ON THE STRUCTURE OF THE RESPIRATORY ORGANS OF THE TERRESTRIAL ISOPODA.

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Plates X.-XVII.

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1. INTRODUCTION.

Terrestrial isopods present problems in respiration because of their change of habitat. With organs of respiration which are homologous with the branchiæ of *Asellus* and other aquatic isopods, they live on land and breathe air. They are found in very varied situations; some require very wet conditions, others can live in comparatively dry places.

In this communication I propose to describe the interesting anatomical features of the respiratory organs of certain species.

In the species treated of, and in the *Oniscoidea* generally, five pairs of abdominal appendages take some part in respiration. I propose to describe these appendages in the female forms only. There are no differences in the essential points of histology and physiology between the male and female pleopods, and the fact that, in the male, reproductive processes are associated with the 1st and 2nd pleopods, brings in an unnecessary complication.

Methods.

Living Specimens: I have indicated the methods in use for examining the abdominal appendages *in situ.*

Abdominal appendages as flat objects: Methylene blue, as a stain for living tissue, as well as for fixed ones, is most useful. Prussian blue gelatine injection has been used to investigate the limits of blood cavities.

Paraffin serial sections: For fixing I have found Fleming's solution the best. Hot 80 per cent. alcohol has given good results with some.

Staining: Delafield's hæmatoxylin followed by eosin in 90 per cent. alcohol. The staining has been done on the slide in dipping jars.

II. SPECIES DEALT WITH.

1. *Trichoniscus pusillus*, Br.

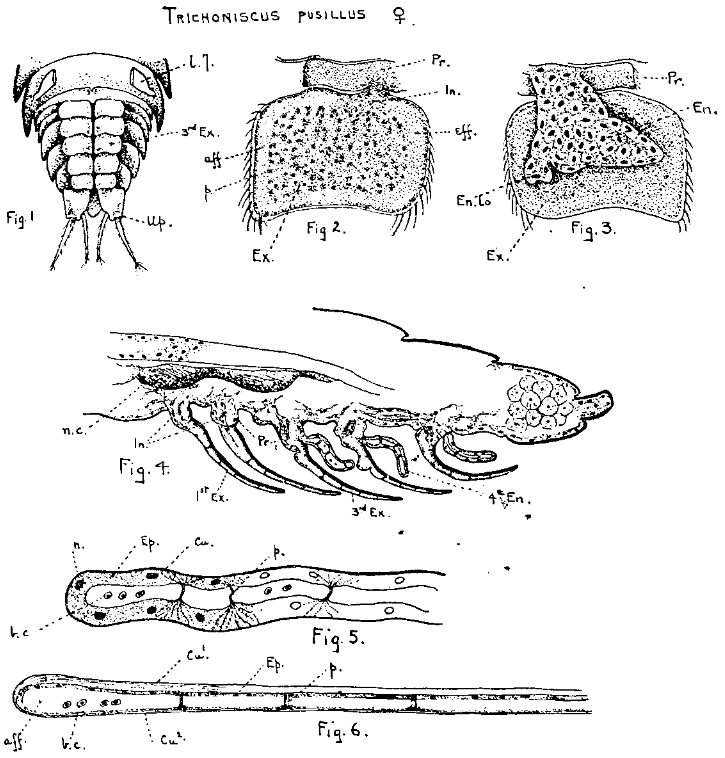
Pl. X., figs. 1-6.

The ventral surface of the abdomen is shown in Fig. 1. It is covered by five pairs of oval plates, which overlap from before backwards, and those of either side meeting together in the mid-ventral line.

Normally each of these plates indicates an abdominal appendage, consisting of a basal part, an outer plate (exopodite) and an inner plate (endopodite), but the endopodites are missing from the first two pairs of appendages. Thus there are five pairs of exopodites and three pairs of endopodites. These are the respiratory organs.

In many forms the structure of all the exopodites is similar and the same applies to the endopodites; it will be convenient, therefore, to take the 3rd abdominal appendage for special study as this is the first complete appendage. Where differences exist between the exopodites of the 1st and 2nd abdominal appendages and that of the 3rd, the description will be extended to include them.

Figs. 2 and 3 show the 3rd abdominal appendage seen from the ventral or outer, and from the dorsal or inner aspect. The exopodite acts as an operculum for its rather smaller and more delicate endopodite. Each plate takes part in respiration. This has been made clear by observation, by experiment, and by the evidence afforded by sections. If a living specimen is observed under a low power of the microscope, the abdominal appendages seem covered with a film of water, at least the endopodites are, for as the exopodites are raised and lowered—an action which, although not absolutely regular, is fairly continuous when the creature is not moving and which is a breathing action—a film of water retreats and advances under the free edges of the exopodites. This shows that the endopodites are kept very wet and are used for respiration in a very damp condition. By using a higher power the circulation of blood can be observed in the exopodites. They are well supplied with blood, and act as additional breathing organs. I proved this by putting the endopodites out of action, in this and in other woodlice, by inserting some vaseline under the exopodites. The creatures lived for very considerable periods. In the control experi-



Trichoniscus pusillus ♀.

ment with the whole of the ventral surface of the abdomen made impervious, the woodlice did not live more than two days at the longest.

It is also clear from the transverse sections that the exopodites are used as organs for respiration, and that the outer or ventral surfaces function to this end. The chitinous cuticle of the ventral or outer wall—the wall towards the air, the oxygen medium—is very thin and the inner or dorsal wall quite thick. If the exopodite functioned as an operculum solely, the outer or ventral wall would be the thicker, as it is for instance in the 3rd abdominal exopodite of *Asellus*. This will be referred to below when the transverse sections are described in detail.

We shall find as we study the woodlice adapted for drier situations, that the exopodites become more and more important as breathing organs. It is in the exopodites that accessory breathing organs are developed; and the endopodites, although three pairs are always present, become less important in consequence.

The Exopodite: The exopodite is roughly oval in outline. (Fig. 2.) When seen under the microscope as a transparent object, either in the fresh living condition or treated with methylene blue, the surface is covered with small dots, which are not arranged evenly over the surface. These dots are the nuclei of the epithelial layer, and here and there where they are grouped together comes an inter-lamellar pillar or bridge (le pilier of Kimus (1)). The space between the two walls traversed by these pillars is the blood cavity. There are no definite blood vessels, but at the sides of the appendage channels can be seen, free from pillars. These are the inhalent and exhalent blood channels, or afferent and efferent canals. It has already been noted that the circulation of the blood can be seen. This is due to the large size of the blood corpuscles. The blood collects into a large ventral sinus in the abdomen and is drawn through the abdominal plates by the pumping action of the heart, which, receiving purified blood, propels it forward to the head and to the body generally. The blood enters the exopodite at the point of attachment, and runs along the inner border in what we may call the afferent canal, finds its way between the two lamellæ, into the efferent canal along the outer border, and so out of the appendage. The blood is prevented from short circuiting from the afferent to the efferent in

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(1) Kimus (see Bibliography).

the proximal part of the exopodite by the presence of a tissue which is continuous with and similar to the tissue found in the body cavity. This is the intermediary tissue to use the name suggested by Kimus (le tissu intermediaire).

If the exopodite be examined by transverse or longitudinal section (Figs. 4 and 6), the details of the two walls or lamellæ can be seen. Each lamella consists of an epithelial part and a cuticle, and the two lamellæ are very different. The inner or dorsal wall has a fairly thick cuticle, and the epithelial lining is quite distinct with its nuclei at frequent intervals. This epithelial lining is a single layer of cells which give rise to the cuticle on its outer face. The cuticle of the outer or ventral wall (or lamella) is very thin, and the epithelial lining is also extremely thin, indeed in most sections it is not seen except in the region of the pillars, but at the time of the formation of a new cuticle the layer is distinctly seen. In a later communication I have described and figured a section through an exopodite at the time when this layer shows best of all (Pl. XIII., fig. 28). Sometimes the very thin remains of the layer is seen when by some action (osmosis) the protoplasmic lining becomes distorted. The pillars pass from cuticle to cuticle. The outer wall of the exopodite is thus adapted for respiration through its very thin wall; the inner wall for protection and for the necessary support of the exopodite itself (Fig. 6).

Stoller (2), to whose work upon the breathing organs of woodlice I shall have occasion to refer and to correct in many important particulars, does not describe *Trichoniscus*, but refers very briefly to *Ligidium hypnorum*. He says, referring to a cross section of the exopodite of which he gives a figure:

"It is seen that the gill (= exopodite) is in principle a " simple sac containing blood. The outer layer of the wall, " composed of chitine, is much thicker on the ventral than " on the dorsal side of the gill. The hypoderm (= " epithelium) everywhere lines the chitine, and in general " varies with it in thickness."

This is the exact opposite of what I find in *Trichoniscus*, and at first I thought that this section of *Ligidium* must have become turned round in some way, or that we were using the terms "dorsal and ventral" in different ways, but a few lines further on he makes it quite clear that he looks upon the inner surface (that is the dorsal surface as the plates are found *in situ*) as the respiratory one, and that it is in

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(2) Stoller (see Bibliography).

use when the air enters the space in which the endopodite lies. By the following extract it is clear that he imagines only one kind of respiration—that taking place in the endopodite cavity, whereas the outer surface of the exopodite is adapted for respiration of a different kind. (See Summary.)

"It is true that as the blood circulates through the gill, " it is separated from the external atmosphere by the rather " thick ventral wall of chitine. But through the movements " of the gill, taking place as described for *Porcellio*, air is " constantly brought into relation with the inner surface " where the chitinous wall is thin." (Stoller.)

It will be best to correct at once this serious mistake in Stoller's account, for it occurs in his descriptions of other species. In his description of the last three pairs of exopodites of *Porcellio scaber*, which are more or less normal in structure and do not possess the air-tree organs, he describes their function as protective covers for the endopodites and their movement causing renewal of air to the endopodites. I agree in these two functions, but do not agree with the observation given below as to the structure of the wall.

"It is possible that the outer gills (= exopodites) in " addition to performing these functions, contitute in them- " selves organs of respiration. The blood circulates between " the two walls of the gills, and whether respiration takes " place depends upon the penetrability of the walls to the " gases to be exchanged. The *ventral wall of chitine is* " *thick*—thicker than the chitinous wall in some other regions " of the body as, for example, the thoracic legs (in which also " the blood circulates). The dorsal wall is, on the other " hand, *moderately thin*. It is, moreover, exposed to the " moist air in the chamber in which the inner gills lie. It " would seem probable, therefore, that to some extent " respiration may take place *through the dorsal wall*." (Stoller.)

This extract goes to show that in Stoller's mind the dorsal wall, the one that is applied to the endopodite, is considered thinner than the ventral wall, the one that is bathed by the external air. I have examined all the common species of woodlice and find the opposite arrangement in every case (except where a great change like the development of an air-tree organ has altered the exopodite). In *Ligia oceanica, Trichoniscus pusillus and roseus, Oniscus asellus, Philoscia muscorum and conchii, Porcellio scaber,* *Cylisticus convexus, Armadillidium vulgare, Porcellionides pruinosus, Platyarthrus hoffmannseggii*, the ventral wall is the thinner, and is normally adapted for respiration. We shall see that some species use this ventral surface more than others, but there is not the slightest doubt but that Stoller is incorrect in his description. A glance at Figs, 4, 25, 53, 57, 59, and 69 will show this.

The Endopodite: It has already been pointed out that there are only three pairs of endopodites. The 3rd abdominal exopodite is the first to have a corresponding endopodite. This latter is slightly smaller in area than its exopodite, but its structure is in marked contrast, as can be seen in figures 3, 4, and 5. The chitinous cuticle is very thin, and the epithelium is, on the contrary, very thick, and the whole appendage is spongy. There is one peculiarity which I have not noticed in the endopodite of any other woodlouse, and that is a lobe which is seen attached to the inner distal corner of the appendage. The blood cavity of the endopodite is continuous with that of this lobe. In Fig. 3 I have attempted to show the nuclei and the large epithelial cells as they are seen after the endopodite has been treated with methylene blue. In Fig. 5 a portion of an endopodite is shown as seen in cross section. The large nuclei are very clear, but the cell boundaries cannot be seen. There are very few pillars running from the epithelium of one wall to that of the other. They are narrow pillars, and as one follows them into the epithelium radiating fibres can be seen. The blood cavity is very variable in size, in some sections the epithelial linings are closely opposed, in others they are widely separated. These observations support Kimus's suggestion that the function of the pillars is partly to assist the flow of blood through the appendages.

The pillars are very similar to the type found in the endopodites of *Asellus aquaticus*, and to which Kimus has devoted so much attention. The chief point to note here is that these pillars are not complete cells, but formed of the fused protuberances which are carried by the large epithelial cells. Kimus in summarising the kinds of pillars found says of this kind—

> "Enfin, le pilier formé par l'union, à travers la cavité "branchiale, de protubérances appartenant à deux larges "cellules épithéliales, qui en possédent plusieurs semblables."

The pillars of the exopodite are quite different. They are formed of the union of two or more cells. The cells of one wall unite with the cells of the opposite wall. The question of these pillars is discussed in the summary.

2. *Oniscus asellus*, Linn.

Pl. XI., figs. 7-16.

The general arrangement and number of the abdominal appendages are the same as in *Trichoniscus pusillus*. Looking at these appendages *in situ*, a peculiar feature is at once seen. The outer border of each exopodite has quite a different appearance from the rest of the exopodite. This outer border appears as a silvery white segment, rather less than a semi-circle in shape and occupying from one-fifth to a quarter of the area of the whole exopodite. (Pl. XI., fig. 7.) This unusual appearance attracted my notice, and I began to study it by observations on living specimens and by means of sections. When watching the breathing action of *Oniscus* under a low power of the microscope, it was clear that these border organs had bubbles of air underneath them, and that the silvery appearance was due to this. With a little patience one could get the air replaced by water, and then the silvery appearance disappeared. By flooding the *Oniscus* with weak alcohol, the air was dislodged, and the alcohol could be replaced by water before any permanent injury was done. In this way I satisfied myself that the silvery appearance was entirely due to the air imprisoned under the corrugated crescentic lobes. I mention this here because below I shall refer to Stoller's work which later caused me to review the whole matter.

This special part is very thin and, having its outer or ventral wall flush with that of the ordinary part, there is a considerable space between its inner or dorsal wall, and the underlying exopodite or the body wall. This is the air or lung cavity, and the air is renewed by the raising and lowering of the exopodites as well as by the flexing of the abdomen and other movements caused by locomotion.

Besides this special arrangement, designed, as we shall see, for more efficient respiration of air, *Oniscus* has exopodites and endopodites which, similar to those already described in *Trichoniscus*, are adapted for breathing of moist air. The endopodites, although not so wet as those of *Trichoniscus*, are yet obviously meant for the same kind of respiration, and the habitat confirms this conclusion: for *Oniscus* is often found along with *Trichoniscus* in very damp situations; but the presence of other breathing organs enables it to exist in places which would be too dry for *Trichoniscus*. I shall refer to this in detail later.

The 3rd Abdominal Appendage: Fig. 8 gives a general view of the appendage from the ventral side, and in Fig. 7 the 3rd exopodite on the right side has been turned back to show its corresponding endopodite. Reference to these drawings will save much description. The ordinary part of the exopodite and the endopodite exhibit much the same structure as those appendages in *Trichoniscus*, although the larger size makes it easier to examine the histology in detail. Reference to Figs. 11, 15, 16, especially to Fig. 16, which is a longitudinal section passing through an exopodite and its endopodite in such a way as to pass through the ordinary part of the exopodite, will show the chief points of interest.

The Exopodite: In the main part of this plate the inner or dorsal wall has a very thick cuticle, carrying still further the arrangement we have noted in *Trichoniscus*, and to which we have already referred at some length. The outer or ventral wall is very thin, and points to the use of the outer face of the exopodite as a valuable breathing organ, for not only is the chitinous cuticle very thin, but the epithelial layer is also very much reduced, so much so that in places it is difficult to make out. Thus the blood which flows through the appendage is brought into close relationship with the air outside, and the necessary interchange is possible.

The pillars are more frequent here than in *Trichoniscus*. They resemble the simpler pillars found in *Asellus*, described by Kimus in his memoir. At the base of the appendage the third tissue, the intermediary tissue, can be seen, pushing a little way into the appendage acting as a partition to direct the flow of blood and to prevent the blood staying in the proximal part of the appendage. This tissue, consisting of elongated stringy cells with prominent nuclei, is seen in sections, and can also be seen in the appendage after treatment with methylene blue, and examined as a flat object. In the special part of the exopodite, this tissue becomes a very thin threadlike partition, sometimes double, continuous with a similar partition in the proximal part of the appendage, especially in the part abutting on the special part. This partition serves to divide the internal blood cavity into an upper and a lower cavity.

The structure of this special part of the exopodite must be dealt with in some detail, for it is here that I find myself in serious disagreement with Stoller. After reading his

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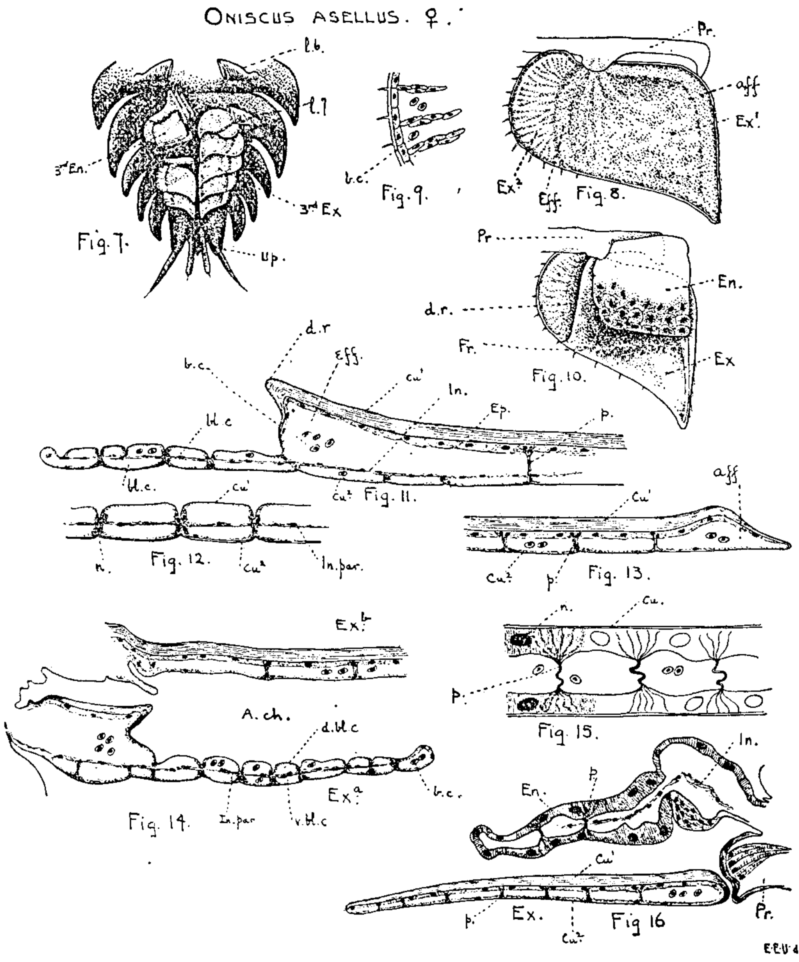


Oniscus asellus ♀.

account I repeated my own experiments and sectionised the appendages again, and also tried the experiments suggested by Stoller. I will first of all give a detailed description of this part as it is seen by me, and then give Stoller's view, pointing out where I think he is in error.

The figures make clear the general structure. We notice that the exopodite as it approached the outer border where this special segment is situated becomes very much thicker, and then suddenly narrows to less than one-third its thickness; the dorsal wall is the one that alters, the ventral wall of the special part and that of the rest of the exopodite are flush with one another. Besides the change in levels the inner or dorsal wall changes in the thickness of the chitinous cuticle. In the ordinary part of the exopodite it is very thick, in the special part it is exceedingly thin, the thinnest cuticle found anywhere in these appendages. The outer or ventral layer of cuticle is very thin, but decidedly thicker than this on the inner surface of the special part. This points to the fact that the inner surface is of more importance from a respiratory point of view. Both surfaces are thrown into corrugations, but these are much deeper on the inner surface.

Turning now to the internal structure. In all sections, transverse or longitudinal, a partition is seen running through about mid-way between the two faces, but the deeper corrugations of the inner or dorsal surface make the cavities on that side rather larger.

This partition consists of elongated threadlike cells with elongated nuclei. The partition in some places is double with a very narrow space between the two threads, but in other places it appears as a single partition. This partition, the intermediary tissue, is continued into the ordinary part of the exopodite for a greater or lesser distance. Near the proximal portion of the exopodite this partition can be traced into the protopodite, but in the distal part it can be traced but a short way.

The internal cavities are interrupted by the pillars which pass from one face to the other. It is usually only at the base of these pillar cells that any trace of the epithelial lining can be made out. This lining is extremely thin. The pillars are of a somewhat different nature here in that they are grouped together into bands. This arrangement, together with the intermediary tissue, divides the cavity into two sets of radial passages, one set of passages on each side of the partition. This can be seen in a surface view, and an attempt to show the radial arrangement of pillars is seen in Figs. 8 and 9. If a living specimen is examined under a low power, it is easy to observe the course of the blood flowing through these radial passages. The blood enters the appendage at its place of articulation, which is near the outer border. The blood stream divides, some of the blood going to the exopodite in the ordinary way passing down the afferent canal along the inner border and working its way across the appendage into the efferent canal, which is the boundary between the two parts of the exopodite, and, by this, out of the appendage: other blood takes a different course, it goes to the special part. The transparent character of this special part makes it comparatively easy to observe the circulation. It is best to remove the last pair of legs, and then invert the creature in a watchglass of water, and rest a cover glass on the creature to restrain its movements. The blood corpuscles travel through the ventral radial passages (the uppermost ones, as the animal is placed) towards the margin of the special part. The partition is so transparent that it is not visible, but its presence is obvious, for as the corpuscles get to the margin they suddenly fall through, as it were, to the lower chamber, and one can see them travel back, slightly out of focus, in the dorsal radial passages. The partition comes to an end just before the margin is reached, which accounts for the observation above. Thus in *Oniscus* we have, besides the main portion of each exopodite, which is similar in function to the exopodites of *Trichoniscus* with its outer or ventral surface adapted for respiration, a set of special breathing organs developed on the outer border of each exopodite. Enough has been said to show that these are most valuable additions to the respiratory powers of this creature. The blood in the passages is only separated from the air outside by the thinnest of walls, and the constant supply of blood and the repeated change of air supply the requisite conditions for an efficient breathing organ.

The account given above differs in several important points from that furnished by Stoller. It will be best to quote from his treatise the paragraphs with which I am in disagreement.

P. 25—" . . . In *Oniscus* the general cavity of the gill[x] " is not a simple cavity as in *Porcellio*, but is separated into " a number of chambers by means of partitions lying parallel " to the walls of the gill.

([x]Gill or outer gill is used for exopodite; inner gill for endopodite.)

"In the general part of the gill there are two of these " chambers, an inner or dorsal chamber and an outer or " ventral one. They contain blood. Each chamber is " bounded above and below by a thin line. It results from " this that the cavities of the two chambers are separated by " a double wall. This appears as two fine parallel lines be- " tween which is a very narrow space. Lying in this space " and occurring at frequent intervals are elongated nuclei. " The outer walls of each chamber lie immediately within " the hypodermic (epithelial) layers on the respective dorsal " and ventral sides of the gill. The outer walls have nuclei, " but they occur at widely separated intervals. The hypo- " dermic pillars cross the blood chambers. Where they occur " the walls of the chambers curve round them, forming " sheaths. Thus the cavities containing blood are every- " where separated from the hypoderm by a boundary wall."

Here are several inaccuracies:—The main portion of the exopodite is certainly a simple cavity crossed by pillars lined by epithelium, thicker on the dorsal than on the ventral side (Fig. 16). In the proximal part of the exopodite and in neighbourhood of the special part this thin partition is present, but not in every part of the exopodite. The nature of this partition; its simplicity in structure to the tissue in the body cavity; its presence in the protopodite and in the proximal portion of the appendage as a blood directing tissue; its presence in the basal part of the endopodite as well; and the fact that a similar tissue is found in *Asellus* and other aquatic isopods are points with which Stoller does not seem familiar. Then he is mistaken when he mentions that the blood cavities have definite boundary walls, that is of cellular structure, other than the epithelial lining and in some cases the intermediary tissue. He, himself, is evidently in doubt as to this, for in a footnote on page 14, added after the treatise was written, he leaves the question undecided. The footnote is meant to qualify the following statement:—

"The blood cavity occupies the whole space within the " hypodermic layer, and is bounded by a very thin wall lying " contiguous to the hypoderm and conforming to its irre- " gularities. In this wall at long intervals lie elongated " nuclei. I infer from the relations of this wall that it is " of mesodermic origin." (Stoller.)

In the footnote he refers to the work of Leichmann, who has described the brood pouch lamellæ of *Asellus aquaticus*, and who found them homologous in structure to the branchiæ, with a simple blood cavity bounded by epithelium. The inner surface of this has a very thin cuticle. Kimus describing the exopodite of *Asellus aquaticus* says:—

“Rappelons que les parois des cavités sanguines sont
“ formeés dans la plus grande partie de leur surface, par
“ les deux lamelles épithéliales tapissées intérieurement d’une
“ mince cuticule.”

This very thin cuticle is more evident in some species, e.g., *Porcellio scaber,* and it is this that Stoller has taken to be a definite cellular layer of mesoblastic origin. This mistake runs all through his treatise, his figures too are incorrect in this particular, but perhaps the most serious of the errors into which he has fallen has reference to the minute anatomy of the special part of the exopodite; serious because it has found its way into such a textbook as “A Treatise on “ Zoology,” Part VII.

He divides the internal cavity of this part into five separate chambers, one below the other, three of these are blood chambers and two are air chambers.

He states (pp. 26 and 27):—“The dorsal and ventral
“ blood chambers of the general part of the gill are con-
“ tinued into the special part of the gill. But in the special
“ part there is present, in addition, a third blood-chamber,
“ which lies between the other two. This middle chamber is
“ formed by the forking of the partition separating the
“ dorsal and ventral chambers in the general part. Each
“ branch of the fork retains the structure of the main parti-
“ tion; that is to say, consists of a double wall, with nuclei
“ lying in the narrow intervening space. While the dorsal
“ and ventral chambers are thus separated along their lateral
“ faces they communicate with each other in certain places
“ at the margin of the gill.”

Then follows a description of the possible communications between the dorsal and ventral chambers, and this so-called middle chamber, which I need not quote. He then proceeds:—

“In addition to the three blood-chambers in the special
“ part of the gill there are other chambers which contain
“ air. These are two in number, situated one on the dorsal
“ and one on the ventral side of the gill. The dorsal air-
“ chamber is bounded outwards by the wall of the gill and
“ inwards by the outer wall of the dorsal blood-chamber.
“ The ventral air-chamber has corresponding relations. In
“ other words, in the special part of the gill there is a space
“ between the general wall of the gill (composed of chitine
“ and hypoderm) and the boundary wall of the blood-cavity,
“ and this space contains air. This space does not com-
“ municate by any opening with the outside of the gill.”

Stoller supports these observations by a number of experiments:—

“As has already been stated, when an animal is placed
“ in water the appearance of air in the gills passes away.
“ This observation led to a number of experiments, the chief
“ purpose of which was to gain evidence, in addition to the
“ evidence derived from direct inspection and from the study
“ of the structure of the gill, that air is normally present in
“ the chambers.

1. “An animal was placed in water until the appear-
“ ance of air in the gills had passed away. It was then
“ killed, and the tissues fixed by hot 33 per cent. alcohol. In
“ sections of the gills prepared from this specimen the air-
“ chambers did not appear empty (as usual), but contained
“ blood without corpuscles, that is, blood plasma (appearing
“ as granulated matter).

“This experiment, having indicated that under the con-
“ ditions imposed the air was replaced in part, at least, by
“ plasma of blood, we next sought to modify the experiment
“ in order to ascertain whether the presence of blood in the
“ chambers was due entirely to the conditions being
“ artificial.

2. “The preceding experiment was repeated, excepting
“ that the animal was placed in normal salt solution instead
“ of water. The result was that the chambers contained
“ blood plasma, but perhaps less in quantity than in the
“ previous case.

“In this case the two fluids were of approximately equal
“ densities and, it may be inferred, tended to replace the air
“ in equal measure. Allowance must be made, however, for
“ the greater thinness of the wall bounding the blood-cham-
“ ber than the outer chitinous wall.

3. “The experiment was repeated, using a concentrated
“ salt solution. The result was that the chambers appeared
“ as empty or nearly so, little blood plasma having entered
“ them.

"In this case it would appear that the more concentrated " fluid replaced, in the main, the air. In all three cases the " results became intelligible on the supposition that the " chambers contain air. Thus, these experiments warrant " the inference that the chambers normally contain air and " not blood." (Stoller.)

Now let me take some of the points raised in the above excerpt—

I do not agree with the description of the partition in the special part. In most sections the partition seems to me to be a single structure composed of two closely applied very thin strands containing elongated nuclei. In some sections the two strands are rather more separated than in others, but I cannot find anything which can be called a middle chamber. The partition here does not differ materially from the partition in the ordinary part, indeed the two partitions are continuous. I have failed absolutely to find the two air-chambers either by surface observation or by sections or by the experiments suggested by Stoller.

In the paragraph from his treatise quoted above, he describes these chambers as being bounded by the epithelium of the outer wall on one side and the wall of the blood cavity on the other. We have already seen that he is in error in describing a definite boundary wall to the blood cavities, and this initial mistake may have led him into the further error of finding air within the appendage. Certainly there is no wall between his so-called air-cavity and the blood cavity: it was not surprising, therefore, to find blood in these cavities.

I have tried every way I could devise to test the question, but have failed to find any air inside the appendage, and I feel convinced that his observations are incorrect, and that the internal cavity of the special part of the exopodite is simply divided into dorsal and ventral blood chambers. In all my sections I have found blood corpuscles in these chambers. Possibly the idea arose after looking at a section in which the protoplasmic lining had contracted leaving a space between it and the chitinous cuticle. This does take place—due, I suspect, to a too rapid method of dehydration or faulty fixation—and this appearance would certainly result after the use of salt solution.

Really a few minutes' observation of a living creature submerged in water and so arranged that the ventral surface of the abdomen can be viewed in a good light would convince anyone that there is no air inside the walls of this special part, but only outside. The following simple observation could be made as well. Take off any one of the exopodites from a living specimen, dip it into alcohol to remove the surface air which clings to the corrugated surfaces, and mount it in water. This need not take more than 30 seconds at the most. The special part of the exopodite is quite transparent, there is no trace of air when seen by transmitted or reflected light. Now, if there were air-chambers, as Stoller suggests, it would have been impossible for the air and water or air and alcohol to have interchanged so rapidly, especially as Stoller agrees there are no openings, and that any interchange must take place by diffusion.

Having convinced myself that Stoller is wrong in his account of these air-cavities, there is no need to follow him further, and point out the errors in his account of their physiological function, for it is based upon error.

Although claiming for these special breathing organs a simpler structure, they are still very wonderful adaptations and illustrate another method whereby gill plates can be used for air-breathing. It is interesting to find these adaptations and to compare them with similar contrivances in other members of the *Arthropoda*. It has seemed to me that the lung books of Spiders may have much in common with the branchial plates of land Isopods.

Before leaving the question of the exopodites, I want to point out a peculiarity associated with the last pair of plate-like abdominal exopodites (that is of the 5th abdominal appendage). The under or dorsal surface of one of these appendages is shown in Fig. 10. There is a curious arrangement of long spines or hairs, which occur in radiating groups in a special band across the exopodite. The arrangement suggests a cheval-de-frise, especially as it occupies the place, just posterior to the endopodite, where protection might be necessary. It is difficult to be sure as to the function of this formidable array of hairs. Protection from enemies or from the "excreta" discharged from the anus, which is close by, do not seem sufficient, and their absence in *Trichoniscus* is against these uses. The only suggestion which occurs to me as likely is the possible use in preventing the drying up of the film of water which covers the endopodites, seeing that the last pair are more exposed when the plates are lifted and when the end of the abdomen is flexed.

The Endopodite: The endopodites of *Oniscus* are smaller in proportion to their exopodites in surface area than those of *Trichoniscus*. This is possibly due to the fact that the exopodites have a greater respiratory importance in the former species. Figs. 10, 15, and 16 will give a good idea of its shape and structure. It is little more than a squarish thick walled bag, the cavity is the blood cavity, and it is crossed by pillars. There is little to add to the description already given for *Trichoniscus*, except to note the larger size of the pillars and the fact that they are more numerous. The pillars are of the same character as described in the case of *Trichoniscus*.

3. *Philoscia muscorum* (Scop.).

Pl. XII., figs. 17, 18.

4. *Philoscia couchii* (Kinahan).

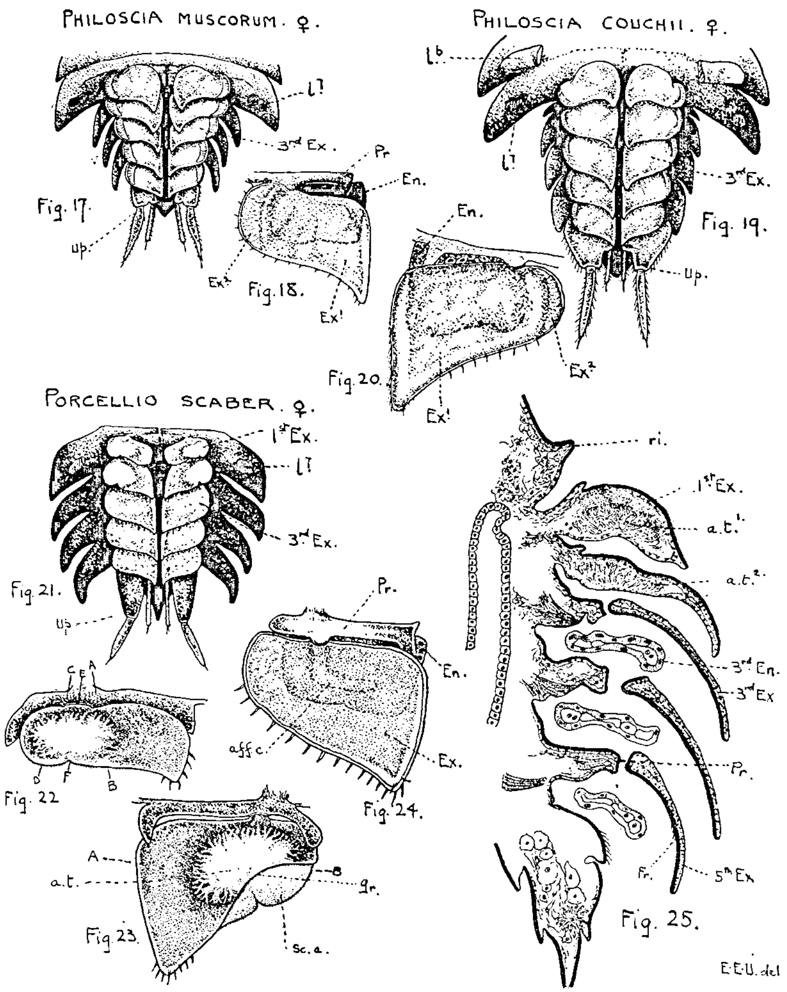
Pl. XII., figs. 19, 20.

The general arrangement and structure of the respiratory appendages of *Philoscia muscorum*, are the same as in Oniscus. Fig. 17 shows a ventral view of the abdomen of a female, and Fig. 18 the 3rd abdominal appendage seen from the ventral aspect. These figures serve to indicate its likeness in details to *Oniscus*. The exopodite with its special respiratory organ, and the endopodite are so similar in structure and function to those already described for *Oniscus* that there will be no need to repeat any part of it here.

The exopodite of the 5th abdominal appendage also shows a similar cheval-de-frise on the dorsal surface.

Philoscia couchii: The general arrangement and structure of the respiratory plates are similar to those of *P. muscorum*; but the special respiratory organs of the exopodites are poorly developed. Fig. 19 shows a ventral view of the abdomen, and in this figure and in Fig. 20 the character of the exopodite can be seen. The endopodites seem rather larger in this species. The structure of the special border organ, although much smaller in size, is identical with that of *Oniscus*, or *P. muscorum*.

I can find no trace of the rows of special hairs—the cheval-de-frise on the exopodite of the 5th abdominal appendage. This fact seems to support the suggestion made that they have some function in connection with respiration, in protecting the cavity in which the last pair of endopodites are found. The very damp habitat of this species making such protection unnecessary.



Philoscia muscorum ♀, *Philoscia couchii* ♀, and *Porcellio scaber* ♀.

5. *Porcellio scaber*, Latr.

Pl. XII., figs. 21-25; Pl. XIII., figs. 26-40.

Fig. 21 gives a ventral view of the abdomen, and from this figure and the longitudinal section drawn in Fig. 25 it will be seen that, apart from the white patches of the first two pairs of exopodites, the general arrangement is similar to that described in the other woodlice.

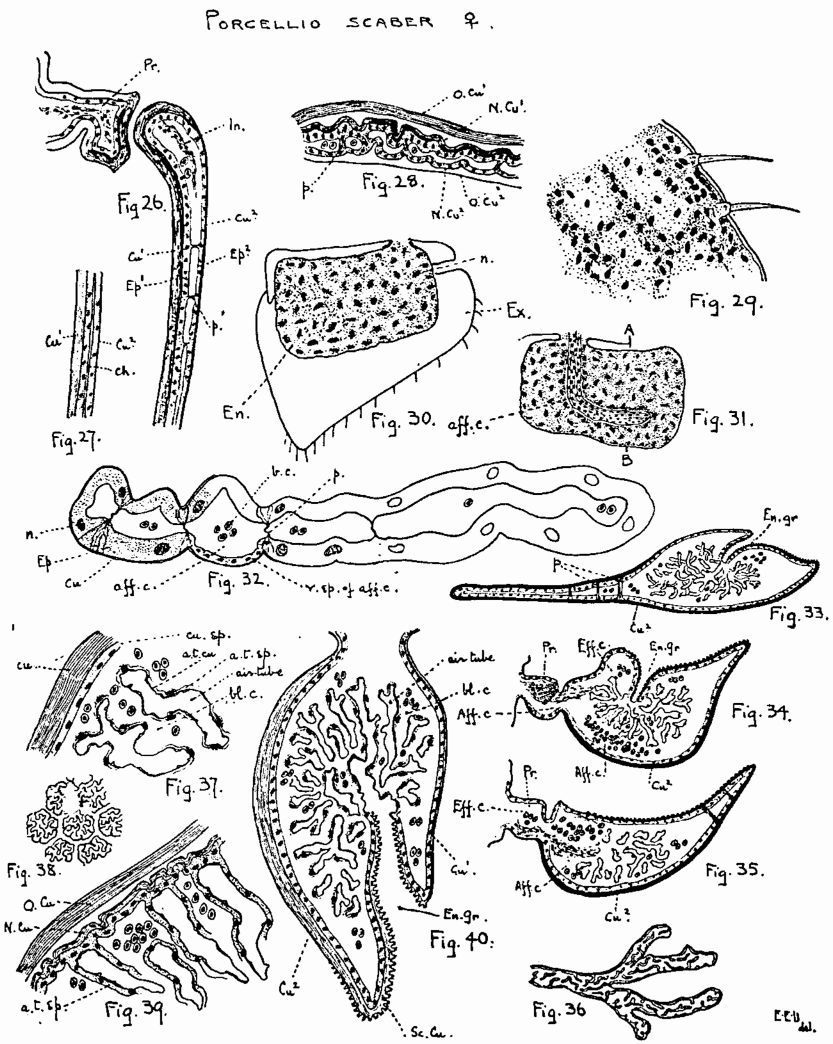
We have to deal here with two distinct methods of respiration. There is the method similar to that described in *Trichoniscus*, using the endopodites and exopodites of the 3rd, 4th, and 5th abdominal appendages, and then the special method which is developed in connection with the air-trees or air-sponges carried by the exopodites of the 1st and 2nd abdominal appendages.

It will be best to examine the more normal method first and for this purpose we will take the 3rd abdominal appendage. The general shape of exopodite and endopodite can be seen from Figs. 24, 30, 31, so that a description need not be given. At first sight there seems but little difference from the structure which we look for in these parts, but both exopodite and endopodite present peculiar features. When the exopodite is examined under the microscope, either in the living condition or after treatment with methylene blue, it is evident that the usual passages for the blood, the afferent along the inward border, the efferent along the outward border, and others traversing the central part, are not present. The exopodite seems to be much more of a regular mass of cells, and only in the proximal part can one make out any sign of blood spaces. These are few, and do not extend far into the exopodite. Fig. 29 gives some idea of these blood spaces seen from the ventral surface. The epithelium appears to be gathered into partitions dividing the cavity into a number of small galleries. Some observations upon the living creature will now be described. I have found it best to use a hollow-ground slide—varying the size of the hollow to suit the size of the woodlouse—and using a rather thicker cover-glass held down by two pellets of paraffin wax. The wax can be melted by a mounted needle, and the height of the cover-glass adjusted so as to restrain the creature with its ventral surface uppermost. It is always best to remove carefully the last two pairs of legs, for they are apt to obscure the abdominal plates.

The breathing action of the exopodites is very evident, and even in such a "dry" species as this, there is a film of water covering the endopodites and the dorsal surface of their exopodites. The film can be seen alternately retreating and advancing as the exopodites are raised and lowered. If working with a table lamp the heat from this is sufficient to cause some evaporation of this water, and one can see the air gradually working its way under the exopodites, as the water recedes, until there is a large bubble of air in the space between the exopodite and the ventral wall of the next exopodite. This air bubble expands and contracts as the exopodites move. When the air has gained access to the space under the exopodites, the silvery appearance of the exopodite resembles very closely the special segment of the exopodites of *Oniscus*, to which attention has already been directed, and confirms the point that their appearance is due to the air imprisoned under those special edges.

The creature in this position is useful for showing the circulation of the blood in the exopodites, and it is usually advisable to run in water under the cover-glass so as to submerge the animal and get rid of the surface reflections. It is interesting in passing to note that when it is submerged, the movement of the exopodites is much more marked. They become widely separated at each movement, no doubt owing to the ease with which they can be moved in the water, and not because of any increase in muscular action, for if the water is drained away, the amplitude of the movements is once more reduced to the normal. It is important to remember that air can gain access more easily than water, and the slight movement of the exopodites sufficient for the purpose of the necessary exchange, will also prevent the desiccation of the endopodites. The circulation of blood in the first two pairs of exopodites will be referred to later. We are concerned with the exopodite of the 3rd and the next two abdominal appendages. I have watched both males and females for hours, but have failed to detect any circulation in the distal region of the exopodites. In the proximal region now and again a blood corpuscle could be seen threading its way from one side to the other, but there is here nothing comparable to the circulation which can be seen in *Trichoniscus* or *Oniscus*.

In the sections examined very few blood corpuscles have been found in the exopodites, indeed the epithelial linings of the two faces are so closely applied, save in the proximal region, that the large corpuscles could not pass through the



Porcellio scaber ♀.

cavity. It is only in the proximal region that there is a normal blood cavity. However, at one special period there is a considerable amount of blood found in the exopodites, and this is when a new chitinous cuticle is being secreted by the epithelial layer. I was fortunate enough to get one or two specimens in this condition, and the sections through the abdominal appendages have been most instructive. If Figs. 26, 27, and 28 are studied, these points are still further illustrated. Fig. 26 shows the protopodite and the proximal one-third of the exopodite in longitudinal section. The epithelium is shown in too dense and definite a form for a normal exopodite. It is like that when the new cuticle is formed, and then the protoplasm becomes vacuolated and stringy, and the exopodite appears in section like Fig. 27. The epithelium has, however, a very definite inner wall, and appears rather like an extremely thin layer of chitin. This persists, and seems especially distinct in *Porcellio*. It is probably this inner boundary of the epithelial cells which led Stoller astray, and induced him to describe it as a distinct layer of elongated cells forming the wall to the blood cavity. Also, there are little irregularities which might be taken for tiny nuclei by a casual observer, but there are no nuclei there, and the whole structure is very clear when exopodites in different conditions are examined. Fig. 28 gives the appearance when a new cuticle is being formed beneath the old one, and it is at such a time as this that blood corpuscles are found in the internal cavity. It is by a comparison of such an exopodite with one during the intermoulting period that the real meaning of this definite boundary is understood. In the distal part of the exopodite the two epithelial layers come so near to one another that the two boundary lines give the appearance, under the low power, of a median line dividing the exopodite into two, but this is not really so. (Fig. 27.)

Both the chitinous cuticle and the epithelium are thicker on the dorsal or inner side. This conforms with the general rule for woodlice, and Stoller's mistake with regard to this has already been referred to. There is no need to repeat his words here.

In the proximal region, especially in the part near to protopodite, a little intermediary tissue can be seen. (Fig. 26.) It blocks up what would otherwise be a large cavity, and so retards the flow of blood both in the protopodite and the exopodite. Another unusual feature is the poor development of the pillars. There are very few pillars, and those that are present appear to be a simple fusion of the epithelial cells of each face, and nothing of the definite structure, which we have referred to in the other forms, is visible here. They cannot be traced from cuticle to cuticle, and are of the simplest form; indeed they appear to be degenerate, for they are much more evident in a specimen which is forming a new cuticle. (Fig. 28.)

This exopodite, as well as those of the next two appendages, was probably useful for respiratory purposes at one time. The very thin chitinous cuticle on the ventral surface points to this, but in course of time when the exopodites of the first two abdominal appendages developed the efficient air-tree organs, it was more economical to concentrate the blood supply in these special organs; consequently the respiratory function of the 3rd, 4th, and 5th pairs of exopodites, became less important, and degeneracy of pillars and epithelium would naturally follow.

The inner or dorsal surface of the 5th pair of exopodites has the curved rows of special hairs, similar to those described under *Oniscus asellus*. Also on the ventral surface of the abdomen at a place covered by this part of the exopodite, there are found large backwardly curved setæ. (Fig. 25.)

The Endopodite: The endopodite is, except in one important particular, similar to that described under *Trichoniscus* and *Oniscus*. It is a flattish bag with thick spongy walls, which are composed of a very thin chitinous cuticle, and a thick epithelial layer containing large nuclei. A few pillars join the cells of the two faces. In these things it is typical. The protopodites which carry the exopodites and endopodites stand out well from the ventral surface, and thus form between adjacent protopodites and exopodites a series of pockets in which the endopodites lie. This arrangement can be seen in Fig. 25, but the exopodites and endopodites in that drawing are not in their natural positions for the killing and subsequent operations incident to sectionising cause the exopodites to gape. In life the exopodites are found resting on one another, and this will close the pocket in which the endopodite rests.

It is usual to find that a mass of intermediary tissue directs the course of the blood as it enters the endopodite from the protopodite, in such a way that the blood will pass down the inward border and out along the outer border. Here there is something quite different.

When the endopodite is examined as a flat object under the microscope, especially after treatment with methylene blue, a curious curved finger-like mark is seen bent to form the letter L. The mark runs from the place of articulation directly backward and then turns towards the inner border. At first sight this had the appearance of a process of cells pushed into the cavity of the endopodite, but neither dissection nor sectionising showed any intermediary tissue either in the proximal or distal region of the endopodite. The sections, however, did show that this appearance was due to a tube with a special wall. If the endopodite is examined with the dorsal surface uppermost, the wall in the region of the tube is in no way different from that of the rest of the face; but if the ventral surface is examined, the thick, large-nucleated cells of the endopoditic epithelium give place to small thin cells with small nuclei in the part where this special tube is situated. This can be seen by altering the focus and bringing into view alternately the dorsal and ventral walls of this tube. Thus, there is a wide tube or channel running from the protopodite into the middle of the endopodite, and this channel is bounded by the ordinary wall on the dorsal side, by a special layer of small cells on the ventral side and laterally by the more or less opposed walls of the epithelial cells with frequent pillars joining the two sides together. The relations of this channel have been followed through a series of sections, and reference to Figs. 31 and 32 will suffice to make clear this unusual feature. This channel is an afferent blood canal bringing blood into the middle of the appendage, and is an effective way of regulating the flow of blood. Stoller gives no hint of this structure in his reference to the endopodite.

The Exopodites of the 1st *and* 2nd *Abdominal Appendages*: We must now consider in detail the interesting breathing organs which are found in the first two pairs of abdominal appendages. They appear as whitish marks to the naked eye, and as air-trees or air-sponges when examined under the microscope. They are an attempt at a more satisfactory method of breathing, and aim at bringing the air and the blood into closer relationship by means of invaginations of the outer wall.

One is reminded at once of the tracheal tubes of insects, but here we are faced with an independent and very much less perfect method and one, furthermore, which is very much restricted; for the air only enters into a part of four abdominal plates, whereas in insects the tracheal tubes ramify throughout the body. The blood in woodlice is therefore of the more importance as a carrying agent of oxygen from these special breathing organs to the rest of the body. These air-tree organs are found in both male and female, and are essentially the same, so that a description of the female exopodites will be given.

Figs. 22 and 23 give a general appearance of these air-tree organs as seen from both the ventral and dorsal aspects. Fig. 22 represents one of the first abdominal exopodites, ventral aspect; Fig. 23 one of the second exopodites, dorsal aspect.

Only a brief account of the general structure of these organs, sufficient to enable anyone to follow the detailed description, is necessary. The cavity of the exopodite is invaded by a tree-like invagination of the wall, and this causes a wide separation of the dorsal and ventral surfaces of the exopodite. The entrance to the air-tree is on the inner or dorsal surface, a little way from the outer posterior border, and the actual entrance is situated in a transverse groove, the opening of which points backwards. The place of the actual opening into the air-tree is indicated by a notch in the ventral posterior border. This notch is very conspicuous in the exopodites of the 2nd abdominal appendage (Fig. 23).

The chitinous cuticle, which is more or less sculptured in all parts of the body, has a very characteristic pattern in the region of this groove. Fairly deep furrows divide up the thickened chitin into hexagonal areas which carry a maze-like arrangement of narrow ridges. Fig. 38 shows a few of the hexagonal patches seen from above. In section the chitin has the appearance of flat-ended processes carrying hairs (Fig. 40). The limits of this specially sculptured chitin are important. Starting from the dorsal edge of the groove, it covers both the sides of the groove and extends to the posterior ventral border and round on to the ventral surface for a short distance. Fig. 40 shows the distribution as seen in a section taken along the line EF in Fig. 22.

The air-tree occupies rather less than half the area of the exopodite. The remaining part is more or less typical in structure, except that, as compared with the exopodites of the 3rd abdominal appendage, there are better pillars and a wider blood cavity. When a living specimen is under observation, it is easy to see that blood corpuscles do penetrate into the normal part of the exopodite, going some little way before sweeping round towards the air-tree, the destination of the blood. The pillars are interesting because of their degenerate condition in the other exopodites. Large, well-defined pillars, running from cuticle to cuticle, mark the place of transition from the swollen, air-tree part and the narrow, normal part; other smaller, yet very well defined, pillars, are scattered near by. Fig. 33 represents a transverse section through such an exopodite as is shown in Fig. 23, the line of section being along the line AB.

It should be noted that the exopodites of the first and second abdominal appendages have thicker chitinous cuticle on the ventral than on the dorsal surface. This exception to the general rule (Fig. 40) has to do with the method of changing the air in the air-trees. This will be discussed below. It has already been pointed out that the amount of blood passing through the exopodites of the 3rd, 4th, and 5th abdominal appendages is very much less than the amount passing through the same exopodites in *Oniscus* and *Trichoniscus*. When, however, we examine the exopodites of the 1st and 2nd abdominal segments in *Porcellio scaber*, a very different state of things is found. In these exopodites there is a good and constant circulation. The blood enters the exopodite by a definite passage or channel from the protopodite on the ventral side of the appendage, and finds its way through the meshwork of air-tubes to the dorsal and posterior side, where, collecting in a large blood space which runs along anterior to the large groove, it passes out by another definite channel into the protopodite and so back to the pericardium and heart. The intermediary tissue or tissue of the body cavity is the limiting tissue of these afferent and efferent blood channels. One can see the blood rushing into the exopodite, and the major part of it at once becoming entangled as it were in the maze of blood passages caused by the branches of the air-tree; some of it, however, as we have noted, travels out into the flatter part and then works back to the air-tree, entering the maze of passages at the side. The blood corpuscles slowly thread their way among the air-tubes until lost to sight in the depths of the tree.

By examining serial sections taken across such an exopodite further details can be made out, and in Figs. 34 and 35 two out of such a series are given. Fig. 34 representing a section taken along the line AB in Fig. 22 shows the afferent channel on the ventral side, leading into a large blood space or sinus from which the blood will be distributed to the air-tree organ. The dorsal sinus (eff. c.) is also shown. In Fig. 34 representing a section taken along the line CD, nearer the outer border, we see the end of the dorsal sinus and the efferent channel leading from it out into the protopodite. I have given the circulation in some detail, for Stoller in his account does not deal fully with it. The function of the dorsal sinus or collecting chamber, which is so important in connection with the even passage of the blood through the sponge-like mass, has been misunderstood by Stoller, who also presents what I feel is a mistaken explanation of the special sculptured region of the chitinous cuticle which surrounds this sinus and the entrance to the air-tree. He looks upon these two things; the dorsal blood space and the grooved wall, as furnishing an important subsidiary respiratory organ. It will be best to quote one or two paragraphs from his thesis:—

"That the larger furrows or grooves separating the poly- " gonal areas contain air may be demonstrated by mounting " a gill in water, when they are seen to appear white by re- " flected and dark by transmitted light. If a gill is placed in " alcohol before examining, the network does not appear dark " under transmitted light. The finer furrows of the poly- " gonal areas do not appear to hold air." (P. 13.)

"It is evident that the gill of *Porcellio scaber* is a struc- " ture adapted to bringing the blood into relation with air. " Two different and independent anatomical structures are " employed in order to secure a ready exposure of the two " media to each other. These are first, the net-work of fur- " rows in the chitine at the exterior of the gill, and second, " the unfolded portion of the chitinous wall, forming the " internal tree." (P. 15.)

"Applying these principles (i.e., permeability and " strength) we see that in the specially modified portion " of the chitinous wall at the exterior of the gill increase of " surface and at the same time thinness of wall is secured " through the furrowing of the chitine. Furthermore, " the furrowed structure is that which in the least degree " compatible with the attainment of these two ends detracts " from the strength of the wall. The arrangement of the " furrows in a net-work is adapted to securing the largest " linear extent of grooving, and at the same time the least " sacrifice of strength of the wall. The shape of the furrows " which as seen in section (Fig. given) is that of an oval " with the long axis at right angles to the face of the wall is, " I conceive, adapted to a threefold purpose, namely: first, " to contain a large amount of air relative to the space oc- " cupied; second, to retaining this air in the groove (by " means of the narrowing of the opening); and third, to re- " duce to the least extent the strength of the wall (by means " of the resistance to fracture secured through the curved " surface to the oval).

"The tree, as a mass, is somewhat spherical in shape " which secures the most favourable distribution of the " branches in the fluid surrounding them. But the sphere is " depressed on the basal side of the tree, leaving a space be- " tween the base and the grooved area of the wall of the gill. " It is evident that this is an adaptation for bringing a re- " latively large amount of blood into rotation with the air " contained both in the grooves and in the basal branches of " the tree." (P. 16, Stoller.)

The special sculpturing of the chitin around the entrance to air-trees is to keep them free from the danger of becoming clogged by water. If a specimen, secured in the way already described, so as to exhibit the ventral surface of the abdomen, is flooded with water, it is clear that unlike the rest of the body, the chitin of these special regions of the first two pairs of exopodites, is not easily wetted. It will be remembered that the special sculpturing extends some little distance on the ventral surface, and it is easy to see the air clinging to this part and keeping the water away from the entrance to the air-trees. If one of these exopodites is removed and mounted in water, it is possible to examine it under the high powers of the microscope and to see that there is certainly air retained in the smaller furrows upon the hexagonal areas just as there is air in the wider furrows between the hexagonal areas. Stoller is not correct in thinking that these smaller furrows do not retain air. It is very easy to demonstrate that they do, by exchanging the water for alcohol and watching the effect. With care, the water can be withdrawn and alcohol substituted without disturbing cover-glass or exopodite. As the alcohol begins to flood the exopodite the air is driven out of both the larger and the smaller furrows. It is obvious that air in these smaller furrows would be useless for respiration.

Then again the distribution of this specially sculptured chitin points to a different use from that suggested by Stoller. Not only is it found on both sides of the entrance groove leading into the air-tree, where the chitin is very thin below the larger furrows, but it extends round the posterior and outer edge of the exopodite and on to the ventral surface, where the chitin is very thick. Then the rest of the dorsal surface, especially the part just anterior to the edge of the groove, is smooth and thin. There is a blood cavity within the appendage at this place, and if the sculpturing aided respiration this seems the very place to have it (cf. Pl. XIII., figs. 34, 35, and 40).

The use of this elaborate sculpturing of the chitin is to prevent water from clogging the entrance to the air-tree, and thus stopping the free current of air so necessary for efficient respiration. It is interesting to remember that aquatic insects exhibit a somewhat similar device for preventing water from entering the spiracles.

The position of these air-tree-holding exopodites so near the ground, and the fact that the other breathing organs, the endopodites, are only functional when coated by a film of water, make some protection essential to the success of the air-trees.

With respect to the minute anatomy of the air-trees I am again in disagreement with Stoller's account. He says, on p. 15:—"The walls of the tubules are thin and show no mark-"ings. Lying outside of the chitinous layer is the likewise "thin hypodermic layer. Outside of this and closely "associated with it is the boundary wall of the blood cavity. "Thus, every portion of the wall of the tree is composed of "three very thin layers. The hypodermic nuclei occur at "frequent intervals." (Stoller.)

There is no need to refer again here to the question of a definite wall to the blood cavities. It has already been shown that this does not exist. There are but two layers separating the blood cavity and the air-tubes, the epithelial (or, to use Stoller's term, hypodermic) layer and its chitinous cuticle. However, as in the other places, this epithelial layer is usually reduced until it appears that only a very thin layer of chitin separates blood and air, but the nuclei of this epithelial layer are prominent, and at certain times the whole layer is very evident. When a new cuticle is being formed beneath the old one, the epithelial layer is seen to best advantage, and Fig. 39 shows a section through a portion of the air-tree of a specimen in this condition. The normal condition of the air-tree in section is shown in Fig. 37. The epithelial layer is much reduced, except the layer which is beneath the surface cuticle.

Further, I do not agree that the chitinous walls of the air-tubes—the branches of the air-tree—are smooth. I find that the walls of all these air-tubes, both great and small, are thrown into ridges which remind one of the ridges upon the surface of the hexagonal areas on the chitin around the entrance to the air-tree.

In another place in his thesis Stoller, speaking of these air-tubes, says:—"The whole structure appears to be hol-"low, with smooth thin walls. The appearance of irregular "markings on the walls is probably due to shrinkage, con-"sequent upon the passing out of air." (P. 13.)

I have examined a very large number of these air-tubes under every kind of condition, both living and dead, with air inside and without air, as flat objects and in section, and I find that the walls have this distinct pattern of ridges. Fig. 36 shows the appearance when the tubes are full of air; and in the various figures of sections across the air-tubes the same irregularities of the wall are indicated (Figs. 37 and 39).

The presence of this distinct pattern on the chitinous lining of the air-tubes is most interesting in comparison with the structure of the tracheal tubes of insects.

The great problem for solution, to which Stoller makes no contribution, is the effective renewal of air in these air-trees. I believe that this pattern on the walls of the branches of the tree plays a part similar to that played by the spiral thread in the insect's tracheal tubes. *But where does it get the pressure?* There is no internal mechanism. At one time I wondered whether there would be pillars running across the swollen area, but this is not so. The only pillars are found in the more normal parts, and their operations would have little effect upon the air-tree organ. Could there be any other way of bringing pressure to bear upon the exopodites? There is the lowering and raising of the exopodites, the normal isopod breathing action, but as we have seen, this movement is very slight in these land-forms, and in the first two pairs of abdominal appendages, the air-tree exopodites hardly move at all. This does not seem effective. The clue came to me whilst watching a number of *Porcellios* which I had placed in different vessels for experiments in duration of life under different conditions of dryness, and varying amounts of carbonic acid gas, and also in water. When the creatures were in difficulty with their breathing, I noticed that the whole abdomen was alternately raised and lowered in an unusual manner. This was especially evident in a specimen placed in carbonic acid gas. When the abdomen was raised and extended the exopodites stood well out from the ventral surface, somewhat as they are drawn in the longitudinal section shown in Fig. 25. When the abdomen was lowered and contracted the exopodites were pressed tightly against one another, and the transverse ridge seen in Fig. 25 as a process just anterior to the 1st exopodite, was pressed against the 1st exopodite.

By experimenting with an inverted woodlouse in a glass cell, which allowed a certain play of the abdomen, I was able to confirm the above statement; and by submerging the creature could get evidence of the effect of the pressure upon the air-tree organs. The ventral wall of those exopodites which bear the air-tree organs, is very thick, whilst the dorsal wall is very thin. (Figs. 40, 34, 35.) The attachment to the protopodite is such that any external pressure would cause the exopodites to respond readily to it. Indeed, the shape, the way in which they press against one another, the transverse fold of the ventral wall which abuts on to the ventral surface of the exopodite of the first abdominal appendage, all support the above suggestion that pressure is exerted by flexion of the abdomen.

The next point to consider was the effect of the pressure upon the air-tubes inside. One of the easiest ways of seeing this, is to remove one of these exopodites from a living *Porcellio* and examine it under the high power of microscope. By cotton wool or some such substance, the cover glass can be kept from pressing on to the exopodite, until such pressure is required. When slight pressure is exerted on to the cover glass, the effect can be watched. The air is seen to leave the finer tubes or branches, and then return when the pressure is relaxed. By careful observation it is clear that the character of the wall of the air-tubes in being strengthened in the way already referred to, is responsible for this return to the normal condition. The ridge-like markings on the walls enabled the tubes to spring open again when the pressure is relaxed, and so allow the air to return unobstructed. Without some such arrangement as this, it would be impossible to get the air into these very minute air tubes.

The pressure on the surface walls of the exopodite will be conveyed by the blood in the blood cavities which surround the air-trees, to the larger and smaller air-tube branches of the air-trees. It seems clear that the mechanism for bringing about the exchange of air in the air-tree is external pressure brought to bear upon the exopodites, by the flexion of the abdomen.

It may be that the legs also play some part in bringing pressure to bear on these air-tree-holding plates, for the last two pairs of legs, when the creature is at rest, are carried bent inwards so that the basipodites rest upon these first two pairs of exopodites. When *Porcellio* is disturbed, the creature usually tries to disarm suspicion and to protect itself by an attempt to roll up the body; the legs are all bent inwards and pressed tightly against the ventral body wall, and the body is flexed to such an extent that it often rolls over on to its back. This special flexion of the body will bring considerable pressure upon the first two pairs of abdominal appendages, and although the action is primarily one of defence, it cannot fail to be of use in respiration.

The whole question of the flexion of the body, carried to far greater lengths in *Cylisticus convexus* and in the *Armadillidia*, is of considerable interest and is, I believe, correlated with this new method of respiration. The matter will be discussed when these other genera are under review and when the whole question of respiration is discussed in its relation to the habitat of the various forms, in a further communication.

6. *Cylisticus convexus* (De Geer).

Pl. XIV., figs. 41-48.

The arrangement and disposition of the abdominal appendages is similar to that described in the other woodlice, except that the lateral plates of the 3rd, 4th, and 5th abdominal segments bend downwards, so as to make a shallow cup-like cavity in which the abdominal appendages lie. This is shown in Fig. 42. A ventral view of the abdomen is shown in Fig. 41, and the five pairs of air-tree organs are indicated.

The 3rd Abdominal Appendage: Fig. 43 gives a ventral view of this appendage. From this the general details of shape and relation of the parts can be determined.

The Exopodite: The exopodite is divided into two regions: the normal, thin, plate-like part and the special swollen part containing the air-tree organ. This latter part is towards the outer border of the exopodite and extends over rather less than half the area of the exopodite. The size of this swollen part diminishes somewhat in the 4th and 5th exopodites, but is about the same size in the 1st two pairs of abdominal exopodites.

When the living animal is observed under the microscope, it is easy to see that the exopodite of this appendage has a good blood supply, and is in this respect much more like *Oniscus* than *Porcellio.* There is a constant and a vigorous stream of blood flowing towards and through the air-tree organ much the same way as has already been described for the first two abdominal exopodites of *P. scaber*. The cause of the blood is also very much the same as already described in *Porcellio,* and is much the same in all the abdominal exopodites. The exopodite of this appendage, as well as of the next two pairs, acts as an operculum as well as an additional breathing organ, and it is so arranged that the one function does not interfere with the other. Fig. 42, in which a section through the 3rd abdominal appendage is drawn, shows this very well. The dorsal wall of the exopodite is so arranged that the alteration in levels, between the swollen air-tree part and the normal part, is abrupt. Thus the endopodite is enclosed in a kind of chamber. The openings into the air-tree organs are on the outer border well away from this chamber, which is kept very moist.

There is no need to give a detailed description of the normal part of the exopodite. It is typical with its chitinous cuticle, epithelial layers, and the pillars transversing the cavity. The dorsal chitinous wall is, in this region, thicker than the ventral one, thus conforming with what has been found to be the general rule in land isopods, but the ventral wall is not very thin, which is what we should expect seeing the respiration will be undertaken by the air-tree organs, and not take place through the ventral wall. Then as the walls approach the region of the air-tree organ, a change takes place, the chitin of the ventral wall becomes much thicker, whilst that of the dorsal wall becomes very thin. We have already commented upon this in the case of the air-tree organs in *P. scaber,* and the reason here is the same as there; the strong curved ventral cuticle, together with the very thin dorsal cuticle, enables the creature to bring pressure to bear on these air-holding appendages by flexing the body, and the appendages regain their normal shape when the pressure is relieved.

The special breathing organ will require rather more attention, for it presents some striking differences from those already described under *P. scaber,* and I do not agree with Stoller when he says that the air-tree organs are similar in the two genera. As one looks at the exopodite as a flat object from the ventral side (Fig. 43), the air-tree appears to be composed of several distinct parts, spreading out towards the middle region of the exopodite. Each of these is

CYLISTICUS CONVEXUS ♀.

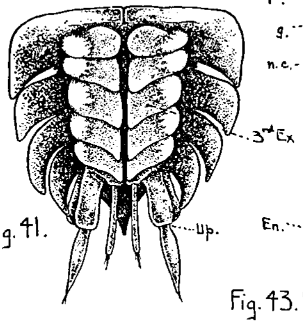


Fig. 41.

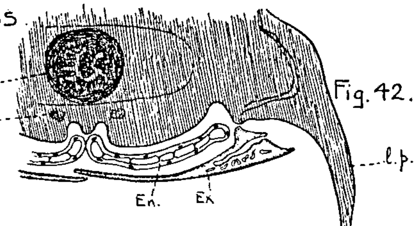


Fig. 42.

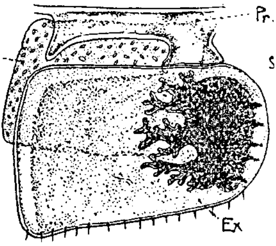


Fig. 43.

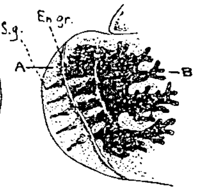


Fig. 44.

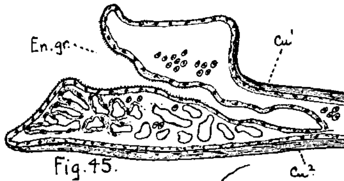


Fig. 45.

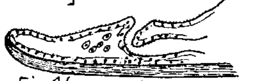


Fig. 46.

Fig. 48

Fig. 47.

PORCELLIONIDES PRUINOSUS. ♀

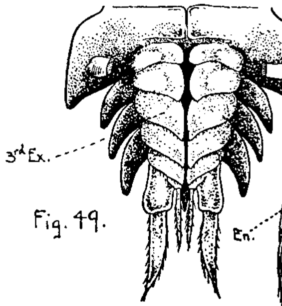


Fig. 49.

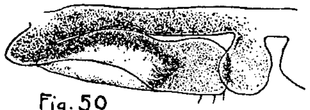


Fig. 50

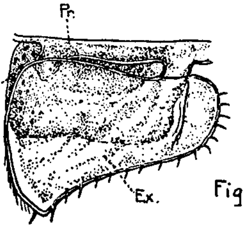


Fig. 52

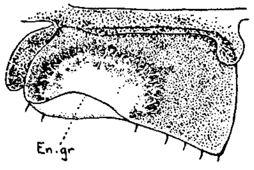


Fig. 51

EEU del

Cylisticus convexus ♀.

Porcellionides pruinosus ♀.

more like a large air cavity ending in smaller branches or tubes than like a tree or bush of many fine inter-locking branches as in *Porcellio*. Fig. 43 represents this organ as seen in transmitted light, the air-holding parts appearing blackish. Towards the outer border four or five dark processes can be seen. They appear white by reflected light. The significance of these will be seen when the dorsal surface is examined. Fig. 44 shows the dorsal surface of this part of the exopodite seen also as a transparent object. It is clear that the main entrances to the breathing trees are situated in a distinct groove, a little distance from the outer border. Into this groove, which runs anterio-posteriorly, open the five or six large air trunks or cavities which have already been referred to. Then the four or five dark bands, extending towards the outer border, are seen to be grooved openings leading down into small air-tubes in the more ventral part of the appendage. These small radial grooves have a very characteristic appearance, which I have attempted to draw in Fig. 47, as it is seen under the high power. It is impossible to indicate clearly the differences in levels, as the groove deepens and widens.

I tested all these apertures with warm alcohol, and also by gentle pressure, and saw air bubbles passing out both from the larger cavities which open into the large groove, and from the small special grooves. Further information was obtained from sections. In Fig. 45 one of the large air-cavities is represented extending a considerable way into the exopodite. In Fig. 46 one of the small apertures is figured as it appears in transverse sections. It leads into smaller branched air-tubes in the ventral part of the exopodite.

The surface of the chitinous cuticle is sculptured in the region of these apertures, but the sculpturing is not nearly so prominent a feature as in *Porcellio*. The whole cuticle of these exopodites, indeed of the whole body, is sculptured to a certain extent, but it is in the region of the entrances to the air-tree organs that it becomes sufficiently prominent to hold air. It is clear that this arrangement will prevent water from easily wetting the surface, and so prevent the minute apertures of the air-tree organs from becoming clogged with water. When an exopodite, removed from a living animal, is mounted in water and examined by transmitted light, the air is seen clinging in these small grooves, and when alcohol is substituted for the water, one can watch the air being dislodged.

I mention these details again here because in Leydig's account to be referred to below, he has misinterpreted the function of these minute sculpturings.

The internal chitinous lining of the air cavities and tubes is raised into ridges, forming a maze-like pattern on the wall (Fig. 48). The use of this is the same as the similar pattern on the air-tube walls in *Porcellio* already described. I was able to see the air-cavities spring open again when external pressure was removed, and confirm the observations and conclusions reached in connection with the exchange of air in the air-trees of *P. scaber*. The question of the bringing external pressure to bear upon these air-holding bodies, is taken a stage further in this woodlouse. We have seen that *Cylisticus* can flex the body to such an extent as to bring the ventral surfaces of the head and abdomen together. This power of folding up will be valuable for many purposes, but one of these will be the pressure brought to bear upon the abdominal exopodites and the consequent exchange of air in the air-trees. There is the same prominent ridge of thick chitin situated immediately anterior to the exopodites of the first abdominal appendages, which will press against these exopodites. Of course, I do not mean to imply that it is necessary for the body to be completely flexed to bring pressure to bear on the abdominal exopodites; naturally when this is done the greatest pressure will be exerted, but any slight bending of the abdomen will have its effect upon these very spongy bodies, and a species with considerable power of flexion will more easily exert the necessary pressure. The entrance to the air-holding region is, as we have seen, quite distinct from the entrances to the damp cavities in which the endopodites are found. There is the same lowering and raising of the exopodites, which we have noticed in the other genera to allow air to gain access to the endopodites. The dorsal surface of the exopodites, indeed the whole of the ventral surface of the abdomen and the appendages, are readily wettable, with the exception of the special part at the entrances to the air-tree organs; and a distinct film of water could be seen underneath the exopodites when a living specimen was examined under the microscope. This woodlouse seemed much damper than *P. scaber*.

The exopodite of the 5th abdominal appendage has the same arrangement of long hairs on the dorsal surface as we have noticed in the case of *O. asellus* and *P. scaber*. The ridge with its rows of long seta-like hairs arranged in fan-like groups is very distinct, and it was in this woodlouse that I first of all became aware of this special "frise" of hairs.

The Endopodite: The endopodite is very similar in structure to that of *O. asellus*. It is larger in proportion to the size of the exopodite than in that form. The same parts are found here, and need not be repeated.

The exopodites of the 1st and 2nd abdominal appendages need not be described in detail, for the structure of the air-tree organ has been given in connection with the 3rd abdominal appendage. In all essentials the air-tree organs of the whole five pairs of exopodites are identical.

Stoller in his account of the respiratory organs of this species says:—

"I have carefully examined, both as seen from without " and in section, the outer gills (i.e., exopodites) of the 1st " and 2nd pairs, and I find that in all essential respects they " are identical in structure with the same parts in *Porcellio* " *scaber*. The only differences are such as relate merely to " comparative form and size. The descriptions and figures " already given for *Porcellio scaber* are applicable to this " species, as respects all essential features of structure."

I have already shown that there are substantial differences. He continues:—

"Inasmuch as I have found the structure and relations of " the air-holding parts of the gills to be essentially different " from what Leydig describes, it may be suitable to quote " those passages of his work in which he sets forth the " results of his investigations in regard to the main points."

Then follow some thirty lines taken from Leydig's paper. I have read Leydig's paper and studied his figures, and although I agree with Stoller that Leydig is incorrect in his descriptions, I do not feel that Stoller has shown that he quite realises Leydig's mistake. Leydig describes in some detail the antennæ, the eyes, the surface of the body including the peculiar hairs on the legs, of a number of woodlice, before describing the exopodites and endopodites of *Cylisticus convexus*.

Beginning with the endopodite, his first sentence: "Es " ist dasselbe nach aussen umgrenzt von einer zarten, doch " von Porencanälen durchzetzten daher senkrecht streifigen " Cuticula, oben und unten,"

causes a doubt to arise as to the correctness of his observations, and I agree with Stoller that there are no pores penetrating the cuticle, although the epithelial layer is certainly striated. The mistake has probably arisen by Leydig misinterpreting surface markings. He remarks that in a previous research he had found something similar in the gill plates of *Asellus aquaticus*. I have examined *Asellus* again, but cannot find what he describes, and Kimus in his valuable researches upon the branchiæ of aquatic isopods shows how incorrect Leydig's observations are. Quoting a description of the branchiæ of *Asellus* by Leydig, Kimus remarks—

"Nous reviendrons plus tard sur celle description et
" nous verrons qu'elle est bien loin de nous donner une idée
" nette de la structure des lames branchiales.

"L'auteur reconnaît qu'il n'est pas parvenu à inter-
" préter les apparences qu'il a eues sous les yeux."

Leydig then turns his attention to the exopodite (decklamelle), and we find a similar error here, but one which is more serious because he professes to upset the observations, crude and incomplete as they are, of Lereboullet, Siebold, and Wagner, who described the "corpora alba" as branching sacs with blind closed ends. Leydig says:—

"In Wirklichkeit bestehen solche blindsackige enden
" nicht."

The earlier investigators did not examine these organs closely, and do not describe histological details, consequently many of their conclusions are incorrect, but Leydig, who makes a closer examination of these exopodites and the air-tree organs, seems to me still further from the real morphological and physiological explanation of these interesting organs. In describing the surface of the cuticle he says:—

"Zerstreut über die ganze Fläche weg vertheilen sich
" noch Kleine pneumatische Räume der Cuticularschicht."

The next extract from Leydig is a part of his paper quoted by Stoller. This, with one or two other extracts from other parts of Leydig's communication, will serve to explain his ideas concerning the air-holding structures.

"Dieselben Zellen scheiden an ihrer freien Fläche, inso-
" fern sie die Bluträume begrenzen, eine zarte, die Blut-
" gänge Auskleidende Cuticula ab und diese letztere ist es,
" welche pneumatisch wird. Die Luft ist in kleinen Höhlen
" der Cuticula enthalten, daher die 'feine Zertheilung' . . . .
" da ja die Luft in der cuticularen Wand der Bluträume
" liegt."

In the course of this description Leydig refers to a figure showing a transverse section through the air-holding part of the exopodite. From this figure and his description (a part of which is quoted above) it is clear that he has mistaken air cavities for blood cavities. The air-tubes with the chitinous wall raised into ridges which we have seen as a characteristic feature of these special organs are marked as blood vessels, and are described as such, and the chitinous pattern on the wall is looked upon as an elaborate arrangement of pneumatic pores and canals.

Near the end of the account, he again refers to this character of the chitin, and it seems likely that the property of retaining air in the fine grooves on the chitinous cuticle (to which I have referred at some length) has deceived Leydig into thinking that the cuticle is full of pneumatic spaces. He says—

"dass auch in der allgemeinen Cuticula der Decklamelle
" ebensolche lufthaltige Höhlen, wenn auch nur in
" Zerstreuter massiger Menge Zugegen sind."

He thus misinterprets not only the structure and function of the chitinous sculpturing both on the surface and on the walls of the air-cavities and branches of the air-trees; but also the circulation of the appendages. The blood flows in wide spaces bounded by the epithelium, and is not confined in definite tubes lined by chitin.

Stoller gives no indication of this serious error in Leydig's account and, as far as I can see, has not fully grasped the details of Leydig's description of the air-holding cuticle, for after quoting from his paper he adds:—"It is true that
" the air-canals have walls of chitine secreted by the hypo-
" derm, but these canals do not open outwards in pores, but
" join one another inwards to form a tree-like cavity which
" communicates with the outside of the gill through a single
" opening." This points to the difference being merely one of the kind of exit from air-tubes, whereas Leydig denies the existence of these air-tubes altogether.

When discussing the physiological functions of the air-holding cuticle, Leydig is obviously in great difficulties, for he can see no method of getting any exchange of air in the pneumatic cuticle. One would have thought that this difficulty might have led him to experiment and in time revise his account of the organs. Instead, he doubts whether they have any respiratory function at all—

"Und sonach darf es wieder fraglich erscheinen ob die "Luft an dieser Stelle etwas mit der Athmund zu schaffen "hat."

I have dwelt at some length upon Leydig's work and Stoller's incomplete description of it, for it is very instructive to realise that both Leydig and Stoller have misinterpreted the function of the surface sculpturings. We have discussed this question in the account upon *Porcellio*. Again, Leydig, although figuring the ridges on the surface of the air tubes in the exopodite misinterprets their significance. Stoller denies their existence or at least dismisses them as wrinkles caused by collapse of the wall. In face of such serious mistakes, there is need for the whole question to be re-stated as plainly as possible, and this I have endeavoured to do.

7. *Porcellionides pruinosus* (Br.).

Pl. XIV. and XV., figs. 49-53.

Like *Porcellio scaber* this species has air-tree organs in the 1st and 2nd pairs of exopodites of the abdominal appendages, and in many ways is similar to *P. scaber*, but the abdomen is narrow, and it is much more delicate in build. It bears the same relationship to *P. scaber* as *Ph. muscorum* does to *O. asellus*.

Fig. 49 gives a ventral view of the abdomen of the female, the general arrangement of the appendages is normal. The exopodites are more curved in these narrow-abdomen forms. This may make up, in some way, for the lack of width in the abdomen. The mass of appendages together form a distinct rounded lump, instead of lying flat as they usually do.

The 3rd Abdominal Appendage: In Fig. 52 the left appendage is drawn seen from the ventral aspect. The parts are fairly typical. Protopodite, exopodite, and endopodite are all indicated. The protopodite stands well out from the ventral surface, this is shown in Fig. 53, which represents a longitudinal section through the abdomen and appendages. The exopodite fulfils the requirements of an operculum, fitting over the endopodite, and having a distinct ridge on the inner or dorsal surface, acting as a boundary to the endopodite cavity on the outer side. This ridge, which runs posteriorly from the place of articulation, can be seen through the exopodite in Fig. 52.

PORCELLIONIDES PRUINOSUS . ♀.

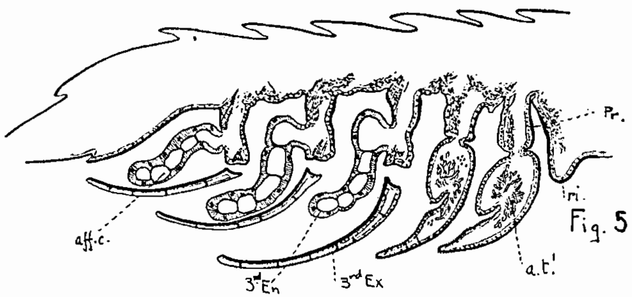


Fig. 53.

ARMADILLIDIUM VULGARE . ♀.

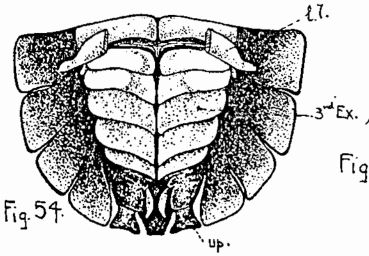


Fig. 54.

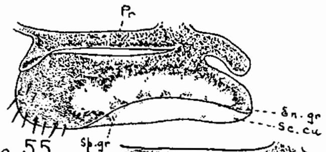


Fig. 55.

Fig. 55A.

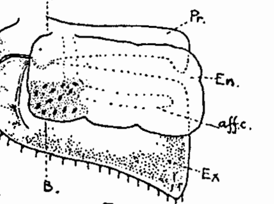


Fig. 56.

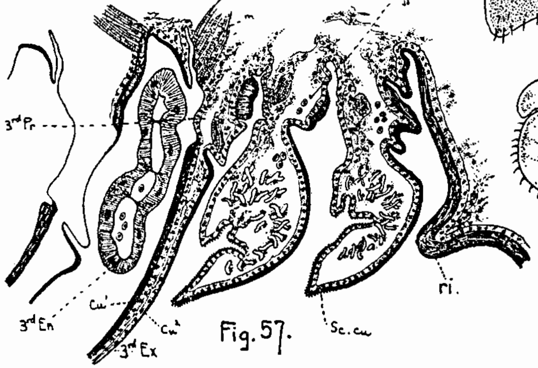


Fig. 57.

E.E.U. del.

Porcellionides pruinosus ♀.

Armadillidium vulgare ○.

The Exopodite: The structure of this exopodite seen as a flat object, and in transverse section, indicates a better blood supply than the corresponding exopodite of *P. scaber*. This is confirmed by observations upon the living creature; but the blood supply is not very good, not nearly so abundant or so vigorous as in the corresponding exopodite of *O. asellus*. The internal structure seen in section shows a wider blood cavity and better developed pillars than in *P. scaber*. The chitinous cuticle of the dorsal or inner wall is much thicker than that of the ventral or outer wall. The outer and posterior margin carries a row of short, stiff, spinous hairs, the inner margin, in its distal region, is covered wth fine hairs.

The Endopodite: This is in every way similar to the endopodites of *P. scaber*. It has a similar afferent canal, similar epithelial layer with large nuclei and well-developed pillars. (Fig. 53.)

The Exopodites of the 1*st and* 2*nd Abdominal Appendages*: These exopodites carry the "corpora alba"—the air-tree organs, the shape of the joint and the organs is shown in Figs. 50 and 51.

When the living specimen was under observation it was very evident that a much greater blood supply went to these exopodites than to the remaining normal exopodites.

The air-tree organs are of the same kind as in *P. scaber*. We notice a similar entrance groove, with the surface of the cuticle in that region sculptured; the internal structure of the tree and of the fine branches is the same; the blood supply is essentially the same also. So that all that has been written and figured for *P. scaber* will apply here.

This woodlouse has the same habit of flexing the abdomen, and of holding itself rigid in a flexed condition in very much the same way as *P. scaber*, when danger threatens. There is a very prominent ridge in front of the exopodites of the 1st abdominal appendage, and the methods in use for changing the air in these air-tree organs is exactly the same as described in *P. scaber* or *C. convexus*.

8. *Armadillidium vulgare* (Latr.).

Pl. XV., figs. 54-57.

The number and arrangement of the abdominal appendages in this species is the same as in the other woodlice, their arrangement, seen from the ventral aspect, is shown in

Fig. 54. This figure shows the shallow cavity, semi-circular in outline, which is formed by the flattening and bending down of the lateral plates of the abdominal segments and the blunt uropods. We saw something of this in *C. convexus*, but it is carried much further here.

There are large air-tree organs in the exopodites of the 1st two pairs of abdominal appendages. This species is stoutly built, the cuticle is thick and the chitin is impregnated with lime to a greater extent than in the other genera. The muscular system of the body is well developed.

The 3rd Abdominal Appendage: There are no unusual features about this appendage; it is very similar to the corresponding appendage in *P. scaber*. Fig. 56 gives a dorsal view of this appendage removed from the body, seen as a transparent object.

The Exopodite: The exopodite of this appendage and also of the 4th and 5th abdominal appendages, is little more than an operculum. In this it also resembles the exopodite of the corresponding appendage of *P. scaber*, but little blood can be seen traversing the blood cavities in the exopodite; and although the ventral or outer wall is much thinner than the dorsal or inner wall, and the exopodite more or less adapted for respiration, yet the same thing, already described in *P. scaber*, has taken place here, and, except at the period of manufacturing a new cuticle, the blood supply is much reduced. This will allow more blood to become available for the more important exopodites of the first and second abdominal appendages which contain the special breathing organs.

Sections through these appendages confirm this observation. The blood cavity in the exopodite of the 3rd abdominal appendage is seen to be much reduced, and a quantity of intermediary tissue—the tissue of the body cavity—is continued into the proximal region of the exopodite, not as a blood directing tissue, but as an obstructing tissue. In Fig. 57, which represents a longitudinal section through the first three abdominal appendages, the 3rd appendage is seen in section taken along a line represented by AB in Fig. 56. The whole length of the exopodite is not shown, but sufficient to show the details of the dorsal and ventral lamellæ with the thick cuticle on the dorsal side and thin on the ventral. The epithelial layers, the intermediary tissue and the reduced blood cavity, are also indicated. The section passes through the protopodite, and the elevator muscle is seen, which moves the appendage for the breathing action. There is a thick ridge of chitin on the anterior surface of this protopodite; a similar ridge, but broader, is found in the corresponding position on the next protopodite, the 4th abdominal. These thick bands of chitin may have some function in connection with the power of rolling and unrolling.

The Endopodite: The endopodite is in every way similar in structure to that described under *P. scaber*. It lies in a cavity bounded by the exopodites, protopodites, and ventral body-wall. It is a cavity but little bigger than the endopodite under normal conditions. In this cavity the endopodite remains in a moist condition covered by a film of water. The boundary walls, viz., the surface of exopodites and ventral body wall, are also damp. If a living specimen is kept under observation under conditions already described on p. 15, the air is seen gradually to work its way under the exopodites as the moisture evaporates in the heat of the table lamp.

The details of structure need only to be enumerated, for they are very similar in essentials to those described in connection with the endopodite of *P. scaber*. The thin cuticle, the spongy epithelial layers, the pillars, the blood cavity, and the special afferent blood channel are all similar. The only difference is in the size of the nuclei of the epithelial layers. They are much smaller in this species than in *P. scaber* or *O. asellus*. Some of these details can be seen in the longitudinal section, but the line of the section AB does not pass through the afferent canal. (Fig. 57.)

The protection of the endopodite by the closely fitting exopodites which reaches an extreme development in this species is related to its power of living in a very dry environment.

The Exopodites of the 1st and 2nd Abdominal Appendages: These exopodites carry air-tree organs, and there is no need to describe them in detail. Figs. 55, 55a show the appendages, as they appear from the dorsal aspect as opaque objects. The air-trees are well developed, and there is the sculptured chitin in the region of the apertures of the air-trees as we have described and figured in *P. scaber*. The air-tree of the 1st abdominal segment is well developed, occupying quite three-quarters of the available space, and it seems composed of several trees with several openings in the main transverse entrance groove. The character of the tree resembles those of *Porcellio* and not those of *Cylisticus*, that is to say, the tree is composed of a large number of branched and interlocking tubes leading off from a main stem. The air-tree nearest the inner border has a special grooved opening which runs in the sculptured face of the dorsal wall opening in a pore not far from the dorso-posterior margin. (Fig. 55.) This groove is similar, in every respect, to the grooves described and figured in the account of *Cylisticus*. There will be no need to repeat here what has already been written as to the structure of the air-tubes, the sculptured wall, the blood supply, and other details of these organs. I have examined and experimented with these air-tree organs in the same way as with those of *P. scaber*, and there are no important differences, apart from the size, the presence of more air-tree organs in one exopodite and the larger entrance groove with several separate passages into the organs.

I have also considered again the question of the changing of the air in these air-tree organs, and the conclusions come to in connection with *Porcellio* and *Cylisticus* are confirmed here. The method of bringing pressure to bear upon these swollen exopodites by flexing the body is very obvious here. In Fig. 57, which represents a longitudinal section through these exopodites, the curious ridge or process can be seen almost touching the outer or ventral surface of the exopodite of the first abdominal appendage. This specimen is only slightly flexed, and it is clear that if the abdomen is still further flexed, pressure will be exerted upon the air-tree holding exopodites. This pressure will drive the air out of the air-tubes, and when the pressure is relaxed by the straightening of the abdomen fresh air will rush into the open air-tubes. The ridges on the air-tube walls cause them to spring open and suck in the air.

The exopodites of the 5th abdominal appendage show on the dorsal surface the transverse ridge of hairs. This ridge is on the surface just behind the limits of the endopodite, and seems connected with the protection of the endopodite. All the exopodites are more hairy than in the other genera. Those of the 3rd, 4th, and 5th appendages have a row of stiff setæ extending along the outer and posterior borders.

9. *Platyarthrus hoffmannseggii* (Br.).

Pl. XVI., figs. 58-62.

If the living creature is examined it is seen that this species resembles *Trichoniscus pusillus* in the structure and function of the respiratory organs. Blood corpuscles can be

PLATYARTHRUS HOFFMANNSEGGII. ♀.

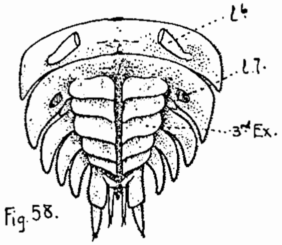


Fig. 58.

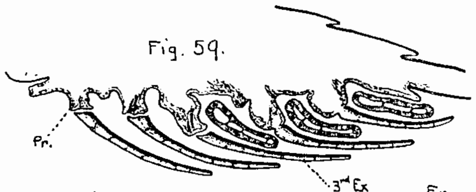


Fig. 59.

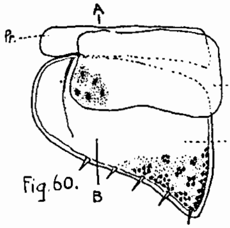


Fig. 60.

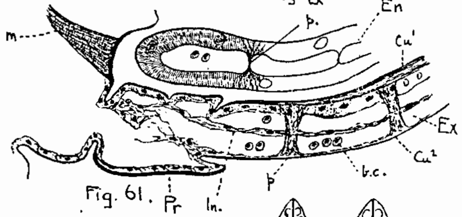


Fig. 61.

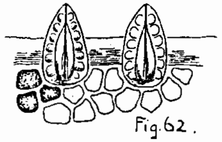


Fig. 62.

LIGIA OCEANICA ♀

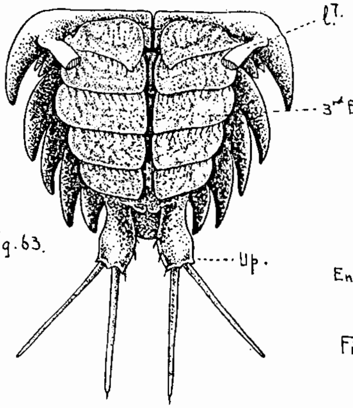


Fig. 63.

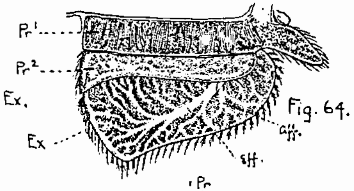


Fig. 64.

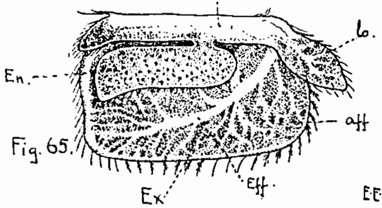


Fig. 65.

E.E.U. del.

Platyarthrus hoffmannseggii ♀.

Ligia oceanica ♀.

seen traversing the blood spaces in the exopodites of all five pairs of abdominal appendages.

There is the same respiratory movement of the exopodites and alternate separation and closing of these plates to allow air to have access to the underlying endopodites. As in the other woodlice the endopodites and all the undersurfaces of the exopodites are damp with a covering film of water. This film of water is seen retreating and advancing when the respiratory movements are watched in an inverted specimen. There are no additional respiratory organs in this form; nothing in the nature of air-trees or the special organs found in *O. asellus* and *P. muscorum*.

The 3rd Abdominal Appendage: This is typical with protopodite, exopodite, and endopodite all of usual form. Fig. 60 represents one of these appendages seen from the dorsal aspect. The same appendage is seen in part as it appears in longitudinal section (Fig. 61). The detailed description follows below.

The Exopodite: This is of the usual form. It is devoid of the curious tubercles, which are scattered more or less thickly over the surface of the cuticle in other parts of the body, and which are such a characteristic feature of this woodlouse. The posterior border carries five or six large, pointed bristles.

Examined as a transparent object after treatment with methylene blue one can see that there are wide blood spaces in which blood corpuscles are found. These blood spaces run between the pillars, which are well formed and abundant. The nuclei of the epithelial layer are also prominent. The circulation as seen in the living specimen is much the same as in *Trichoniscus*. The blood enters the exopodite at the point of articulation with the protopodite, and travels towards the inner border. From here it passes down and across the expodite to find its way out through the efferent canal which runs along the outer border.

The transverse and longitudinal sections confirm these observations, and supply further details. From dorsal to ventral one finds a thick cuticle, a thick layer of cuticular epithelium, a wide blood cavity, a very thin layer of epithelium, almost nothing in places, and a very thin cuticle. Joining the cuticles together are the pillars, and if the section passes through the proximal part of the exopodite, near to the articulation, some intermediary tissue will be found. These points are all shown in Fig. 61. All these details help to make the resemblance to *T. pusillus* still more marked.

The Endopodite: This also is very similar to the endopodites of *Trichoniscus* and *Oniscus*. It is a flat, thick walled sac. The wall is composed of a thick, epithelial layer, with large nuclei, carrying a very thin chitinous cuticle on the surface. A few pillars of the normal type join the epithelium of one side to that of the other. These pillars are very similar to those in the endopodites of *Asellus aquaticus*, which are described in great detail by Kimus in the memoir already mentioned. The pillar really consists of a number of long threads which run from cuticle to cuticle. The narrow part between the two lamellæ consists of the bundle of threads which separate fanwise in each epithelium. The threads mark out a pattern rather like an hour glass in shape or like two cones applied apex to apex.

There is no need to refer to the 1st and 2nd abdominal appendages, for the exopodites of these appendages are similar in every particular to those of the 3rd appendage, which has been described.

I have referred already to the curious tubercles that are present on the surface of the cuticle of the body and limbs. These tubercles are scattered over the dorsal surface in fair profusion and less thickly on the ventral surface. They are especially evident on the edges of the lateral plates and on the dorsal posterior edges of the thoracic and abdominal segments. They give a toothed appearance to these edges. Each tubercle is a flattened scale-like body, not standing out at right angles to the surface of the cuticle, but bent posteriorly at a small angle, so that when the carapace is examined under the microscope, one sees the tubercle almost as a flat object. Its appearance in this position is shown in Fig. 62. There appears to be a central part in the shape of a cone drawn out to a fine point with a surrounding border consisting of an expanded vacuolated wall. There seems to be a canal down the middle of the tubercle or at least some connection with the threadlike extension of the cone. The surface of the cuticle has a characteristic marking, being covered by a pattern of hollows sculptured out of the thickness of the chitin. The absence of pigment and the presence of these tubercles and the sculptured cuticle are responsible for the characteristic white colour of this woodlouse, which is blind and lives as a "pet" in ants' nests.

10. *Ligia oceanica* (Linn.)

Pl. XVI., Figs. 63-65.

Pl. XVII., Figs. 66-71.

The Abdominal Appendages: At first sight it seems that the number and arrangement of the abdominal appendages are the same as in the other woodlice. Fig. 63 shows the five pairs of plate-like exopodites overlapping in the usual manner; but upon examination it is found that the 1st and 2nd appendages still retain some traces of endopodites or at least of inner plates in a similar place to the endopodites.

Hewitt says:—"There are five pairs of abdominal appendages or pleopoda and a terminal pair of uropoda. Each pleopod consists of a pear-shaped superior lobe covering a small inferior lamella."

I agree insofar as the 3rd, 4th, and 5th appendages are concerned. The 2nd appendage carries a very small endopodite, but I can find no trace of an endopodite in the 1st abdominal appendage, although the basal part of the appendage, the protopodite to which the exopodite is attached, is large and is divided into two well-defined parts. A full description of these appendages will be given later, after the more normal appendage has been considered.

Observations upon the living creatures confirm Hewitt's short account of the course of the circulation in the exopodites, but his description is too general to be of any value. I, therefore, add a description as seen when the living *Ligia* is observed with the abdominal plates in view.

The blood enters the exopodite at the place of articulation with the protopodite and travels in a wide vessel along the anterior and inner borders.

Branches are given off from this afferent branchial vessel as it passes along the anterior border and down the inner border. These branches subdivide and disappear in the maze of interlocking vessels. There are two other main afferent vessels, distributing blood to the ventral surface: the one, arising from the principal afferent vessel near its proximal end at the place of articulation, passes backward

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I am retaining the terms used throughout, namely, ventral or outer for the surface, which is obviously ventral, as the plates are found, and as they are shown in Fig. 63. Hewitt uses the term "anterior" for this face; strictly speaking it may be anterior, but with the plates lying almost horizontal, the terms ventral and dorsal seem more suitable here, and I have also used anterior, posterior, inner and outer borders to denote the boundaries of the plates regarding them as they appear *in situ*.

across the middle of the exopodite, giving off branches which subdivide still further as they approach the posterior border; the other, a smaller vessel, has a similar course nearer to the outer border. These afferent vessels are plainly nearer to the ventral surface than the other vessls which cross under them. The blood is returned from the exopodite in a system of efferent vessels which, as we have noted, are more dorsal in position, and they open into a large, very prominent efferent vessel, which runs diagonally across the exopodite from the inner posterior corner to the place of articulation. This course of the circulation is substantially the same in all the five pairs of exopodites, Figs. 64, 65, and 66. This feature of the exopodites, the presence of distinct vessels which are plainly visible to the naked eye, is unique among the woodlice.

The same respiratory movements of the appendages are seen here as in the other genera described. Also the endopodites and the exopodites are damp, indeed this form gives me the impression of being able to retain a great deal of moisture under the exopodites. No doubt the presence of salt may help in this. The exopodites, besides being intersected by blood vessels and, as we shall see, respiratory in function, act as opercula to the more delicate endopodites, and the dorsal surface is curved in such a way as to enable the exopodite to fit down over the endopodite, and a transverse ridge on the dorsal surface will help to close the cavity in which the endopodite is enclosed.

It will be best to follow the plan which has been adopted in the other species and describe in detail the third abdominal appendage, and then deal with the differences found in other abdominal appendages.

The 3rd Abdominal Appendage: This is the largest of all the abdominal appendages. It consists of the three parts: a small horizontal basal part, the protopodite; an outer plate, the exopodite; and an inner plate of smaller size, the endopodite. The shape and general structure will be seen best by examining Figs. 66 and 67, which represent the left appendage seen from both ventral and dorsal aspects. The protopodite is not very different from the protopodite of many of the woodlice (see various figures). The posterior border is fringed with long, spinose bristles and the lateral extension which is somewhat leaflike in outline is fringed with fine hairs.

The Exopodite: The shape and the fringe of feathered bristles are seen in Fig. 66 in which an attempt has been

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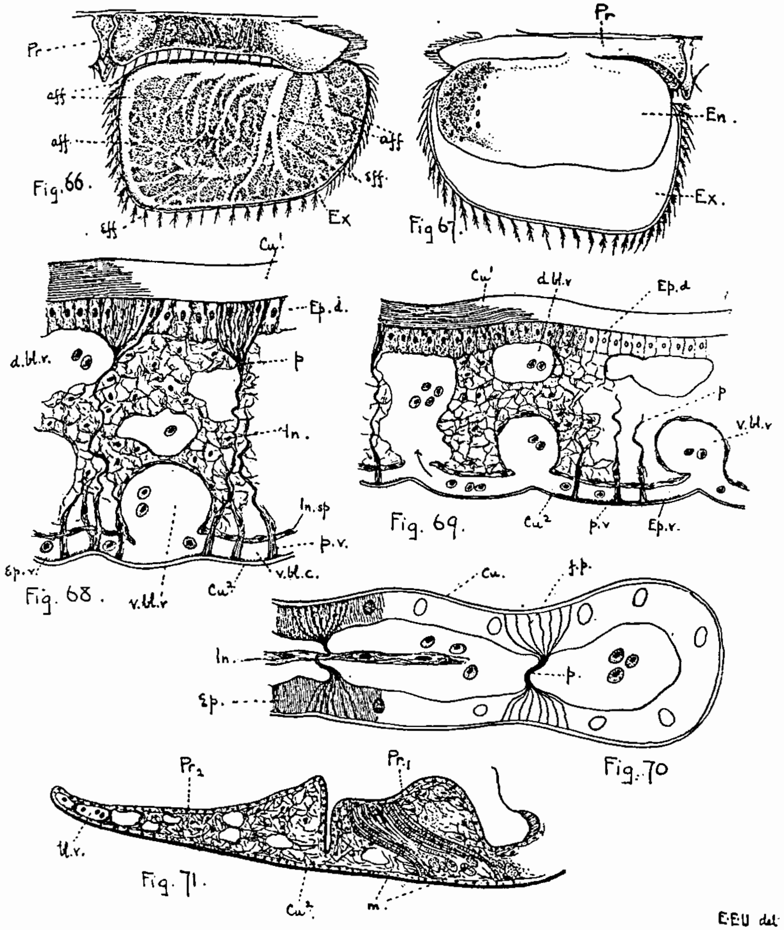
LIGIA OCEANICA. ♀.



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Ligia oceanica ♀.

made to show the characteristic appearance of the exopodite when seen either by transmitted or reflected light. The surface is covered by large and small blood vessels, which interdigitate all over the surface, and if the exopodite is treated with methylene blue it is possible to trace with considerable accuracy the afferent and the efferent vessels. There is no need to repeat here what has already been written about the circulation, but in such a preparation of the exopodite one can see plainly the more ventral position of the afferent vessels. One can see them pass on the ventral side of the efferent vessels. By careful focusing one can pass from one wall to the other inspecting the various tissues which lie between the two cuticles. It is clear that the blood vessels on the ventral or outer surface have a different external wall from the vessels near the dorsal surface. The dorsal blood vessels are examined through a thick cuticle and a very uniform layer of epithelium. One can see the regular pattern formed by the nuclei of this layer; whereas the ventral blood vessels can be seen to have a very thin and clear wall, in most cases merely a thin cuticle, or if any epithelium extremely thin and without nuclei. Blood corpuscles can be seen with great clearness lying in small cavities just under the cuticle. The cavities are marked off by what appear to be the ends of pillars, in which nuclei can be seen. If the middle part of the exopodite is examined, a mass of intermediary tissue can be seen filling the exopodite save for the blood vessels.

The cavity of the exopodite, which, in most of the other genera, is a simple blood cavity between the dorsal and ventral epithelial layers, is here invaded by a large quantity of this tissue—very like the body cavity tissue—which has nothing to do with the cuticular epithelium—and which forms the boundary walls of the numerous blood vessels.

Further information is obtained by examining serial sections through this appendage. It is abundantly evident when we examine a section of the exopodite (Figs. 68 and 69), that the ventral surface is adapted for respiratory purposes, for bringing the blood into such a position that only a very thin wall separates it from the air.

The dorsal wall consists of a thick cuticle and a layer of epithelial cells, which are uniform in size, in appearance something like a shallow palisade tissue. The nuclei of this layer are of a good size, and the whole layer is a well formed tissue.

The ventral wall is very different. There is a very thin cuticle, about one-tenth of the thickness of the dorsal cuticle. The epithelial layer is very poorly developed, indeed it is extremely difficult to make out, except in the neighbourhood of the pillars, the ventral ends of which are attached to the cuticle.

The intermediary tissue is remarkable in its great development here. In the exopodites of the woodlice already examined there is very little intermediary tissue. *Oniscus asellus* is the only one in which much is found; in the majority it is restricted to the proximal region in the part near to the place of articulation. Here, however, the exopodite is packed with the tissue. Most of it is like a ground tissue, loose stringy cells with nuclei scattered about. It is obviously a filling-up tissue, and in this it resembles the tissue found in the body cavity. It forms the boundary walls for the blood vessels, and is of great importance in connection with the circulation. The cells are not full of protoplasm, they do not stain deeply, but are rather vacuolated. The nuclei are rather smaller than the nuclei of the dorsal cuticular epithelium.

The tissue is more compact where it forms the wall of a blood vessel, and there is a distinct layer of more compact cells, forming a well defined and constant layer running parallel to the ventral wall a little distance from it. The cells of this layer are more elongated, and the nuclei seem longer also. The effect of this layer is to form a narrow blood cavity all over the ventral surface, just within the very thin cuticle. This cavity is interrupted by the ventral ends of the pillars, so that in the transverse sections the appearance is of a number of cavities side by side. (Figs. 68 and 69.)

The importance of this arrangement of the tissue is obvious, when the respiratory function of the exopodites is remembered. The ventral surface is the surface in contact with the air, the cuticle is thin, there is little or no epithelium, so that with the blood flowing in these cavities the conditions for effective respiration are fulfilled. Thus, the whole ventral surface becomes adapted for the interchange of gases between the blood and air. The width of this blood cavity is such that the blood will travel slowly, and so help in the more efficient interchange. These blood cavities, just beneath the thin cuticle traversed by the pillars, remind one of the arrangement found in the special respiratory organs on the outer border of the exopodites of *O. asellus*.

The study of transverse and longitudinal sections enables one to carry further the description of the circulation in these exopodites. Dorsal blood vessels from their position and arrangement are little more than conducting vessels belonging to the efferent system already outlined. They are bounded by the thick dorsal wall on the one side and the intermediary tissue on the other. The ventral vessels show very clearly the connections between them and the special cavity of the ventral wall, and here and there the sections show the passage from this ventral cavity to the dorsal system of vessels. So that the blood entering the exopodite is distributed by means of the ventral afferent vessels to the special respiratory cavities which lie just within the ventral cuticle, and then travels from these cavities into the dorsal efferent vessels and so out of the exopodite. (Pl. XVII., Figs. 69 and 66.)

The pillars have already been mentioned, but a rather fuller account of them must be given, for they are rather different from the pillars found in the exopodites of the other genera in the *Oniscoidea.*

A casual inspection of a section through the exopodite might miss the pillars, for the presence of so much intermediary tissue makes them less distinct, but inspection of the ventral wall gives the first clue to their presence, and with care they can be traced across the exopodite from cuticle to cuticle.

If we start from the dorsal wall, the pillar fibres arise from 2 or 3 epithelial cells, to judge by the nuclei, and the fibres which are widely separated to start with run together into narrow bundle. The dorsal part of the pillar has, therefore, a fanlike arrangement of the fibres. The central part of the pillar is in the form of this twisted rope or bundle of fibres which threads its way through the mass of intermediary tissue, to again spread out as the ventral surface is approached. The ventral part of the pillar is, however, very different from the dorsal, the individual fibres do not separate into a fan, but into three or four groups of fibres which, pushing through the special layer of the intermediary tissue, cross the special blood cavity and fasten on to the ventral cuticle. These smaller bundles possibly represent the remains of the ventral cuticular epithelium, for nuclei can be seen in them, and it is what one would expect considering the formation of the pillars as worked out by Kimus in the aquatic isopods. Although I have given a description passing from one side to the other, the pillar is really formed of cells from each wall, which meet and fuse in the middle.

I have attempted to draw two of these pillars as they appear in a section through the appendage (Pl. XVII., Fig. 68).

The Endopodite: The endopodite need not detain us long, for it is very similar to the endopodites of *Trichoniscus* and *Oniscus*. The general form and size as compared with the exopodite can be seen in Fig. 67. Fig. 70 shows the endopodite in transverse section. The thin cuticle, the thick epithelium, the pillars arising from the conical lumps, with their fibres spreading fanwise before becoming attached to the cuticle on either side, are all typical. If the section passes through the proximal region of the endopodite, especially near the place of articulation with the protopodite, a thin layer of intermediary tissue will be found, acting as a tissue directing the flow of blood into or out of the endopodite.

The 1st and 2nd Abdominal Appendages: These appendages need some further description, for not only do they differ from Hewitt's description, but they also differ from the general plan found in the other members of this sub-order *Oniscoidea*. We have seen that the woodlice already described in this investigation have lost the inner segments or endopodites of these first two abdominal appendages. *L. oceanica* still retains traces of these inner segments.

The 1st Abdominal Segment: When the abdomen of *Ligia* is examined under the simple microscope and the exopodite of the first appendage is lifted up by a needle, a prominent ridgelike inner segment is seen. By moving the exopodite to and fro, it is clear that the exopodite is articulated with the proximal part of this inner segment near to the outer border.

The inner segment is divided into two distinct parts by a transverse suture. The two parts are about equal in area, but are very different in appearance.

If one of these appendages is removed and examined under the microscope further details can be made out. Fig. 64 represents such an appendage seen from the dorsal side as a transparent object. The proximal part of this inner segment to which the exopodite is attached is obviously the protopodite or a part of the protopodite. The presence of a pointed lobe on the outer border of the protopodite beyond the place of the exopodite articulation is a usual feature in the woodlice, and a similar structure can be seen in Figs. 22, 23, 51, and 55. This seems to confirm the protopodite character of this proximal part. To this is attached another lobe, which looks like a special extension of the protopodite rather than an endopodite. For one thing it is attached along the whole length of the posterior border, for another it resembles in no way an endopodite, rather it more closely resembles an exopodite, as one sees it as a flat object under the microscope. I have attempted to show the structure of the various parts of this appendage as seen in the flat, and the proximal part of this inner segment is full of muscle. The fibres can be seen through the dorsal wall. In the distal part there are blood vessels ramifying through the interior of the plate, which is packed with intermediary tissue. A fairly thick cuticle and epithelium is found on both surfaces, and the free edges are fringed with feathered bristles. Further details are obtained by taking longitudinal sections through the abdomen, and in Fig. 71 is drawn a longitudinal section through this inner section which is under consideration. The proximal part with its mass of muscle, some fibres running from the dorsal to the ventral wall, others at right angles to the section; the distal part with the blood vessels and intermediary tissue and the epithelial layer showing prominently on both walls. Considering all these points I am inclined to the opinion that this inner segment is a two segmented protopodite, and that there is no real endopodite present.

The 2nd Abdominal Appendage: The second appendage is quite different from the first. There is clearly here an endopodite, as well as protopodite and exopodite; all three parts are distinct and well defined and normal in structure. Fig. 65 gives a dorsal view of this appendage. A large exopodite with blood vessels similar to those in the exopodite of the 3rd abdominal appendage, a small endopodite, about one-third of the size that it should be if it were normal, and a protopodite to which these two plates are attached. The lobe of the outer border is here unusually large and leaflike, and has a system of blood vessels very much the same as the exopodite. The small endopodite as seen in transverse section is typical in every way.

It is interesting to find these differences in the first two pairs of abdominal appendages. The woodlice, which are established further inland, have lost the endopodites of these first two appendages. It is clear from their structure and by comparison with aquatic forms, that the endopodites are respiratory organs for use in water, and that they are useless on land unless they can be kept very damp. The exopodites have, on the other hand, become adapted for air breathing only, and function in a drier state. The first two abdominal appendages are in a favourable position for air breathing, but unfavourable for the endopodite or gill respiration, and this may have caused the loss of these parts in most of the *Oniscoidea*. Whether this is so or not, *L. oceanica* is nearer to the aquatic types than any other member of the *Oniscoidea*, and the fact that there is no endopodite in the 1st and a small one in the 2nd abdominal appendages, helps us to bridge the gulf between marine isopods and the land isopods.

SUMMARY.

GENERAL REMARKS.

It seems best to attempt a brief summary of the main points of interest which have been brought to light in the foregoing investigations, and to give a general account of the respiration of land isopods in light of these researches.

Abdominal Appendages: We have seen that the first five pairs of abdominal appendages take some part or other in respiration. A typical appendage consists of a basal part—the protopodite, an outer plate—the exopodite, and an inner plate—the endopodite.

In *Trichoniscus, Oniscus, Philoscia, Porcellio, Porcellionides, Cylisticus, Armadillidium,* and *Platyarthrus,* the 1st and 2nd abdominal appendages have no trace of endopodite. In *Ligia* only the 1st abdominal appendage is without the endopodite, although the protopodite of this appendage is very large and divided into two distinct parts (Fig. 64). The endopodite belonging to the 2nd abdominal appendage is small, about one-third the normal size (Fig. 65).

The arrangement of the abdominal appendages is the same in all the various genera; the exopodites are ventral and external, overlapping from in front backwards and covering the endopodites as opercula. (Figs. 1, 7, 17, 19, 21, 41, etc.) Both exopodites and endopodites are respiratory in function.

The Exopodite: Normally an operculum, it has become adapted for respiration by having the ventral or outer wall extremely thin, so that the blood within the exopodite is only separated by a very thin membrane from the air outside. In the aquatic genera if there is any difference in the walls, the ventral wall is the thicker. This is seen in the exopodites of the 3rd abdominal appendage of *Asellus*, and in all the exopodites of *Cirolana*.

The simplest form of exopodite is found in *Trichoniscus* and *Platyarthrus*, that is to say, in these genera the exopodite closely resembles the normal type seen in the aquatic isopods, except for the thickness of the ventral wall. The exopodite consists of a flattened sac in which a simple blood cavity is found between the dorsal and ventral walls, which are formed of a cuticular epithelium and a chitinous cuticle. Crossing the cavity are the pillars, epithelial structures joining the wall of one side to the wall of the other. (Figs. 6, 61.) Another tissue is found in the exopodites, although it is much less evident than in the aquatic genera. It will be seen in the protopodite and extending a short way into the exopodite as a blood directing tissue. (Figs. 4 and 61.)

Although this is the normal type of exopodite there are not many genera which retain this simple form; perhaps the nearest being the exopodites of the 3rd, 4th, and 5th abdominal appendages in *Porcellio, Porcellionides,* and *Armadillidium,* and the chief part of the same exopodites in *Oniscus* and *Philoscia*. In the case of the former three genera, the blood cavity is much reduced, and there is but little respiration performed by them, the reason for this is the formation of very efficient breathing organs in the exopodites of the first two abdominal appendages. These air-tree organs take over, as it were, the type of respiration performed by the exopodites as a whole, and so, although originally adapted for the purpose, these last three pairs of exopodites lose their respiratory function.

Leaving *L. oceanica* for the moment, there are two quite different ways in which the exopodites of certain genera are modified to make them more efficient respiratory organs. The one kind of special respiratory organ is found in *Oniscus* and *Philoscia*—the other kind in *Porcellio, Porcellionides, Cylisticus,* and *Armadillidium.*

The first kind is a special thin extension of the outer border of the exopodites, forming small lung chambers; the second kind is an invagination of the outer wall of the exopodite to form a branching tree of air-tubes, which have very thin walls. In the first case, the blood flows through radial passages in the thin walled plate, and the air bathes the surface of the special organ: in the other, the blood within the cavity of the exopodite bathes the surface of the air tubes, which have a large opening on the posterior dorsal surface of the exopodite. In each case air is brought into intimate relation with the blood, so that only a very thin membrane separates the two media.

In *L. oceanica*, however, we meet exopodites of quite a different type. Instead of the cavity of the exopodite being a simple blood cavity crossed by the pillars, and in places divided into two parts by a plate of intermediary tissue, the cavity has been invaded by the intermediary tissue to such an extent as to confine the blood to a definite system of blood vessels, the walls of which are partly formed by the cuticular epithelium and partly by this intermediary tissue—a tissue of mesoblastic origin. There are ventral vessels, the afferent system, leading into a network of narrow cavities which cover the ventral surface and lead into dorsal vessels—the efferent system.

We have here a very different type of exopodite from any of the other members of the *Oniscoidea*, and indeed the amount of intermediary tissue is greater than in any of the aquatic forms described by Kimus. The reason for this difference seems to me to be associated with its large size and the fact of becoming terrestrial. The large exopodites of *Ligia*, especially in comparison with the genera most nearly related, e.g., *Trichoniscus* and *Ligidium*, do require an internal supporting tissue in a way that the exopodites of the others do not. The intermediary tissue is the same kind of tissue which is found performing the same kind of supporting and filling-up functions in other parts of the body. The point to notice here is that the circulation is so arranged that the blood in the exopodite is conducted to the small cavities on the ventral face where there is only a very thin cuticle separating it from the air. In this way the exopodite is adapted for respiration in air.

The Endopodite: Unlike the exopodites which exhibit considerable variation, the endopodites are practically identical in structure throughout the sub-order *Oniscoidea*. In every genus examined, the endopodite can be described as a thick walled, flattish sac containing blood. The wall is very constant in composition, being formed of a thick spongy epithelium, the cells of which are not easily distinguished except by the large nuclei. The protoplasm of the cells has much the same character in all the species—a striation

running at right angles to the surface. The epithelial layer carries thin cuticle on its outer surface, and on its inner surface is in the form of conical protuberances which join across the cavity in pairs to form the characteristic pillars. The spreading fibres of the pillars can be traced through the protoplasm to the cuticle to which they appear to adhere. The endopodites of *Asellus* are very similar. Intermediary tissue is found in the protopodite to which the endopodite is attached, and in some genera it extends a little way into the endopodite. In this case its function is similar to that of the intermediary tissue found in the proximal region of the exopodite, namely, the proper directing of the blood entering and leaving the plate.

In three of the genera examined, *Porcellio*, *Porcellionides*, and *Armadillidium*, the arrangement for the blood is rather different. A special afferent canal is formed by an alteration in the thickness of the ventral epithelial wall at one place. Instead of the thick spongy layer, one finds a narrow layer of quite small cells, rather like intermediary tissue cells, forming an arched wall in a narrow band running back from the place of articulation, tracing out, in the larger endopodites, the letter L. The details of this tube are fully described in *P. scaber*. Also see Figs. 31, 32, 53, 56.

I do not propose to discuss here the minute histological details of the various tissues of these respiratory appendages. Kimus, in his account of *Asellus* and other aquatic isopods, to which reference has been made, has described in considerable detail the histological features of tissues which are similar in every way.

I do not feel able, however, to pass over the question of the pillars and the intermediary tissue without some little attention, for some of the chief points of interest in the work of Kimus are centred around the pillars and the intermediary tissue. Taking the pillars first, it will be well to see how they compare with those found in the aquatic genera.

Kimus distinguishes several different kinds of pillars:—

"Certaines cellules épithéliales d'une face s'unissent à
" des éléments de l'autre face au travers, de la cavité
" branchiale pour former des piliers multicellulaires.

"Parmi ceux-ci, on en distingue de bicellulaires, formés
" par l'union d'une seule cellule d'un côte avec une seule
" cellule de l'autre. Cette disposition s'observa dans les
" piliers de l'exopodite de la Cirolana.

"D'autres sont au contraire formés d'un plus grand " nombre d'éléments voisins appartenant à chacune des faces. " Ce sont alors des colonnes formées par la juxtaposition " de plusieurs piliers bicellulaires. Nous avons signalé cette " variété chez l'Anilocra, la Cymothoa, l'Idotea, et dans la " zone protectrice d'exopodite de l'Asellus. Une cellule " épithéliale peut contracter des rapports, non avec une cellule " de la lamelle d'en face, mais directement avec la cuticule de " cette dernière. Pour cela, elle a dû écarter certaines cellules " de la couche cuticulaire, dénuder la cuticule, et s'y fixer par " son extrémité. Ces cellules constituent des 'piliers simples' " et unicellulaires. Ici se présente aussi le cas où les piliers " sont formés par la juxtaposition de plusieurs éléments " appartenant à la même face. Ce sont alors des piliers multiples et unicellulaires. Enfin certaines cellules contractent " avec une cellule située en face des rapports plus complexes " que ceux que nous venons d'indiquer.

"Au lieu de s'abuter pars une extrémité simple avec une " extrémité semblable de la cellule opposante, elles " présentent une série de protubérances qui s'unissent " à des productions toutes semblables appartenant " à des cellules qui leur font face. Ces diverses protubérances sont bien distinctes, isolées les unes des autres: le " sang circule entre elles.

"Chacune de ces cellules contribue donc à former non " pas un seul pilier, mais plusieurs. On peut leur donner le " nom de cellules multicolonnaires. Ces éléments, extrêmement remarquables, s'observent chez l'asellus aquaticus, " dans les lames internes (endopodites) et dans la zone " brancilale des lames externes."

The pillars found in the sub-order *Oniscoidea* are for the most part of the simpler kind. In the exopodites of *O. asellus*, *T. pusillus*, and *Platyarthrus*, "piliers simples" are found and "piliers bicellulaires" also. (Figs. 6, 13, 61.) These are very similar to the pillars figured and described by Kimus in the operculum of *Asellus* and in the exopodites of *Idotea.*

We have seen that in the genera *Porcellio*, *Cylisticus*, *Porcellionides*, and *Armadillidium* pillars are not well developed. In the exopodites which contain the air-tree organs, one or two rather prominent pillars are found joining the dorsal and central walls together around the outskirts of the air-tree organ, where the two faces come into normal relationship to one another. (Fig. 33.) These are of the bicellular type and "multiple." The endopodites of all the genera have pillars which resemble in every way those figured and described, by Kimus, in the endopodites of *Asellus*. They are not formed of complete cells, but by the fusion of processes from the large epithelial cells—les cellules multicolonnaires. However, in most genera these cells are not so large as those found in *Asellus*, and do not carry so many pillars. (Figs. 5, 15, 16, 32, 61, 70.) The most unusual type of pillars are those found in the exopodites of *L. oceanica*. (Figs. 68, 69.) They resemble in a general way the type found in the endopodites, that is to say, radiating threads or fibres can be traced to each cuticle, but they are fundamentally different from these, for they are multicellular. Several cells on each face give rise to them. A full description has already been given of these pillars in *Ligia*.

Function of the pillars:—

1. They will prevent the too wide separation of the dorsal and ventral walls. "De longues colonettes minces comme " celles de la lame externe de l'Asellus ou des Cloportes, ne " peuvent évidemment servir qu'à limiter l'écartement des " deux lamelles." (Kimus.)

2. The more robust pillars would prevent the flattening of the plates when external pressure is applied. "L'un et " l'autre de ces mouvements exagérés doivent être " évités pour le fonctionnement regulier de l'organe. En " effet, si les deux lamelles pouvaient s'écarter librement, " l'organe tendrait à prendre une forme vésiculeuse,—c'est " une loi physique,—à la moindre perturbation qui pourrait " se produire dans le courant efférent, le canal afférent con- " tinuant à déverser le sang dans l'organe. Dés lors, une " stagnation plus ou moins accusée du sang respiratoire " pourrait se produire. Si au contraire une pression " extérieure s'exerçait sur les lamelles, la cavité pourrait se " trouver complêtement effacée et la circulation branchiale " serait arrêtée. Il semble donc certain qu'en toute hypothèse " les piliers jouent ce rôle passif." (Kimus.)

3. Contractility: Kimus goes further and described the power of contractility possessed by many of the pillars. Some of the genera studied by him—*Cirolana*, *Anilocra*, and *Cymothoa*, have large and very extraordinary pillars, with a striking resemblance in structure to muscle-fibres.—"L'im " pression," he says, "qui nous reste de l'étude de tous les " piliers que nous avons examinés est que la substance des

"faisceaux délimités présente une structure plus semblable "à la structure musculaire. Qu'aucune autre production "cellulaire dont nous ayons connaissance."

Other facts are brought forward, the innervation of the pillars; direct observation of a fluttering movement in the lining branchiæ of *Asellus*, the different sizes of the internal cavity in the case of the endopodites, when seen in transverse section, and they lead up to the conclusion.—"La structure, les "réactions, l'innervation des piliers et l'observation des "organes vivants ou fixés, concourent à nous démontrer que "ces productions sont donées d'une contractilité semblable à "celle des fibres musculaires.

"Il existe donc chez les édriophthalmes des cellules épithélio-musculaire."

In the *Oniscoidea* as a whole the pillars of the exopodites are not particularly well developed. They are mostly of a simple type, and not present in great numbers. Their function here seems of the passive kind preventing the collapse or the too great widening of the internal cavity. Possibly the small size of the exopodites in most genera would account for the lack of the contractile character. In the case of *Ligia oceanica*, it seems feasible that the pillars in the wide exopodites will have a contractile function, for the presence of the intermediary tissue and the consequent formation of blood-vessels will do away with the dangers of collapse and over extension. Yet the pillars are quite distinct, and the fibres united into bundles "faisceaux de fibrilles" run from cuticle to cuticle. Their appearance too favours the contractile nature, and also the advantage, in promoting more efficient circulation in the ventral cavities, of the power of contractility, is obvious. I examined the ventral surface of the exopodites of a living specimen, and there did appear to be some slight movement of the surface, something to which the name "fluttering movement" might be given, but I am in doubt as to the wisdom of counting this observation as evidence, for it is difficult to be quite sure of such movements, and I may have been influenced by Kimus's account. However, I offer the observation for what it is worth. It seemed clear to me at the time.

The pillars in the endopodite certainly appear to be contractile. The chief evidence apart from structure, is the very varied size of the internal cavity, as seen in transverse section.

The Intermediary Tissue: Kimus has given this name to the tissue which is found in the cavity between the two epithelial walls of the exopodite and endopodite, and which in the proximal region of either plate is continuous with the same kind of tissue in the protopodite and in the body cavity. Its use is to direct the blood. This function will be seen illustrated in several of the Figs., especially in the exopodites which bear air-tree organs. (Figs. 34, 35, 61.) In *Oniscus* its use is still further extended. As a rule in the exopodites and endopodites its presence is restricted to the part near by the place of articulation, but in *Oniscus* it is found acting as a horizontal partition in the special breathing organs (Figs. 11, 12, 14.) *L. oceanica* is also an exception, and differs from the other *Oniscoidea* in having the exopodites packed full with this tissue. This special case has been already dealt with in the communication on *Ligia*.

Although this tissue is more prevalent in the aquatic isopods than in the terrestrial forms (except *Ligia*) there are no differences in structure to note, and reference should be made to the memoir by Kimus.

General Remarks upon Respiration: The whole problem of respiration in the terrestrial isopods is much more complicated than in their aquatic relatives. Organs adapted for absorbing oxygen that is dissolved in water, cannot easily be made to act in the air. It seems to me that the woodlice have two rather distinct methods of respiration, the one method not very different from that of the aquatic forms; the other adapted more for obtaining oxygen from ordinary air.

The obvious respiratory organs for aquatic life seem to be of the "endopodite" type, that is to say, a blood sac with a thick spongy wall composed of an epithelial layer and a thin cuticle. In *Asellus aquaticus* even the exopodites have somewhat this structure, and the same thing is found in *Anilocra* and *Cymothoa*. Kimus devotes some attention to the matter, and concludes that the thick wall of spongy protoplasm is a most efficient wall for the respiratory exchange, and that the living protoplasm plays some important part in obtaining the oxygen. He concludes by saying:—

"Le gaz qui a traversé la cuticule et pénétre dans la mass "protoplasmatique vivante, dans ce laboratoire de la cellule "où se produisent tant de réactions, va-t-il passer en totalité? "Ou bien ce protoplasme ne va-t-il pas, au contraire, le "retenis, en grande partie et former des corps, oxydés qu'il

" utilisera lui-même ou déversera peut-être dans le sang?
" Rien ne prouve que l'épithélium lamellaire laisse passer tout
" l'oxygène qu'il absorbe. On peux faire la même remarque
" chez d'autres animaux, les vertébrés par ex. Chez les
" édriophthalmes, le fait que la couche de protoplasme qui
" sépare le sang du milieu extérneur est plus puissante dans
" les positions qui doivent étre les plus respiratoire, est une
" indication sérieuse. Elle parait montrer que, chez ces
" animaux au moins, le protoplasme vivant joue un rôle dans
" l'absorption et l'utilisation de l'oxygéne."

Now the endopodites of woodlice are without exception of this same type—having thick spongy walls. One may conclude, therefore, that they are adapted for a similar method of respiration. How is this possible in a terrestrial habitat? We have seen how that the endopodites of all the woodlice have been found to be very damp, to be covered with a distinct film of water, and this, not only in those living in damp situations, but in the "drier" species too. And it seems clear to me that in retaining the "gill-like" character of the endopodites, the woodlice have perforce to retain a film of water around these endopodites to act as the medium for oxygen and carbonic acid gas. The layer of water will have its available oxygen constantly renewed, as the air is drawn beneath the exopodites during the breathing action, and the endopodites are then able in some way to absorb this oxygen through the medium of this film of water. Of course, this is not a very satisfactory method, and there is the great danger of "drying up"—a peril very real to all the woodlice.

The other method of respiration is an attempt to solve the problem by obtaining a very thin membrane between the blood and the air. This extreme thinness of the respiratory membrane is found in the case of the air cells in the lungs of vertebrates, and seems as important for ordinary air breathing as the thick wall was for the aquatic method.

The exopodites are adapted for this purpose. The simplest adaptation is to use the whole ventral surface as a respiratory surface. This is what we find in *Trichoniscus, Platyarthrus*, and in a different way in *Ligia*. That this has been, as it were, the first and simplest method is shown by the fact that in all the genera the ventral or outer wall is thinner than the dorsal. The normal arrangement is the direct reverse of this.

In the other genera of *Oniscoidea* methods are found whereby the respiratory surface is obtained in a still thinner condition. In *Oniscus* and *Philoscia* special thin-walled border organs are found, and in *Porcellio, Porcellionides, Cylisticus*, and *Armadillidium* a much more satisfactory method has been developed in which there is much less likelihood of the danger of desiccation. This is by the formation of the air-trees, invaginations of the outer wall of the exopodite in the form of branching air-tubes. The term "lung-trees" might be used, for they are restricted in extent, and the blood plays an important part. We have here an independent attempt to solve the problem of aerial respiration in the *Arthropoda*, and in many ways it is comparable to the methods found in the *Insecta* and *Arachnida*. However, the woodlice are severely handicapped in the matter of respiration by the small size of these organs and their inability to do without the endopodites. These facts have caused the range of the woodlice to be rather limited, for they have to seek for places where conditions will be favourable for both methods of breathing.

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EXPLANATION OF PLATES.

PLATES X. TO XVII.

Abbreviations used in all figures.

Cu., cuticle.
Cu^1., cuticle of inner or dorsal wall.*
Cu^2., cuticle of outer or ventral wall.**
Ep., epithelium of wall.
In., intermediary tissue.
Pr., protopodite.
Ex., exopodite.
En., endopodite.
1st Ex., 3rd Ex., etc., exopodite of 1st or 3rd abdominal appendages, etc.
p., pillar.
b.c., blood corpuscle.
n., nucleus.
l^6, l^7, 6th of 7th walking legs, in all cases cut short or removed entirely.
up., uropods.

Other references are given under the details of each figure.

*, **. The terms "dorsal" and "ventral" are used to distinguish the two walls of the exopodite or endopodite.

"Ventral" is the obvious ventral face taking the appendage as being practically horizontal (= inferior, external, anterior).

"Dorsal" is the obvious dorsal face (= superior, internal, posterior).

PLATE X.

Trichoniscus pusillus.

Fig. 1. Ventral view of the abdomen of female. × 15.

Fig. 2. Ventral view of the 3rd abdominal appendage of left side. × 50.
aff., afferent canal running along inner border.
eff., efferent canal running along outer border.
Blood spaces between the groups of dots, which represent pillars.

Fig. 3. Dorsal view of the 3rd abdominal appendage (left). × 50.
En. lo., lobe of the endopodite.

Fig. 4. Longitudinal section through the abdomen. Semi-diagrammatic. × 75.
n.c., nerve cord.
4th Endo., endopodite of 4th abd. appendage.
This figure illustrates arrangement of exopodites, endopodites, and protopodites. Note thin *ventral* wall of exopodites.

Fig. 5. Transverse section of Endopodite (a part only shown.) × 350.
n., nucleus of the thick epithelium.
p., pillar with radiating fibres attached to the dorsal and ventral cuticle.
b.c., blood corpuscle in the blood cavity.

Fig. 6. Transverse section of Exopodite (a part only shown.) × 350.
aff., the afferent blood canal.
Ep., the epithelium of the dorsal or inner wall.
The epithelial layer of ventral wall is very thin as is the ventral cuticle Cu^2.

PLATE XI.

Oniscus asellus.

Fig. 7. Ventral view of abdomen of female. × 4.
The 3rd appendage of the right side is turned forward to show the protopodite and endopodite.
Notice also "special breathing organs" on the outer borders of exopodites.

Fig. 8. Ventral view of 3rd abdominal appendage (endopodite omitted) of the right side. × 15.
Methylene blue treatment:
Ex^1, the ordinary part of exopodite.
Ex^2, the special respiratory part.

Fig. 9. A small part of Ex^2 of Fig. 8 more highly magnified. Radial blood cavities shown.

Fig. 10. Dorsal view of 5th abdominal appendage. × 15.
This shows the special row of hairs "like a cheval-"de-frise." Fr.
dr., the dorsal ridge marking the boundary between the two parts of the exopodite.

Figs. 11, 12, 13, 14. Illustrate details of the Exopodite seen in T.S. & L.S.

Fig. 11. The outer part of Exopodite in transverse section. × 75.
dr., the dorsal ridge as above.
bl. c., blood cavity.
In., intermediary tissue.

Fig. 12. Portion of "special respiratory organ" of Exopodite in T.S. × 100.
n., nucleus of simple epith. pillar.
In. par., intermediary tissue forming partition.

Fig. 13. The inner part of Exopodite in T.S. × 75.

Fig. 14. Longitudinal section through parts of the 1st two abd. Exopodites. × 75.
Ex^{a}, special respiratory part of 1st.
Ex^{b}, ordinary part of 2nd.
d. bl. c., dorsal blood canal.
v. bl, c., ventral blood canal.
In. par., partition of intermediary tissue.
A. ch., "air pocket" or "lung cavity." The air retained in this cavity gives the silvery appearance.

Fig. 15. Semi-diagrammatic transv. section of Endopodite.

Fig. 16. Longitudinal section through the 3rd abd. appendage. × 50. The line of section is through the place of articulation of Endopodite with Protopodite.

PLATE XII.

Philoscia muscorum.

Fig. 17. Ventral view of abdomen of female. × 7.

Fig. 18. Ventral view of 3rd abdominal appendage, right side. × 15.
(Seen as a transparent object.)
Ex^{2}, special respiratory part of Exopodite.
En., Endopodite (shaded in to show up).

Philoscia couchii.

Fig. 19. Ventral view of abdomen of female. × 7.

Fig. 20. Ventral view of 3rd abd. appendage of left side. × 15.
Note the small size of the respiratory part.

Porcellio scaber.

Fig. 21. Ventral view of abdomen of female. × 6.
Air-tree organs in Exopodites of appendages 1 and 2.

Fig. 22. Ventral view of the 1st abdominal appendage of right side. × 18.
(Seen as an opaque object.)
The letters refer to sections represented later.

Fig. 23. Dorsal view of the 2nd abdominal appendage of right side. × 18.
(Seen as an opaque object.)
a.t., air-tree organ.
gr., the main entrance groove leading to air-tree.
sc. a., sculptured area of the cuticle.
AB, line of section Fig. 33.

Fig. 24. Ventral view of 3rd abdominal appendage of left side. × 18.
(Seen as a transparent object.)
aff. c., aff. blood canal of Endopodite shown in outline.

Fig. 25. Longitudinal section through the abdomen. × 25.
ri., transverse ridge, important in connection with exchange of air in air-trees.
a.t.^{1}, air-tree organ of 1st abd. appendage.
a.t.^{2}, air-tree organ of 2nd abd. appendage.
Fr., the "frise" of hairs.

PLATE XIII.

Porcellio scaber (continued).

Fig. 26. Part of a longitudinal section of 3rd abd. appendage. × 45.
(Endopodite omitted.)
Ep^{1}, Epithelium of dorsal wall.
Ep^{2}, Epithelium of ventral wall.
The specimen was one which had just moulted. Epithelium very distinct.

Fig. 27. Small part of Exopodite in L.S. × 45 from normal specimen. The epithelium is vacuolate, nuclei prominent; distinct inner boundary wall of tissue—(ch.); very narrow blood cavity.

Fig. 28. Small part of a longitud. section of an exopodite shortly before ecdysis. × 50.

Notice the character of cuticular epithelium, and size of blood cavity.

O. Cu^1, old cuticle of the dorsal wall.
N. Cu^1, new cuticle of the dorsal wall.
O. Cu^2, old cuticle of the ventral wall.
N. Cu^2, new cuticle of the ventral wall.

Fig. 29. Small portion of the Exopodite in the proximal region seen as a transparent object after treatment with methylene blue. The lighter patches represent the blood spaces.

Fig. 30. Dorsal view of the 3rd abdominal appendage of right side. × 18.

Methylene blue treatment.
Protopodite and Exopodite shown in outline only.

Fig. 31. Ventral surface of Endopodite (methylene blue). × 18.

aff. c., the ventral wall of afferent blood canal.
AB. line of section of Fig. 32.

Fig. 32. Longitudinal section of Endopodite (along AB in Fig. 31). × 100.

n., nucleus of epithelium, Ep.
aff. c., afferent blood canal.
v.e. aff. c., ventral wall of same.

Fig. 33. Transverse section of the 2nd abdominal Exopodite. × 35 (line of section AB in Fig. 23).

En. gr., main entrance groove.
p., pillars in the normal part of Exopodite.
Cu^2, ventral cuticle, *thick.*

Figs. 34 and 35. Longitudinal sections through the 1st abd. Exopodite taken along lines AB and CD in Fig. 22. × 35.

These figures illustrate the blood supply to the air-tree.

aff. c., afferent canal. Eff. c., Efferent canal.

Fig. 36. One of the small branches of the air-tree organ. × 100.

Note character of the wall.

Fig. 37. Portion of the outer part of the air-tree organ in L.S. × 150.

cu., cuticle of the wall of Exopodite with its epithelium (cu. ep.).

a.t.cu., cuticle of air-tube. Note the ridges on the walls.
a.t. ep., epithelium of the air-tube represented by trace of protoplasm round the nuclei and the persistent chitinous niner boundary of tissue.
bl. c., blood cavity.

Fig. 38. Small portion of the sculptured cuticle from sides of entrance groove (surface view).

Fig. 39. Similar section to that in Fig. 37 taken at a time when the new cuticle is being formed. The epithelium of air-tubes is very distinct at this time. Compare it with the epithelium in Fig. 37.

Fig. 40. Longitudinal section of 1st abdom. Exopodite taken along line EF in Fig. 22. × 75.

This shows the general structure of the Exopodite and air-tree organ.

Cu^2, thick cuticle of ventral wall.
Cu^1, thin cuticle of dorsal wall.
En. gr., entrance groove to air-tree.
Sc. cu., sculptured cuticle—the limits of this area are shown.

PLATE XIV.

Cylisticus convexus.

Fig. 41. Ventral view of abdomen of female. × 7.

Fig. 42. Part of a transverse section through the abdomen in the region of the 3rd abd. appendage. × 20.

Ex., Exopodite containing air-tree organ.
En., Endopodite.
l.p., lateral plate of abdomen.
g., alimentary canal.
n.c., nerves from n. cd.

Fig. 43. Ventral view of the 3rd abdominal appendage. × 25.

(Seen as a transparent object.)

Fig. 44. Dorsal view of the outer part of Exopodite. × 25.

En. gr., main entrance groove to air-tree.
s.g., special entrance groove.

Fig. 45. Transverse section through the Exopodite (along AB in Fig. 44). × 75.

En. gr., main entrance groove.

Fig. 46. Transverse section of same passing through a special entrance groove. × 75.

[Only a portion of the sections drawn in Figs. 45 and 46.]

Fig. 47. One of the special entrance grooves seen as a transparent object, with the air retained within. × 100.

The shallow sculpturing of the surface cuticle is shown.

Fig. 48. Small portion of wall of air-tree organ showing the ridge markings. × 75.

Porcellionides pruinosus.

Fig. 49. Ventral view of the abdomen of female. × 12.

Fig. 50. Dorsal view of the 1st abdominal appendage of left side. × 35.

Fig. 51. Dorsal view of the 2nd abdominal appendage of left side. × 35.

(Both seen as opaque objects.)

Fig. 52. Ventral view of the 3rd abdominal appendage of left side. × 35.

(Seen as a transparent object.)

PLATE XV.

Porcellionides pruinosus (continued).

Fig. 53. Longitudinal section through the abdomen. × 35.

a.t.[1], air-tree organ of 1st abd. appendage.
aff.c., afferent blood canal of Endopodite.
ri., ridge for pressure on air-tree for expiration.

Armadillidium vulgare.

Fig. 54. Ventral view of the abdomen of female. × 5.

Fig. 55. Dorsal view of the 1st abd. appendage of right side. × 12.

(Seen as an opaque object.)

En. gr., main entrance groove.
Sc. cu., sculptured cuticle.
Sp gr., special entrance groove.

Fig. 55a. Dorsal view of the 2nd abd. appendage of right side. × 12.

(Seen as an opaque object.)

Fig. 56. Dorsal view of the 3rd abd. appendage of left side. × 12.

(Seen as a transparent object.)

Underlying parts (e.g., aff.c., the afferent canal of Endopodite) shown by a broken line.

Fig. 57. Part of a longitudinal section through the abdomen. × 25.

Only the details of the first three appendages are shown.

ri., transverse ridge.
Aff. bl., afferent blood canal passing through the protopodite bounded by intermediary tissue.
Sc. cu., sculptured cuticle. The limits of this can be seen.

The section of the 3rd appendage passed through the place of articulation of the exopodite and protopodite. The endopodite, therefore, does not show the afferent canal in section. See AB in Fig. 56 for line of section.

PLATE XVI.

Platyarthrus hoffmannseggii.

Fig. 58. Ventral view of the abdomen of female. × 15.

Fig. 59. Longitudinal section through the abdomen. × 45.

Arrangement of appendages and parts as in the other sections of similar kind.

Fig. 60. Dorsal view of the 3rd abdominal appendage of left side. × 50.

(Seen as transparent object.)

Fig. 61. Part of a longitudinal section of the third abdominal appendage such as along the line AB in Fig. 60. × 150.

Fig. 62. Two tubercles from edge of telson. They are drawn as they appear from above, as transparent objects. The figure also shows the cuticle with its shallow polygonal cavities.

Ligia oceanica.

Fig. 63. Ventral view of abdomen of female. × 3.

Fig. 64. Dorsal view of 1st abdominal appendage of right side. × 7.

(Seen as transparent object.)

Pr^1, proximal division of Protopodite showing the muscles within.
Pr^2, distal division of same containing blood vessels.
Ex., Exopodite showing afferent (aff.) and efferent (eff.) vessels.

Fig. 65. Dorsal view of 2nd abdominal appendage of right side. × 7.

Pr., Protopodite with large outer lobe, lo.
En., Endopodite.
Ex., Exopodite with afferent and efferent vessels.

PLATE XVII.

Ligia oceanica (continued).

Fig. 66. Ventral view of 3rd abd. appendage of left side. × 7.

(As transparent object with Endopodite omitted.)
The Exopodite shows the circulation.
aff., the afferent vessels, ventral.
eff., the efferent vessels, dorsal.

Fig. 67. Dorsal view of the 3rd abd. appendage of left side. × 7.

Exopodite shown in outline.
Endopodite with small portion showing details.

Fig. 68. Transvere section of the 3rd Exopodite. Only a small part shown, to illustrate the pillars. × 150.

d. bl. v., dorsal blood vessels (efferent system).
v. bl. v., ventral blood vessels (afferent system).
v. bl. c., special ventral blood cavity for respiratory purposes.
Ep. d., Ep. v., epithelium of dorsal and ventral walls.
In., intermediary tissue.
In. sp., special layer of this tissue.
p., pillar. p.v., ventral termination of pillar.

Fig. 69. Another part of an Exopodite in T.S. × 100.

References as in Fig. 68.
Here the connection between the ventral cavities and the afferent and efferent systems is shown.

Fig. 70. Part of a transverse section of an Endopodite. × 100.

p., pillar; f.p., fibres of pillar attached to cuticle.

Fig. 71. Longitudinal section through the protopodite of the 1st abd. appendage. × 50.

Pr^1, Pr^2, the two parts of Protopodite.
bl. v., blood vessel.