are considering will be very closely overlapped by the endites of the limb in front. The only entrance to the inter-limb space even when the filtratory setæ have been penetrated will be through this mat of densely set setules and these all point against the direction of any inflow ; they must, therefore, offer a great resistance to the passage of water.

In the Anostraca they may act partly in the same way but in these forms the limbs are set further apart so that water can enter the inter-limb spaces directly through the filtratory setæ.

The first endite or gnathobase is an extremely complicated structure separated sharply from the more distal endites. It is roughly triangular in frontal section, the base of the triangle representing its median face and the apex fitting closely into the exit groove of the inter-limb space behind the limb considered, fig. 23, *a* and *c*. From a median view also the gnathobase appears triangular but the sides of the triangle are curved towards the body and forwards, the hinder margin of the triangle being thus convex, the front concave. The point of the gnathobase terminates in a complex blunt claw and there is a long curved spine which projects forwards from the anterior margin and is always characterised by a peculiar bend about the middle of its length, fig. 22, limbs 3 and 4.

On the outer surface of the gnathobase, that is, on the surface facing the wall of the food groove, there is a marked ridge running from the distal end of the anterior margin in an almost straight line to a point about a third of the way up the posterior margin. In fig. 22, limb 2, the median portion of the gnathobase has been removed so as to expose it. From this ridge there extends forwards a row of curved setæ which, for about half their length, are so closely set that they touch each other, while their distal halves are extremely fine and armed with lateral setules, so fine and closely set that they can only be seen with an immersion lens. As can be seen from fig. 22, limbs 2 and 3, the setæ diminish in length from the base of the food groove up to the attachment of the gnathobase to the limb. In this way they form a triangle which covers accurately the exit groove from the inter-limb space, fig. 22, limb 7. These setæ form, in my opinion, the main filtratory part of the limb, and I term them the filtratory setæ of the gnathobase. The portion of the gnathobase in front of the ridge from which these setæ arise, that is, the triangle terminating anteriorly in the blunt claw, I call the claw process of the gnathobase and as will be seen later, I consider it a separate part which is a later development of the claw-bearing ridge of the primitive gnathobase.

On the hinder margin of the gnathobase there are two distinct sets of setæ, an inner and an outer, fig. 22, limb 3. The inner set are all straight and extend over the whole of the length of the margin. They are widely separated and increase in length towards the middle of the margin, the longest extending back as far as the tip of the gnathobase but one behind, and all approximately point towards this region.

On limb 4, fig. 22, the inner set of setæ have been removed so as to expose the outer.

These extend only about two-thirds of the way up the hinder margin of the gnathobase, and each consists of a stout basal portion, which is straight, and a thin terminal portion which is curved and bent at a distinct angle to the basal part, the direction of curvature being shown in fig. 22, limb 5. The terminal parts are covered with setules which project all round the setæ, that is, they are brush setæ.

The more distal setæ lie in one plane so that their terminal portions lie close against the median face of the gnathobase behind, but towards the tip of the gnathobase the terminal portions bend sharply on the basal portions so that they lie across the floor of the food groove.

At the upper end of the gnathobase there is a small groove curving downwards (limbs 3 and 4), the area in front of which, down to the tip, is covered with setules, the direction of which is indicated on limb 5. The walls of the food groove are covered with similar setules and their direction is indicated at the base of limbs 6 and 7, but the channels of the exit grooves leading from the inter-limb spaces are devoid of setules.

The movement of the gnathobase can be determined by its relation to the other parts of the limb and by the position of the muscle insertions. The walls of the food groove do not move, for they are formed of comparatively thick chitin and there are no muscles attached to them which could bring about their movement. The limbs are attached to the tops of the walls and, as in the Cladocera, the gnathobases hang down into the food groove. Hence, as the limb as a whole moves backwards, the gnathobase moves forwards, that is, the limb pivots about a point somewhere between the gnathobase and the second endite. Also on the front and hind surface of the limb, about the level of the attachment of the gnathobase there are two regions where the chitin is thin and folded into ridges running across the limb, fig. 22, limb 6, A and P, which must mark the points of the flexure of the limb chitin. The point about which the limb pivots must then be on the line joining these two points and from the shape of the outer surface of the gnathobase and the adjacent wall of the food groove, it is probable that the centre occurs at the spot marked with a star on limb 6, fig. 22.

The movement of the gnathobase, however, cannot be simply a backward and forward rotation. It has already been stated that the gnathobase fits closely into the exit groove from the inter-limb space, fig. 23. Such a movement would therefore bring the gnathobase at once against the hinder wall of the exit groove. Also the filtratory setules curve forwards from the exit groove into which the gnathobase fits, to the next anterior groove, round the curved ridge between the two grooves, fig. 23, *a*, so that there can be little, if any, direct backward movement of the gnathobase.

Now the gnathobase has attached to its upper end, two muscles, fig. 23, *b*, from the position of insertion of which it can be deduced that their only action must be to rotate the gnathobase about an axis running along the length of the limb, that is, normal to the body. The gnathobase thus has two rotary movements. Considering now the forward movement of the limb, the first rotation about an axis across the body tends to move the point of the gnathobase posteriorly and ventrally (away from the floor of the food groove); the second about an axis normal to the body, tends to move the gnathobase laterally and anteriorly. The combined action of these rotations, I believe, results in the gnathobase fitting closely into the exit groove throughout the whole of its movement.

The apex of the triangle of filter setæ, fig. 22, limb 7, is approximately at the centre, about which the gnathobase pivots, while its curved base coincides with the hinder margin of the exit groove. Hence it follows that, as the gnathobase pivots backwards, the exit channel is at every instant covered by this triangular filter.

On limb 7, fig. 22, it can be seen that the triangle of the filter setæ covers an area of setules on the wall of the food groove. The direction of the setules, indicated by arrows, coincides exactly with the length of the filter setæ, and from fig. 23 *a* and *c*, it can be seen that they project between the latter.

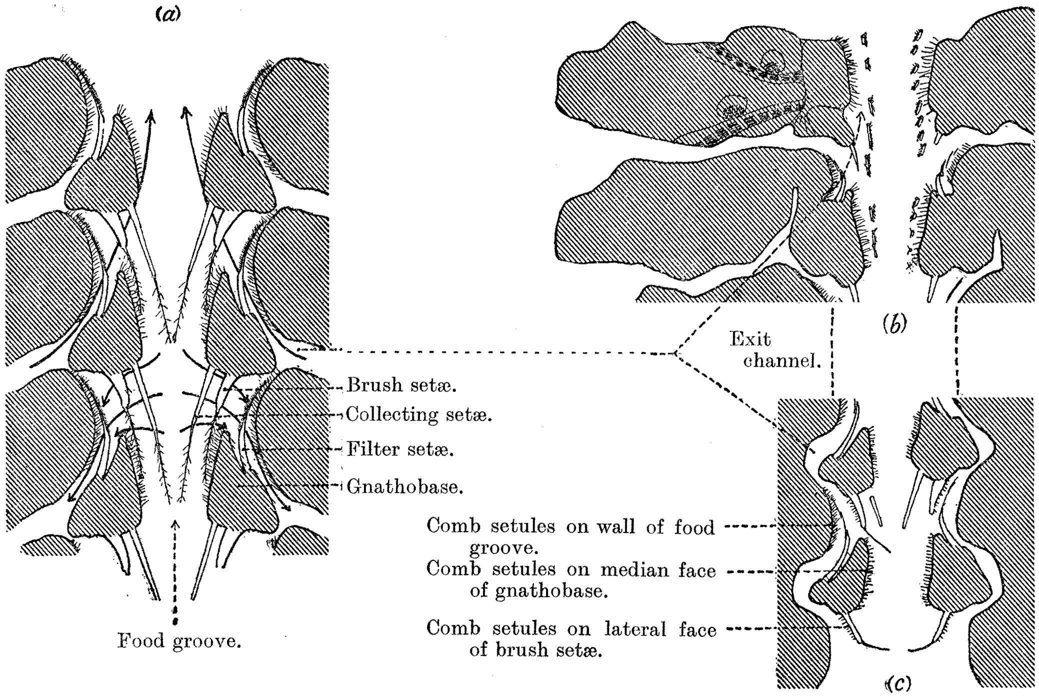

FIG. 23.—(*a*) Diagram of frontal section through gnathobases of *Estheria*, showing filter currents and anterior food current, and also the relation of the setæ to each other and to the setules on the wall of the food groove and on the median faces of the gnathobases; (*b*) and (*c*) Frontal section through the food groove of *Estheria* showing above, the anterior gnathobases cut near their attachment to the limb and below, more posterior gnathobases cut near their tips. The top left-hand gnathobase shows the musculature which rotates it about the axis of the limb.

The conditions of these filter setæ are the same as those of the proximal end of the basal endites of the Anostraca, both as regards position and related setules, and hence, on the forward movement of the *Estheria* limb, food particles must be strained off on to these filter setæ, at the same time being scraped off by the underlying setules. The food particles will then be blown forwards by the oral food currents on the next back-stroke of the limb.

This method of food collection is probably the most efficient and also, as will be seen later, the most primitive. I have reasoned out its mechanisms by comparison with the Anostraca where direct observation is possible, but I believe that the other setæ on the gnathobase also assist in food collection and that their method of functioning can be deduced with a considerable degree of certainty.

I have previously explained (p. 310) that the second to sixth endites are provided with two sets of setæ, a posterior row for filtering and an anterior comb row for scouring the filter setæ of the limb in front. Now, by comparing the second endites of limbs 2, 3 and 4 in fig. 22, it will be seen that the most proximal setæ of the filter row—about the first sixteen in the limb figured, marked by a dotted line on limbs 2 and 4—are not served by scouring setæ of the limb behind. These setæ, occurring at the base of the limb are near the region of maximum suction, and hence a considerable amount of food will be deposited on them; also, as in the Anostraca (p. 278), there will be little or no tendency of the particles to be blown off the setæ on the next backstroke of the limb, and the residue will remain to be removed in some other way.

On the forward movement of the limb the endites will be sucked against the limb behind. The proximal filter setæ which we are considering will press against the median face of the gnathobase of the limb behind. Now this is armed with setules, limb 5, fig. 22, which take the place of the comb setæ and scrape off the residue. This, however, is not scraped into a food groove and hence there will be no current to blow it forward but is, I believe, swept off by the peculiar brush setæ of the outer row on the hinder edge of the gnathobase in front. The bottle brush ends of the more distally placed of these setæ lie against the inner face of the gnathobase of the limb behind, fig. 23, *a*, and extend only over that area of the gnathobase which is covered with the setules.

Further, when the limb is at the end of its forestroke, the mat of setules will be charged with particles scraped off the endite setæ of the limb in front during that forestroke, but also, during the forestroke, the gnathobase of the limb in front will have rotated about an axis normal to the body. This rotation causes its hinder margin to move laterally and brings the brush setæ close up against the inner face of the gnathobase behind, so that they are caused to press on the mat of setules behind and any particles deposited there must be swept downwards towards the tip of the gnathobase; finally, they will be brushed off the tip on to the floor of the food groove.

Here they will be swept forward by the more proximal of the same series of brush setæ which, as I have explained (p. 313) and attempted to figure, fig. 22, limbs 3 and 4, project backwards and inwards, thus lying obliquely across the floor of the food groove.

The filtered food thus consists of two portions, one the residue collected by the filter setæ on the anterior edge of the gnathobase, and the other collected by the brush setæ on the hinder margin. The former is blown forwards by the currents from the exit grooves, and so is the latter, although at first sight it might seem as if the residue were passed forward from limb to limb. This, however, cannot be as there is no structure for removing the filtered residue from the brush setæ of one gnathobase and depositing it on the gnathobase in front. The method by which the brush setæ are relieved of their residue can best be explained by considering limbs 4, 5 and 6 in fig. 22. Considering limb 5 at the limit of its backstroke, limb 6 will have just commenced to move forward and water will be forced out from the inter-limb space between limbs 5 and 6 down the exit channel. Now this channel opens in just that region occupied by the proximal brush setæ of the gnathobase of limb 4 and these setæ project postero-medially. The outflow of water from the exit groove enters from a postero-lateral direction so that the brush setæ lie across the current and will thus be forced apart and blown clear by each blast from the exit channel.

The only setæ which I have not dealt with are the inner set of straight setæ, which I call the collecting setæ. In the oscillation of the gnathobase, these must roughly move up and down towards the floor of the food groove. Their armature of setules is too coarse for dealing with fine particles, and I believe that they catch the larger particles from the current passing between the limbs to the food groove and pass them directly on to the proximal brush setæ to be dealt with along with the filtered residue.

So far, except for the last paragraph, I have dealt only with the mechanism by which *Estheria* abstracts minute particles from the water currents, but *Estheria* is a mud-living form and at times comparatively coarse particles must be disturbed by the currents, and if not too large, sucked into the median space between the limbs. These are dealt with by a separate mechanism on the hind limbs.

All the trunk limbs of *Estheria* slope backwards, the angle with the body becoming more acute in the posterior limbs. In their oscillations the limbs thus all beat towards the hind end of the food groove, and I believe that large particles are gripped by the comb setæ of the second to sixth endites and passed in this direction. The comb setæ it will be remembered, project inwards and backwards while the filtratory setæ project directly backwards. Large particles will therefore be caught on the tips of the stout comb setæ and will not come into contact with the more lateral filter setæ.

The last twelve limbs, or thereabouts (there are twenty-seven trunk limbs in all), show a gradual but marked change in structure from the more anterior limbs. The filter setæ on the second to sixth endites lose their filtratory armature of setules and become brush setæ, that is, the setules project all round the setæ. They are naturally shorter as the limbs themselves are shorter and also more crowded and this makes them more robust. The comb setæ similarly are much shorter and are, in fact, powerful claws.

The gnathobase shows the most marked change in structure. It becomes relatively much larger and actually larger than the second endite. The conspicuous triangular claw process diminishes so that its base, from which the filtratory setæ arise, becomes more and more terminal until at about the twentieth or twenty-first limb the claw process, as such, does not exist, while the blunt claws which terminate the claw process become actually larger and point medially rather than anteriorly. The filter setæ, brush setæ and collecting setæ, all diminish rapidly in numbers from the fifteenth limb backwards. Extra claws appear on the median face which may represent transformed collecting setæ but, in addition, a group of new claws appears near the upper hinder margin of the gnathobase. The setules on the median face become irregular and comparatively long.

In this way the gnathobase of the twenty-second limb consists of a powerful spinous jaw process pointing inwards and slightly forwards. Behind this all the limbs become very small and all the structures are simplified.

These posterior heavily armed limbs form the masticatory apparatus of *Estheria*. Larger food particles are gripped between them and as I have explained, passed down on the backstroke of the limb to the food groove, during which process they are torn and crushed by the inwardly pointing claws holding them. The final crushing, however, is carried out by the immense armed posterior gnathobases. Now these point forwards and, as in the most anterior limbs they move forwards as the remainder of the limb is on its backstroke. The mass of food will thus be pushed forwards and will be ground by the opposing gnathobases during the process, but it does not move forwards quickly, as there is no anteriorly directed food current in this region. There are no exit grooves from the inter-limb spaces and, more important, the floor of the food groove is transversely ridged, not smooth as in the anterior region, and this ridging would effectively stop any such anterior current.

By the time that the crushed food mass reaches the sixteenth trunk limb, I believe it is sufficiently triturated to be passed forwards. If a large particle did pass forwards, that is, if the posterior limbs could not masticate it, I imagine, that it could be removed by the caudal furca.

The food mass is now transferred forwards by the more anterior gnathobases. This is carried out by the brush setæ aided by the currents from the inter-limb spaces which commence in this region.

The claw processes of the anterior gnathobases must also assist in pushing forwards the food mass but I believe that this function diminishes as the food passes forwards. In fact, I do not believe that the main function of the claw process is gnathobasic. If it were so, it is difficult to see why it has lost the claw armature which is so conspicuous in the hinder limbs, for its terminal claws, in fact, the only claws it retains, progressively diminish in actual size in the anterior limbs although the gnathobase itself becomes considerably larger.

The function of the claw process is, I believe, to assist in directing forwards the spurts of water leaving the inter-limb spaces. The exit channels from these spaces are covered on their median side by the gnathobase and water is forced from the inter-limb space when the limb is at the end of its backstroke. In this position the gnathobase with its claw process will just cover the whole of the length of the exit groove. The shape of the exit groove itself directs the water forwards but the presence of the covering gnathobase prevents the water passing medially, and at the same time, converts the exit groove effectively into a tube and so makes the current more powerful. In addition, the claw process of the gnathobase probably protects the exceedingly delicate filter setæ from the coarse mass of food passing forwards to the mouth.

NOTOSTRACA.

In this order I have only had the opportunity of examining one living specimen of *Lepidurus*, which I reared from the egg.

The feeding mechanism differs greatly from that of other phyllopodous Branchiopoda. While all the other forms I have described are mainly, and certainly primitively, filter feeders both *Apus* and *Lepidurus* feed mainly on large food particles (LUNDBLAD, 1920, p. 81).

The lateral aspect of the trunk limbs is similar to that of typical Branchiopoda, that is, the exite series project backwards, overlapping similar structures on the limb behind and forming a lateral valve to the inter-limb space, while the tips of the limbs similarly curve backwards. The limbs are very close together so that any movement relative to each other must produce large changes in the volumes of the inter-limb spaces, and they exhibit a very marked metachronial rhythm of the typical type. Hence there must be a continual suction of water into the inter-limb spaces and an outflow laterally between the exites just as in other Branchiopoda.

The peculiar type of the feeding mechanism is due to the shape and arrangement of the endite series. The limbs are well-known (see LANKESTER, 1881) and I have not figured them. The endites are marked off from the corm of the limb to a much greater degree than in any other Branchiopod. The most important difference, however, from the point of view of the feeding mechanism, is that they do not project markedly backwards and overlap the corresponding structures of the limb behind, for apart from the gnathobase, they project approximately medially.

Considering a typical trunk limb (see CALMAN, 1901, p. 39) of *Apus* and *Lepidurus*, each endite (omitting the gnathobase) consists of an elongated lobe ending in a knob heavily armed with short stout spines and flattened in the plane of the limb. Across the front and hind surfaces of each lobe a complex row of longer spines project obliquely towards the middle plane. The hinder spines of one endite thus touch the front spines of the corresponding endite of the limb behind.

In the rhythmical movements of the limbs water which enters the inter-limb spaces must pass between these endite series, all other directions being closed by valves. The armature of setæ on the endites can thus retain coarse particles from this stream but there is no separation of fine particles as in other forms. The separate spines are filter setæ in that they are armed in a typical manner with setules, but the latter are short and do not touch those of the neighbouring seta, and hence the row of setæ as a whole does not present a filtratory plate.

The rhythmical movement results in a relative movement of the limbs and hence of the endites, to each other and, as a result, the endites automatically clean each other, a particle retained on the hinder setæ of an endite being scraped off again by the front setæ of the endite behind.

The first eleven pairs of limbs project markedly laterally from the body so that all their endites are clearly visible in ventral view. In their oscillation they beat backwards and inwards towards the hind end of the body, the endites slightly projecting backwards over the limb behind. Coarse particles are thus handed on from limb to limb towards the hind end and at the same time, towards the middle line.

Behind the eleventh limb the limbs project more ventrally than laterally so that in their backstroke they beat, on the whole, towards the body. In this region particles will be passed down towards the mid-ventral line.

The endites of the twelfth limb and those posterior to it show a gradual change. The terminal knob of the endite becomes relatively larger so that in the hindmost limb the endites consist mainly of this knob and its armature of stout spines, while the rows of spines on the front and hind surfaces become irregular and merged into these terminal spines. I believe that when coarse particles are abstracted from the water currents by the anterior limbs, they are passed back to the hinder limbs and in this region the main function of the endites is to triturate the food so obtained.

The food collected in this region will now be passed forwards from limb to limb by the gnathobases. They are devoid of filter setæ, but are armed with a group of stout forwardly directed spines, fig. 24. Each gnathobase projects obliquely forwards and overlaps the gnathobase in front on its median side; hence, as each limb beats backwards its gnathobase projects forwards pushing its collected food mass level with the gnathobase in front, then as this same limb commences its forestroke just before the limb anterior to it, it will comb off its food mass on to the gnathobase of the limb in front. There is thus a direct transference of food from gnathobase to gnathobase forwards towards the maxillæ.

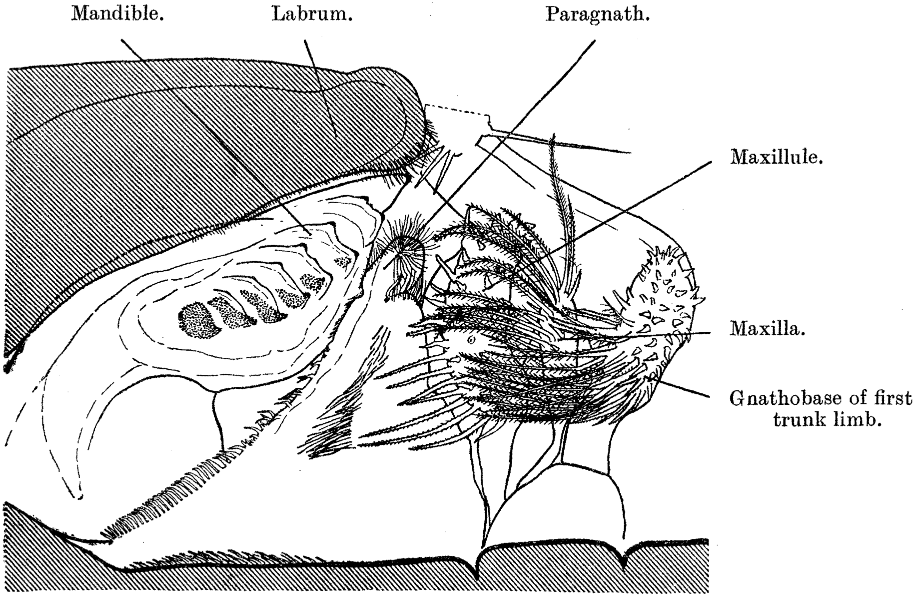

Fig. 24.—Median view of the mouth parts and gnathobase of first trunk limb of *Lepidurus macrurus*. (Drawn by Miss F. M. C. Leak, Ph.D.)

There is no marked food stream along the mid-ventral lines. I have been unable to detect any current at all, but LUNDBLAD (1920, p. 82) describes a weak forward current; it is not clear, however, that he was dealing with a current and not with a forward transport of the carmine particles he was using. From the anatomy of the limbs it could be predicted that no such current would exist. The forward current in other forms is due to the sudden expulsion of water from the inter-limb space through a channel directing it forwards into the deep food groove. In the Notostraca the whole of the median side of the inter-limb space is always open as the endites do not curve backwards to close it, and furthermore, the endites are of such a shape that they could not completely close the space. Also, there is no food groove and this is a character in which the Notostraca differ from all the forms with which I have dealt. The limbs are attached on the flat ventral surface of the body on either side of the middle line and not on the top of the walls of the median groove. Another morphological point which indicates the absence of a forward current is that the median cuticle is ridged, each ridge marking a segmental boundary. This corresponds to the hinder part of the food groove of *Estheria*, and, as in that form, the ridges may help in removing the food from the gnathobases.

The maxillæ are similar in structure to the gnathobase and overlie the proximal parts of the maxillules which are also armed with setæ pointing towards the mouth. The food passed forwards by the gnathobases is transferred to the maxillæ and maxillules direct on to the mandibles.

In addition to abstracting coarse suspended matter from the surrounding water, the Notostraca can feed on large food masses (LUNDBLAD, 1920). In this process, the anterior trunk limbs curve towards the mouth and hold the food mass against the mouth parts. The endites of the anterior limbs can probably bite into the food mass, but I believe the most important jaws are the distal parts of the maxillules where the stout setæ point directly inwards forming a definite biting jaw, fig. 24.

DISCUSSION.

Apart from the work of STORCH, very little has been published on the feeding mechanisms of the Branchiopoda. NAUMANN (1921) has dealt with *Sida* and *Holopedium* but his analysis consists mainly of a description of the feeding currents, while LUNDBLAD (1920) described briefly the feeding mechanisms of *Tanymastix* (Anostraca), *Estheria* (Conchostraca), and *Lepidurus* (Notostraca). Neither of these workers, however, go into any detail as to the mechanism by which the water currents are produced. They both agree that in the Anostraca and the Ctenopoda there *is* a forwardly directed current along the mid-ventral line towards the mouth, but LUNDBLAD ascribes this to the sweeping action of the gnathobases. LUNDBLAD also describes the method by which the comb setæ on the limbs of *Estheria* scour the residue off the filter combs, but in *Tanymastix* he appears to consider that the isolated EKMAN'S setæ are more important in this respect than the mat of setules at the base of the filter setæ.

Recently ERIKSSON (1928) has described the feeding mechanism of *Sida*, but, as he has incorrectly described the metachronial rhythm of the limbs—he states (p. 103) that they appear to move in waves which pass backwards instead of forwards—his results are of little value.

STORCH, on the other hand, in 1924, published a lengthy study on the feeding mechanism of that most specialised of all Branchiopoda—*Daphnia*—and followed it up with a series of theoretical papers on the Branchiopoda generally (1925, *a*) and on the Trilobita (1925, *b*, 1926). Finally (1929) he published an experimental analysis of the feeding mechanism of *Sida*. Now all these later papers are based on his first work on *Daphnia,* so that STORCH has attempted to derive the simpler processes from the most complex. While this method is legitimate, it is, I maintain, both difficult and dangerous. The method of comparative functional morphology should be where possible, to investigate the simplest processes first, and from them to evolve the more complex. Otherwise, any mistake or misinterpretation in the investigation of the highly specialised processes is apt to find its way into the analysis of the more primitive functionings. On the other hand, a mistake made in the study of a primitive mechanism is almost certain to become evident in any attempt to study more specialised processes which have evolved from this simpler process. Now it is with STORCH's original description of the feeding mechanism of *Daphnia* that I am in disagreement, so that a criticism of his later papers would clearly be of little use, and it is to this first paper that I am confining my remarks.

A concise description of STORCH's views is to be found in his article on the Cladocera (1925, *c*, pp. 35–36). He states that during the forward movement of the limbs—by this he means the third and fourth trunk limbs—water is sucked into the inter-limb spaces because of the low pressure in them ; they are enlarging, their valvular system is closed and hence the inter-limb space will be a suction region. This agrees so far with what I have described, but then he states that on the backstroke of the same limbs their edges, that is, the edges of their gnathobases, come together in the middle line and so enclose the water in the median space (1924, fig. 20 or 1925, *c*, fig. 6). The filter combs press on this water and, the pressure in the inter-limb spaces being normal because their valves are open ; "... in den Seitenkanälen mit ihren nun geöffneten Ventilen Normaldruck herrscht . . ." (1925, *c*, p. 36), there is now high pressure in the median space compared with that in the inter-limb spaces. Hence, water is pressed from the median space into the latter, and the filtration process is thus continuous. During the forward stroke of the filter limbs, it is suction filtration and during the backstroke it is pressure filtration. ERIKSSON (1929), has accepted this view.

There are two important points in this description with which I cannot agree. As the third and fourth trunk limbs beat back the pressure in the inter-limb spaces behind them *cannot* be normal. It must be high pressure, that is, it must be higher than the surrounding pressure for the limbs are forcing the water backwards out of the open valves. It is physically impossible for a limb to press its way through water without producing a region of high pressure on the side towards which it is beating: even with a slow-moving limb this condition must obtain. Or, if there was no high pressure during this phase of the limb movement, there would be no force to produce the posterior outflow of water, since water at one level will only flow from regions of relatively high pressure to relatively low.

It may be argued, however, that while there is high pressure behind the limbs as a result of their backward beat, the pressure in the median space due to their opposing gnathobases pressing on each other is still greater. But I can find no evidence that they do come together during their backstroke. The point can be settled by anyone studying a living *Daphnia* on its back, or, better still, a living *Simocephalus* which naturally feeds on its back. I have observed both, and found that while the limbs move in and out to a slight degree during their backwards and forwards movements their edges never touch. This is evident from the fact that it is possible to observe the floor of the food groove accurately throughout the limb movement. If the limbs touched at any time during their motion this would cut off the view of the food groove, and with limbs moving with such a low frequency as those of *Daphnia*, an interruption of this sort would completely obscure the food groove. Not only can the food groove be seen, but the tips of the moving filter combs can be watched.

If the limbs moved with very high frequency such as do those of *Diaptomus*, it would be possible to see through them, though the view obtained would not be clear, but with limbs moving with the frequency of those of *Daphnia* the " flicker " produced is sufficient to obscure all details underlying them.

It is difficult to understand how STORCH came to his conclusions, because he most emphatically denies the existence of a forward current in the food groove (1924, p. 230). If he is so certain of this he surely must have seen clearly into the food groove, but, on the other hand, if the gnathobases come together in the middle line during the backstroke, he cannot have done so.

STORCH believes that the residue filtered on to the filter combs is sucked towards the mid-ventral line and transported to the mouth, not by a food current, but by the setæ on the gnathobasic lobe of the second trunk limb. The middle group of setæ on the gnathobasic lobe, he states, sweep the food forwards because of their curvature and the fact that they move in the arc of a circle, but only in the case of the anterior three or four does the lower part of the arc through which they swing, point very slightly forwards; all the others sweep backwards on their downstroke towards the floor of the food groove. But even supposing that STORCH were correct, the hindmost of the middle group of setæ only reaches as far as the anterior edge of the fourth trunk limb gnathobase. Thus all the residue behind this, that is, all that collected on the fourth limb and on more than half of the third limb, has to be transported forwards somehow to reach the middle group setæ.

This he states is carried out by the posteriorly directed spines which scrape off the residue and transport it forwards; " . . . die Partikelchen flott machen und nach vorn kehren" (1924, p. 230). How setæ beating backwards and down into the food groove without any forward component in their motion can beat particles forwards he does not explain. By comparing figs. 14, *b*, 13 and 20, the path swept by these posteriorly directed setæ can be seen and clearly, while they can beat particles backwards there is no possibility of their sweeping them forwards. A comparison of fig. 14, *b*, with fig. 16, which represents the first and second trunk limbs of *Holopedium*, emphasises this point. On the second limb of *Holopedium* there is a gnathobase similar to the gnathobasic lobe of *Daphnia*. Its long posterior spine beats backwards and downwards into the food groove, but on the first there is a gnathobase on which, while it is otherwise similar, a posterior spine has curved forwards; now this cannot function in any other way than in pushing food forwards.

The account given by STORCH of the method by which food is transferred to the mouth is the second great difference between our views, for he denies the existence of a forward current not only in *Daphnia* but in all other Branchiopoda. As far as I am aware, STORCH is alone in this view. Thus LUNDBLAD (1920, p. 41) in *Tanymastix*, and NAUMANN (1921, p. 9) and ERIKSSON (1928, p. 105) in *Sida*, all describe a forward stream to the mouth. In addition, as I have explained above (see p. 274), I demonstrated by experiment a forward current in *Chirocephalus*.

STORCH, however, objects to my experiment on the grounds that injection of the methyl blue will interfere with the rhythmical movement of the limbs. A repetition of my experiment would have shown him that this is not so, as any of the inter-limb spaces can be injected and no disturbance of the rhythm of the limbs is produced. Then he makes the remarkable objection that the experiment would produce a region of high pressure in the inter-limb space, but with an aqueous solution of methyl blue, whose viscosity must be practically the same as that of water, it would be impossible to maintain a region of high pressure in a mass of water for more than a fraction of a second. I stated definitely that I simply filled the inter-limb space—I did not say that I forced a continuous stream through it; if I had done so, then STORCH's criticism might have been admissible. However, in his further remarks, he maintains that if any such current exists, it would be produced by the sweeping action of the proximal setæ of the gnathobases as they move forwards on the backstroke of the limb. "Dasz die Schübe immer in Rückschlage erfolgen, ist in Einklang mit meiner Deutung" (1929, p. 55). But again, this is not what I said. I stated that the anterior current is produced in a series of jerks, "each jerk coinciding with the *end* of the backstroke of the limb behind which the dye has been injected" (1928, *a*, p. 811)—not *during* the backstroke as STORCH misquotes me. It is obvious that I might have stated with equal truth, that the spurt coincided with the beginning of the forestroke of the limb in front of which the dye had been injected. If I had done so, STORCH could not have brought this argument against me.

I have now pointed out the two main differences between STORCH's views and my own. Firstly, the nature of the movement of the third and fourth trunk limbs of *Daphnia*.

This would be a matter of detail were it not for the fact that STORCH in his investigation of other Branchiopoda assumes that all filtratory limbs move in the same way as those of *Daphnia*. Now if STORCH with his elaborate cinematographic apparatus would photograph a Daphnid on its back and focus, not on the edges of the third and fourth trunk limbs, but on the floor of the food groove, I am convinced that he would always obtain a clear image. This would be a critical experiment as a camera has no "after image," so that, if at any instant the third limbs came together in the middle line, this would obscure the food groove and it would be recorded on the photograph.

The second difference is as to whether or not an anterior food current exists along the food groove of the Branchiopoda. The results of my experiment on *Chirocephalus* satisfy me and I consider that before disputing the existence of this current, STORCH should at least attempt to repeat my experiment.

Throughout this paper I have accepted the general view that the gnathobase is simply the most proximal of a series of lobes, the endites, arising from the inner margin of the limb, and this was the view adopted by LANKESTER (1881) when he defined a gnathobase. The posterior limbs of *Lepidocaris* are armed with endites which are all alike, while on the anterior limbs, the basal endite has been transformed into a gnathobase. In an embryo *Sida* the gnathobases appear as rounded knobs indistinguishable from the distal endites. In certain Ostracods, *e.g.*, *Conchoecia*, the gnathobases, together with the adjacent endites, become modified in a similar fashion to form composite jaws. There is thus considerable evidence that the gnathobase is a modified endite. It would be expected then that if the endites show a common structural plan, this would also be visible in the structure of the gnathobase.

The simple endite of the primitive Branchiopod limb was undoubtedly a flat lobe. The elongated stalked endite of *Apus* is a specialisation; it is unique, but then the Notostraca are unique among the Branchiopoda in bearing limbs which project laterally from the body instead of ventrally in parallel rows.

The whole limb must have been slightly concave posteriorly so that the endites projected backwards to a small degree. This, I think, is a safe assumption as there is no such thing as a flat phyllopodium; even in *Lepidocaris* the inner margin of the limb is curved backwards. The posterior concavity must have increased the efficiency of the limb to force water backwards.

The current of water so produced was probably originally a respiratory stream. The swimming activities would have been carried out by the biramous antennæ which I consider must have been present in the ancestral adult Branchiopod. They are present in *Lepidocaris* and to-day occur in adult Conchostraca, Cladocera and in all Branchiopod nauplii. The increasing power of the trunk limbs to produce a respiratory stream, however, led to new possibilities for the mass of water set moving in this way had a momentum. Hence, if it was thrown backwards it would automatically move the animal forwards and so the respiratory stream became the respiratory-swimming stream.

Probably, along with the development of the posterior concavity of the limb, a rearrangement took place so that the exopodite, together with the exites, came to act as a lateral valve (CANNON, 1928, p. 818). The importance of this development was that it forced the water to take a definite path and again, this may have been primarily an improvement of the respiratory system. On the forward movement of the limbs, water entering the enlarged inter-limb spaces could not enter distally because of the endopodite flapping down on the limb behind. Similarly, it could not enter laterally because of the lateral valves and so it was forced to pass from the median space and, on the backstroke of the limb, for the greater part, found its exit laterally and distally from the now open valves. A stream of water was thus produced in one direction over the gills.

Now since the endites are curving slightly backwards any setal armature that they may carry tends to project backwards across the median entrance to the inter-limb space. Hence, water sucked into this space must pass through, or at least across, any such armature.

From a comparison of the endites (omitting for the time being the gnathobase) of the series of forms I have described, it is clear that the setæ on the endites of *Lepidocaris* represent a type from which all others can be derived. Each endite carries a row of setæ on its posterior edge sloping backwards, another on its anterior edge which slopes back to a smaller degree, and, in between, a group of powerful spines or claws on the ridge between pointing more or less directly inwards. This arrangement is found again in the Notostraca, the difference here being that the ridge of the endite has extended inwards leaving the anterior and posterior rows of setæ in their original position, but carrying the claws on its tip.

In all the forms, apart from the Lipostraca and Notostraca, the posterior row of setæ has developed enormously to form the backwardly directed filter setæ

In the Anostraca the front row have become transformed into a mat of comb setules. The claws have either disappeared or are represented by the isolated stout spines which occur near the bases of the filter setæ and are called EKMAN'S setæ.

In the Conchostraca the claws have disappeared but the front row still persists as a row of powerful setæ pointing backwards and inwards.

In the Cladocera Ctenopoda also, the claws have disappeared, but they are interesting, in that they show a series of stages in the transformation of the front row setæ into a mat of comb setules. The endites of *Sida* are armed with a front row of short but comparatively stout comb setules, those of *Holopedium* are finer and more closely set, while those of *Diaphanosoma* are extermely fine and so close together that they form a mat.

There is thus, in my opinion, sufficient morphological evidence from which to deduce that there was a definite grouping of setæ on the primitive endites, and further, because of this arrangement, that the endites must have acted as food gatherers. Particles carried on the respiratory-swimming stream would be held by the zig-zag of anterior and posterior setæ—if they were large enough. Smaller particles would pass through with the stream. The limbs moved with the typical metachronial rhythm (CANNON, 1928, p. 816) and hence particles so carried would be passed backwards from limb to limb, each limb combing the limb in front as it commenced its backstroke. At the same time the limbs in their backstroke would beat towards the body so that particles would gradually gather in the hinder region of mid-ventral space between the limbs, that is, in the manner that *Apus* gathers its food. The claws, again as in *Apus*, may have ground up the residue in its passage between the limb rows.

Now I maintain that the ancestral Branchiopod certainly, and most probably, the ancestral crustacean, was a minute form. My reasons for this are first, that it is impossible to consider any limb of a modern crustacean other than that of a minute form, which is sufficiently unspecialised from which to derive all other crustacean limbs. It will scarcely be denied that all such limbs are derivable from a common type, but any modern limb is either large and specialised as in the Anostraca, or else small, but occurs on a form which is so specialised in itself as to preclude the possibility of its being an ancestral form, *e.g.*, *Daphnia*. And secondly, a comparison of the internal anatomy of the various orders of Crustacea shows that this is based on quite a simple plan. Thus in minute forms the gut, heart, excretory organs, musculature, etc., are all comparatively simple and similar. For major differences we have to go to larger Crustacea ; in other words, it is possible to derive the various differences among the Crustacea from a hypothetical minute form, whose anatomy we base on our knowledge of modern minute forms, while this is not possible if we start with a large form.

I consider that in the Branchiopoda the various lines of evolution were brought about primarily by an increase in size for this led to a change in the type of particle sucked in between the limbs. In the small ancestral form obviously only the minutest particles could be sucked in, but with increase in size larger particles in addition would be drawn in. Two distinct lines of evolution then took place, both involving a specialised method of transport forwards of the filtered residue to be used as food.

The first was the development of a gnathobase such as occurs in the Notostraca. This was brought about simply by the enlargement of the basal endite which turned forwards so that it came to overlie the similar structure on the limb in front. As the limb moved backwards the gnathobase moved forwards, only slightly, but sufficient to reach the gnathobase in front. Directly the limb commenced to move forwards the gnathobase would move backwards and so leave its residue on the setæ of the gnathobase in front. This gnathobase would repeat the process and so the collected residue would pass forwards.

This is as near a true gnathobase as can be found in the Branchiopoda, but even so, it does not agree with LANKESTER's original definition. Its essential feature is that it hands on the residue from one gnathobase to the other on the same side, but it does not work against the gnathobase of the opposite side as a jaw. Its function was not primarily masticatory. This process was carried out where necessary by the claw processes of the second and more distal endites. Obviously, if any pair of gnathobases were to function as true jaws, this would block the passage towards the mouth for the time being and lead to congestion posteriorly. Such gnathobases have been developed for example, on the hind limb of *Estheria* (p. 317) but this form is a true filter feeder, and filtered food as well as large particles which require breaking up enter the food stream along the whole length of the animal, so that congestion in the hinder region is of little importance.

As to the armature of this gnathobase, I can say very little. In *Apus* and *Lepidurus*, the gnathobase is covered with an irregular group of powerful spines pointing forwards, but it must be remembered that the modern Notostraca are comparatively large and any primitive arrangement of spines on the gnathobase has probably been lost. I think all that can be said is that the primitive arrangement of setæ became lost in the development of a group of stout spines. The gnathobase had one function only and hence it would be expected that only one type of setæ would be retained on it, but it is possible that, since the food accumulated more at the hind end of the body, before its transference to the mouth, than further forwards, the claw process of the gnathobase may have persisted or even enlarged on the hindmost limbs, but there is no direct evidence for this.

The second line of evolution was quite different from that which led on to the Notostraca, and it was brought about by the development of a food groove. The Branchiopoda, with the exception of the Notostraca and the Cladocera Gymnomera, and possibly certain specialised Daphnids, are characterised by the possession of a deep gully along the mid-ventral line to the tops of the walls of which are attached the limbs. This character, as far as I am aware, differentiates these Branchiopoda from all other Crustacea.

The ventral gully developed, I believe, to accommodate the food collected by the endites. Obviously the development of such a groove would place the food below the level of the attachments of the limbs and therefore below the level of the first endite, so that as the food groove evolved there must have been a compensatory development in the method of transport of food to the mouth.

This, I consider, was brought about by the modification of the first endite into a gnathobase of a type from which evolved the gnathobases of all those Branchiopoda possessing a food groove.

I have explained above that owing to the posterior concavity of the limb all the endites projected slightly backwards. As the food groove developed, so the basal endites projected backwards and downwards into it, and this was brought about by a rotation of the axis of the endite. While its lower end remained stationary its upper end extended backwards and towards the body wall. In this way the gnathobase came to overlie the gnathobase behind—the opposite arrangement from that of the Notostraca.

During this development, I believe the claw process was the structure of the greatest importance and this enlarged. It functioned simply by pushing food forwards in the food groove, that is, as the limb beat backwards the claw process on the gnathobase swung towards the body and slightly forwards.

Now I have explained (p. 275) that, owing to the metachronial rhythm of the limbs and to the shape of the inter-limb spaces, maximum suction into those spaces takes place at the base of the limb, that is, in the region of the gnathobase. If, in the development of this gnathobase the claw process alone had persisted and the posterior and anterior setæ disappeared, as might be expected if it were to function merely as an instrument for pushing the food forwards, this would have left a gap unguarded by setæ in just that region of maximum suction. Accordingly, as the food groove developed, that is, as it increased in depth, not only did the claw process extend down into it, but the posterior setæ also grew down against its walls. They increased in length to such an extent that even when the limb was in its anterior position, the region of maximum suction into the inter-limb space was guarded by them. They then became typical filtratory setæ.

This development I have explained, led to a gnathobase being covered over by the gnathobase in front, but it would only be the hinder corner of the gnathobase which could rest against the gnathobase behind. Clearly, the anterior part equal in length to the distance between two successive limbs rests against the wall of the food groove. Now the latter developed an armature of setules which projected between the hind row setæ of the gnathobase and combed off its filtered residue.

The front row setæ of the developing gnathobase must have given up their original function. By the change of axis of the basal endite they were placed in a position such that they could not comb the hind row setæ of the endite in front. They became a horizontal row which in the movement of the gnathobase beat downwards into the food groove. They would thus assist in food collection by sweeping particles into the groove.

Now in *Lepidocaris* we have this state of affairs in the anterior limbs. The distal endites curve slightly backwards while the proximal endite is a gnathobase extending backwards and lying against the gnathobase behind. It carries a large posterior claw on a claw ridge. Its median face is covered with setules which I take to represent the anterior row and on its outer face just outside the claw ridge is a row of typical filtratory setæ extending down against the walls of a food groove, which, although it has not been figured, must have existed to accommodate them.

It is probable that the walls of the food groove developed an armature of setules such as I have suggested. In all modern filter feeding Branchiopoda the food groove is thus armed and I think it extremely probable that these were present in *Lepidocaris*, but I have not been able to settle this point.

The next development of the Branchiopod limb was the marked backward extension of the distal endites and their rows of posterior setæ. That is, the inner edges now projected backwards like the exite series and so completed the bath-shaped limb such as occurs in the modern Anostraca. This ensured that the whole of the median entrance to the inter-limb space became spanned by a sheet of setæ. Now, unless a particle could pass between the setæ of the distal endites it could not enter the inter-limb space and so was confined to the median space. The setæ then became typical filtratory setæ such as occur on the distal endites of all modern Branchiopods.

The anterior row setæ by this development, projected through the posterior rows of the limb in front and so became comb setæ. In the original limb the setæ formed a more or less continuous zig-zag and the backward extension of the endites made this interlocking more close, and, at the same time, flattened out the filtratory surface.

The backward extension of the endites not only converted the limbs into typical filter limbs but it led to the production of the anterior currents in the food groove. These currents are produced, as I have explained (p. 273), by two consecutive limbs approaching each other and forcing the water out of the inter-limb space between them. Until the endites projected backwards the water had a free exit into the median space, but afterwards, this passage was closed as the flat endites extended back from one limb to the other. The only exit now was at the bases of the limbs into the food groove. From the position of the limbs in this phase—the anterior sloping back and just finishing its backstroke and the posterior just commencing to move forwards—the water would be given a forward momentum along the food groove. To accommodate these streams the exit channels in the wall of the food groove developed.

Food was now blown forwards instead of being pushed forwards by the claw process of the gnathobase. The claw thus lost its original function and so either disappeared or became modified in different ways in relation to new functions. This change and all other changes in the gnathobase must be looked upon as results of the swinging backwards of the endites.

In the Conchostracan, *Estheria* (p. 317) the hinder limbs have become modified for mastication, the claw-bearing ridge has enlarged, and all the setæ on the gnathobase, together with the claws, form a complex jaw.

The anterior limbs bear gnathobases which form the ultimate filtratory surface of the limb. The posterior row of setæ have extended to form a curved plate of filter setæ, which accurately covers the exit groove at all positions of the limb; these setæ, I consider, form the most perfect filtratory surface in the whole of the Branchiopoda. The claws on the claw process have dwindled, but the process, that is, the original ridge of the endite, has extended down as a flat plate to act as a protection to the excessively fine filter setæ. At the same time, this plate acts as a cover to the exit groove and so directs and increases the strength of the forward spurt from the inter-limb space.

The hinder margin of the anterior gnathobases of *Estheria* is armed with two sets of peculiar setæ, the collecting setæ and the brush setæ (p. 312) whose function is partly to collect food off the median face of the gnathobase behind and partly to sweep it forwards. Whether or not these setæ represent modification of the posterior row of the primitive endite it is impossible to say. The collecting setæ from their position, may do so, but the brush setæ I am inclined to think are new developments. They are unique in their structure in the whole of the Branchiopoda.

In the Ctenopod Cladocera the main modification of the gnathobase has been the transformation of the claw from a toothed structure which beat downwards and forwards in the food groove into a long setose spine projecting backwards which thus beats downwards and backwards. Its function now is to beat the food into the food groove where it is blown forwards. This change must be looked upon as a definite advance, since the beating down of the posterior spine is an additional method of collecting food for transport to the mouth.

Within the tribe Ctenopoda the gnathobase shows the interesting trend of becoming merged into the distal endites. In the three forms *Sida, Holopedium* and *Diaphanosoma* the hinder corner of the gnathobase swings up towards the edge of the second endite. Thus, the change which led to the development of the primitive gnathobase of *Lepidocaris,* the swinging down of the upper end of the first endite, has reversed.

If this had taken place by the simple shifting back of the gnathobase to its original position, a gap would have opened up at the base of the limb in the region of maximum suction, and so, as this process advanced the filter setæ on the gnathobases became proportionately longer. Thus the filter setæ of *Diaphanosoma* are longer than those of *Holopedium* and those of the latter longer than those of *Sida.*

But the longer the filter setæ, the greater is the filter surface offered, hence this again is a definite advance, as it leads to an increased filter surface. Now the process seen taking place in the Ctenopoda is completed in the Anostraca; the gnathobase has returned to alignment with the second endite, and now forms with it a single filter plate which has reached the limit of its size; no further improvement is possible in this direction.

This view of the relation of the Anostracan limb to that of other Branchiopoda is based on a comparative study of their functions, but EKMAN (1902, p. 15) states that the long proximal endite of the trunk limbs of *Polyartemia* develops by the fusion of two endites, which are distinct in the larva. If this is so these represent the gnathobase and the second endite.

All traces of the claw ridge have disappeared in the Anostraca, and as far as I know, there are no forms which show even a trace of it; if there were, it would be possible to settle at once whether my contention that the gnathobase is the lower part of the proximal endite were correct. This disappearance need not be considered as leading to a decrease in efficiency. As I have stated, directly the distal endites turned backwards the anterior food stream developed and the claw process became superfluous. It is possible that along the Anostracan line it disappeared at this level.

In the Daphnids the evolution of the various limbs must be considered separately. The first and fifth limbs gave up their filtratory function. They retained their primitive rhythmical movements and by altering the phase in relation to other limbs assisted in producing the very definite currents along the food groove to the mouth and through the filter limbs respectively.

The third and fourth limbs specialised as filters. In this, the main filtratory part of the limb, the gnathobase, persisted and enlarged, while the more distal parts dwindled and lost all their filter setæ. In *Moina* the posterior spine of the claw process on the third limb persists to beat the residue off the limb behind into the food groove, but it has disappeared on the fourth limb as the fifth has given up its filtratory function.

In *Daphnia* the enlargement of the gnathobases is enormous. The gnathobase of the third limb has extended forwards to the base of the second limb, and backwards so as completely to cover the fourth limb gnathobase. The posteriorly directed spine is thus useless and has dwindled to a short seta. In addition, the tips of the filter setæ on the third limb where they cover those of the fourth, have developed a modification for cleaning the latter—an entirely new development.

Finally, the second limb has specialised as a food gatherer, sweeping the residue off the filter limbs into the food groove. All the filter setæ on its distal endites have disappeared while those on its gnathobase have become modified as brush setæ combing the anterior filter setæ of the third limb. The posteriorly directed seta of the claw ridge has persisted in *Moina* and sweeps the residue off the filter combs. In *Daphnia*, in addition, a long spine from the second endite has fused with the gnathobase for the same purpose.

The various lines of evolution I have suggested are summarised in fig. 25. This scheme is not meant to indicate a phylogenetic series, but rather to illustrate the various evolutionary trends of the filter systems of the Branchiopoda. Thus it is not suggested that *Diaphanosoma* is in any way ancestral to the Anostraca but the series *Sida-Diaphanosoma-Chirocephalus* exemplifies an evolutionary tendency.

The main division between the filtering systems is between the Notostraca on the one hand and the rest of the Branchiopoda on the other. In *Apus* we have a gnathobase projecting forwards whose function is to push the collected food to the mouth. In all the others, the gnathobase projects backwards, and, what is more important, functions as the main filtratory part of the limb. If a new term is required for this type of gnathobase I suggest the word " Siniobase " (Gr. sinion = a sieve).

The stimulus which led to the transformation of the basal endite into a gnathobase was undoubtedly the swinging round of the exopodite from a terminal position on the limb to a lateral position, where it acts, together with the terminal endopodite, as a valve causing water to pass in one direction from the median space laterally over the gills. This change I consider, was chiefly a response to increased size. In a hypothetical minute form with a double row of flat paddle limbs a sufficiency of oxygen was obtained merely from the comparatively irregular currents resulting from the limb movements. Increasing size did not lead to a more complex gill with a relatively greater respiratory surface. The gills of modern Branchiopoda are, on the whole, as simple as they can be, and therefore, since the respiratory surface did not increase, the supply of water to the gills increased.

Again, in this hypothetical form, I have previously pointed out (1928, *a*, p. 812 and fig. 6, p. 813) that its limb movements would collect food particles between the limb

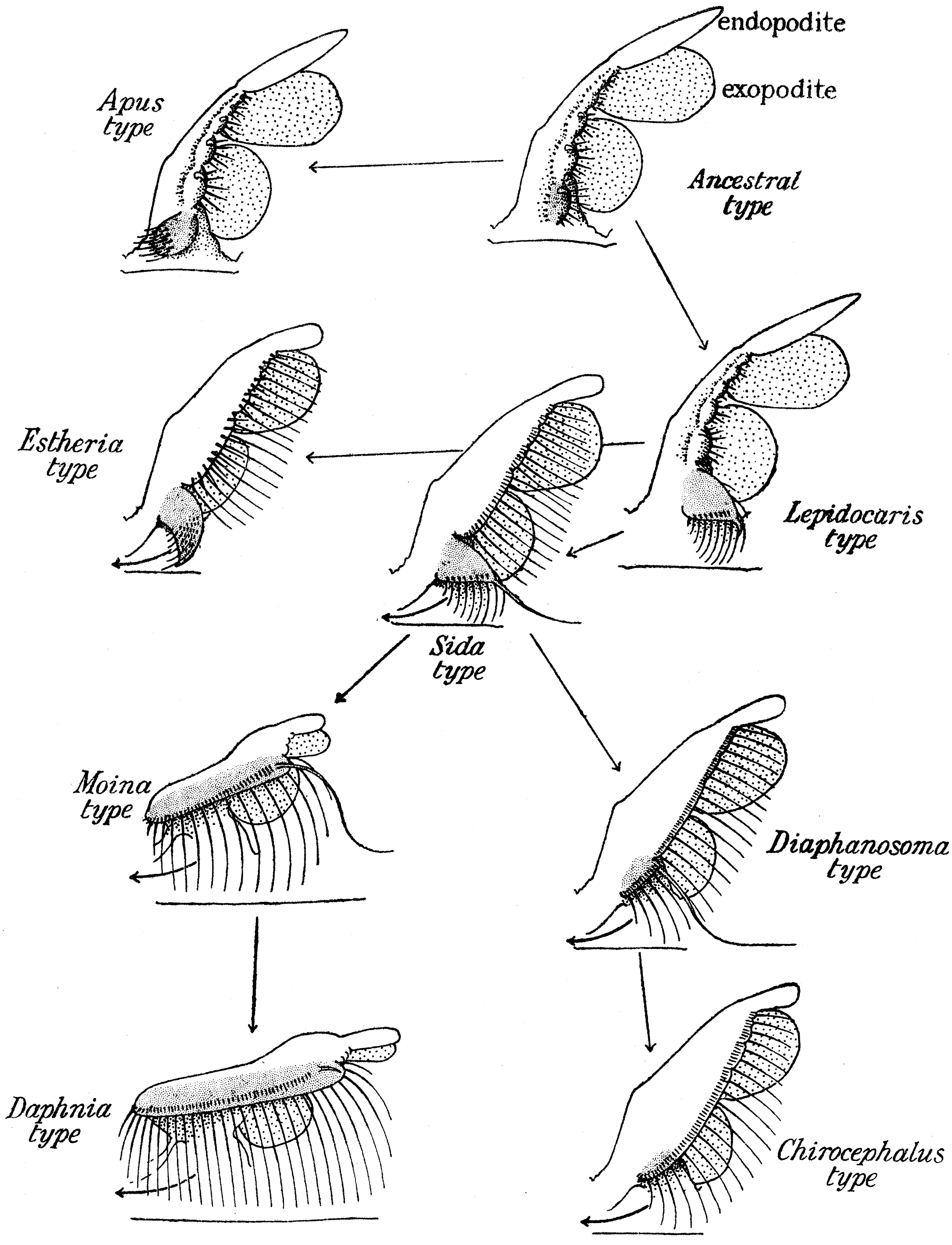

FIG. 25.—Scheme illustrating the suggested inter-relationship of the filtering trunk limbs of the forms dealt with in this paper. The gnathobase in each case is indicated by machine stippling.

and that as a result of the metachronial rhythm of the limb movements " there must have been produced a series of regions of high pressure alternating with regions of low pressure which passed continuously forwards in the mid-ventral space between the limbs and this must have resulted in a transport of the particles towards the mouth." Now the Branchiopoda with the exception of the Notostraca possess degenerate maxillæ and reduced maxillules (see Appendix). It is probable that the common ancestor of the Branchiopoda and Malacostraca possessed a well-developed maxilla which functioned as a feeding mechanism as in modern Malacostraca (CANNON, 1928, *a*, p. 820). The forward stream of particles along the mid-ventral line to the mouth may have been an accidental result of the primary respiratory stream. In fact, that particles were retained at all in the mid-ventral space resulted from the elaboration of the setal armature along the inner edges of the limbs and this may have been primarily to get rid of those particles. The self-cleaning system of setæ on the endites may have been the method of keeping the limbs clean so that the current of water over the gills was not impeded.

Thus in the original minute Branchiopod the anteriorly directed food stream was a secondary result. Judging by modern Crustacean standards it could not have been an efficient method of food collection, as only a fraction of the particles sucked in would find their way into the mouth; nevertheless, it formed part of the total feeding mechanism. Now increasing size resulted in an increased amount of suspended matter and an increase in the individual size of particles sucked in, but at the same time, the effect of the suctions passing forwards to the mouth diminished. Firstly, they would not be so effective with the larger particles and secondly the increased space between the limb rows would lead to much more irregular currents. Hence, as a compensatory result the basal endites became transformed into structures capable of pushing the food particles forwards.

This took place along two distinct lines. Along the Notostracan line the endite projected forwards and became a true gnathobase pushing the residue forwards. This development did not increase the filtratory efficiency of the limbs and hence the early Notostraca probably relied on their maxillary feeding mechanism as much as on the trunk-limb mechanism. Thus the modern Notostraca still retain well-developed maxillues and maxillæ.

Along the other line leading to the remainder of the Branchiopoda the endite projected backwards. This was undoubtedly the result of the development in these forms of a mid-ventral gully to accommodate the collected residue. If the endite had projected forwards, as in the Notostraca, where a food groove is absent, it would have tended to push particles away from the body out of the groove on the backstroke of the limb, but projecting backwards, it beat the particles towards the body and slightly forwards.

It now developed its posterior armature as a row of filter setæ. This was to guard the entrance from the food groove into the inter-limb space. It was a necessary development. Its necessity did not arise in the Notostraca where there is no food groove, but in the remaining Branchiopoda, as I have already emphasised, *if these* *filter setæ had not developed, a gap would have been left unguarded at the base of the limb in the region of maximum suction,* and this would have upset the whole of the filtratory mechanism. The endite thus became just as much a structure for filtering as for pushing food forwards. This is the type of structure on the anterior limbs of *Lepidocaris* and can be called sinio-gnathobase.

In the remaining forms the distal endites have curved backwards and overlap the limb behind so that their posterior setæ now form a continuous filter surface on either side of the median space. This is obviously an increase in the efficiency of the filter system and, again, I consider that it was a result of increased size. *Lepidocaris* is a minute form, its sinio-gnathobases are efficient filters, but its distal endites point inwards and hence form a primitive type of filter. With increasing size the area of filter surface became insufficient and the endites curved backwards as a compensatory development. As an inevitable result, as explained on p. 329, the forwardly directed intermittent spurts of water developed along the food groove. The gnathobasic function of the basal endite became superfluous and so was given up and the endite then developed as a siniobase.

Occurring as it does at the region of maximum suction it would be expected that in the further elaboration of the filter system, this filtering organ would be the structure to persist. The main evolutionary trends from this point culminate, on the one hand in the Daphniids where the filter organ consists of an enormously developed siniobase, and on the other, in the Anostraca where the siniobase has enlarged to its utmost and fused with the distal endites to form a complete filter functionally the same as the filter of *Daphnia*.

The ultimate filtering limb of the Branchiopoda has been termed a phyllopodium, that is, the leaf-like leg. The conception of a leaf-like structure is something which is flat, but the idea that the Branchiopod phyllopodium, or in fact, the Malacostracan phyllopodium, is flat, has arisen simply because these limbs have been studied after having been removed from the body and flattened under a coverslip. The Branchiopod phyllopodium wherever it occurs, consists of a thickened corm from which the exites, endopodite and endites all project backwards, and I have shown throughout this paper that the functioning of the limb depends *absolutely* on this arrangement. Together with the body wall at its base, the shape of the limb is that of a bath and I suggest as an appropriate term to designate this type of limb the word " droitopod " (Gr. δροίτη = the bath in which Agamemnon was murdered).

SUMMARY.

The numbers at the end of each paragraph refer to the appropriate figures.

General.

1. The trunk limbs of all Branchiopoda exhibit a marked metachronial rhythm in their oscillations. Any limb commences its backstroke just before the limb immediately

anterior to it, and as a result the limbs appear to move in waves which pass forwards. 1, 10.

2. The filtering trunk limbs of all Branchiopoda are armed laterally with a series of exites, the distal being the exopodite, which projects backwards and touches the limb behind. The endopodite forms the distal part of the limb and similarly projects backwards over the limb behind. 4, 25.

3. Except in the Notostraca there is a median food groove along the mid-ventral line on the tops of the walls of which are attached the limbs. 1, 2, 9, 10, 13, 22.

4. Except in the Lipostraca and in Notostraca the inner edge of the limb is produced into backwardly projecting endites armed with filter setæ. In these two groups the inner edge of the limb points medially and only very slightly posteriorly.

Anostraca.

5. As any two successive limbs move forwards the space between them (the inter-limb space) is enlarged and water is thus sucked in. It cannot pass in laterally or ventrally, as the exites and endopodites act as valves preventing this, and so it is sucked in from the middle line. In this way a constant stream of water is sucked into the mid-ventral space between the two rows of trunk limbs. 1.

6. Of this water, some enters the inter-limb space towards the tips of the limbs but the majority enters at the base (see para. 7). Hence, there is a movement of water in the median space towards the body. 1.

7. The inter-limb space is triangular in parasagittal section, the base being the body wall between the two limbs, the apex, the point where they touch. As the limbs move forwards this triangle swings through the arc of a circle. It increases in area at a maximum rate at the base and hence suction into the inter-limb space increases to a maximum at the bases of the limbs. 1.

8. As the limbs move backwards they extend as rigid plates, and water from the inter-limb spaces is thrown out postero-laterally and distally; this produces the swimming stream. 1, 4.

9. As the limbs move backwards they press on the water in the inter-limb space behind. This pressure acts on the filter setæ of the endites and blows off the residue collected during the previous forestroke, back again into the median space. The pressure at any point is proportional to the speed with which the adjacent part of the limb is moving. Hence, at the tip of the limb the pressure is greatest and all the residue is blown off the filter setæ. Part will be thrown out with the swimming stream while the remainder will be sucked on the water stream towards the body. At the base where the limb is not moving there is little pressure and the residue remains to be removed in another way. Hence food is concentrated between the tips of the limbs and filtered towards their bases. 4.

10. At the base of the filter setæ, along the length of the endites, is a strip of setules

which project medially through the filter setæ of the limb in front. These assist in sweeping the residue off the distal filter setæ. 2.

11. The proximal filter setæ of the basal endite, which are in the position of maximum suction project down towards the body against the wall of the food groove. This wall is armed with setules which project between these setæ. The residue sucked on to the setæ is combed off by the setules. 2.

12. When any limb is just about to end its backstroke the limb immediately behind it commences to move forwards. Thus momentarily the two limbs move in opposite directions and tend to obliterate the inter-limb space; this suddenly forces out the remaining water. The limbs are in contact from the point of flexure down to the base of the limb and this divides the lower part of the inter-limb space into a lateral and a median chamber. The water in the lateral chamber and behind the distal half of the limb is thrown out backwards into the swimming stream; that in the median chamber has only one exit at the base of the inter-limb space, into the exit groove. 1, 3.

13. The exit groove is a channel in the wall of the food groove curving from the base of the inter-limb space towards the floor and forwards towards the mouth. Water is thus suddenly expelled down this channel and blows the residue off the setules on the food groove wall towards the mouth. 1, 2.

14. The anterior food stream towards the mouth is thus an intermittent series of spurts occurring at those levels where the limbs are changing over from backstroke to forestroke. 1.

15. Owing to the nature of the metachronial rhythm (para. 1) the regions where these spurts occur pass forward in a regular sequence to the mouth. There is thus a false impression of a continuous orally directed food stream.

16. The feeding mechanism of the typical Conchostraca, Cladocera Ctenopoda and Anomopoda is based on the same principles as that of the Anostraca. Thus in each group the food is ultimately blown forwards to the mouth on an intermittent oral current. These groups differ from the Anostraca in that the basal endite is modified as a gnathobase. The gnathobase, occurring at the base of the limb in the region of maximum suction forms the main filtratory part of the limb. 1, 10, 20.

Lipostraca.

17. These filtratory gnathobases can be derived from those occurring on the anterior trunk limbs of the Devonian form *Lepidocaris*. The gnathobase of this form consists of a quadrangular lobe hanging down towards the body against the wall of the food groove. Its lower edge consists of a ridge terminating posteriorly in a powerful claw. On the lateral face, that is, against the food groove wall, there occurs a row of perfect filter setæ which hang down against the wall and curve forwards towards the mouth. The median face of the gnathobase is covered with setules. 5, 6, 7, 8.

Cladocera Ctenopoda.

18. In *Sida* the second to fifth trunk limbs form the main filtratory system. At the bases of the filter setæ on the median face of the endites there occurs a row of short setules which project medially between the filter setæ of the limb in front. These comb the residue off the filter setæ into the median space. 9.

19. The gnathobase is armed as in *Lepidocaris* with a row of filter setæ arising from the outer face along the lower edge. The posterior claw is replaced by two long setæ, the hinder of which projects backwards. This is armed with projecting setules and sweeps the filtered residue off the limbs behind into the food groove. The inner margin of the lower edge carries a row of short comb setules, which comb the residue off the proximal filter setæ of the distal endites of the limb in front. 9.

20. The residue ultimately filtered on to the filter setæ of the gnathobase is combed off by semicircular strips of comb setules arranged across exit channels in the food groove wall so as to correspond exactly to the position of the gnathobases. This residue is then blown forwards by the anterior spurts from the inter-limb spaces. 9, 10.

21. In *Holopedium*, the hinder corner of the gnathobase has swung upwards so as to approach the edge of the distal endites. In *Diaphanosoma* this process has extended further so that the setæ of the gnathobase and of the distal endites are almost in alignment at their bases. The limb of *Diaphanosoma* thus closely resembles the Anostracan limb. 11, 12, 16.

22. The anterior of the two long setæ at the hind end of the claw ridge of the gnathobases of all the three Ctenopoda studied curves posteriorly and then medially. Its function is uncertain. On the first trunk limb of *Holopedium* it curves forwards so as to reach as far as the most anterior filter seta. It functions in pushing the collected food on to the maxillules. 9, 11, 12, 16.

Cladocera Anomopoda (*Daphniidæ*).

23. Among the Daphniidæ the third and fourth trunk limbs only are filters. The endites which bear the characteristic long fringe of filter setæ are the gnathobases. The remaining endites have dwindled and given up their filter setæ. The posteriorly directed spine, marking the hind end of the claw ridge, occurs on the third trunk limb of *Moina* as a long curved seta. In *Daphnia* it has dwindled to a short stout spine. 13, 14, 18.

24. The gnathobase of the second trunk limb persists in *Moina*, but has given up its filtratory function and its filter setæ are modified as brush setæ. In *Daphnia*, the gnathobasic lobe of the second trunk limb consists of the gnathobase fused with at least the second endite. Its filter setæ also have become brush setæ. 14, 15.

25. The gnathobases of the first and fifth trunk limbs have disappeared. 14.

26. The primitive filter setæ of the gnathobasic lobe of the second trunk limb of *Daphnia* comb the filtered residue off the anterior part of the third gnathobase, while

the posterior part is scoured by the comb setules occurring on the fourth gnathobase at the base of its filter setæ. The filter setæ of the fourth gnathobases are combed by the posterior filter setæ of the third gnathobase which are modified at their tips for this purpose. 14, 21.

27. The metachronial rhythm of the limb movements of *Moina* is closely similar to that of *Sida*. In the case of *Daphnia*, the rhythm has become modified to increase the anteriorly directed food stream. 19.

28. In *Daphnia* the third and fourth trunk limbs beat backwards almost together. Water from their inter-limb spaces is forced forward. At this instant, the first limb moves forwards away from the second and water is thus sucked out of the food groove. The oral current is thus produced by pressure from behind and suction in front. 20.

29. The fifth limb does not move backwards and forwards as a whole. Its inner margin remains stationary and the limb swings about this edge as a door on its hinges. It swings forwards just as the fourth limb is finishing its backstroke and so helps to force the water out of the inter-limb space. In *Moina* it swings forwards precociously and so increases the anterior current. 19, 20.

Conchostraca.

30. The anterior trunk limbs form a filtratory system. The hind limbs are modified as jaws.

31. At the bases of the filter setæ on the median face of the endites of the filtering limbs, there occurs a row of stout setæ which project postero-medially between the filter setæ of the limb in front and comb off its residue into the median space. 22.

32. The gnathobase is armed with a row of perfect filter setæ on a ridge on its outer face. These all curve forwards towards the mouth. The claw ridge has extended forwards as a triangular plate—the claw process—covering the greater part of the filter setæ on the median side. 22.

33. The exit grooves are extremely well defined. They are covered over exactly by the claw processes of the gnathobases. The function of the latter is to protect the extremely delicate filter setæ and at the same time to enhance the spurts of water from the inter-limb spaces by converting the exit channels into complete tubes. 22, 23.

34. The gnathobases are armed along their posterior margins with two rows of peculiar setæ whose function is partly to sweep the residue off the gnathobase behind, and partly to sweep the residue forwards along the food groove. 22, 23.

Notostraca.

35. The endites are elongate lobes extending medially and slightly posteriorly from the edge of the limb ; each endite ends in a heavily armed knob. Across the front and hind surfaces a row of long spines project towards the median plane ; this armature of setæ retains particles in the median space.

36. Owing to the metachronial rhythm of the limbs and the slight posterior direction of the endites, the collected food is passed backwards and downwards to the mid-ventral line.

37. The gnathobases differ from those of all other Branchiopoda in that they point forwards and overlap the gnathobase in front. The food collected in the mid-ventral line is passed forwards from gnathobase to gnathobase to the mouth. 24, 25.

38. The suggested evolution of the various types of filter mechanism is described on pp. 324–334. 25.