Herpyllobius arcticus.

By

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With Plate 22 and 4 Text-figures.

CONTENTS.

I. INTRODUCTION.

AMONG parasitic copepods Herpyllobius is remarkable for the extreme degeneracy attained by the adult male and female, both of which are entirely devoid of appendages. The female has a globular body 2 to 4 mm. long, which bears two large egg-sacs. It is attached to its host, a polychæte worm, by means of a chitinous fixing organ, through this there protrudes into the worm a mass of vacuolated tissue, recalling in its structure and nutritive function the root system of the parasitic Rhizocephala amongst the Cirripedes. It seems hardly likely that an endoparasitic stage is included in its life-history, but of this we are entirely ignorant. The adult males have a sac-like body, which remains enclosed in the last larval skin; they live attached to the body of the female in the region of the genital apertures.

Steenstrup and Lütken (**12**), who first described this species, Herpyllobius arcticus, found it parasitic on certain polychæte worms from Greenland, and recognised that the body consisted of two parts, the external body and the part within the host, joined together by a thin stalk. The external body was rounded, and bore a pair of large egg-sacs, whilst the internal portion they believed to vary in shape according to the amount of space available within the worm. They found no males.

Two years later Kröyer (**7**) published an account of a parasite, which he called Silenium polynœs, found infecting Polynœ cirrata in Greenland. He only described the portion of the parasite external to its host, but he was more fortunate than Steenstrup and Lütken, in that he found the males, four or five in number, attached near the egg-sacs of the female; they were minute Cyclops-like forms, about ·13 mm. long and half as broad, the anterior end of the body being drawn out and inserted firmly into the body of the female. He gave some details of the appearance of both male and female, which will be dealt with later in discussing the anatomy of these forms.

In 1874 Claus (**1**) published a paper, in which he placed Silenium among the Lernæopodidæ, and suggested that it was identical with the Herpyllobius described by Steenstrup and Lütken. Further light was thrown on the systematic position of this animal by Levinsen (**9**), who, in an account of some parasitic copepods, gave a summary of the generic characters of Herpyllobius and the specific characters of the two species then known, H. arcticus (Stp. and Ltk.)

and H. crassirostris (Sars). In this paper Levinsen also dealt with the different theories concerning the significance of the portion of the parasite inside the worm, and gave a concise account of his own observations on the subject.

Giard and Bonnier (2) in 1893 published the results of their observations on Sphæronella, and suggested including the Herpyllobiinæ as a sub-family equivalent to the Choniostomatinæ, under the heading of Sphæronellidæ. This classification was not acceptable to Hansen (4), who criticised their conclusions in his work on the Choniostomatidæ, and objected to Herpyllobius being linked with that family on the grounds of extreme structural differences exhibited by the two forms.

In 1900 Jensen published an account of Herpyllobius and Rhizorhina (6), and later on in the same year Hansen (5) wrote a paper on the same subject. Both these observers were able to make a minute investigation of these forms, with the result that their structure was worked out with greater detail than had before been possible.

As will be seen from this short account of the literature on Herpyllobius, almost all that has been written on the subject is in Danish, and hence not easily available. In the summer of 1911 Mr. F. A. Potts, of Trinity Hall, Cambridge, collected some specimens of this interesting parasite from Departure Bay (Vancouver Island), Victoria, and San Juan Island, in Puget Sound, and on his return to England very kindly gave them to me to describe. This provided me with opportunity of writing an account of the animal in what I trust may be a more accessible form for English readers than at present exists.

I should like here to thank Mr. Potts for the help he has given me in writing this paper, and also Mr. H. M. Chadwick, of Clare College, and Miss Lehmann, of Newnham College, Cambridge, for their assistance in translating the Danish papers, and to acknowledge the kindness of Dr. H. J. Hansen in sending me his paper on Herpyllobius, and of Dr. W. T. Calman in reading my proofs.

I should also like to thank the trustees of the Bathurst Fund, Newnham College, for a grant awarded to me in the summer of 1911.

II. Material.

The copepods were found attached to specimens of the polychæte worm Harmothoë, and all were fixed in corrosive and acetic and preserved in 70 per cent. alcohol.

There were seven worms and ten parasites, distributed as follows: three worms had one parasite each on the head, two worms had one parasite each on a parapodium, one worm had a parasite on the head and another on a parapodium, and one worm had three parasites on the head. The parasites were always attached to the dorsal surface of the host.

III. Anatomy.

A. The Female.

1. External Appearance.—The female is entirely devoid of appendages, and the portion outside the host is globular in shape, except for swellings at the bases of the egg-sacs; in some of the smaller forms, which are probably young as their egg-sacs are not developed, there is a tendency for the body to be flattened ventrally. Levinsen (**9**) describes Herpyllobius arcticus as being triangular in outline and laterally compressed, but Kröyer's description (**7**) of a sac-like body seems to tally better with this form. The body is smooth and of a white or yellowish colour, and some specimens show the slight longitudinal grooves, mentioned by Steenstrup and Lütken (**12**), which, as they were observed in fresh specimens by Mr. Potts, cannot be due to shrinkage in spirit, as was suggested by these observers.

The length of this part of the parasite is from 1 to 1·3 mm.; Levinsen (**9**), in his summary of the specific characters of H. arcticus, gives the length as 1·5 to 2 mm., but on p. 367 he gives lengths varying from 0·6 to 2 mm., so that there is evidently a good deal of variation. This portion of H. crassirostris, according to the same observer, is $\frac{2}{3}$ mm. long, while Hansen (3) describes H. affinis as being 3 to 4 mm. in length.

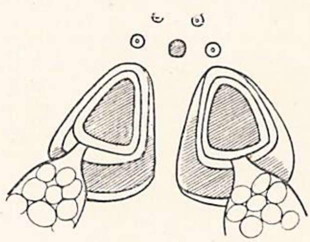
The paired egg-sacs naturally vary a good deal in size according to the stage of development, and they may be larger than the body; they are rounded or sausage-shaped, and in one individual flattened and leaf-like. Each egg-sac is borne on a strong chitinous swelling, which is somewhat shield-shaped, with the point directed upwards; these two structures, according to Levinsen, consist of concentric rings of chitin (Text-fig. 1, and Pl. 22, fig. 2). The eggs, owing to their being tightly packed, are polygonal in outline. Above the bases of the egg-sacs are some small apertures with chitinous edges. I could not make out the arrangement of these as they only became apparent in my specimens after they were sectioned. Levinsen, however, describes and figures them as four in number and forming an arc, in the centre of which is a small process previously described by Steenstrup and Lütken (Text-fig. 1). Jensen (**6**) figures two more similar apertures, one at the apex of each chitinous boss. On the ventral surface are two small chitinous bodies which Kröyer suggested might be lenses. This, however, seems unlikely, as an examination of the sections shows no trace of any lens-like structure in this, or any other region. Kröyer was probably misled by his assumption that the whole of the parasite was external to the worm, whereas it is now generally accepted that the visible portion is hardly one half of the whole animal. The diminutive males live attached to this posterior region close to the egg-sacs of the females (Pl. 22, fig. 2).

The external portion of the parasite is joined to the part lying within the host by a narrow stalk, on either side of which some specimens show a light-coloured area. Just underneath the skin of the host the stalk becomes chitinised and expands into a hold-fast, which is collar-shaped with serrated edges (Pl. 22, figs. 5 and 7).

2. Part embedded in the host.—This part of the

parasite is generally called the "anterior portion" or "proboscis," presumably because other parasitic copepods, such as Lernæa and Pennella, are attached by what is obviously the anterior end, and it is not likely that Herpyllobius would depart from the general rule, especially as the males are attached anteriorly; it is also evident that the external portion must be posterior because of the presence of the egg-sacs. Owing, however, to the extreme degeneracy attained by this animal, the "anterior portion" has lost any characteristic structure it may have had and become merely absorptive, thus recalling a similar state exhibited by the

Text-fig. 1.



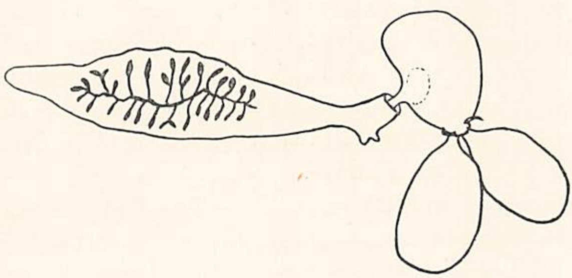
(After Levinsen.)

Rhizocephalan Cirripedes; for this reason I propose to speak of this portion of the parasite as the "root system."

This was not visible in my specimens until the worms were sectioned. Levinsen (**9**), however, was able to see it within the host by simply removing the elytra of the worm. He described it as a thin red streak lying parallel to the worm's gut, and on removing the worm's skin it appeared as a long, narrow, tongue-shaped body lying free beside, or underneath the pharynx of its host; posteriorly it emerged from the worm's head and was continuous through the stalk with the external part (Text-fig. 2). The length of the root system of the parasite according to this observer was 4 to 5 mm., the breadth 1 mm., and the thickness $\frac{1}{3}$ to $\frac{1}{2}$ mm.; the broadest part was just behind the middle, and posterior to this it tapered, broadening again just before the stalk, where it gave off two small processes. Along almost the whole length there were red dendritic markings, but no cell boundaries were visible: in spirit specimens some lacunæ showed.

This structure has been the source of some controversy; Steenstrup and Lütken (**12**) first described it as part of the parasite, but Kröyer (**7**) some years later regarded the chitinous "sucker" as the end of the parasite, and Schiödte (**11**) agreed with Kröyer that no integral part of the parasite was inside the worm. He recognised two terms used by different observers, "opsvulnet" and "tungedannet,"

TEXT-FIG. 2.



(After Levinsen.)

and explained their meaning by translating the first as a "tumour" formed by the worm, and the second as a "tongue-shaped body" hanging from the sucker and caused by some excretion from the parasite coagulated by spirit. Sars (**10**) also agreed with Kröyer, but as his specimen of H. crassirostris was still attached to the host, the part in question would not show. Claus (**1**), describing H. arcticus, thought that the front part was pathological.

Levinsen (**9**) then went thoroughly into the question, and found by making a cut through the stalk that the cuticle surrounding the root system appeared to be continuous with that of the stalk. He also made careful measurements of the two portions of fourteen individuals, and obtained the following results: the top figures giving the length in mm. of the roots, whilst those below give that of the external portion:

$$\frac{5}{2}\quad\frac{5}{2}\quad\frac{4\cdot5}{1\cdot5}\quad\frac{4\cdot5}{1\cdot5}\quad\frac{4}{2}\quad\frac{4}{1\cdot6}\quad\frac{4}{1\cdot6}\quad\frac{4}{1\cdot5}\quad\frac{4}{1\cdot3}\quad\frac{3\cdot6}{1\cdot6}\quad\frac{3\cdot5}{1\cdot5}\quad\frac{3\cdot3}{1\cdot3}\quad\frac{3}{1}\quad\frac{1\cdot5}{0\cdot6}$$

showing that the root system is from two to three times as long as the part outside the worm. He therefore concluded that there is a definite body inside the worm which is connected with the external parasite, and is either part of the parasite or a pathological formation caused by it, but that the former is the case as this structure is always the same shape, it lies free in the worm's body, and is proportional in size to the external body. Other observers—Hansen (**3**) and Jensen (**6**)—also figure the roots as being in direct communication with the external part of the parasite.

The suggestion that the internal part of the parasite had a nutritive function was put forward by Levinsen (**9**), but this question will be dealt with in the next section, together with a description of its structure.

3. Microscopical Structure.—The first specimens cut were unfortunately detached from their host, as I did not then know that any part of the parasite was within the worm; subsequently the worm was cut at the same time as the parasite. The specimens were first stained in paracarmine, dehydrated and cleared, and then as much as possible of their structure was studied and drawn before they were sectioned; after being cut the sections were stained on the slide in hæmalum.

(a) External Part.—Examined as a solid object the anatomy of this portion of Herpyllobius is not easy to make out. The body is always covered by thick structureless cuticle from which the internal organs frequently shrink away. In most forms (Pl. 22, fig. 3) the body is almost filled with a mass of eggs, which may show clear spaces running through it, all converging at the point where the stalk arises, in which place there is often an opaque structure which runs down the stalk and may extend up the clear spaces. The strong chitinous buttresses that support the egg-sacs are well supplied with muscles. The external skin is continuous down the stalk, at the end of which it becomes chitinous, and, turning up, forms a collar (Kröyer's "sucker"), which is embedded in the tissue of the host, and acts as a hold-fast. Some of the internal organs run down the stalk and are directly continuous with those of the root system.

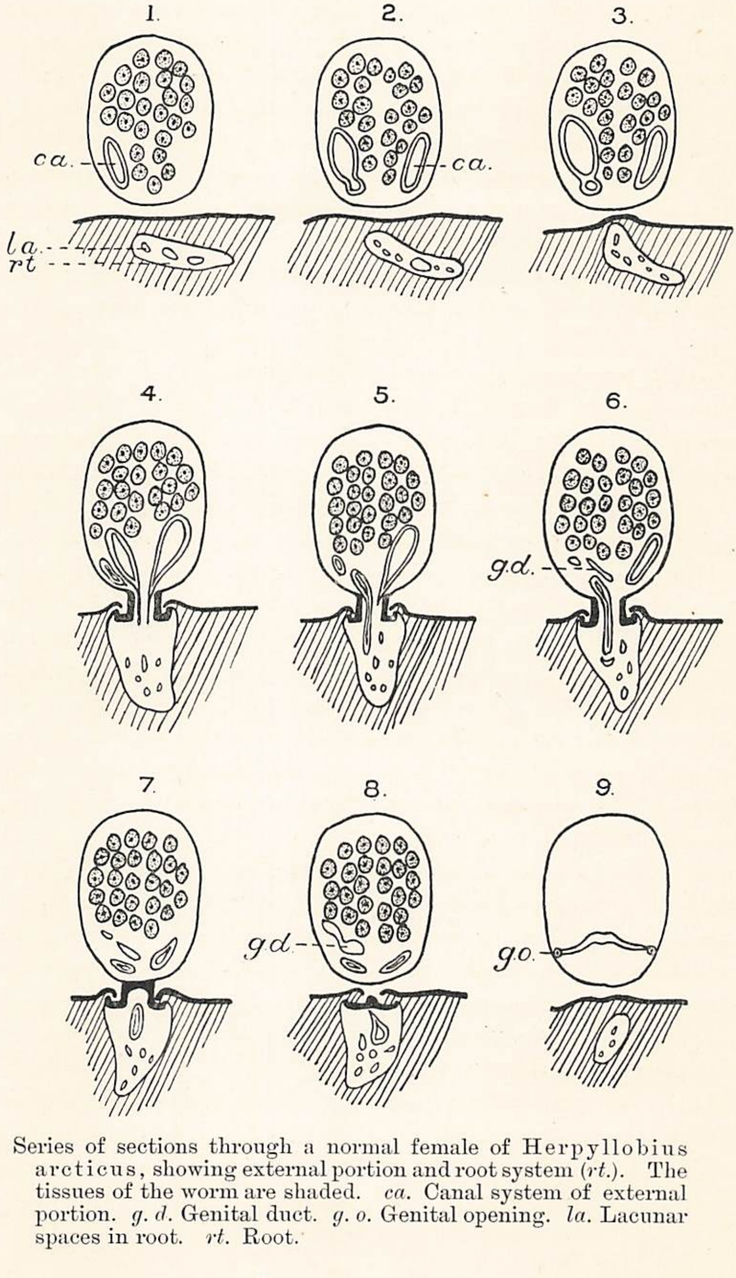
When cut in sections and examined under the microscope, the cuticle of these animals appears as a thick layer, slightly chitinous and traversed by a number of fine wavy fibres running parallel to the surface; externally it is bounded by a thin layer which stains more deeply than the rest of the skin.

Lying beneath the cuticle and at intervals sending up fine processes into it is a thin layer (Pl. 22, fig. 6, *hyp.*) with nuclei scattered along it; it usually appears to be without any definite structure except in one case (Pl. 22, fig. 4, *hyp.*), when in longitudinal section this layer appears to be composed of epithelial cells; longitudinal sections of other individuals, however, do not show this structure. This layer probably represents the hypodermis, but it shows a tendency to shrink away from the cuticle and applies itself closely to the internal organs; the processes running into the cuticle may be caused by a folding of the sections. In the anterior region of this external portion some sections show canal-like openings through the skin, but there is no alteration in the tissues below them, so it is likely that these are also due to folding caused by shrinkage.

Posteriorly there are several chitin-lined apertures (Text-fig. 1), according to Jensen (**6**) six in number, to which, he says, are attached the males, although they are not the genital openings. Opening into each of these there is a peculiar gland, which he figures (**6**, Tab. ii, fig. 12). I have examined these glands in my own sections and can find no other opening except through these apertures.

The genital openings are large slits placed on the end of the chitinous supports of the egg-sacs, and from them a duct may be seen running to the inside of the animal where it

TEXT-FIG. 3.



Series of sections through a normal female of Herpyllobius arcticus, showing external portion and root system (*rt.*). The tissues of the worm are shaded. *ca.* Canal system of external portion. *g. d.* Genital duct. *g. o.* Genital opening. *la.* Lacunar spaces in root. *rt.* Root.

becomes confused with the other spaces (Text-fig. 3, and Pl. 22, fig. 4, *g. d.*).

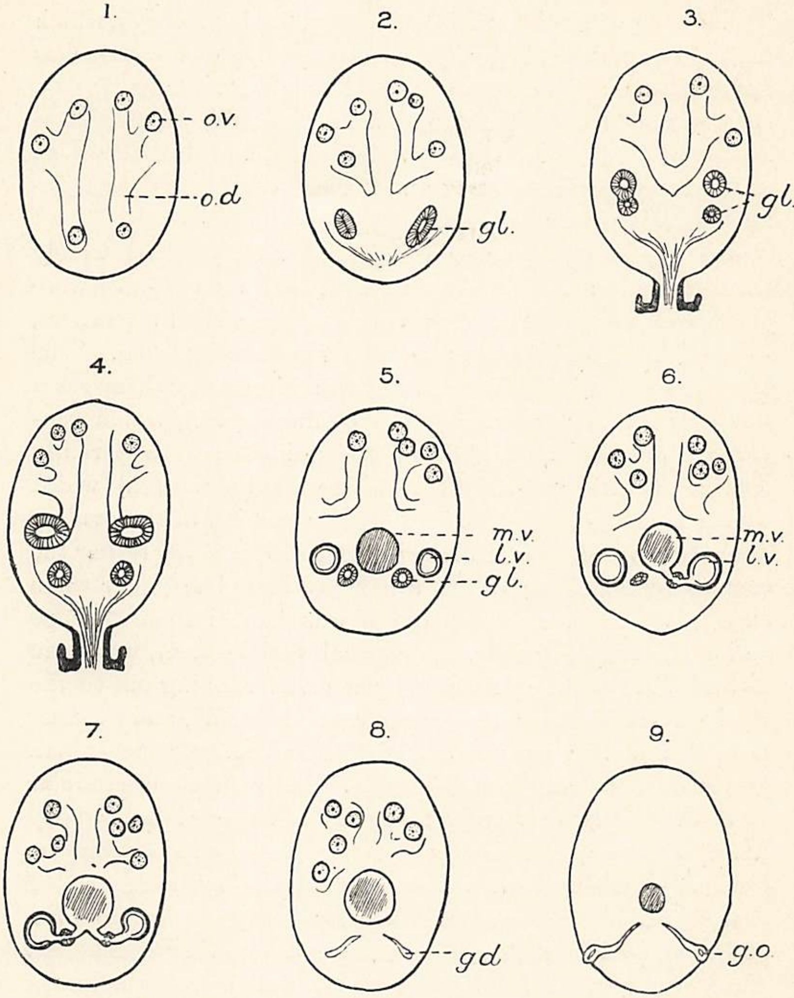
The body of the animal is frequently filled with eggs, which tend to be arranged in groups surrounded by strands of fibrous tissue which radiate from a central mass (Pl. 22, fig. 4, *fb.*). Running from the stalk along each side of the animal there is a canal (*ca.*) surrounded by thick walls, and drawn out so as to extend down the stalk and become continuous with the lacunar system of the roots.

One specimen, however (Pl. 22, fig. 5), differed widely from the rest; it was rather small, and its egg-sacs were just beginning to form. It was less opaque than the others, so that the internal structure was more easily seen. The body was well filled with eggs, and running among them was a series of canals, presumably the oviducts (*o.d.*), which converged towards the middle of the animal, and apparently opened on either side into a thick-walled duct (*gl.*) which would homologise with the glandular portion of the oviduct described by Marcus Hartog[1] in Cyclops as secreting the cement by which the eggs are agglutinated together when expelled. Each of these ducts was bent into a ⊐-shape and opened into, or near, a spherical vesicle (*l. v.*), which, in its turn, led to the exterior by a canal running out to the chitinous support of the egg-sac of that side, and opening near its apex. From this there extended an extremely small egg-sac, containing but few eggs. Between the glandular ends of the two oviducts there lay a large globular body (*m. v.*) containing a darkly staining mass, and having no obvious connection with the rest of the system; this, I thought, might be the spermatheca, as it lay not far from the place to which males were attached in other specimens. None of these structures extended down the stalk, the lumen of which was completely filled with non-vacuolated tissue.

An examination of sections made from this specimen also shows that its anatomy is very different from that of other

[1] Hartog, M., "The Morphology of Cyclops and the Relations of the Copepoda," 'Trans. Linn. Soc. Zool.,' v, 1888, pp. 1–46.

TEXT-FIG. 4.



Series of sections through another female Herpyllobius arcticus, showing the arrangement of the genital ducts. *g. d.* Genital duct. *gl.* Glandular portion of oviduct. *g. o.* Genital opening. *l. v.* Lateral vesicle. *m. v.* Median vesicle. *o. d.* Oviduct. *ov.* Ovum.

forms (Text-fig. 4). Directly beneath the hypodermis are a number of eggs (*o. v.*) lying in blind diverticulæ of the oviducts (*o. d.*); about the centre of the animal these converge into a single canal, which almost immediately divides again into the two glandular ducts (*gl. d.*) mentioned before, which run forward for a little way and then bend sharply back on themselves, so that each appears double in a considerable number of sections. Midway between these two tubes is a hollow sphere (*m. v.*) partially filled with a mass of tissue, frayed out at the edges into what, under an oil-immersion lens, looks remarkably like spermatozoa, and I have thought that this was a single spermatheca, such as is found in some Copepods. Such an interpretation is at variance with Jensen's statement that large spermatophores are found in the male and fixed by means of a cement to the upper end of the long genital aperture of the female (see his figure, (**6**), Tab. ii, fig. 11A, *hls.*), and I give it with reserve.

At the lower end of this median vesicle there is, at either side, a tube with swollen lips, which leads outwards to another vesicle (*l. v.*), which is smaller than the median one, surrounded by thick walls, and apparently empty. Into each of the ducts, from the median to the lateral vesicles, there opens the glandular oviduct, and from it there runs posteriorly another duct (*g. d.*), which opens to the exterior by a long slit, the genital aperture (*g. o.*) at the end of each of the chitinous bosses; these openings naturally only show when no egg-sacs are present.

Even in the sections there was no trace of any canal running down the stalk.

(b) Stalk and Root System.—As mentioned above, the skin of the external portion may be traced down the stalk to the chitinous hold-fast; this has a serrated edge to which are attached strands of muscle-fibres (Pl. 22, fig. 7, *m. f.*). Down the lumen of the stalk the tissues of the two parts of the copepod may be seen in direct communication, whilst the lacunar system of the roots may also be shown to communicate with certain spaces in the external portion, as noted before.

This last fact would seem to prove that Steenstrup (**12**) was right in his statement that the "Fordφjelsesvej" (literally "way of digestion") goes through the stalk. As Hansen (**5**) points out, he avoids calling this system the gut, for in a degenerate form like this no definite gut can be traced. Sections in this region show that these canals have very thick walls, which might be the remnants of gut epithelium—an additional reason for supposing that these spaces have a nutritive function.

The minute structure of the portion of the parasite embedded in the host has been the subject of a good deal of dispute. According to Levinsen (**9**), it is surrounded by a thin cuticle which appears to arise in the region of the sucker, and Jensen (**6**) describes this cuticle as being a direct continuation of the sucker, and pressed against the bent-up portion of it; Hansen (**5**) agrees that this suggestion is plausible, but points out that Jensen does not draw this cuticle separate from the skin he describes as formed by the worm round the parasite (**6**) (fig. 10). Jansen further suggests that it is this membrane, formed by the worm, that Levinsen described as the cuticle of the parasite, but Jensen considers it to belong to the host on the grounds that a section shows that the cells forming it lie to the outside, that is on the side remote from the parasite. In this connection he refers to Giard and Bonnier,[1] who describe a similar formation among crabs infected by Entoniscans. Hansen, however, does not believe that there is any other skin than that belonging to the parasite, and fails to find any trace of a membrane arising from the worm. He believes that an apparent membrane is due to the tissues of the worm being pressed against the roots of the parasite causing a certain amount of degeneration, and compares it with Rhizorhina,[2] the roots of which pass into the gills of Ampeliscas with no trace of membrane round them.

A careful study of my sections leads me to believe that

[1] Giard and Bonnier, 'Contributions à l'étude des Bopyriens,' 1887, p. 97.

[2] Hansen, H. J., "Rhizorhina ampeliscæ," 'Ent. Meddel,' IIIB, H. 5, 1892, p. 207.

Jensen is right in stating that a membrane formed by the worm is present. In cases where the parasite and host have been cut together the epidermis of the worm folds in over the hold-fast (Pl. 22, fig. 7, *ep.*), and although the actual connection is not evident, the membrane (*mb.*) surrounding the roots seems to be a part of this. In sections of a whole worm from which the parasite had become detached the epidermis of the host (Pl. 22, fig. 8, *ep.*), although broken at the critical spot, is probably continuous with the membrane (*mb.*). This membrane may be traced down the worm as far as the roots of the parasite extend, although all the proximal part of the root system was withdrawn when the copepod was removed. A section lower down the worm (Pl. 22, fig. 9) shows the distal end of the roots of Herpyllobius surrounded at some distance by a well-marked membrane (*mb.*), and sections of another worm infested with three parasites show the root system of each surrounded by a membrane, which is always separated by some distance from the tissue of the root, and therefore is not likely to belong to it, as the root itself does not appear to be at all shrunken. Giard and Bonnier[1] state that in the case of crabs the parasitic Entoniscan is always entirely surrounded by a thin transparent membrane, except at one spot which is the opening to the invagination caused by the penetration of the young Entoniscan into its host; this membrane presents the same histological structure as the hypodermis of the crab. As a like process is probably effected by Herpyllobius it may then be described as an ectoparasite.

As to the cuticle of the roots themselves, I am inclined to think that if this is present it is extremely thin, and only evident in the region of the hold-fast (Pl. 22, fig. 7, *cut.*[1]); in sections of the worm with the parasite roots, these are not surrounded by any well-marked cuticle (Pl. 22, fig. 9).

The tissue of the root system is fibrous and does not show any definite cell boundaries; these fibres are strongly developed round the hold-fast, to the serrated lower edges of

[1] Loc. cit.

which they are attached (Pl. 22, fig. 7, *mf.*). All through this mass of tissue there is a branching system of lacunæ surrounded by a fairly definite lining of cells; the main one (*ca.*) runs up the stalk, and dividing into two is continued as a pair of lateral spaces in the external body; these, as mentioned above, have thick walls, which are also characteristic of this main canal for a short way along the root.

B. The Male.

The males are diminutive, and live attached to the female in the region of the egg-sacs; there are usually two or three to each female, and according to Jensen (**6**) they fix themselves to the openings of the peculiar glands mentioned before as occurring in this region. As, however, these glands are only six in number at the most, it is difficult to see how they could accommodate the twenty males found by Hansen (**3**) on one female of H. affinis.

The cephalic segment, which occupies about one half of the body (Pl. 22, fig. 10) has a thoracic segment fused to it, for in addition to a pair of three-jointed antennæ it bears a pair of maxillipeds; these are four-jointed, the last joint being hooked and serving for attachment to the female. There are three thoracic segments, each bearing a pair of biramous swimming legs; the first two pairs are alike, each consisting of two basal joints, a one-jointed inner ramus and a two-jointed outer one, each bearing bristles. The third pair resembles the first two except in having a one-jointed outer ramus. The abdomen consists of three narrow segments, the first two being about equal in size, whilst the third is about twice their length and bears a forked telson, each prong composed of two joints and bearing three stout bristles.

According to Jensen, however, this chitinous investment is merely the last larval skin of the male, the adult being sac-like and enclosed, all except the anterior end, in the skin; the anterior end is drawn out and is embedded in the female, being kept in position by a rough surface. The two genital openings (*go.*) lie side by side at the base of the drawn-out anterior end, and near its apex there appears to be another opening (*m.*) which is not so obvious as the genital apertures, but its position is indicated by a strand of tissue running up to it. This is the "mouth" described by Jensen, and he further finds a pair of mandibles and two pairs of small processes, possibly rudiments of appendages, on the hinder pair of which there open a pair of glands which secrete cement for fixing the male to the female. My specimens, however, showed no mandibles or processes, and their existence is denied by Hansen (**5**), who furthermore declares that there is no mouth opening at all; I am, however, inclined to believe that a mouth is present, although it is degenerate and probably functionless.

The body part of most of the males is chiefly occupied by two large spermatophores (*sp.*) oblong, in shape and provided with long necks (*sp. d.*), which emerge through the genital opening; these are evidently for insertion into the female and may be of great length; in one of my specimens they are twice as long as the whole animal. A similar structure has been described by Hansen in the allied genus Rhizorhina.[1] Jensen believes that the cement for the spermatophores is derived from two large glands occupying all the ventral and part of the dorsal surface anterior to the single testis (**6**, tab. ii); none of my specimens, however, showed this gland; and Hansen considers that the cement is derived from the vas deferens. The spermatophores, according to Jensen, are shed from the body of the male, and he figures them (**6**, fig. 11A) attached to the female close to the genital openings; they were not to be found on any of my specimens.

The anterior position of the genital openings of the male is an unusual occurrence among crustacea, and Hansen (**4**) questions whether it can be said to occur in this case. He describes the male larvæ as attaching themselves to the female at an early stage, and subsequently undergoing a

[1] Loc. cit., tab. iii.

profound morphological change during which all the larval organs vanish, and the testes together with their efferent ducts are formed. Owing to this transformation Hansen states that the morphological orientation of the adult is uncertain. As, however, the larva is attached by its anterior end, it seems unlikely that the developing male would revolve round in its larval skin, so as to reverse its anterior and posterior ends, hence it is in all probability safe to speak of the openings as occurring at the anterior end of the male.

The loss of the alimentary canal is also interesting, especially as it has practically gone in the female as well, though in this case its place is taken by the absorptive root system. The male seems to be without the means for obtaining nourishment.

IV. Relation of Parasite to Host.

The most frequent position of the female Herpyllobius is on the head of the worm, although it is sometimes attached to a parapodium. Levinsen (**9**) describes the root system of the parasite as forming a tongue-shaped body lying by the side of the gut of the host, and I have been able to confirm this statement by means of sections. In the worm sectioned the parasite was attached to the head, and the roots actually pierced through the cerebral ganglion of the host (Pl. 22, fig. 8) to reach the alimentary canal, and further on (Pl. 22, fig. 9) could be seen lying by the side of the œsophagus, which had been pushed over to one side by this intrusion. The internal economy of the worm with three parasites on its head must have been extremely deranged, but unfortunately it did not cut well and I was unable to make out the relative positions of the three roots.

The roots obviously have an absorptive function, and the process must be carried on in spite of the protective envelope formed by the worm round it. The lacunar tissue of the root system is in continuation through the stalk with vacuolated tissue in the external body, as well as with the "gut" spaces, and it is probably by this means that nourishment is carried to the reproductive organs, which occupy practically the whole of the external body.

As to the life-history, there is nothing known. There is probably a free-swimming stage in the female, as in the allied Lernæopodidæ, as otherwise one cannot account for the infection of new worms. It is probable that the males become attached to the female at an early stage, as is the case in Rhizorhina; having no gut and no apparent means of absorbing nutriment they must be short-lived.

No stages of development were to be found in the eggs.

V. Comparison with Allied Genera.

Hansen, in his work on the Choniostomatidæ (4), gives an account of the relationships of Herpyllobius and the allied genera. Previously[1] he had established the family Herpyllobiidæ containing the seven genera: Herpyllobius (Stp. and Ltk.), Eurysilenium (M. Sars), Rhizorhina (H. J. H.), Trophoniphila (McIntosh), Œstrella (McIntosh), Saccopsis (Lev.), and Bradophila (Lev.).

Trophoniphila bradii is described by McIntosh[2] as adhering to the bases of the branchiæ of the worm Trophonia, while Œstrella levinseni[3] is described by the same author from Ehlersiella; in both cases, however, an extremely short description is given, so that it is only possible to refer them to this family without any comparison with the other groups. The female of Rhizorhina forms a short slender stalk which pierces the skin of the gill of its host (Ampelisca); in this stalk are two tubes which, on entering the skin of the host, separate and ramify irregularly through the gill, sometimes entering into the body of the host. In Herpyllobius and Eurysilenium the stalk pierces the

[1] Hansen, "Rhizorhina ampelisca," loc. cit.

[2] McIntosh, "Report on the Annelida Polychæta," 'Report Scient. Results of H.M.S. "Challenger,"' xii, 1885, p. 368, pl. xxxviA, fig. 4.

[3] McIntosh, loc. cit., p. 477, pl. xxxixA, fig. 11.

skin of the host and there expands into a collar-like hold-fast, from which there depends an oblong or irregularly-shaped body, which is homologous with the tubes of Rhizorhina and has the same function of supplying nourishment to the external body. Levinsen (**9**) has found that Saccopsis and Bradophila have stalks, but he has found no expanded body at the end of it in the body of the host; Hansen (**4**), however, is of the opinion that some tubes must run into the body of the host, otherwise it is difficult to see how the parasites get their food.

A comparison between the two best-known genera of the family Herpyllobiidæ, Rhizorhina and Herpyllobius, shows important differences in the stalk of the female, as mentioned above, and also in the male. In both forms the larva fastens itself to the female, after which the tissues of the larva contract, thus forming a sac-like adult, without visible internal organs except the gonads and their efferent ducts. In Rhizorhina the male remains entirely inside its larval skin, pushing its generative ducts out through a hole in front of the mouth of the dead case. In Herpyllobius the skin of the larva bursts and the male is fastened by the anterior end, the generative ducts proceeding through the split produced by the bursting of the larval skin.

VI. Affinities of Group.

Giard and Bonnier (**2**) regarded the Herpyllobiidæ as closely resembling the Choniostomatidæ, for although they considered the females too degenerate to admit of comparison, they believed that the males, especially the larval males, strongly resembled one another both in the mouth parts and in the position of the generative opening. For these reasons they proposed to make a new order, Sphæronellidæ, containing two subdivisions, the Herpyllobiinæ and the Choniostomatinæ.

Hansen (**4**), however, points out that there are structural differences in the two groups that render such a classification unsatisfactory. The female Choniostomatid is less degenerate, having mandibles, maxillæ and maxillipeds, while the females of the Herpyllobiidæ are entirely without appendages. The description of the males is at fault, for the adult male of Herpyllobius and Rhizorhina is limbless and degraded and cannot be said to possess mouth parts, while the male Choniostomatid is highly developed and has well-formed mouth-parts.

It therefore seems best to retain the two as separate families, equivalent to the Chondracanthidæ, the Lernæopodidæ and others.

It might be of interest at this juncture to make some comparison between the Herpyllobiidæ and the Rhizocephala, as each may be considered the most degraded form of the Copepoda and Cirripedia respectively. In both the adult female consists of two parts, one inside and one outside the host, the outside portion containing the reproductive system, whilst the part inside the host forms a root system for absorbing nutriment and conveying it to the external part. Some analogy might also be traced between the chitinous ring of the Rhizocephala and the chitinous hold-fast of Herpyllobius. There is of course a great difference in the method of infection: Sacculina, for instance, obtains entrance into the body of the host as a larva, and undergoes metamorphosis as an endo-parasite, the adult being evaginated at maturity; while Herpyllobius fixes itself to the outside of the host, probably at an early larval stage, and, if it is true that a protective membrane is formed by the worm, remains as an ecto-parasite throughout life.

The Rhizocephala are as a rule hermaphrodite, thus differing from the unisexual Herpyllobiidæ, but this is not always the case, for G. Smith[1] has found in the mantle cavity of Duplorbio what appear to be extremely degraded, but still functional males. In the ordinary individual no testes are found, as is also the case in Sylon, but in the latter no male individuals are known.

[1] Smith, G., "Rhizocephala," 'Fauna und Flora des Golfes von Neapel.,' Monogr. xxix, 1906.

Another interesting parallel is afforded by the Pedunculate Cirripede Anelasma squalicola, which is parasitic on the Selachian genus Spinax. G. Smith[1] describes this form as having a root system which arises from the region of fixation and penetrates into the flesh of the shark, probably serving to nourish the parasite, although the gut is not degenerate. The roots closely resemble those of Sacculina, having a chitinous investment, below which is a regular epithelium, while the inside is occupied by a lacunar tissue of vacuolated cells. This lacunar tissue is distributed over all parts of the body and may carry nourishment, thus recalling a similar structure in Herpyllobius.

Dr. Calman has kindly drawn my attention to the fact that absorptive "roots" are also developed by some parasitic Isopods. Prof. Caullery[2] describes Wanalia as forming a tubular prolongation in the region of the mouth which penetrates into its host, Inachus, but it is at first separated from the body cavity by a membrane. Two pairs of processes are then formed at the distal end, the mouth opens between them, and the whole system pierces through into the body cavity of the crab. This "proboscis," as Caullery calls it, serves the double purpose of fixation and of absorbing nourishment. A similar organ is found in the genus Cryptoniscus.

We thus find a remarkable case of convergent evolution in the development of absorptive roots in the Copepoda, Cirripedia and Isopoda.

VII. Systematic.

Generic Characters of Herpyllobius.

Female.—Body consists of two parts joined by a stalk. The anterior part (root system), which lies within the host, is soft and elongated, composed of lacunar tissue, and provided

[1] Smith, G., loc. cit.

[2] Caullery, "Récherches sur les Liriopsidæ," 'Mittheilungen aus der Zool. Station zu Neapel,' xviii, 1907-8, p. 583.

with a chitinous fixing organ where it penetrates the tissue of the host. The external posterior part is subglobose, white, and lacking any vestige of limbs. Posteriorly are two chitinous buttresses which support the large egg-sacs, and above are six chitin-surrounded pores, near to which the males are attached. The stalk is joined to the middle of the lower surface of the external part, the interior of which is principally occupied by the reproductive organs.

Male.—Minute and sac-like, consisting only of reproductive organs, anteriorly drawn out into a conical prolongation which is inserted into the female. Forms two large spermatophores with long necks. Most of the body of the adult remains enclosed in the last larval skin, characterised by the following characters: Cephalothorax with two pairs of appendages, antennæ and maxillipeds, the latter with their last joint hooked. Three free thoracic segments, each bearing a pair of biramous swimming legs. Abdomen three-jointed; last joint longest and bearing telson with long bristles.

Specific Characters.[1]

H. arcticus (Stp. and Ltk.).—Female: Anterior portion 4–5 mm. long, $\frac{1}{3}$–1 mm. broad. External portion $1\frac{1}{2}$–2 mm. long (without egg-sacs). Stalk very thin, diameter one-eighth of the length of the external portion. Male (Larval skin): $\frac{1}{8}$–$\frac{1}{7}$ mm. long. Antennæ three-jointed. Maxillipeds four-jointed. First and second pairs of thoracic legs with external rami two-jointed.

Habitat.—Greenland, on two species of Polynoid—Harmothoë imbricata and Eunoë œrstedi. Gulf of St. Lawrence, on Nychia amondseni.[2] Gulf of Georgia Puget Sound, on Harmothoë: Antarctic, on three species of Polynoids.[3]

[1] Levinsen (9).

[2] McIntosh, 'Ann. Nat. Hist.,' 4th series xiii, 1874, p. 262.

[3] Gravièr, C., "Sur quelque Crustacés parasites annelidicales provenant de la seconde expédétion antarctique française," 'Comptes Rendues,' xliv, 1912, p. 830.

H. crassirostris (Sars).—Female: Anterior portion unknown. External portion ⅔ mm. long. Stalk very broad, diameter one quarter of the length of the external portion. Male (Larval skin): No antennæ (?). Maxillipeds three-jointed. External ramus of swimming legs one-jointed.

Habitat.—Norway, on Polynoë imparis.

H. affinis (H. J. H.).[1]—Female somewhat similar to H. arcticus, but double the length. Body half as broad as long, subovate. Egg-sacs half as broad as long, fusiform. Length of body 3–4 mm. Male indistinguishable from that of H. arcticus.

Habitat.—Kariske Hav, Northern Siberia, on Harmothoë badia.

There seems no reason for separating the species of Herpyllobius of Puget Sound from H. arcticus, first described by Steenstrup and Lütken; the size of the female seems the same, and the males appear identical. I therefore propose to call this species Herpyllobius arcticus, only recording as a new locality for it the west coast of North America, and it remains as another example of the similarity in the fauna of the North Pacific and Atlantic sides of America.

VIII. Summary.

(1) The female Herpyllobius is entirely without appendages, and consists of two portions united by a thin stalk.

(2) The rounded posterior or external portion contains the reproductive organs and bears two large egg-sacs. In it are certain spaces with thick epithelium-like walls, which probably represent the gut.

(3) The anterior portion or root system is an elongated body lying within the host, and composed of vacuolated tissue penetrated by a lacunar system.

(4) The lacunar system of the root unites into a main branch, which runs up the stalk and is continuous with the gut spaces in the external portion.

[1] Hansen (3).

(5) The root is, therefore, in all probability an absorbing organ, nourishment being carried to the external portion of the body, which contains the important reproductive organs, by means of the lacunar system.

(6) In one specimen (fig. 5) the body contained numerous eggs lying in the diverticula of the two oviducts, each oviduct terminated in a thick-walled glandular portion. In the posterior region of the animal was a median vesicle communicating on each side with a lateral one; into the duct between the two there opened the glandular oviduct, and from there a short duct led to the exterior.

In this specimen there was no trace of a gut.

(7) The parasite is usually attached to the head of the worm, and in the two specimens cut the root pierced the cerebral ganglion and lay by the side of the œsophagus (figs. 8 and 9).

(8) Herpyllobius is one of the seven genera of the family Herpyllobiidæ.

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EXPLANATION OF PLATE 22,

Illustrating Kathleen Haddon's paper on "Herpyllobius arcticus."

Fig. 1.—Adult female on Harmothoë imbricata, showing the attachment of the parasite to the dorsal surface of the worm's head.

Fig. 2.—Dorsal view of an adult female, showing two males attached posteriorly. On either side of these are the chitinous buttresses supporting the egg-sacs.

Fig. 3.—Side view of a stained specimen after clearing; external portion of the parasite only. The opaque gut lies in the centre sending out radiating channels. Posteriorly is shown a chitinous buttress for the support of an egg-sac.

Fig. 4.—Longitudinal section through an adult female.

Fig. 5.—Side view of the peculiar type, after staining and clearing, showing the arrangement of the genital organs.

Fig. 6.—Transverse section of the above specimen.

Fig. 7.—Transverse section of a normal female, showing the external portion, and the root embedded in tissues of the host.

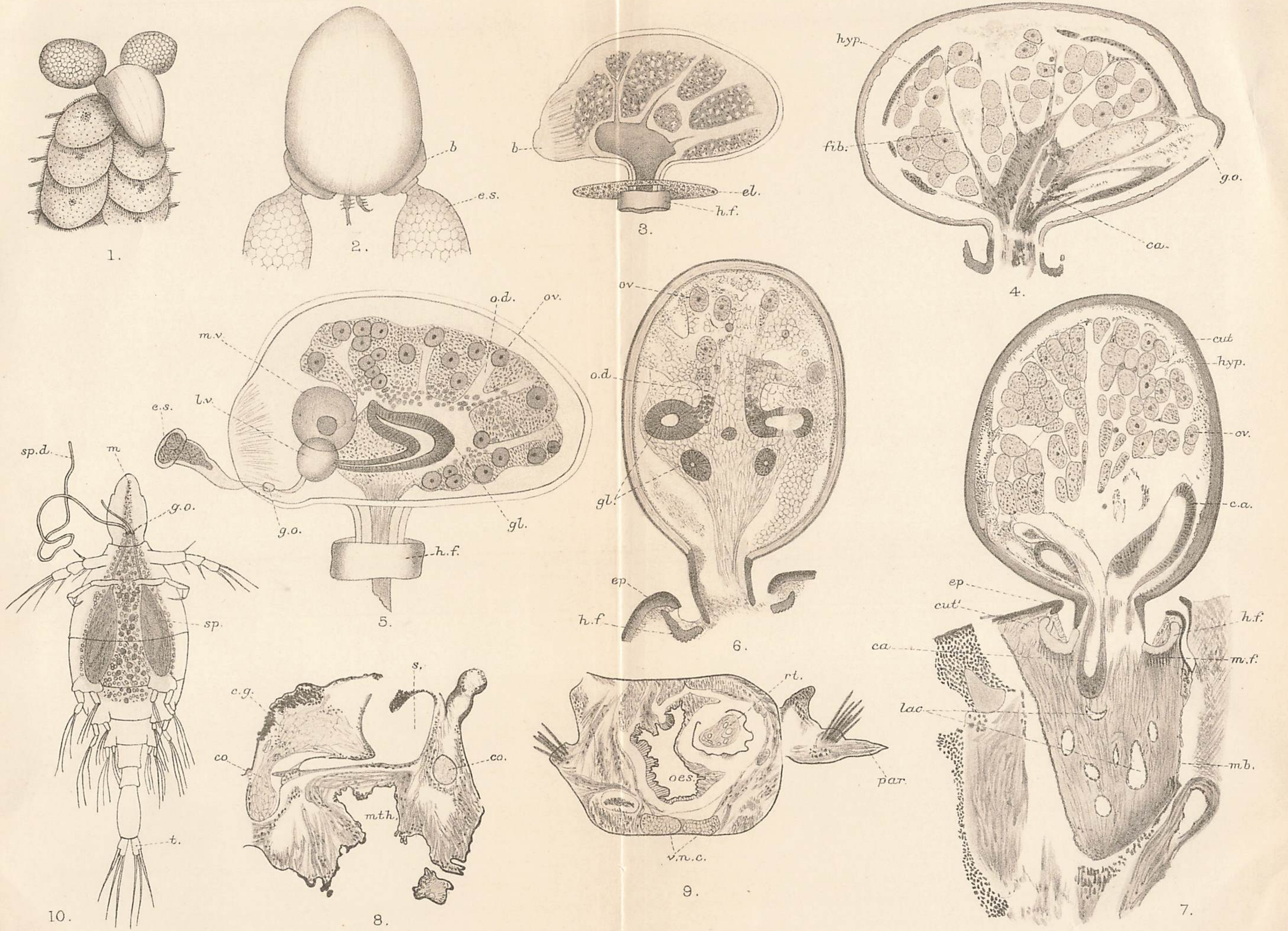
Fig. 8.—Transverse section of worm's head, showing space (*sp.*) formerly occupied by the roots of the parasite. This pierces the cerebral ganglion of the worm.

Fig. 9.—Transverse section of the same worm farther back, with the root of the parasite (*rt.*) lying beside the œsophagus of the worm.

Fig. 10.—Dorsal view of a male Herpyllobius enclosed in its last larval skin.

Lettering.

b. Buttress supporting egg-sac. *ca.* Canal system of body. *cg.* Cerebral ganglion. *co.* Commissure. *cut.* Cuticle. *cut.*[1] Cuticle of root. *el.* Elytra of worm. *ep.* Epidermis of worm. *es.* Egg-sac. *fib.* Fibrous tissue. *gl.* Glandular oviduct. *g.o.* Genital opening. *hf.* Hold-fast. *hyp.* Hypodermis. *lac.* Lacunar system of root. *l.v.* Lateral vesicle. *m.* Mouth. *mb.* Membrane formed by worm. *m.f.* Muscle-fibres. *mth.* Mouth of worm. *m.v.* Median vesicle. *od.* Oviduct. *œs.* Œsophagus. *ov.* Ovum. *par.* Parapodium. *rt.* Root of parasite. *s.* Space occupied by parasite. *sp.* Spermatophore. *sp. d.* Duct of spermatophore. *t.* Telson. *v. n. c.* Ventral nerve-cord.



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