ON THE

ORGANS OF RESPIRATION OF THE ONISCIDAE.

BY

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With 2 Plates.

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Part I.

Introduction.

The family Oniscidae is distinguished from the other families of the order Isopoda by the habit of living upon the land. The appendages of the abdomen which in the aquatic isopods constitute organs for respiration in water subserve in the Oniscidae the function of respiration in air.

In the systematic treatise of Budde-Lund published in 1885, 37 genera and 282 species of land-isopods are described. Of these 10 genera and 22 species are described as found in Germany.

Since the structural features of the organs of respiration vary with genera and sub-families rather than with species, in the present work I have studied a number of forms representative of genera, as followe: *Porcellio*, *Cylisticus*, *Armadillidium*, *Ligidium* and *Oniscus*. I have used fresh material collected in the vicinity of Leipzig.

The respiratory organs of the Oniscidae are constituted in general by the appendages of the first five segments of the abdominal region of the body. These appendages are of the morphological type common in the Crustacea: each consists of a basal joint and an outer and an inner branch. The outer divisions are uniformly present in full number; but the inner divisions, as a rule, are lacking for the first two segments.

The outer branches have generally been designated by authors as gill-covers. They form two longitudinal rows of plates, constituting the ventral aspect of the abdomen. When at rest the inner margins of the plates meet at the middle line of the body and the posterior margins slightly overlap one another from in front backwards, thus forming a closed, imbricated surface. This surface is convex transversly and slightly so from before backwards. It is broadest in front and gradually narrows backwards.

This description, applicable to the females, requires a slight modification for the males. In this sex there are attached to the basal joints of the first and second pairs of the appendages the stylets of the reproductive organs. They lie along the middle line of the body extending posteriorly to the extremity of the inner margin of the second pair of outer gills. The stylets, thus disposed, separate the inner margins of the first and second pairs of outer gills.

The gills are movable downwards and sidewards by means of muscles connecting them with the basal joint. Those of each pair move simultaneously; and the series of pairs move successively from before backwards. The movements, as a whole, take place in rythmical order.

In certain genera, including *Porcellio* and *Armadillidium*, the first two pairs of gills (in some species of *Porcellio* all five pairs) present peculiar modifications. To the eye these modified parts appear as whitish flecks and they have therefore been designated by some authors as corpora alba.

They lie in the outer and posterior portion of the plates and the posterior margins of the same plates present indentations. These mark the places where small bubbles of gas pass out from the interior of the corpus album when a gill is placed under water and pressure applied. The use of the microscope is requisite for this demonstration.

In the genus *Oniscus* the outer branches of all the abdominal appendages (the gill-covers of authors) present also definite modifications but morphologically entirely different from those of *Porcellio* and *Armadillidium.* The outer and posterior portion of each gill is thinner than the rest and is marked by lines arranged in a radiate manner. To the eye these lines appear as glistening whitish spaces, suggesting the presence of chambers containing air. When an animal is placed under water these spaces gradually disappear; when the same animal is returned to air the original appearance is gradually regained.

The inner divisions of the abdominal appendages are, excepting in *Ligidium,* uniform in structure and relations for all genera which I have examined. They consist of three pairs of delicate flattened sacks attached to the third, fourth and fifth abdominal segments. They lie within the corresponding outer divisions and share with them movements through the muscles of the common basal joint.

These organs have been designated as gills by all authors.

In *Ligidium* all five of the inner branches of the appendages are represented. Those of the first pair consist of thin plates resembling in general the outer divisions. The inner branches of the second pair are rudimentary gills. The other three pairs are identical in general features with the corresponding parts in the other genera.

Part II.

Review of the Literature.

The animals composing the modern family Oniscidae were classed by the early systematists with the Insects. Naturally it was not until their affinities with the Crustacea were recognized that the question of their mode of respiration attracted attention. This relationship was established by the labors of CUVIER and was first published in his Tableaux élémentaires de l'histoire naturelle des Animaux in 1798. The same author in his Histoire des progrès des Sciences naturelles, records that LATREILLE was the first to fill the gap in Zoölogy due to a lack of knowledge of the mode of respiration in the Cloportides. He refers to an announcement made by LATREILLE to the French Institute in 1814.

"Er weisst an vieren der fraglichen Blätter einen kleinen gelblichen Teil nach, welcher von einem Loch durchbohrt ist und in seinem Innern kleine Fäden enthält, welche er mit denen der Schnecke und des Scorpions vergleicht, denn ob sie gleich bei diesen anders angeordnet sind, so findet doch zwischen beiden, sowohl hinsichtlich der Struktur als auch der Verrichtung, die grösste Aehnlichkeit statt."[1]

To these observations LATREILLE later added another to the effect that the parts contain air. In his systematic treatise on the Crustacea, published in Règne Animal, first edition, 1817, describing the genus *Armadilles* he says:

"Les écailles branchiales et supérieures du dessous de la queue ont une rangée de petits trous, donnant passage à l'air."

Two years later TREVIRANUS published a somewhat elaborate article on the anatomy and physiology of the terrestrial isopods.[2] He reached quite different conclusions from those of LATREILLE to whose work he makes no reference. He considered the first two pairs of appendages in *Porcellio* to be wholly concerned with the reproductive function. The openings associated with the corpora alba serve, he states, in the male for the discharge of the seminal fluid and in the female for the admission of the male intromittent organ. He says:

"Zwischen den beiden oberen Platten an derselben Stelle, wo bei dem Männchen die Wurzel der Ruthe liegt, befindet sich ohne Zweifel die äussere, zur Aufnahme des männlichen Gliedes bestimmte Oeffnung der weiblichen Zeugungsteile."

After referring to the other pairs of plates, lying posteriorly to the two concerned in reproduction, as similar but of simpler structure, he states that under these lie the organs of the

[1] Translation of Dr. F. A. Wiese, Leipzig, 1829.

[2] Vermischte Schriften, Göttingen, 1816.

breathing-hole. These are the gills, consisting of three pairs of simple membranous (häutige) leaves. He then describes them in detail as to form.

This appears to be the first published description of the inner gills.

Brandt[1] in 1833 expressed the same opinion as Treviranus as regards the nature of the first two pairs of appendages in the genus *Porcellio*.

Milne-Edwards[2] in 1839 announced that he had confirmed through his own observations the conclusions reached by Latreille. He stated that the branched air-canals were rightly to be compared with the tracheae and lung-sacs of the Insects and Arachnids.

The same author in his Histoire naturelle des Crustacés, published the next year, says concerning the Cloportides terrestres: "Mais le caractère le plus important . . . est fourni par le mode de conformation des fausses pattes abdominales des deux ou quatre premières paires. Ces appendices servent à la respiration comme chez tous les autres Isopodes; mais au lieu de constituer des branchies, ils remplissent les functions de poumons, car ils renferment des organes creux dans l'intérieur desquels l'air atmosphérique pénètre directement à travers des ouvertures diversment disposées."

A more thorough study than any hitherto made was that of Duvernoy and Lereboullet published in 1841.[3] These authors give a detailed account of the general anatomy of the respiratory organs of the land-isopods and also describe a series of experiments made upon *Porcellio* and *Armadillio* to determine their comparative vitality in dry and in moist air, in water and when exposed to the direct rays of the sun.

The following is a summary of the conclusions reached by these investigators:

The external organs are composed of two leaves (the outer of much greater consistence than the inner) the space between which has a double communication with the blood system, receiving on the one hand blood to be respired and on the other giving back that respired.

The "corps blanc" is not present in all the Cloportides as Latreille had announced[4] but only in the genera *Porcellio* and *Armadillis*. In these two genera it is constant in the first two pairs of lames operculaires and in two species, *Porcellio armadilloide* and *Porcellio à trois bandes*, in all five pairs.

The corps blanc has a tree like, spongy and vascular appearance. It is a simple modification of the lames branchiales operculaires, through the inward folding and division of the membranous leaf of the lames.

It absorbs the moisture of the air and maintains the moistened condition of the lame branchiale [the inner gill].

On the posterior borders of the lames enclosing the corps blanc is a cleft which one of the authors had observed to dilate and contract and out of which they had seen a fluid to pass. „Il s'en échappe, suivant notre observation commune, de très petites quantités de liquide aqueux dans lequel du moins, nous avons constaté qu'il n'existe pas des globules."

[1] Medizinische Zoologie, II. Band, Berlin, 1833.

[2] L'Institut, 1839.

[3] Essai d'une Monographie des organes de la respiration de l'ordre des Crustacés Isopodes. Annales des sciences naturelles. Ser. 2, Tom. XV, 1841.

[4] In this Latreille was followed by Milne-Edwards. See, Histoire naturelle des Crustacés, 1840. But in his Physiologie Comparée, 1857, he refers to the corps blanc as present only in the two genera named above.

As a general result of their experiments they had found that *Porcellio* resists for a longer time than the other Cloportides the action of dry air and of light. "Sans doutes ces expériences ne suffisent pas encore pour en tirer des conclusiones incontestables. Mais on peut au moins en déduire que l'eau et l'air sec et chaud, sans l'action de la lumière ou avec cette action, sont mortels pour ces animeaux, et que leurs organes de respiration, quoique formés, pour l'essentiel, sur le modèle des branchies de cette classe, ne sont pas plus propres à respirer l'eau, ni l'air sec, que ceux de certains crabes terristris. Leur respiration normale ne peut avoir lieu que dans un air humide, condition essentielle de la durée de leur existence."

It will be to our purpose to quote also from these authors their description of the outer gills of *Oniscus*, in so far as they refer to that portion of the gills which, as will be shown in the body of the present work, constitutes a special structure adapted to the respiration of air.

"Il résulte de cette disposition, que la portion externe de chaque lames, celle qui forme un segment de cercle, est entièrement et uniquement constituée par la membrane délicate qui forme le feuillet viscéral. C'est pour cette raison que cette portion externe est beaucoup plus mince, plus transparente que le reste de la lame. Il est à supposer que c'est principalement dans cette portion externe que se fait l'hématose; on y distingue une apparence de réseau très fin, formé de traits en relief qui affectent une direction plus ou moins rayonnée."

Siebold,[1] in 1842, in connection with a review of the work of Duvernoy and Lereboullet, stated, as the results of his own investigations upon *Porcellio*, as follows:

"Die weisse Farbe jener eigentümlichen vier Körper der beiden ersten Paare von Decklamellen rührte nur von der in denselben sehr fein zerteilten Luft her. Die eigentümlichen Körper bestehen nämlich am äusseren Rande der Decklamellen aus einem zwischen den beiden Platten derselben befindlichen sehr feinen Luftgefässnetze, welches sich nach innen hin als ein vielfach baumförmig verzweigter Gefässbüschel ausbreitet; die Wände dieser Luftgefässe sind ausserordentlich zart und werden durch Pressen zwischen Glasplatten sehr leicht zerstört, wobei die in ihnen enthaltene Luft als grössere Luftperlen hervorquillt und die weisse Farbe verschwindet."

Lereboullet,[2] in 1852, in an elaborate work described the external anatomy and relations of the organs of respiration of the Cloportides in still greater detail than in his work published jointly with Duvernoy, noted above.

Referring to the corps spongieux, he says: "Ces organes considérés anatomiquement, sont donc des poches aériennes, c'est-à-dire, des poumons. Mais sous le rapport functionnel, ils peuvent être considérés comme des branchies, tout aussi bien que les vésicules et les lamelles operculaires elles-mêmes, car ces poches ne fonctionnent bien que dans l'air humide; seulement ces branchies sont intérieures au lieu d'être libres et flottantes, et c'est l'air humide au lieu de l'eau qui remplit leurs ramifications.

On voit, en resume, que la fonction si importante de la respiration s'exerce, chez les Cloportides, par trois moyens qui ne sont en réalité que des modifications les uns des autres: les lames operculaires, les vésicules et les cavités aériennes ramifées. Cette diversité de moyens, pour atteindre le même but, montre les liaisons étroites qui existent entre la respiration aérienne proprement dite et la respiration branchiale."

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[1] Müller's Archives, 1842, p. 141.

[2] Mémoire sur les Crustacés de la Famille des Cloportides, qui habitent les environs de Strasbourg. Strassburg, 1852.

In regard to the outer gills of *Oniscus* he says: „Dans le genre Cloporte le bord externe de chaque lame s'arrondit en un lobe très mince; ce lobe est aussi formé de deux feuillets, mais l'externe est aussi mince que l'interne. Les canaux qui donnent passage au fluide nourricier affectent, dans cette partie, une disposition rayonnante."

Leydig[1] announced, in 1855, that he had confirmed Siebold's conclusion that the corpora alba coutain very finely divided air. He stated that the air passages form a finely-meshed network, similar to the capillaries in the lungs of vertebrates.

N. Wagner[2] in an article entitled Appareil circulatoire des Porcelliones, published in 1865, stated that the outer lames, taken together, form a kind of respiratory chamber, holding moist air which is indispensable for the inner gills. The corpora alba resemble very much the respiratory organs of the arachnids and insects. They are in reality a sort of pulmonary sac or trachea, serving as organs supplementary to the gills. He refers to certain histological features. The gills are filled with a spongy tissue "tissu spongieux". The walls are composed of two layers, the inner of which consists of "celles sous-epidermiques". Within the gills, mainly aggregated in one place, are the "gouttelettes de la graisse".

The last work that has appeared relating to the breathing-organs of the land-isopods is that of Leydig, published in 1878.[3] This author essayed to make an investigation of the histological structure of the gills of *Porcellio armadilloides*. Full comment upon this work is given in the body of the present treatise. It will be to our purposo to notice here the conclusions which he reached in regard to the main points previously investigated by zoölogists, as noted above.

In agreement with his previous determination (see above) Leydig finds that the corpora alba contain finely divided air. But this air does not enter or pass out, as had been reported by others and as he himself had formerly believed, through an opening on the posterior margin of the gill-cover. Scattered over the entire surface of the gill are small pneumatic spaces of the cuticle. "Die Luft ist in kleinen Höhlen der Cuticula enthalten, daher die 'feine Zerteilung' . . . Man sieht hier innerhalb der feldrigen Abgrenzungen die vorhin schon erwähnten kleinen schräg liegenden mit Luft erfüllten Höhlungen und indem wir genauer die Fläche durchmustern, können wir wahrnehmen, dass sie wohl auch in gewöhnliche Porenkanäle übergehen, somit nur eine besondere Form der letzteren darstellen."

Previous authors were in error in their estimation that the air-holding part was a branching divided sack with blind closed ends, after the form of a glaud. "In Wirklichkeit bestehen solche blindsackige Enden nicht, da ja die Luft in der cuticularen Wand der Bluträume liegt."

What appears to be an opening is in fact a depression or recess in which a leaf-like extension of the basal joint lies. That air comes out at this place under pressure can be explained by supposing that the bottom of the depression in thinner there than the skin elsewhere is.

Concerning the significance of the organisation described, the author states that it is not to be regarded as morphologically corresponding with the tracheae of insects, nor, on the physiological side, is the conception of a kind of lung-breathing warrantable. It is in fact questionable whether the air in this situation has anything to do with respiration.

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[1] Müller's Archives, 1855.

[2] Annales des Sciences naturelles, 1865.

[3] Über Amphipoda and Isopoda, Zeitschrift für wissensch. Zoologie, Band 30, Supplement, 1878.

It is seen from the above review of the literature that, although the organs of respiration of the *Oniscidae* have been the subject of investigation by a considerable number of zoölogists, scarcely anything concerning their more intimate characters can be said to have been finally settled. Leaving out of account the aberrant views of TREVIRANUS and BRANDT, the only point as to which there had been some approach to unanimity of opinion was that the corpora alba are organs containing air. Even as to this DUVERNOY and, at the time of the publication of their joint work, his collaborator, LEREBOULLET, were at least in doubt. They record that they observed a clear liquid to pass out from the aperture associated with the corpora alba, and their final conclusion was that the organ served to abstract the moisture from the air.

As to the precise structure of the same organ, the statements of the several authors are widely divergent. In its general features it has been compared variously to a tree, a sponge and a net-work. As to its physiological nature it has been regarded at times as a form of trachea, again as a lung, and again as a modified gill.

The only histological investigation made has been that of LEYDIG and the conclusions reached by him, in regard to the corpora alba, were contradictory, in respect to nearly all essential points, to those reached by his predecessors. Moreover, a reading of LEYDIG's article shows that as an histological study it is incomplete.

The investigations hitherto made upon the special modifications of the outer divisions of the respiratory appendages have been confined to the genera *Porcellio* and *Armadillidium*. It has not been hitherto discovered that also in the genus *Oniscus* there are highly specialized structures, though quite different in their morphological characters, adapted to the performance of the respiratory function in air.

It is evident that a thorough investigation, employing the resources of modern laboratory methods, was to be desired in order to add to our knowledge of these interesting organs. The writer believes that the work here submitted is a contribution to that end.

Part III.

The Anatomy and Physiology of the Organs of Respiration of Porcellio, Cylisticus, Armadillidium, Ligidium and Oniscus.

Porcellio scaber LATREILLE.

The general external anatomy and relations of the gills of *Porcellio* have been well described by several of the authors above mentioned, especially LEREBOULLET. It will be sufficient, therefore, in the present work, as a preparation for an account of the histological anatomy of the outer gills and the included corpora alba, to describe the outward appearance of a single gill. The features presented by the inner surface of the first right outer gill of *Porcellio scaber*, male, are as follows:

The general outline (Fig. 1) is that of a triangle with broadly rounded corners. Along the anterior side which is slightly curved inwards is situated the articulation of the gill with the basal joint (Art.). The inner side which lies contiguous to the stylet along the middle line of the body is convex outwards; the lower two-thirds of its margin is beset with about 15 stout hairs. The outer and posterior side forms an irregular line marked by a sharp angle directed inwards.

The face of the gill falls into two parts: the general part, making up more than one-half of the whole and the special part which includes the corpus album. The general part is marked by dots which along the margin are aggregated into a broad continuous line and elsewhere are scattered or irregularly grouped. The marginal line of dots lies immediately contiguous to the chitinous wall of the gill at the junction of the inner and outer faces.

The special part may be seen best by mounting a gill in water and examining under a low power of the microscope with reflected light. In the outer portion is seen a whitish body presenting the general appearance of a deuse clump of bushes (Fig. 1, tr.). The base of the bushy mass lies toward the angle on the posterio-lateral margin of the gill and the branches are arranged radiately arount the base terminating in minute twigs. By focussing at different levels it becomes evident that this body lies within the gill which in this region is much thicker than elsewhere. Since by transmitted light the body appears dark, it may be inferred that it contains air. Furthermore, by pressing upon the cover-glass a bubble of gas may be seen to pass out at the angular indentation on the margin of the gill.

A portion of the wall of the gill overlying the white body shows very marked modifications (Fig. 1, Gr. a). This portion has well defined boundaries, being included within a curved line, convex inwards, lying at the surface of the gill, and two shorter curved lines, convex outwards, the intersection of which forms the marginal angle referred to above. The surface of this region presents the appearance of a net-work. The meshes of the net-work appear as dark lines under transmitted light, indicating that they are furrows in the chitinous wall of the gill and contain air.

Minute Anatomy. Examined with a high power of the microscope, the several parts just noticed present the following features:

The chitinous wall of the general part of the gill shows superficial markings, consisting of minute pits which appear as dark points. They are arranged so as to form a pattern composed of polyginal areas (Fig. 2).

The bodies referred to above as dots are seen to present the appearance of nuclei. They lie immediately under the chitine and are of irregular sige and form. By focussing at different levels it may be seen that associated with many of the nuclei are strands of tissue which extend from the dorsal to the ventral wall of the gill. These form pillars and will be further described below.

In that portion of the special region of the gill where the wall presents the appearance of a net-work the chitine is sculptured in a peculiar way. The surface in thrown into irregular polyginal areas which are separated by furrows (Fig. 3b; P. a, Gr.). The areas themselves are sculptured by much finer furrows, lying in short angular lines. The elevations and depressions thus formed give the surface of each area the appearance of a pattern.

That the larger furrows or grooves separating the polyginal areas contain air may be demonstrated by mounting a gill in water, when they are seen to appear white by reflected and dark by transmitted light. If a gill is placed in alcohol before examining the net-work does not appear dark under transmitted light. The finer furrows of the polyginal areas do not appear to hold air.

Underneath the chitine presenting these special modifications may be seen corpuscles which here occur somewhat in accumulation. When pressure is applied to the cover-glass these corpuscles move independently. Examination of a drop of blood taken from the body of a living animal shows the same corpuscles present in the blood. They are of two kinds, namely: spherical, nucleated cells and larger, highly granular, nucleated cells of irregular form. The former which are much more numerous than the latter are the ordinary blood corpuscles; the latter are leucocytes.

The two forms of blood corpuscles may be seen elsewhere in the gill but occurring sparsely as compared with the special region above mentioned. It would appear that Wagner (see reference p. 10) in referring to the "gouttelettes de la graisse" and in stating that they occur aggregated chiefly in one place in the gill had observed the corpuscles distributed as above described.

A portion of the marginal region of the white body presents an appearance somewhat resembling a piece of branching coral (Fig. 5). The whole structure appears to be hollow, with smooth thin walls. The appearance of irregular markings on the walls is probably due to shrinkage, consequent upon the passing out of air.

Internal Anatomy. Fig. 4 represents a cross-section of the gill taken in the direction of the line s s' Fig. 1. The gill is seen to fall into two portions, a thinner and a thicker; these correspond, respectively, to the general and special parts, described above. The chitinous wall (Ch) is in general thicker on the lower or ventral side than on the upper or dorsal side. Within the chitine is a layer of tissue with conspicuous nuclei — the hypoderm (Hy). The hypodermic layers lining the two opposite chitinous walls are not entirely separated but, in the general portion of the gill, are connected by extensions, forming pillars (Pl.). The space crossed by these pillars is the general cavity of the gill and contains blood (B.c.). The blood cavity is bounded by a thin wall which lies immediately within the hypodermis (W.b.c.).

In the special portion of the gill there are no pillars but the blood-cavity is penetrated by a system of branching canals. This system is in fact a single much divided cavity, tree-like in form, and communicating with the outside of the gill through an opening (Op.). In other words, it is morphologically an infold of the wall of the gill.

It is evident that this tree-like structure is a section of the corpus album.

The tree, as a whole, divides that portion of the blood-cavity of the gill in which it lies into numerous small communicating spaces, containing blood (B.sp.). But at the base of the tree and surrounded externally by that portion of the chitinous wall which is sculptured into furrows that contain air is a large space or chamber (B.ch.). The quantity of blood contained in this chamber gives the appearance of an accumulation of blood corpuscles, referred to above.

Minute Internal Anatomy. The cellular structure of the hypoderm is indicated only by the nuclei, no cell-walls being visible. The layer varies in thickness in different parts of the gill. It is best developed in the general part where the nuclei are large and surrounded with cell-protoplasm. In the special part, along the two walls of chitine, the layer becomes thinner and the nuclei are flattened. Along the infolded portion of the chitinous wall, forming the tree, the cell-protoplasm is greatly reduced and the layer becomes very thin, except where the nuclei occur (Hy. Nu.). The nuclei are everywhere marked by clearly defined boundaries and are highly granular. The pillars consist of hypodermic tissue and at their ends are structurally continuous with the respective dorsal and ventral hypodermic layers. They contain one or more nuclei which are elongated in the direction of the axis of the pillar.

The blood cavity occupies the whole space within the hypodermic layer and is bounded by a thin wall lying contiguous to the hypoderm and conforming to its irregularities (W.b.c.). In this wall at long intervals lie elongated nuclei. I infer, from the relations of this wall that it is of mesodermic origin. [1]

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[1] Since the present treatise was written my attention has been called by Professor CHUN to the work of LEICHMANN, Beiträge zur Naturgeschichte der Isopoden, published in the Bibliotheca zoologica, Heft 10. Cassel 1891. It appears from this work that the brood-sacks of the Isopoda are in their general features homologous with the gills. As shown by this author the brood-sacks arise as folds of the hypoderm and at an early stage of development the hypoderm cells become grouped in such a way as to leave a net-work of spaces between the opposite walls of the sack. A cross-section of the brood-lamella of *Asellus aquaticus* (a figure of which is given) taken at this stage of development shows an identity in structural plan with that of the gills of the Oniscidae, in the cases where the latter have undergone no special modifications in adaptation to air-breathing, as in the last three pairs of outer gills of *Porcellio scaber*. According to LEICHMANN, the net-work of spaces in the brood-lamellae which, as in the gills, contain blood, are lacunose. He figures these spaces as bounded by a clearly defined line, but he regards this line as merely the boundary of the hypodermic walls and pillars. In my description of the gills, as above given, I have considered this boundary line as forming a definite wall surrounding the blood-spaces and probably of mesodermic origin. I was inclined to this view from the fact that nuclei occur, though very sparsely, along these lines where they immediately adjoin the hypodermic wall.

According to my conception a layer of mesodermic origin which bounds the body-cavity extends into the gills and forms a boundary wall of the blood-spaces of the gills. On the other hand LEICHMANN finds in the brood-lamellae no such layer but considers that the spaces are lacunae and that the blood lies immediately in contact with the hypoderm. The clearly defined line surrounding the spaces is the inner marginal line of the hypodermic tissue. LEICHMANN speaks of the "innere Chitinlamelle".

In view of this discrepancy I would leave as undetermined in the present work the nature of the wall in question. I hope at a future time, through the study of the embryology of the gill, to determine the point finally.

Where the hypodermic pillars intersect the blood cavity the dorsal and ventral boundary walls of the cavity become continuous, forming sheaths which surround the pillars. The ramifications of the tree are also accompanied by folds of the boundary wall of the blood cavity (Fig. 6, W.Bc.). In this situation the wall becomes very thin but it may be seen as a clearly defined boundary of the communicating blood spaces formed by the divisions of the tree.

The structure of the tree is well seen in sections taken parallel with the faces of the gill (Fig. 7). The opening through which the ramified cavities of the tree communicate with the outside, here appears as a rather narrow passage and the chitinous walls along the passage are sculptured in the same manner as the specially modified portion of the exterior chitinous wall (Op. tr.; Gr. ch.). The grooved structure of the exterior wall is in fact continued in the infolded portion and gradually becomes simplified to the plain wall of the branches of the tree. The passage widens into a shallow bowl-shaped cavity from which pass out in radiate arrangment the tubular cavities of the primary branches of the tree (Br. tr.). These divide repeatedly and the final terminations approach closely to the walls of the gill (Fig. 6). The mode of branching does not appear to conform to any definite law, excepting that the divisions lie at approximately uniform angles with one another. Where a division occurs the size of the tubules is reduced only to a moderate extent, so that the final branches have a relatively large diameter. The branches terminate in rounded ends.

The walls of the tubules are thin and show no markings. 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 (Fig. 6; Ch., Hy., W.b.c.). Thus every portion of the wall of the tree is composed of three very thin layers. The hypodermic nuclei occur at frequent intervals.

It is seen from the above that the study of the internal anatomy of the gill establishes the conclusions of those authors quoted above who found the corpus album to be a branching, tree-like cavity communicating with the exterior through an opening. The conception of Duvernoy and Lereboullet that the tree is morphologically an inward folding and division of the inner wall of the gill is verified. Incidentally to the study of the anatomy it has been shown, as has been hitherto generally believed, that the cavity contains air.

The Physiology of the Gill. In considering the physiology of the parts described above it may first be noted that the gill as a whole has no function that is merely relative to the inner gills. The name gill-covers usually given by authors to the outer branches of the appendages is not applicable to the first and second pairs, since the three pairs of inner gills lie within the last three pairs of the outer branches.

As regards the use of names it may be remarked that it seems most suitable to employ simply the terms inner and outer gills, using them in their morphological values.

The function of the tree and the grooves. It is evident that the gill of *Porcellio scaber* is a structure 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 furrows in the chitine at the exterior of the gill and second, the infolded portion of the chitinous wall, forming the internal tree.

In considering the physiological significance of the details of structure of these two parts it is helpful to bear in mind the mechanical conditions requisite to securing the general end. These are first, an extension of the wall interposed between the two media, in order to afford a large surface of exposure, and second, a thinning of the same wall, in order to secure the permeability requisite for a ready exchange of elements between the two media.

But modifications of structure in each of these two directions are subject to limitations imposed by other mechanical conditions. Increase of surface is limited by the requirement of a moderate and proportionate size of the part; and the thinning out of the wall is limited by the requirement of strength.

Applying these principles 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 thiness 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 arrangment 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. 3 a, gr.) is that of an oval with the long axis at right angles to the face of the wall is, I conceive, adapted to a three-fold purpose, namely: first, to containing a large amount of air relative to the space occupied; second, to retaining this air in the groove (by means of the narrowing of the opening); and third, to reduce to the least extent the strength of the wall (by means of the resistance to fracture secured through the curved surface of the oval).

In spite of these adaptations, it is evident that the grooved portion of the wall of chitine has not the same strength as the rest of the wall. As a compensation for this the marginal region of the grooved area is depressed below the level of the plain area and is bounded by a ridge of chitine (Rd. Fig. 4) formed by a thickening of the wall at the line of junction of the two areas.

This ridge is the curved line, convex toward the middle of the gill, mentioned above in the description of the appearance of the inner face of the gill. Furthermore, the grooved area as a whole is bounded by convex surfaces — a means of increasing its strength.

In the tree extent of surface is secured by the folding of the wall and permeability by the thinning out of the same. The protected position of the tree inside the gill permitts a high degree of tenuousness of the wall. The tubular form of the branches, as well as their rounded form at the ends, afford the greatest degree of strength consistent with their extreme thinness.

The tree, as a mass, is somenhat spherical in shape (Fig. 1), which secures the most favorable distribution of the branches in the fluid surrounding them. But the sphere is depressed on the basal side of the tree, leaving a space between the base and the grooved area of wall of the gill, as noted above (p. 22, see also Fig. 4, B. ch.). It is evident that this is an adaptation for bringing a relatively large amount of blood into relation with the air contained both in the grooves and in the basal branches of the tree.

The circulation of the blood in the gill. From my observations I am lead to infer that all of the blood in the course of its circulation through the gill passes through the space or chamber, just referred to. By mounting a living animal in water the movements of the blood corpuscles within the gill can in part be observed. The blood enters the gill at its connection with the basal joint and is first distributed through the cavity of the general part of the gill. Due to the position of the gill in relation to the joint the course of the current is directed toward the inner and lower sides of the blood cavity. But owing to the curvature of the inner side of the cavity (corresponding to the curved outline of the side of the gill lying toward the middle line of the body) the blood particles are swerved in their course toward the special part of the gill. They may be seen in part to enter among the branches of the tree and in part to enter the large space above described, at its posterior end. I have not found it possible to trace further the course of the circulation but it would appear that the blood, entering among the branches of the tree, passes through the tree into the cavity, there mingling with that which entered at the posterior end of the cavity. The current would then pass upwards and outwards toward the excurrent channel at the base of the gill.

The comparatively large size of this special blood space causes a slower movement of the blood through the space and thus permits a longer exposure to the air contained in the grooves and in the basal branches of the tree.

The composition of the air in the tree. I have thus far spoken of the contents of the tree and the grooves as consisting of air. It is to be understood, however, that it is air altered in composition through the respiratory process. And inasmuch as there is no mechanism for renewing the supply of air, this alteration must be carried to a considerable degree. In general it may be considered that its composition is that of ordinary air to which has been added in the respiratory process a quantity of carbonic acid from the blood and from which has been taken a corresponding quantity of oxygen.

We have next to consider the condition of the air in the tree in respect to presence of moisture. Concerning this point Duvernoy and Lereboullet in their joint work went so far as to state that the white body absorbs the moisture of the air. Lereboullet in his later work reached the conclusion that the body contains air but that it is indispensable for the functional action of the gill that the air taken up from without should be charged with moisture. Other authors have made no express statements upon this point.

In considering this question we are first met by the fact that the animals live in situations where the air is damper than ordinary atmospheric air. One may suppose, however, that this is in adaptation to the functional action of the inner gills only. Next, there are phylogenetic considerations which appear rather adverse to the view that the gills are adequate to breathing ordinary air. The ancestral Isopoda were aquatic animals and their descendants comprising the modern family of the Oniscidae have acquired the terrestrial habit of life by a gradual process. It would appear that the modifications of the gills in adaptation to the respiration of air may not have been carried to the extent that they are capable of breathing ordinary dry atmospheric air.

Notwithstanding these considerations I have reached the conclusion that the outer gills of *Porcellio* (and its congeners) are capable of functioning in a medium of atmospheric air in its ordinary condition as to quantity of moisture present. First, on the basis of the structure of the gill it would appear that there is warrant for the inference. Since the tree corresponds in structural principle with the tracheae of insects which in general live under ordinary conditions as to atmosphere, it would seem probable that it is capable of the same functional action. Moreover, I conceive that the form and situation of the respiratory tree are adaptations to this end. The tree, indeed, in its general build and relations possesses a two-fold adaptation. The first we have considered above, namely, the bringing of air into relation with blood. The second is to secure the protection of the blood against dessiccation from the air in the process of respiration. We have seen that the mass of air present in the tree is changed very slowly, due to the shope of the tree (having only a single orifice) and the lack of any mechanism for inspiration and expiration. This secures also a retardation in the escape of the water of respiration — that passing off from the blood — to the outer air. It results that the water of respiration becomes distributed through the mass of air in the tree and thus prevents a dessiccating action of the air upon the blood. Thus while it might happen that if ordinary dry atmospheric air were brought into relation with the respiratory surface of the blood cavity it would be fatal to the respiratory process, yet it remains true that the outer gills are capable of functioning when the animals are surroundet by the ordinary atmospheric medium.

As supporting this view we have the fact that the animals will live for a considerable length of time under ordinary atmospheric conditions. I have found that *Porcellio scaber* lives from 24 to 36 hours when kept in air under the conditions of an ordinary living-room. I infer that under these circumstances the breathing process takes place mainly in the outer gills and that finally death ensues through the dessiccation of the inner gills only. (See also below under physiology of the inner gills.)

Conclusions. From the foregoing facts and considerations I reach the following conclusions in regard to the nature of the outer branches of the first and second pairs of abdominal appendages in *Porcellio scaber*.

1. From the stand-point of morphology they are gills, homologous with the true gills of aquatic isopods.

2. But from the stand-point of physiology they are organs for the respiration of air.

3. The special respiratory organ forming the tree is in morphological principle homologous with the tracheae of insects but it is different in structural plan, especially as having only a single external opening and as lacking spiral folds of the chitinous wall.

4. In its general physiological value the tree corresponds to tracheae, but it differs from tracheae in the respects first, that it is adapted to retaining for a time the water of respiration in the air-cavity and second, that it is an organ lying in a particular region of the body to which the blood is brought, to be aerated, instead of a system of tubes penetrating the body in order to carry air to the blood.

5. In the respect last mentioned the tree is analogous to the lungs of vertebrate animals, but

6. Morphologically the tree differs from lungs, first, in that it lacks any associated muscular mechanism for forcing air in and out and, second, it is an infold of the external wall of the body, instead of the wall of the enteric cavity.

The last three pairs of outer gills. These lack the respiratory tree and the area of grooved chitinous wall. That is to say, they have no special modifications adapting them to the respiration of air. In other respects they correspond in structure to the first and second pairs.

As regards their physiological office it is evident from their form and position that they serve as covers for the corresponding three pairs of inner gills. And since the inner gills can perform their function only in air charged with moisture (see below) it would appear that the outer gills exercise their protective function mainly in sheltering the inner gills from the dessiccation that would follow from direct exposure to air.

The movements of the outer gills have already been referred to (p. 5). It is evident that the object of the movements in to afford a renewal of the supply of air to the inner gills. In a living specimen under a lens one can see the gills separate and a layer of air enter between each lateral division and the one that lies next posterior to it. As the gills come together again, this layer of air appears to be pressed into the cavity in which the inner gills lie. The outer gills thus possess an active as well as a passive function with respect to the inner gills.

It is possible that the outer gills, in addition to performing these functions, constitute in themselves 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.

I conclude, then, that the function of the last three pairs of outer gills is chiefly a relative one, namely, that of protecting the inner gills from dessiccation and of supplying air to them; but that they also act independently, as organs of respiration, though limited in this function.

The Inner Gills. The general external features of the inner gills of *Porcellio* have been studied by several authors: first by Treviranus and later by Duvernoy, Lereboullet and Leydig, The last named author also investigated their internal structure in the species *Porcellio armadilloides.*[1] I find that the figure he gives for this species applies also in general to *Porcellio scaber.* (Full notice of Leydig's account of the histology will be given below under *Cylisticus convexicus.*)

A cross-section of the inner gill of *Porcellio scaber* presents the appearance shown in Fig. 8. It is seen to consist of a flattened sac the cavity of which contains blood. The wall of the sack is composed of an outer thin layer of chitine and an inner thick nucleated layer — the hypoderm. The hypodermic layers on the two opposite dorsal and ventral sides of the gill are connected by pillars. The lines representing the structural elements of these pillars are seen to be continuous at each end with the structural elements of the hypodermic layer.

Examined as to its minute anatomy the hypoderm is seen to consist of a continuous layer of granular and striated matter. In other words there are no cell-boundaries, the cell structure being indicated alone by the nuclei. The striae of the protoplasm are arranged at right angles to the surface of the gill. The nuclei are large and in general ovoidal in shape. They show a definite arrangment, — the long axis of the ovoid being at right angles to the face of the gill and the narrow end on the side toward the cavity of the gill. The granules of chromatine of the nuclei also conform to a law of arrangment, namely, they tend to be aggregated at the narrow end of the nucleus, toward the cavity of the gill. It would appear that these structural features have a significance in reference to the passage of the gases concerned in respiration through the hypodermic layer.

The hypoderm at its inner margin is bounded by a clearly defined line which is immediately in contact with the blood within. The appearance of this line is such as to suggest that it is the dense (chitinized?) inner surface layer of the hypodermic tissue. Whether this is the case or whether the line represents a remnant of a mesodermic layer bounding the blood cavity, I have not had an opportunity, through the study of the embryology of the gill, to ascertain.

Physiology of the Inner Gills. The function of the inner gills is that of respiration in a medium of moist air. That the animals require air charged with moisture as a condition for

[1] Concerning the identity of this species, see p. 20.

continued existence is evident from their habits of life and is readily susceptible of demonstration by experiment. That it is the inner rather than the outer gills whose function is conditioned by the presence of moisture would seem evident from the following considerations, as well as from those given above in the account of the physiology of the outer gills:

The inner gills are protected from direct exposure to the surrounding atmospheric air, while the outer gills function under such exposure.

Those genera of land-isopods which lack special respiratory structures in the outer gills, such as *Ligidium*, live only in very moist situations.

Considerations as regards the phylogenetic history of the land-isopods: As the ancestral aquatic forms gradually acquired the habit of terrestrial life, the outer gills underwent far greater modification than the inner gills. In all they became converted into covers for the inner ones but in this transformation probably did not entirely lose their functional capacity as gills. In certain genera, as *Ligidium*, the process of modification stopped at this point. In other genera, as *Porcellio*, a new form of modification set in, namely, that of the development of tracheae-like structures. This was in adaptation to the respiration of ordinary atmospheric air. But the inner gills acquired only a certain measure of adaptation to respiration in a medium of air; hence the presence of moisture in the air surrounding them is still indispensable to their functional action.

Porcellio Ratzburghii Brandt.

In this species all five pairs of the outer gills possess the special respiratory structures described for *Porcellio scaber*. They are best developed in the first pair and gradually decrease in size to the last pair. I find that in all essential structural features the outer gills are identical in the two species. The respiratory tree and grooves present the same characters in both, differing only as regards the minor features of size and form.

It is worthy of remark, as bearing upon the question of the function of the outer gills, that this species lives in situations where the air is charged with moisture only in a moderate degree in excess of that of ordinary atmospheric air. Their habitat is under the bark of dead trees and they may often be found a meter or more above the ground.

Cylisticus convexicus Budde-Lund.

This is the species which under the name of *Porcellio armadilloides* was investigated by Leydig.[1] I have established the identity as to species of the animals studied by Leydig and those studied by myself not only by reference to the list of synonyms given in Budde-Lund's work but also by a comparison of preparations of the gills with the figures of the same given by Leydig.

In this species all five pairs of the outer gills have the special respiratory structures — the tree and the grooves. I have carefully examined, both as seen from without and in section,

[1] Über Amphipoda und Isopoda; Zeitschrift für wissenschaftliche Zoologie, Bd. 30, Suppl. 1878.

the outer gills of the first and second pairs (where the corpora alba are best developed) 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.

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.

The author states that in his investigation he placed before himself especially the question: "Wo und in welchem Gewebstheil befindet sich denn eigentlich die fein zertheilte Luft?" He reports as follows:

"Man unterscheidet auf dem Durchschnitt der Decklamelle zunächst wieder die schon erwähnte das Ganze umfassende und abschliessende Cuticula. Unter ihr folgt als matrix eine Zellenlage und diese, indem sie nach einwärts ein Balkenwerk entwickelt, zerlegt den gemeinsamen Blutraum in ein Netz von Blutgängen. In der dünneren Partie der Decklamelle heben sich die Zellen als inselartige Stellen zwischen den Bluträumen ab.

Dieselben Zellen scheiden an ihrer freien Fläche, insofern sie die Bluträume begrenzen, eine zarte, die Blutgänge auskleidende Cuticula ab und diese letztere ist es, welche pneumatisch wird. Die Luft ist in kleinen Höhlen der Cuticula enthalten, daher die 'feine Zertheilung'. Suchen wir uns verständlich zu machen, welchen Bildungen etwa sonst die pneumatischen Höhlungen zu vergleichen sind, so giebt die nähere Prüfung der äusseren Cuticula des Rückenblattes der Decklamelle Aufschluss. Man sieht hier innerhalb der feldrigen Abgrenzungen die vorhin schon erwähnten kleinen, schräg liegenden, mit Luft erfüllten Höhlungen und indem wir genauer die Fläche durchmustern, können wir wahrnehmen, dass sie wohl auch in gewöhnliche Porencanäle übergehen, somit nur eine besondere Form der letzteren darstellen. Die Decklamelle im Ganzen und bei geringer Vergrösserung betrachtet, zeigt durch den Lauf der Bluträume die pneumatische Partie von dreifacher Form: gegen den freien Rand zu erscheint sie dicht netzförmig, weiter nach hinten wird sie noch engmaschiger, und gerade diese Stelle besitzt das schwammige Wesen und bei auffallendem Licht die schneeweisse Farbe; dazwischen verlieren sich weitere gefässartige Züge.

Die bisherigen bildlichen Veranschaulichungen leiden an dem Fehler, dass sie die lufthaltige Partie als einen ästig getheilten Sack darstellen, mit blind geschlossenen Enden, nach Art einer Drüse. In Wirklichkeit bestehen solche blindsackige Enden nicht, da ja die Luft in der cuticularen Wand der Bluträume liegt.

Die französischen Beobachter beschreiben ferner am hinteren Rande der Decklamelle eine Spalte . . . . Obschon ich selbst früher eine derartige grössere Oeffnung wahrzunehmen glaubte, muss ich eine Täuschung insofern darin erblicken, als die bezügliche Stelle, oben nahe der Einlenkung der Decklamelle, sich jetzt mir nicht als Spalte oder Oeffnung darstellen will, sondern das Aussehen einer Furche oder muscheligen Vertiefung an sich hat, in welche ein blattartiger Fortsatz des Gelenkstückes sich legt. Dass die Luft sich an diesen Stellen durch Druck hervorpressen lässt, liesse sich durch die Annahme erklären, dass der Grund der Spalte zarthäutiger als die übrige Haut ist.

Is is evident from the above that LEYDIG misapprehended the morphological relations in general of the pneumatic part. His conception is that the cuticula (chitine) secreted by the cells of the matrix (hypoderm) becomes penetrated by air-canals which independently open at the surface. It is true that the air-canals have walls of chitine secreted by the hypoderm 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.

I have carefully examined the dorsal chitinous wall of the gill both as seen from without and in sections, but fail to find pore-canals. The author gives a figure of the structures he thus designates and I find that his error arose through mistaking very small chitinous hairs for canals lying in the chitinous wall.

The correllative error in Leydig's account, namely, that then is no opening at the margin of the gill, is made evident by sections (figures 4 and 7). It is true that there is no opening near the articulation of the gill with the basal joint but at a point on the opposite margin of the gill. That Leydig was deceived in regard to this becomes understood by the fact that in the species he studied the marginal indentation, indicating the position of the opening, is small and inconspicuous.

Leydig appars to have observed the net-work of air-holding furrows, since he refers to a portion of the pneumatic part as presenting the appearance of a close net-work; but he was evidently under the impression that the net-work was inside the gill and formed a portion of the general pneumatic part.

The Inner Gills. I find that the figure of a section of the inner gill given by Leydig is applicable to my own preparations excepting as regards the nuclei. In his figure nucleoli are represented which I do not find to be present. Further he represents the nuclei as evenly granular throughout while I find the chromatin to be situated mainly on the side lying toward the cavity of the gill.

In his description of the inner gill he mentions one structural feature which I am not able to identify in my preparations. He says:

"Es ist dasselbe nach aussen umgrenzt von einer zarten, doch von Porencanälen durchsetzten, daher senkrecht streifigen Cuticula, oben und unten.

Sodann erscheint die Zellsubstanz von deutlich streifigem Wesen und starke Vergrösserung bei gehöriger Aufmerksamkeit lässt wahrnehmen, dass die Streifen von Längscanälen oder Lücken herrühren, welche das Protoplasma durchsetzten. Die Zellen von der Fläche angesehen zeigen sich wie von feinsten, dicht beisammenstehenden Löchelchen durchbohrt."

Contrary to the above I find that the chitine is not penetrated by pores. I find that the protoplasm of the hypoderm is striated, as stated by Leydig, but I do not find that actual canals or lacunae are associated with the striae.

Armadillidium vulgare Zoddach.

I have examined the first two pairs of outer gills in this species, both as seen from without and in sections, and I find that in all essential features they are identical with the corresponding parts in the genera already described. The respiratory tree and grooves present the same characters in both. The only differences are such as relate merely to comparative form and size.

Armadillidium granulatum Brandt.

I have compared alcoholic specimens of this species, collected by Dr. zur Strassen in Dalmatia, with the preceding species in respect to the external form and structure of the first two pairs of outer gills. I find that they correspond in all respects, differing only as regards comparative size and form.

Ligidium Hypnorum Budde-Lund.

In this species the outer gills have no special modifications of structure in adaptation to the respiration of air. In general they resemble in structure the last three pairs of outer gills in *Porcellio scaber.*

External Appearance and Structure. Fig. 9 shows the appearance of the right outer gill of the first pair, as viewed on the inner or dorsal surface. It is seen to be of a general quadrilateral shape and is broader than long. The attachment with the basal joint is at the outer anterior corner of the gill. The face of the gill is dotted and the dots are so arranged as to leave open spaces. These are paths for the flow of the blood through the gill. The incurrent path or channel — beginning at the union of the gill with the basal joint — extends laterally across the gill and gives off branches toward the middle region of the gill. Here the branches become lost in the small irregular spaces lying among the dots. The excurrent path or channel lies along the posterior and outer margin of the gill. It has no branches but is in free communication with the spaces in which the branches of the incurrent channel terminate.

Examining the gill under higher magnification it is seen that the dots are nuclei, lying immediately within the chitine and belonging (as further shown by the study of sections) to the hypoderm. By focussing at different levels it may be seen that associated with many of the nuclei are strands of tissue which run from the upper to the lower layer of hypoderm. These form supporting columns or pillars, such as have already been described for *Porcellio scaber.* It is due to the grouping of these pillars that spaces and channels for the passage of the blood through the gill, as above described, are formed. Along the channels the pillars tend to be arranged in rows, forming a kind of broken wall to the channel. Elsewhere they are scattered and stand either singly or in irregular groups.

Internal structure. Fig. 10 represents a cross-section of the outer gill, taken in the direction of the line 55′, Fig. 9. It is seen that the gill 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 everywhere lines the chitine and in general varies with it in thickness. It is very thin on the dorsal side and its nuclei for the most part lie in the extensions of the hypoderm forming the pillars. The blood-cavity is everywhere bounded by a very thin wall in which at distant intervals elongated nuclei occur. From its relations I infer that this layer is mesodermic in origin.[1]

Function of the outer Gills. The structure of the gill as above described appears

[1] See Foot-note, p. 14.

to me to warrant the inference that it functions directly as an organ of respiration of air. 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. It seems probable that the conditions requisite for an exchange of gases between the blood and the air are here satisfied.

In addition to the respiratory function the outer gills serve as covers for the inner gills.

The Inner Gills. The last three pairs of inner gills of *Ligidium* are in all respects identical in general structure and relations with those of *Porcellio scaber.* The first two pairs, as already stated, p. 6, are rudimentary.

Oniscus murarius Cuvier.

In the genus *Oniscus* the anatomy of the outer gills differs greatly from that of the genera thus far described. They lack any trachea-like structures but in their place possess special modifications adapted to the same functional end.

The first right outer gill of the male, examined on the inner or dorsal surface is represented in Fig. 11. It is seen that the gill is somewhat triangular in general outline, with rounded corners. The articulation of the gill with the basal joint (art) is situated on the anterior and outer side. The inner side lies parallel with the middle line of the body and is nearly straight. The side lying outwardly and posteriorly is deeply indented, the angle thus formed dividing this portion of the gill into two unequal lobes. The outer of these lobes is the portion of the gill specially modified in adaptation to the respiration of air. Viewed from above it is seen to constitute the outer-posterior portion of the gill and to comprise about one-third of the whole surface. Its margin is semi-circular in shape and its line of union with the general part of the gill is slightly convex toward that part. Along this line is situated a broad channel which, as will be shown below, conducts blood, after being aerated in the gill, back to the body and may be designated the main excurrent channel. Communicating with this channel is a series of small channels, arranged in a somewhat radiate manner, and occupying the whole area of the special part of the gill. Another broad channel is situated along the anterior and inner margin of the gill. As will be shown below, this receives blood from the body and it may be designated the main incurrent channel.

The boundaries of all the blood-channels are marked by rows of dots. Such dots are also seen scattered over the middle region of the gill, more or less aggregated into groups.

The chitinous covering of the gill is seen as a somewhat broad line along the entire margin of the gill. It is provided with stiff hairs on the outer and posterior border.

If the gill of a living animal is examined with a hand lens the special part presents the appearance of containing air. This may be better seen by placing a specimen in water under a cover-glass and examining with a low power of the microscope. Corresponding with the radiate channels above noted are seen a series of wave-like elevations and depressions which under reflected light appear silver-white and glistening. Most of the waves divide toward the margin of the gill, becoming Y-shaped, thus giving rise to the radiate arrangement of the parts, as a whole. Underneath the wave-like elevations the corpuscles of the blood may be seen to circulate.

This appearance lasts but a short time. The waves gradually become flatter and narrower and in the course of 10 minutes pass away altogether. The shining white aspect gives place to the ordinary appearance of the rest of the gill. If the animal is then restored to air the original appearance gradually comes back and in about 30 minutes is fully regained.

Minute External Anatomy. Under high magnification the chitinous wall shows superficial markings forming a pattern-work similar to that already described for *Porcellio scaber*. The dots, as in the species already described are the nuclei of the hypodermic layer. The pillars of the hypoderm come into view by focussing at different levels. Along the margins of the blood-channels these pillars are arranged in rows, forming a kind of broken wall to the blood-channels.

Within the cavity of the gill blood-corpuscles may be seen. They consist of the two forms of cells already described for *Porcellio scaber*.

Internal Anatomy. Fig. 12 represents a cross-section of the gill taken in the position of the line ss′, Fig. 11. It is seen that the gill is of moderate thickness throughout and that the outer fourth (right side of the figure) is much thinner than the rest. This thin portion of the gill in the special part; that is to say, the part specially modified for respiration and containing in the living animal, as noted above, air. The remaining thicker portion constitutes what we have designated above the general part of the gill.

The chitinous wall of the gill varies in thickness in different regions. It shows its greatest development on the dorsal side of the general part, where the chitine makes up nearly one-third of the breadth of the gill. On the ventral side it is everywhere thin, but less so in the general than in the special part. In this latter part the chitinous wall is thrown into elevations and depressions (see also Fig. 13).

The hypoderm consists of a continuous layer of tissue lying immediately within the chitine and, in addition, the bridges or pillars of tissue referred to above. In general the hypoderm layer varies in thickness with the chitine. The nuclei are conspicuous and vary widely in respect to size, form and position. Where the layer is thick the nuclei are large and tend to be elongated in form and arranged with the long axis at right angles to the wall of the gill. Where the layer is thin the nuclei are flattened and lie parallel with the wall of the gill. In the special portion of the gill where the hypodermic layer is very thin the nuclei appear to be withdrawn from the layer and to be associated with the tissue of the pillars (Fig. 13, Hy. pl.). It is seen further that the layers of hypoderm between the bases of the pillars are arched outwards. In other words, where the pillars occur the opposite dorsal and ventral hypodermic layers are drawn inward, thus being thrown into the form of waves. On this account the chitinous wall of this part of the gill has, as noted above, an undulated form.

The structure and relations of the general part of the gill. In *Oniscus* the general cavity of the gill 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.

In the general part of the gill there are two of these chambers, an inner or dorsal chamber and an outer or ventral one (Fig. 12, d.b.c., v.b.c.). They contain blood. Each chamber is bounded above and below by a thin wall. It results from this that the cavities of the two chambers are separated by a double wall (Pt.). This appears as two fine parallel lines between 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 layers on the respective dorsal and ventral sides of the gill. The outer walls have nuclei, but they occur at widely separated intervals.

The hypodermic pillars cross the blood chambers. Where they occur the walls of the chambers curve round them, forming sheaths. Thus the cavities containing blood are everywhere separated from the hypoderm by a boundary wall.

It is seen (Fig. 12) that the dorsal chamber becomes very wide where the general part of the gill adjoins the special part. This enlarged portion of the dorsal chamber is (as seen in section) the main excurrent blood-channel. By examining a series of sections, proceeding from the one figured toward the proximal side of the gill, it is seen that the rest of the dorsal chamber becomes gradually narrower and finally disappears, while the enlarged portion continues to the union of the gill with the basal joint. The gradual narrowing of the dorsal chamber (apart from the portion forming the excurrent channel) is correllated with the gradual widening, toward the proximal side of the gill, of the ventral chamber. Finally, where the dorsal chamber disappears the greatly enlarged ventral chamber becomes the main incurrent channel.

These relations may be described in other words by saying that the partition separating the dorsal and ventral chambers gradually approaches, in the direction of the proximal side of the gill, the outer wall of the dorsal chamber and finally becomes in contact with it, excepting along the region where the general part of the gill adjoins the special part.

By examining a complete series of sections, proceeding from the one figured to the distal side of the gill, it will be found that the partition separating the dorsal and ventral chambers comes to an end and that the end lies free in the cavity of the gill (excepting as supported by the pillars). This results in a communication of the dorsal and ventral chambers in the distal region of the gill.

The structure and relations of the special part of the gill. The dorsal and ventral blood-chambers of the general part of the gill are continued 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 (Fig. 13, d.b.c., m.b.c., v.b.c.). This middle chamber is formed by the forking of the partition separating the dorsal and ventral chambers in the general part (Fig. 12, Fk.). Each branch of the fork retains the structure of the main partition; 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. This is shown in Fig. 13 which represents a portion of a section of the gill taken in the direction of the line rr′, Fig. 11. It is seen that communication is afforded through the continuety of the outer boundary wall of the dorsal blood-chamber with the corresponding wall of the ventral chamber. At these places of communication of the two outer chambers the middle chamber ends blindly. I have not been able to satisfactorily demonstrate places of communication between the middle chamber and the other two. But since the middle chamber contains blood with corpuscles, I conclude there are such communications; further, as the middle chamber is blind at its inner end (lying between the branches of the fork) these communications must be along the margin of the gill.

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 (Fig. 13, d.a.c.). The ventral air-chamber has corresponding relations (v.a.c.). In other words, in the special part of the gill there is a space between the general wall of the gill (composed of the chitine and hypoderm) and the boundary wall of the blood-cavity. and this space contains air. This space does not communicate by any opening with the outside of the gill.

I find that in many preparations of sections the hypoderm does not appear to be present as a layer lining the chitine in the special part of the gill (excepting at the free end of the gill). I am inclined to the opinion that the hypoderm may become withdrawn from the chitine and centered in the pillars. As already observed, in this region of the gill the hypodermic nuclei are found only as associated with the pillars. It would seem possible that such a withdrawal of the hypoderm may take place periodically with moulting as soon as a new chitinous layer has been formed.

The hypodermic pillars in the special part of the gill are arranged in rows which divide the chambers into a series of compartments separated by broken walls. The appearance of these compartments, as seen when the gill is examined from without has already been referred to, p. 47, as being a series of radiating blood channels communicating with the main excurrent channel. It will be understood, however, that the compartments of the dorsal blood-chamber only open directly into the main excurrent channel.

Physiology of the outer gill. The course of the circulation of the blood. The course of the circulation of the blood in the outer gills of *Oniscus* can be seen by removing the first two pairs of thoracic legs, placing the animal in water in a watch-glass, putting on a cover-glass, and examining under a low power of the microscope. Fig. 14 is based upon examinations thus made. The dotted arrows represent the courses taken by the in-flowing or venous blood and the lined arrows the courses taken by the out-flowing or arterial blood. The blood, entering the gill at the basal joint, for the most part takes the path of the main incurrent channel. But as the inner boundary of this channel is a broken wall (formed by a row of hypodermic pillars) the blood constantly escapes from the channel and spreads over the entire region of the general part of the gill. This distribution of the blood further depends upon the curvature of the outer wall of the main in-current channel (the marginal wall of the gill) from which the current of blood is constantly being reflected.

That portion of the blood which thus makes its way to the distal region of the gill then turns in its course and enters the main excurrent channel. The rest of the blood passes from the general to the special part of the gill, entering the radiating channels and proceeding directly outwards toward the margin of the latter portion. Here it turns in its course and, following the radiate channels but in the reverse direction, enters the main excurrent channel. A small portion of the blood, however, does not enter this channel but joins the outflowing stream directly at the basal joint.

A portion of the blood, entering at the basal joint, does not go to the general part of the gill but to the special part and appears to circulate as follows: It tends to spread over the region of the special part but mingling with the currents flowing from the general to the special part, its course is gradually lost in these currents.

If now we apply the facts of structure and relation gained by the study of the anatomy of the gill to the explanation of the course of the circulation as observed from without, and above described, we are led to the following results:

The blood enters the ventral blood-chamber and spreads out through the entire cavity. In the distal part of the gill where the partition separating the ventral from the dorsal chamber comes to an end the blood passes into the dorsal blood-chamber and immediately into that portion of it forming the main excurrent channel. The blood entering the ventral chamber of the special part of the gill flows through the compartments of that chamber to the places where they communicate with the corresponding compartments of the dorsal chamber and there enters the latter. It flows through these to the main excurrent channel, excepting a small portion which passes into the excurrent channel at the basal joint.

The function of the blood-chambers. The function of the ventral chamber is obviously to receive venous blood from the body and distribute it over the entire outer face of the gill. It is there separated from the external atmosphere by its own wall and the ventral wall of the gill. As this wall of the gill is rather thin it would appear that an exchange of gases may take place between the blood in the ventral chamber and the external air. (This statement is intended to apply here only to the general part of the gill; the exchange of gases in the special part is considered below.) The function of the dorsal chamber is evidently to expose the blood still further to the action of air (as described below) and finally to collect the purified blood into a channel through which it passes back to the body. The use of the middle chamber appears to be passive rather than active. The space taken up by it reduces by so much the depth of the chambers above and below and thus secures the exposure of a very thin stream of blood to the action of the air in the air-chambers.

The function of the air-chambers. When the blood enters the ventral chamber of the special part of the gill it is separated from the air in the corresponding air chamber only by the single thin membrane which forms the outer boundary wall of the blood-chamber. The ordinary conditions of the respiration of air are thus satisfied. As the blood passes at the margin of the gill into the dorsal chamber it is further exposed to the action of air in the dorsal air-chamber and the respiratory process is here completed.

The air-chambers, as already noted, do not communicate by openings with the exterior of the gill. The contained air must therefore enter by penetration through the wall of the gill. The wall, as we have seen, is here very thin, the hypoderm, as a rule, appearing to be withdrawn and leaving only a very thin layer of chitine.

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]

1. An animal was placed in water until the appearance of air in the gills had passed away. It was then killed and the tissues fixed by hot 33 % 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 conditions 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.

[1] These experiments were suggested to me by Dr. ZUR STRASSEN.

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-chamber 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 become intelligible on the supposition that the chambers contain air. Thus these experiments warrant the inference that the chambers normally contain air and not blood.

In considering more precisely the function of the air chambers we must first take account of the fact that they do not serve to increase the area of respiratory surface. They are not, as in the case of *Porcellio* and its congeners formed by an inward fold of the wall of the gill but are simply spaces filled with air, lying between the parallel walls of the blood cavity and the gill. But it is to be noted that a provision for exposure of a large surface of blood to air is made by the expandet dimensions of the special part of the gill and by the presence of these parts in all five pairs of the outer gills.

In studying the outer gills of *Porcellio* we reached the conclusion that the respiratory tree is an adaptation having a two-fold purpose; namely, first, to provide for a large surface of exposure of blood to air and, second, to secure the protection of the blood against dessiccation from exposure to air in the process of respiration. Now, in *Oniscus*, the former of these purposes being provided for by the means just noted — an increase of the total area of the special respiratory surface — it is left to the air-chambers to prevent a too great loss of water from the blood in the process of respiration. One may easily conceive that if nothing intervened between the blood and the outside atmospheric air but the two very thin membranes of the wall of the blood cavity and the chitinous wall of the gill, the two being in contact, dessiccation would follow. Again, phylogenetic considerations lead us to expect that the respiratory surfaces must be maintained in a moist state as a condition of their functional action.

In the respiratory process the air of the chambers becomes charged with water of respiration. The only means of escape of this water to the outer atmospheric air is by passage through the chitinous wall. This process takes place slowly and secures the maintenance of the moist condition of the air in the chambers. This air is thus separated from the blood by only a very thin moist membrane. Thus conditions most favorable to respiration are provided; the blood is both shielded from dessiccation and at the same time separated from air by only a very slight barrier.

I reach the conclusion that through the possession of these special modifications, the outer gills of *Oniscus* constitute organs for breathing ordinary dry atmospheric air. The several collateral reasons in support of this conclusion that have already been given for *Porcellio* apply also for *Oniscus*.

The Inner Gills. The inner gills of *Oniscus* agree in all essential features with the corresponding parts in *Porcellio* and the other genera already described.

Explanation of the Plates.

Plate I.

Fig. 1. The first right outer gill of *Porcellio scaber,* male, as viewed from the inner or dorsal side.
Tr., — the respiratory tree.
Gr.a., — the grooved area of chitine.
Ch., — chitine at the junction of the two faces of the gill.
Art., — articulation of the gill with the basal joint.

Fig. 2. Markings of the chitine on the inner face of the general part of the gill.

Fig. 3a. Section of the grooved area of chitine.
Gr., — groove.

Fig. 3b. The grooved area of chitine.
Gr., — groove.
P.a., — polyginal area, showing markings.

Fig. 4. Cross-section of the gill of *Porcellio scaber,* taken in the direction of the line ss′, Fig. 1.
Ch., — chitine.
Hy., — hypoderm.
Hy. Nu., — hypodermic nuclei.
Pl., — pillar.
B.c., — blood cavity.
B.ch., — blood chamber.
B.sp., — blood space.
Op., — opening of tree.
Cv.tr., — cavity of tree,
Rd., — ridge of chitine.

Fig. 5. Portion of the respiratory tree, showing terminations of the branches.

Fig. 6. Section of a portion of the respiratory tree and the adjoining wall of the gill.
Ch., — chitine.
Hy., — hypoderm.
Hy. Nu., — hypodermic nuclei.
B. Sp., — blood space.
W.b.c., — wall of blood cavity.
Tr., — cavity of branch of the tree.

Fig. 7. Section of a portion of the respiratory tree at its base; the section was taken parallel with the faces of the gill.
Gr.ch., — grooved chitine.
Bd.chm., — blood chamber.
Op.tr., — opening of tree.
Br.tr., — branch of tree.
W.b.c., — wall of blood cavity.

B. Sp., — blood space.
Hy. Nu., — hypodermic nuclei.
B.c., — blood corpuscle.
Leu., — leucocytes.

Fig. 8. Section of the inner gill of *Porcellio scaber*.
Ch., — chitine.
Hy., — hypoderm.
P., — pillar.
B.c., — blood cavity.

Plate II.

Fig. 9. The first right outer gill of Ligidium hypnorum, as viewed from the inner or dorsal side.
In.ch., — incurrent channel.
Ex.ch., — excurrent channel.
Art., — articulation of the gill with the basal joint.

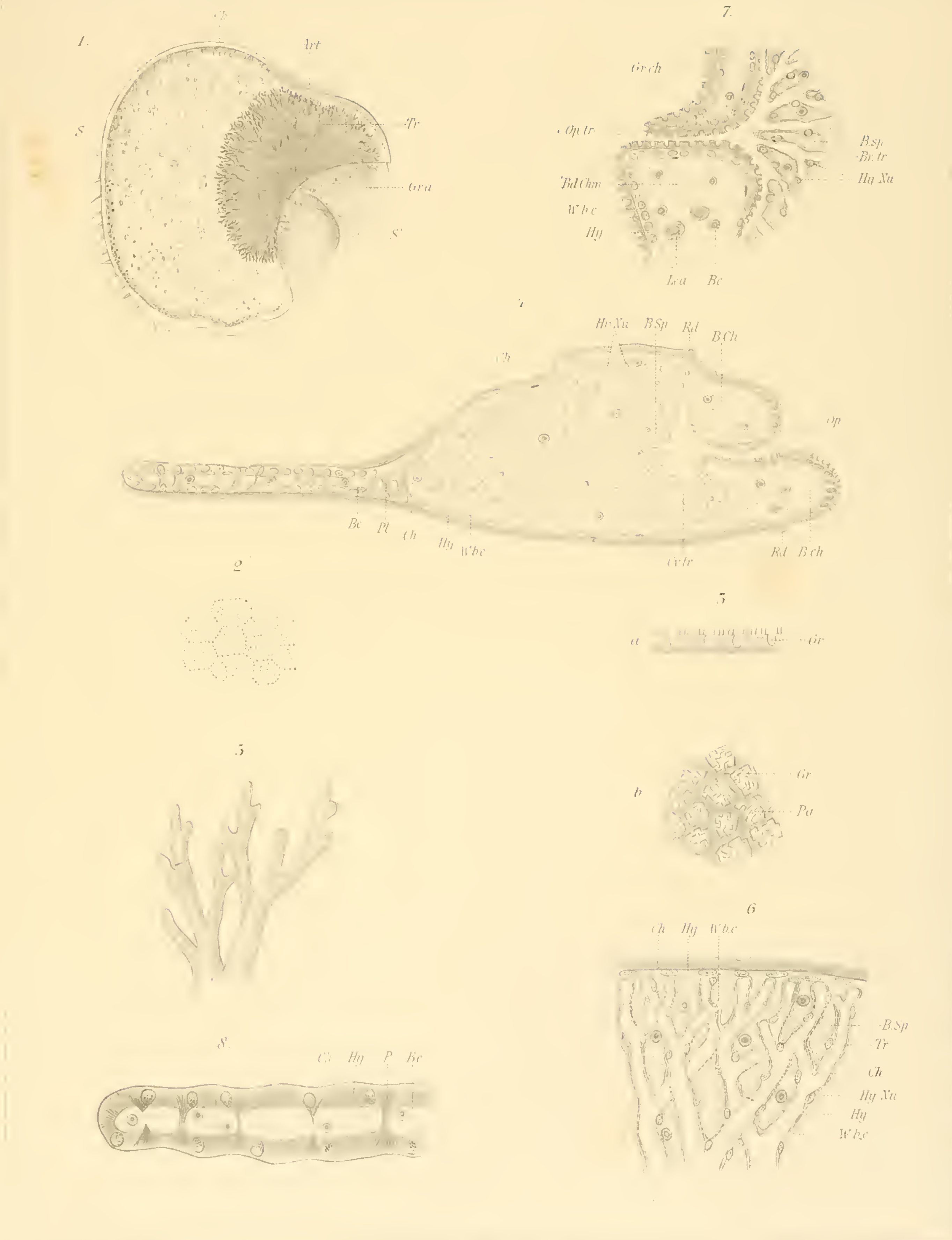
Fig. 10. Cross-section of the gill of Ligidium hypnorum, taken in the direction of the line ss', Fig. 9.
Ch., — chitine.
Hy., — hypoderm.
W.b.c., — wall of blood cavity.
Ex.ch., — excurrent channel.

Fig. 11. The first right outer gill of *Oniscus murarius*, male, as viewed from the inner or dorsal surface.
In.ch., — incurrent channel.
Ex.ch., — excurrent channel.
Rd.ch., — radiating channels.
Art. — articulation of gill with the basal joint.

Fig. 12. Cross-section of the gill, taken in the direction of the line ss', Fig. 11.
Ch., — chitine.
Hy., — hypoderm.
Hy.pl., — hypodermic pillar.
v.b.c., — ventral blood chamber.
d.b.c., — dorsal blood chamber.
Pt., — double-walled partition between the dorsal and ventral blood chambers.
Fk., — forking of the partition.
W.b.c., — walls of blood chambers.
In.ch. — incurrent channel.
Ex.ch., — excurrent channel.

Fig. 13. Cross-section of the special part of the gill, taken in the direction of the line RR', Fig. 11.
Ch., — chitine.
d.a.c., — dorsal air chamber.
v.a.c., — ventral air chamber.
d.b.c., — dorsal blood chamber.
v.b.c., — ventral blood chamber.
m.b.c., — middle blood chamber.
Hy.pl., — hypodermic pillar.
W.b.c., — walls of blood cavity.

Fig. 14. The course of the circulation of the blood in the gill of *Oniscus murarius*. The dotted arrows show the direction taken by the particles of incurrent or venous blood; the lined arrows that of the excurrent or arterial blood.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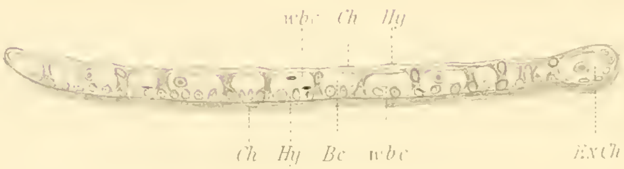

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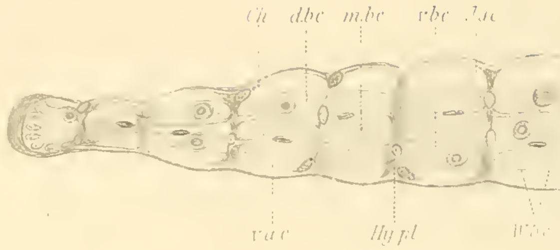

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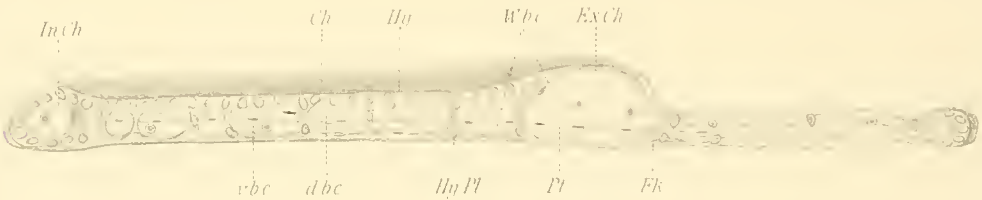

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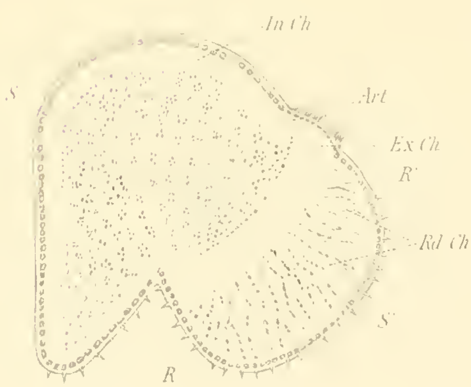

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