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ON THE RHIZOCEPHALAN GENUS THOMPSONIA AND ITS RELATION TO THE EVOLUTION OF THE GROUP.

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Two plates and twelve text-figures.

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INTRODUCTION.*

The Rhizocephala are a group of undoubted Cirripedes having nevertheless a structure and life-history in which the departure from the normal type is probably greater than in any other parasitic Crustacea. They are found upon Decapod Crustacea and in the adult form have lost all trace of segmentation and appendages. Each one consists of an *external sac* communicating by a peduncle with an *internal root system* which traverses the body of the host and absorbs food from the blood. The absence of an alimentary canal and the development of an absorptive root system are characters which have been independently acquired in other parasitic crustacea, to wit, the Copepods *Herpyllobius* and *Rhizorhina*, which yet retain signs of segmentation and vestigial appendages. Moreover, in some parasitic Isopods (*Wanalia* and *Cryptoniscus*) and in the Cirripede *Anelasma* there is an incipient root system, although the gut does not degenerate. The modification of the reproductive phenomena is very considerable in the Rhizocephala, for it has involved the supression of the male sex and the conversion of the other into self-fertilising hermaphrodites or, in a few genera, parthenogenetic females.

The criterion of the Cirripede affinities of the Rhizocephala is to be found in the Nauplius and Cypris stages, which occur in their early larval history. Without the evidence of embryology it would be difficult to refer the adult even to the Crustacea. The external sac, in *Sacculina*, consists of a mantle surrounding a *visceral mass* but separated from it by the *mantle-cavity* or brood pouch (which opens to the exterior by a mantle opening) except along the surface of attachment to the host, where there is a communicating *mesentery*. A *nerve ganglion* and the small tubular *testes* lie in the mesentery; the main bulk of the visceral mass is occupied by the *ovaries* and there are present on each side an *oviduct* and a *vas deferens* opening into the *mantle cavity*. Geoffrey Smith (**9**), by comparing the arrangement of these organs with those of the typical Cirripede, has made a plausible attempt to homologise the external sac with the body of other Cirripedes. This brief summary of the typical Rhizocephalan structure is designed to show that, while structural reduction has proceeded far, it is by no means

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* Service as a Lieutenant in the English Army has prevented Mr. Potts from revising the proofs of this paper.—A. G. M.

complete. But the retention of the mantle and the mantle cavity is due to the exigencies of the reproductive method in these forms, which compels an elaborate mechanism of ducts and incubatory spaces.

The most remarkable feature of the group, however, is the endoparasitic life-history, which has its only parallel in the Crustacea in the copepod family Monstrillidæ. The Nauplius and Cypris larvæ resemble those of other Cirripedes except in the absence of a gut. The latter fix at the base of hairs on the carapace of crabs and an internal mass of cells leaves the larval cuticle and passes through the gap in the carapace, which the articulation affords, into the body-cavity of the host. After a period of wandering it becomes attached to the intestine in the region of the abdomen and here it grows, absorbing nourishment from the blood and differentiating into a root system and a body destined to become the external sac. The internal stage of development is terminated by a moult in *Sacculina*, the sac-like body eating its way through the muscle and epithelium of the abdominal wall so that it emerges when the chitinous exoskeleton is cast. In adult life connection with the internal root system is maintained through the narrow peduncle occupying the aperture which served for escape.

Though it has been pointed out above that other parasitic Crustacea possess a root system, this is always developed, so far as is known, by a secondary inpushing of tissue from the externally situated body.

The complete description by Delage (**2**) of the development of *Sacculina* was published in 1884, but so extraordinary was its nature that for a long time doubt was cast upon the correctness of the account. In particular the late Alfred Giard maintained that the Cypris larva underwent metamorphosis into the adult at the precise position of fixation, as proved by his personal observation. It was not in fact until Geoffrey Smith, in 1906, published a striking confirmation of Delage's story that the matter was put beyond doubt. That an endoparasitic stage occurs in the life-history of *Sacculina* and *Peltogaster* is now certain; but it has not been actually proved to occur in any other genera of the group. For the most part they are similar in structure and habit and it may be safely assumed that their development runs through a course not unlike that of *Sacculina*. But, in one genus at least, *Thompsonia*, which forms the subject of this paper, the facts that an enormous number of external sacs are associated on the same host and that these sacs have an exceedingly simple structure seem to suggest that a different method of development may occur here. The endoparasitic stage must have been interpolated in the life-history and it is not perhaps unreasonable to suppose that amongst the many forms of the Rhizocephala one should be found to exhibit a simpler and, in its omission of the endoparisitic stage, more primitive life-history than that of *Sacculina*. Coutière (**1**), who has described the forms of this genus which infest Alpheids, under the name of *Thylacoplethus*, has reverted to the theory of Giard, supposing that each of the external sacs represents a Cypris larva which has fixed and metamorphosed in that identical position. The simple structure of the sac is another primitive feature, and we are led to believe that the more complex structure of *Sacculina* is due to progressive evolution from a form like *Thompsonia*. This view has also been taken by the few workers who have studied material of this Indo-Pacific form. The conclusions which are arrived at in this paper combat decisively the claim that the genus represents in any way the ancestor of the group Rhizocephala. As is so often the case, a form which seems at first sight to fill a gap between a group and its relations proves on closer examination but to illustrate an extraordinary capacity for specialised development in the group to which it belongs. But though the problem of *Thompsonia* thus changes with widening evidence, it is yet a form of great importance to the student of comparative anatomy and general biology.

PREVIOUS WORK ON THOMPSONIA.

In 1874 Kossmann (**6**) published a description of the Rhizocephalous Crustacea collected by Semper in the East Indies. In this class he placed a parasite, two examples of which were found on the walking legs of *Melia tessellata*. He named this animal *Thompsonia globosa*, the generic name being given in honour of that distinguished Irish naturalist who first recognised the Cirripede affinities of the Rhizocephala. The new genus was characterized by its globular shape and small size, long stalk with peculiarly thickened chitinous ring, absence of a mantle opening, reduction of the visceral mass, and retention of the larvæ until the Cypris stage was reached. Only two examples of the parasite occurred on this host, so the most striking feature of the genus, the presence of large numbers of external sacs of equal development, is not here recorded.

In 1902 Coutière (**1**) described a new type of Rhizocephalan parasitic on various Alpheids from East Indian and Australian waters and remarkable for the fact that each host carried under its abdomen, attached to the appendages, a great number of parasites, which resembled the eggs somewhat in volume and aspect. This parasite, for which he proposed the name of *Thylacoplethus* (several species of the genus were described) approaches *Thompsonia* in its form, but must, he says, be separated generically, first and foremost because its host, the shrimp *Alpheus*, is so different from the host of *Thompsonia*, which is the crab *Melia*. Besides, *Thylacoplethus* is distinct as the first example of a truly gregarious Rhizocephalan. I shall deal later with my own reasons for setting aside these conclusions of Coutière and treating the name *Thylacoplethus* as a synonym of *Thompsonia*.

The most interesting point in Coutière's papers is his daring supposition as to the significance of *Thylacoplethus* in the origin and evolution of the Rhizocephala. He remarks that the adult parasites exist on the pleopods in almost the very situation in which the attached larvæ of *Sacculina*[*] are found, and also that the root systems of adjacent parasites, if not entirely independent, are at any rate largely localised. These observations show that here at least infection of the host takes place by direct metamorphosis of the larva into the adult at the position of fixation, without the intervention of such a stage of internal parasitism as characterises the life-history of *Sacculina.* This conclusion points to *Thylacoplethus* as a primitive or even ancestral form and explains the "gregarious habit" as due to the simultaneous fixation of large numbers of larvæ.

The latest researches on *Thompsonia* have been made by Häfele (**4**) and Krüger (**5**) on material brought back by Professor Doflein of Munich from Japanese waters. The host in the larger number of cases was a species of *Pilumnus* (a Xanthid crab). Häfele was not able, owing to the absence of illustrations in Coutière's rather meagre descriptions, to decide whether his form was identical with *Thylacoplethus*[†] or not. But the possession by the latter of a distinct mantle and a cloacal opening led Häfele to suppose that the two forms might be safely placed in different genera.

In this paper the first attempt is made to give adequate figures of the parasite. Series of sections were cut to trace the course of the root system, but unfortunately a curious error of identification of the root tissue is made. This is corrected by Krüger from examination of material in the same collection. But both authors agree with Coutière in supposing that *each* of the external sacs is an individual formed by metamorphosis from a Cypris larva. Krüger alone seems to contemplate the existence of an internal stage in the life-history as a possibility.

In 1913 Dr. A. G. Mayer, Director of the Department of Marine Biology of the Carnegie Institution of Washington, kindly invited me to accompany the expedition of his department to Torres Straits. In arranging my programme for this purpose, it occurred to me that Coutière's observations were partly made on specimens from the very field of work to which we were journeying. I kept in view, then, the interest which an examination of fresh and specially fixed material of this form could not fail to possess, and was fortunate enough to procure specimens which throw a great deal of light on this obscure form.

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[*] In reality the larvæ of *Sacculina* do not fix more readily on the appendages than elsewhere.

[†] "La faible extension des racines, leur localisation dans les bourrelets saillant, dus à l'irritation causée par les parasites le grand nombre de ceux-ci, leur fixation dans une cupule deprimée de dehors en dedans, la presence de parasites adultes tres voisins sur les pleopodes d'*A. malleodigitatus*, ou de *Thompsonia* sur les pattes d'un Crabe la où s'effectuerait surtout l'inoculation des larves de Sacculine au stade Kentrogone; tous ces faits montrent que, chez *Thylacoplethus* au moins, l'infestation de l'hôte doit se faire par fixation directe des larves à leur place définitive, sans l'inoculation ni le stade de parasite interne qui paraissent caractériser l'évolution de *Sacculina carcini* Thompson."

PRELIMINARY DESCRIPTION OF MATERIAL.

During the first few days of our stay at Murray Island at the North end of the Great Barrier Reef, I sought for the Rhizocephalan parasite of *Alpheus* amongst the species dwelling in burrows on the reef (such as *A. edwardsi*), but without any success. On September 30, Dr. H. L. Clark brought to me a few specimens of a dark-coloured Alpheid (*Synalpheus brucei*, sp. n.), which he had found sheltering amongst the arms of a large Comatulid. One of these was distinguished from its fellows by the possession of numberless little pink egg-like* sacs attached to the thoracic legs and contrasting strongly with the purple colour of the cuticle of the host. These sacs were found to contain Cypris larvæ, and so little doubt remained that I was dealing with the creature described by Coutière under the name of *Thylacoplethus*. The next few days proved that, on the south reef of the island of Maër, there lived under every loose stone and within the branches of the living coral a teeming population of crinoids, of which the majority belonged to the species *Comanthus annulatum* (Bell). Within the living basket formed by the arms of the crinoid, a pair of Alpheids, male and female, were generally to be found, and a small proportion of the whole population were infected with the parasite. So numerous were the crinoids and their commensal Alpheids that they could be depended upon to provide a sufficient quantity of material for the study of the parasite. Only toward the edge of the reef, however, were the crinoids numerous, and as the spring tides waned it became more difficult to locate the crinoid with the water glass, to plunge beneath the water which covered its retreat, to extricate, by means of the brutal hammer or the persuasive hand, the unwilling echinoderm from amongst branching corals, to which it clung with desperate energy, and finally to prevent the escape of the agile Alpheid when the crinoid was raised above water. It was such experiences, however, which gave additional zest to our life at Murray Island.

I was eventually able to obtain nearly twenty Alpheids infected by *Thompsonia* in various stages of development. The external sacs varied from tiny bodies barely 0.5 mm. long to those a little more than 1 mm. in length and 0.6 mm. in breadth. In the latter stage the Cypris larvæ, with their dark eyes, could be plainly made out through the mantle. They were nearly always situated on the limbs. Some Alpheids only showed them on the abdominal swimmerets, where they were to be distinguished from the eggs of the host by their inferior size and different colour, but in the majority of hosts they occurred both on the abdominal and thoracic limbs. On some of the ambulatory limbs as many as a dozen were found, but in a late stage of development they were greatly crowded, as is shown in plate 1, figure 2. As

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*The eggs of the Alpheid are, however, green and are larger than the parasite.

recorded by Häfele,they are clustered thickly on the proximal part of the limb, while the last two or three joints are entirely free. Occasionally external sacs are found on the chelipeds and even the third pair of maxillipeds, though I have never seen them, as Häfele notes, on the eye-stalks of the host. Posteriorly they extend to the uropods and to both surfaces of the telson when the infection is heavy. Rarely, too, they spring from the pleura of the abdominal segments, but never from the terga and sterna.

On the last day of work at Murray Island (October 25) I obtained a swimming crab, *Thalamita prymna,* which was parasitised by another species of *Thompsonia* (pl. 1, fig. 3). The thoracic legs, including both the chelæ (text-figure 1), were thickly beset with elongated lemon-yellow sacs containing Cypris larvæ, much larger than those on *Synalpheus.* The sacs were nearly 3 mm. in length, counting the peduncle. It was impossible, as we were on the eve of departure, to obtain further material of this form, but the capture gave me an opportunity of examining the genus on its typical host, a Brachyuran. Since the swimming crab is much larger than the Alpheid, the number of external sacs is much greater on the former; a single ambulatory limb may have nearly a hundred external sacs upon it. Altogether there were certainly more than 500 on my specimen of *Thalamita,* while the number on *Synalpheus* never reaches 200.

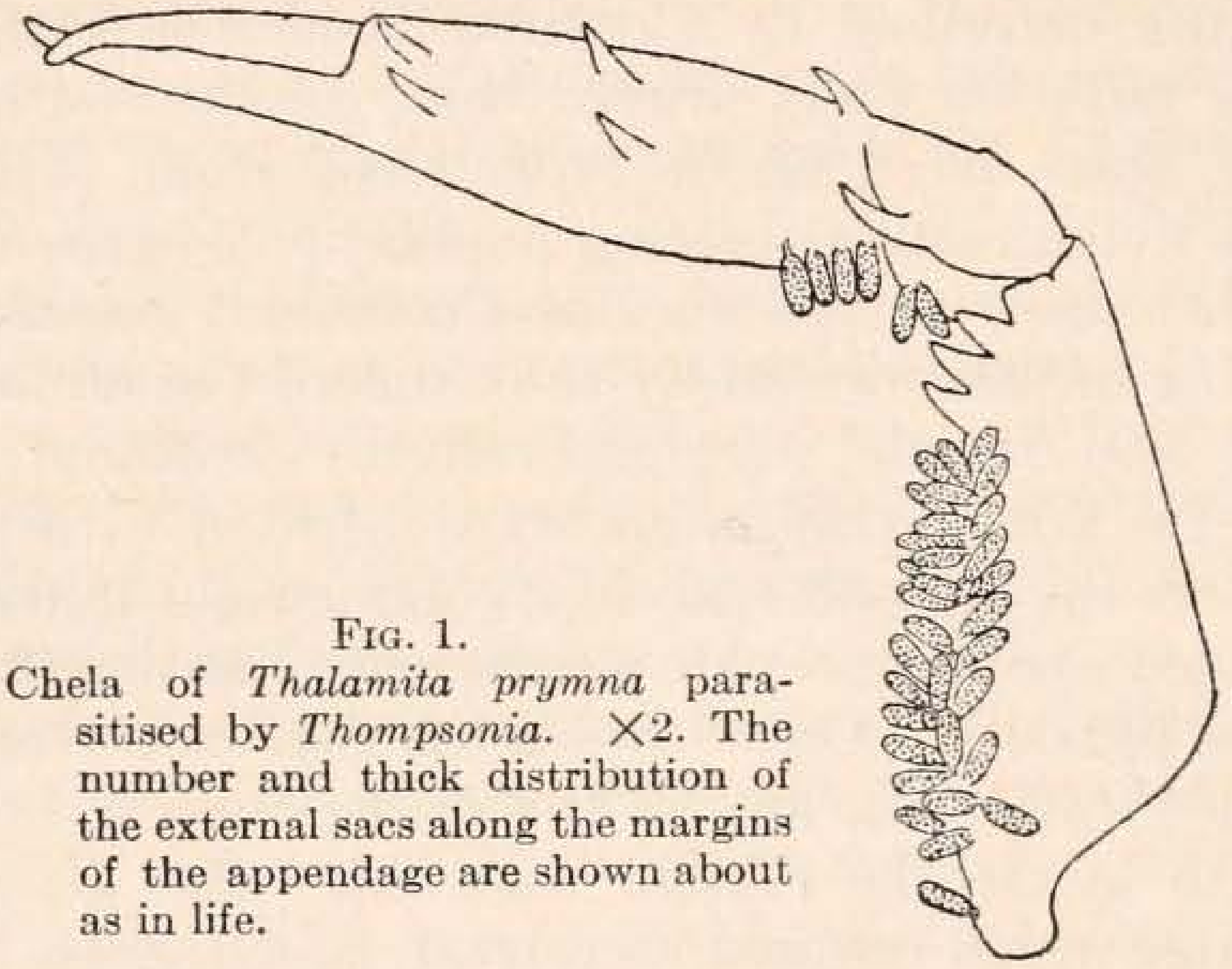

FIG. 1.
Chela of *Thalamita prymna* parasitised by *Thompsonia.* ×2. The number and thick distribution of the external sacs along the margins of the appendage are shown about as in life.

Dr. W. T. Calman, of the Natural History Department of the British Museum, has been kind enough to entrust to me a specimen of *Actæa ruppellii* (pl. 1, fig. 4) from South Africa, which also bears a large number of sacs of a species of *Thompsonia.* This species probably differs from that found on *Thalamita,* the sacs being much smaller and pear-shaped.

As far as I am able to judge, there is no essential difference between the forms of *Thompsonia* which infest Macrurous and Brachyurous

Decapod Crustacea respectively, although, owing to the scantiness of my material, I was unable to investigate thoroughly those of the latter class. The account which follows is based almost entirely on the parasite of *Synalpheus*.

THE ROOT SYSTEM.

The root system is the characteristic organ of the Rhizocephala. Delage and Geoffrey Smith have shown that it appears first in the course of endoparasitic development and is well established before the visceral mass begins to form. There is no doubt as to its existence and importance in all genera, with the exception of the doubtful form *Duplorbis*, but it has been exactly described only in *Sacculina*. The following brief description is condensed from the account of Delage:

> The tissue of the peduncle is bounded by the *basilar membrane* and from this the roots originate. For the most part they originate in a small number of large trunks which immediately ramify and spread. At first the roots follow the intestine, which they envelop with a close network. Some then pass into the distal part of the abdomen of the crab, penetrate the muscular layers of the body wall, and enter the abdominal appendages. Others pass forward and divide into two groups: the first follows the intestine and passes on to the stomach and into the interstices of the liver lobes and the genital glands; the second, not quite so important, accompanies the nerve chain, its branches following the lateral nerves into the limb muscles and penetrating into all the appendages, limbs, antennæ, and even the peduncles of the eyes. All the organs are invaded except the gills and heart.
>
> The roots branch with an irregular dichotomy. The separate branches never anastomose. In diameter they usually vary from 30 to 40μ, but the largest may measure 200μ. Histologically they consist of the following elements: (1) an exceedingly thin external layer of chitin; (2) a layer of cells forming a complete internal investment; (3) the interior of the root is occupied by star-shaped cells, the processes of which anastomose with each other and with the marginal cells. In the largest roots the centre is empty. Refringent drops or granules of yolk occupy the meshes. The root system of *Peltogaster*, though similar to that of *Sacculina* in details of histology and method of branching, has a very different distribution. It constitutes a compact mass which is concentrated in the neighbourhood of the peduncle, not invading the spaces between the tissues of the host in the manner characteristic of *Sacculina*.

Such accounts of the root system of *Thompsonia* as have been given by the earlier observers are conflicting and obviously influenced by a predisposition to accept the theory that each external sac is a metamorphosed larva. It is, moreover, exceedingly difficult to demonstrate the root system of Rhizocephala when preserved by usual methods, for the roots, owing to the impenetrability of their cuticular envelope, take up stains much less readily than the surrounding tissues. In addition, the highly refringent yolk globules, which make the roots easily distinguished in life, disappear under the action of alcohol or even formalin. And lastly, the roots are even more delicate than in *Sacculina*, so that we can well understand why Coutière and Häfele were unsuccessful in tracing the course of the system.

Coutière was nevertheless able to make out some details of their distribution. His description may be given in full:

> "Celles-ci s'ont bien différentes de ce que l'on remarque chez *Sacculina carcini* par exemple; elles sont même plus réduites que dans le genre *Sylon*, ou Hoeck les a décrites. Ces racines occupent uniquement le bourrelet transversal du pléosternites dont elles ont vraisemblablement provoqué la formation anomale; on n'en trouve nulle trace autour de l'intestin ni entre les muscles. Elles envahissent, par contre, les lames concentriques du neurilème externe, tres épaissi chez *A. edwardsi* et *A. avarus*. Elles ont un diametre de 25 μ a 30 μ et se montrent ramifiées et coutournées en tous sens."

Though Coutière is mistaken in supposing that the roots are localised in the neighbourhood of the sternum, his observations as to their absence round the intestine and concentration round the nerve cord agree with mine.

In *Pilumnus*, Häfele had a particularly unfavourable host for studying *Thompsonia*. The external sacs are all situated on appendages with an enormously thick cuticle. The only possible method of studying the root system was by prolonged treatment of the appendage in Perenyi's fluid to soften the chitin, after which sections could be cut. From an examination of these he concluded that there was a root system of an exceedingly simple kind. Krüger from a more careful examination of material from the same source, overstaining his sections and washing out carefully, was able to demonstrate a root system of a normal kind and show that the chromatin-rich nuclei which Häfele had taken to belong to the root system were actually in the connective tissue and blood cells of the host. The root system, then, Krüger decides, does not support the claim that *Thompsonia* is primitive, and, on the other hand, the omission of the Nauplius stage is a mark of specialisation. This is perfectly correct, and if he had suspected that the roots of adjacent sacs were continuous Krüger would have been able to complete his chain of reasoning.

My own conclusion is that there is a single root system continuous throughout the host, from which all external sacs are budded off so that each host is parasitised by a single individual and not by a hundred or more gregariously inclined Rhizocephalans.

I was first able to see the root system in the abdominal appendages of an infected *Synalpheus*. Those which bore external sacs were cut off from the living animal and examined under a low power of the microscope. The endopodites and exopodites are greatly flattened and the cuticle is thin and unpigmented. The whole organ is thus transparent and the roots are visible as slender strands to which the presence of innumerable highly refringent yolk granules gives a greyish colour. Usually a single root strand entered each ramus and this gave off a secondary root to each external sac and generally a number of others which ended in club-shaped swellings. The significance of these last will be explained later.

It thus became evident that the root systems of adjacent sacs at least were continuous, and since all the sacs upon one host are in the same stage of development, it was hardly to be doubted that the one system is common to all. Dissections of the trunks of infected Alpheids were made and carefully examined for roots. A perfect network of slender grey roots was seen to exist in the ventral body wall and to be concentrated particularly in the neighbourhood of the nerve cord.

The course of the root system in the body of the host particularly was best demonstrated, however, in preserved material. The infected animals were preserved for further study by fixing either with corrosive sublimate solution or Flemming's fluid. In those treated in the former manner the results are not very satisfactory. It is only possible to trace the roots because they take up stains so much more slowly than the surrounding tissue. In text-figure 2 an abdominal appendage is represented which bears a number of young external sacs. This was stained in a very dilute solution of borax-carmine for several days. The roots connecting the sacs are shown as colourless channels in the well-stained epithelial tissue of the appendage.

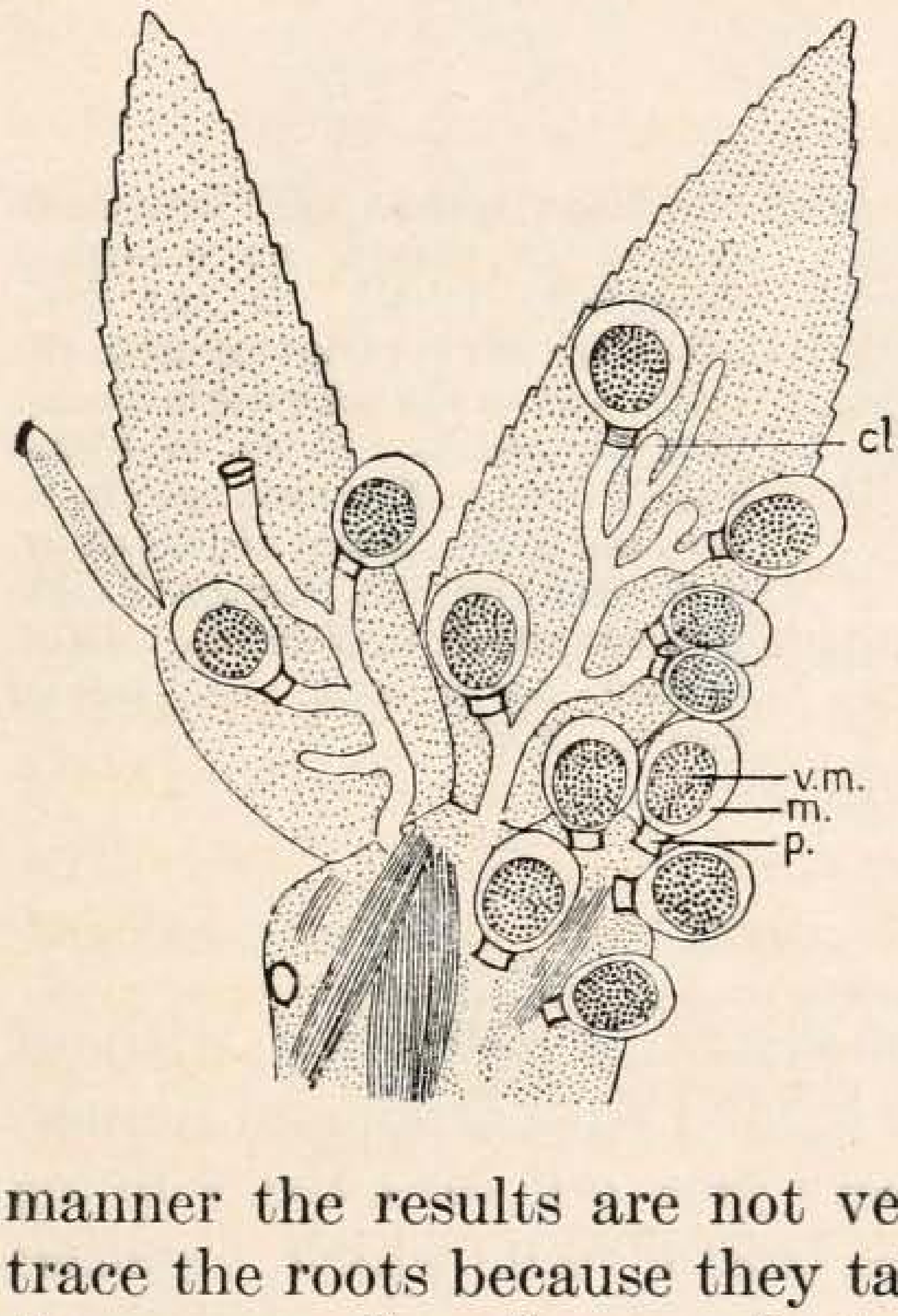

FIG. 2.—Abdominal appendage of *Synalpheus brucei* infected by *Thompsonia*; to show the branching root system connecting a number of very young external sacs. The specimen was fixed in corrosive sublimate and stained with borax-carmine. The roots have therefore taken up very little stain compared with the tissues of the host and are shown unshaded. *v.m.*, visceral mass; *m.*, mantle; *p.*, peduncle; *cl.*, internal bud of root system, which after further development will become an external sac. ×35.

But much clearer preparations were obtained from the individuals fixed in Flemming's fluid. In appendages from these mounted in Canada balsam without any further staining, the course of the roots is shown with the greatest clearness by the yolk granules, which are blackened by the osmic acid in the fixing fluid. The majority of the drawings which I reproduce here to illustrate the root system have been made from preparations of this kind.

The root system is not localised, then, in the neighbourhood of the external sacs; on the contrary, the main development is in the ventral body wall of the abdomen and often, too, the thorax, where it exists as a network of thin roots underneath and on both sides of the nerve cord, giving off frequent branches into the longitudinal musculature (see text-figure 3). In the thorax the roots extend into the lateral and dorsal body wall as well. Their distribution is not so wide as that of *Sacculina,* in that the intestine and stomach are not surrounded, but roots occur between the lobes of the liver. In the concentration of roots round the nerve cord rather than the alimentary system *Thompsonia* resembles *Mycetomorpha* (**8**), the root system of which has, however, a much more restricted distribution.

Branching is dichotomous and anastomosis of neighbouring divisions certainly does sometimes occur, a feature unknown in *Sacculina.*

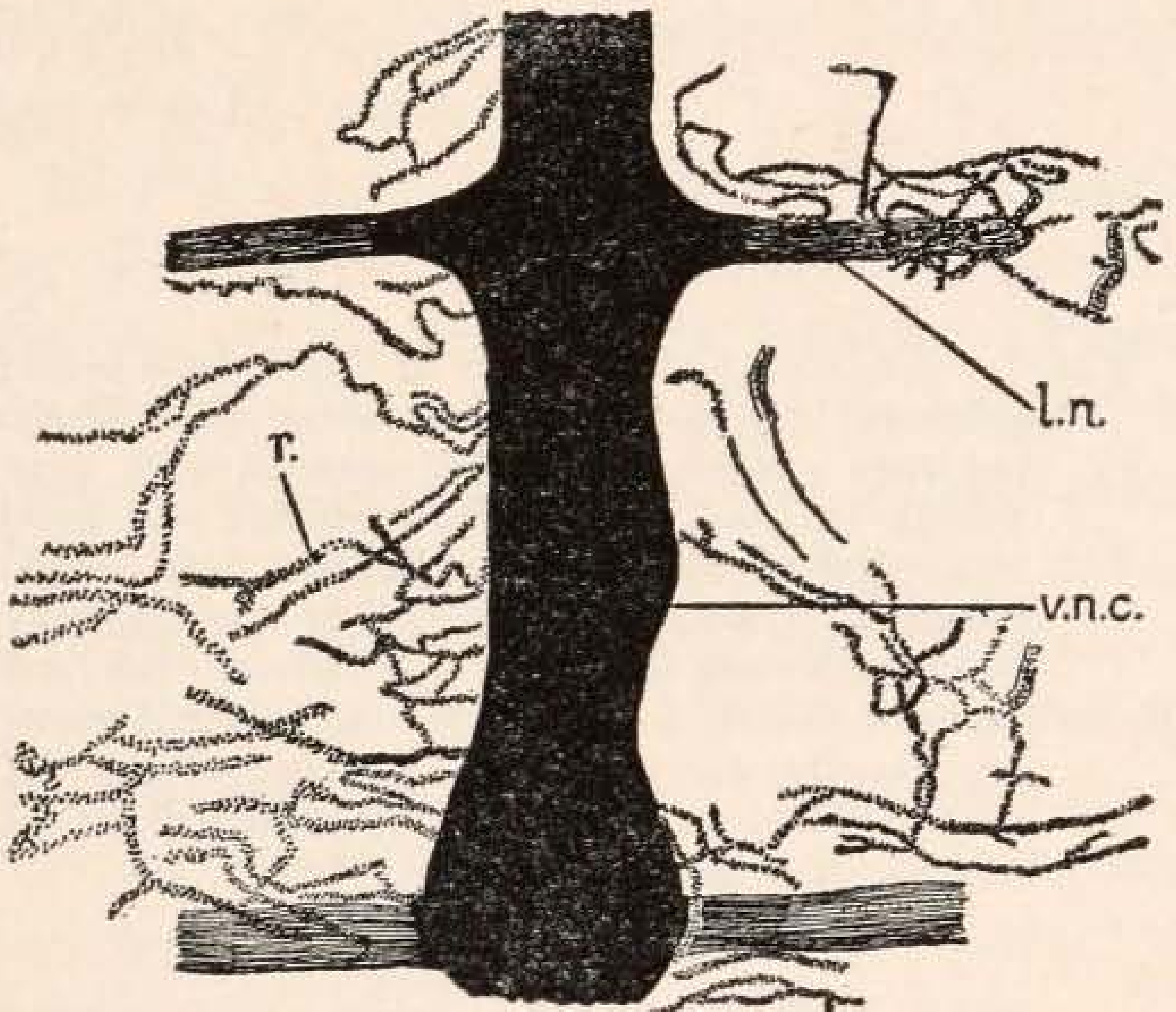

FIG. 3.—Root system of *Thompsonia* around the ventral nerve cord of *Synalpheus brucei.* It has been partially torn in removing from the body, and so the network is incomplete in places. Fixed in Flemming's fluid. The root system *r.*, here and in the figures which follow, is revealed by the blackened yolk globules which it contains. *v.n.c.*, ventral nerve cord; *l.n.*, lateral nerve. ×38.

This *central* or *internal* part of the root system is concerned, without doubt, with the *nutritive* function and is loaded with large and numerous yolk granules. From the trunk there pass out into the walking legs, abdominal swimmerets and tail-fans, lateral roots which, together with their branches, may be distinguished as the *peripheral* division of the system. It gives rise to the external sacs and its function is *reproductive.* The yolk granules, though numerous, are small.

In the case of the abdominal appendages a single root usually enters the protopodite, but it immediately divides and as a rule both the endopodite and the exopodite are invaded by secondary roots, which divide further, as mentioned above. Where the roots enter the abdominal appendages there is sometimes also an invasion of the space within the adjacent pleuron. Such a case is figured here (text-figure 4). A complicated knot of roots of the nutritive kind occupies the wider part of this space near the attachment of the muscles of the appendage and from this are given off two branches which pursue a tortuous course within the broad area of the pleuron. One of these branches has given rise to an external sac, of which the peduncle (*ped.*) alone is shown, but sacs occur only rarely in this position.

Similar wide extension of the system occurs when the tail fans and telson are penetrated, as is shown in text-figure 5. The single root whose course is followed divides into two, each of which gives rise to numerous short rootlets and finally anastomoses with its fellow. The rootlets usually end in club-shaped enlargements, but two have fully formed external sacs.

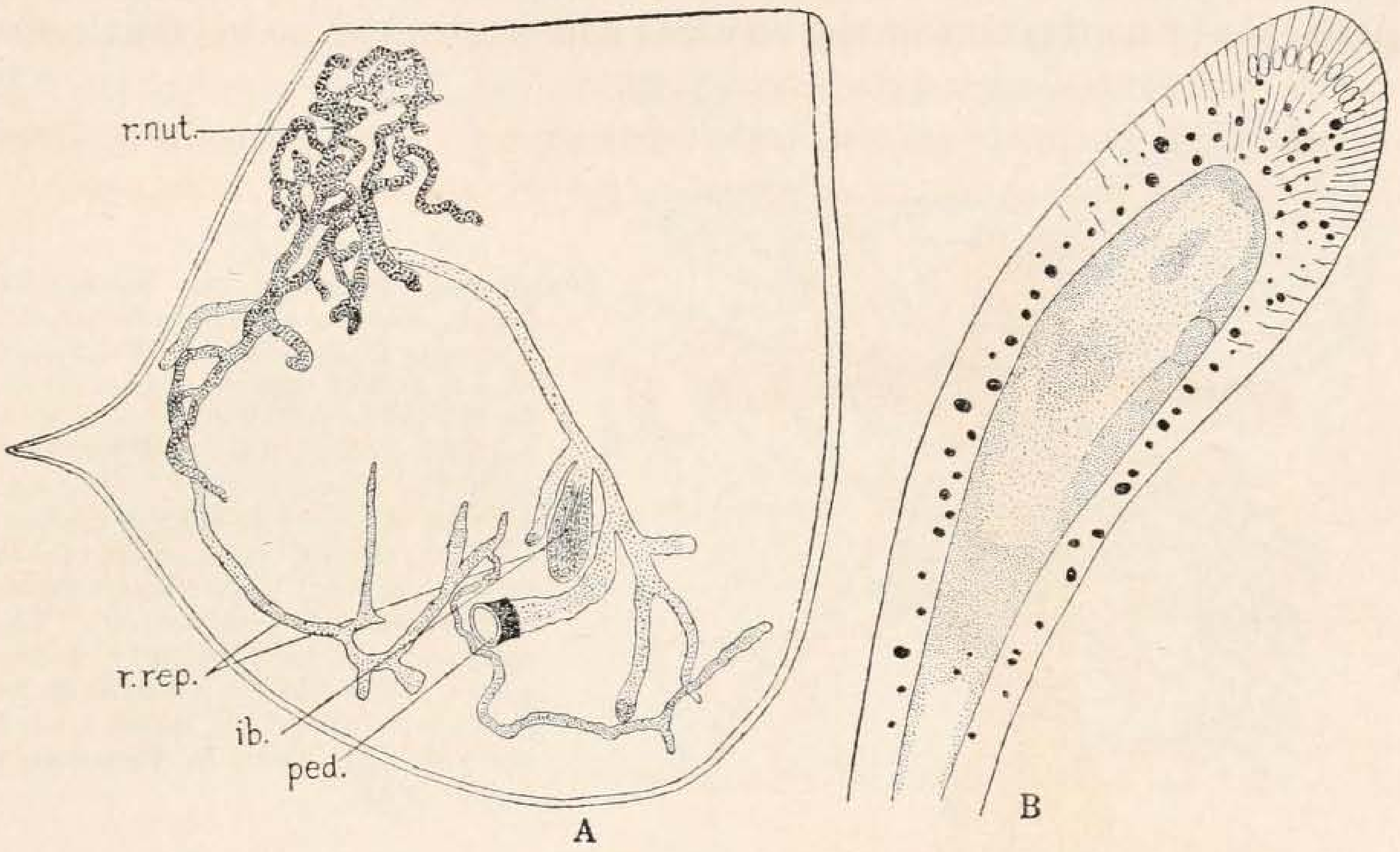

FIG. 4.

A. Pleuron of abdominal appendage of *Synalpheus brucei*, showing root system of *Thompsonia*. *r.nut.*, a number of roots like those of the interior of the trunk with large yolk globules; *r.rep.*, roots of the peripheral system with much smaller yolk globules. These give off one branch to an external sac, which, however, has been detached, leaving the peduncle, *ped.*, another process, *ib.*, which will shortly become an external sac, probably at the next moult, and numerous others which are not at all developed as yet. Fixed in Flemming's fluid. ×75.

B. Internal bud of *Thompsonia*. This is *ib.* of fig. A more highly magnified. ×450.

The histology of the internal roots (text-figure 6A) is similar to that described in *Sacculina*, with some modification perhaps due to the fact that they are thinner than those of the last-named form. In diameter they vary from 10 to 20 μ. There is a very thin cuticular investment covering a syncytial external layer, which contains a number of nuclei dispersed at irregular intervals. In the middle is a lacunar space, but I have not been able to demonstrate a lacunar tissue of stellate cells, such as is found in *Sacculina*. It is possible that this may be absent owing to the thinness of the roots. The large and numerous yolk globules are placed in the syncytial layer.

The roots of the peripheral part of the system (text-figure 6B) show two well-marked differences. The first of these I have already mentioned, namely, the smaller size of the yolk globules indicating that consumption rather than accumulation of food stores is the physiological condition in this region. The second is the occupation of the lacunar space by masses of small rounded nuclei with a scanty cytoplasmic investment. The external layer is, on the other hand, free from nuclei, which thus appear to have migrated internally. The origin of this lacunar tissue must be looked for in the external syncytium. Its function is undoubtedly reproductive; it accumulates particularly as the end of the rootlets which give rise to external sacs.

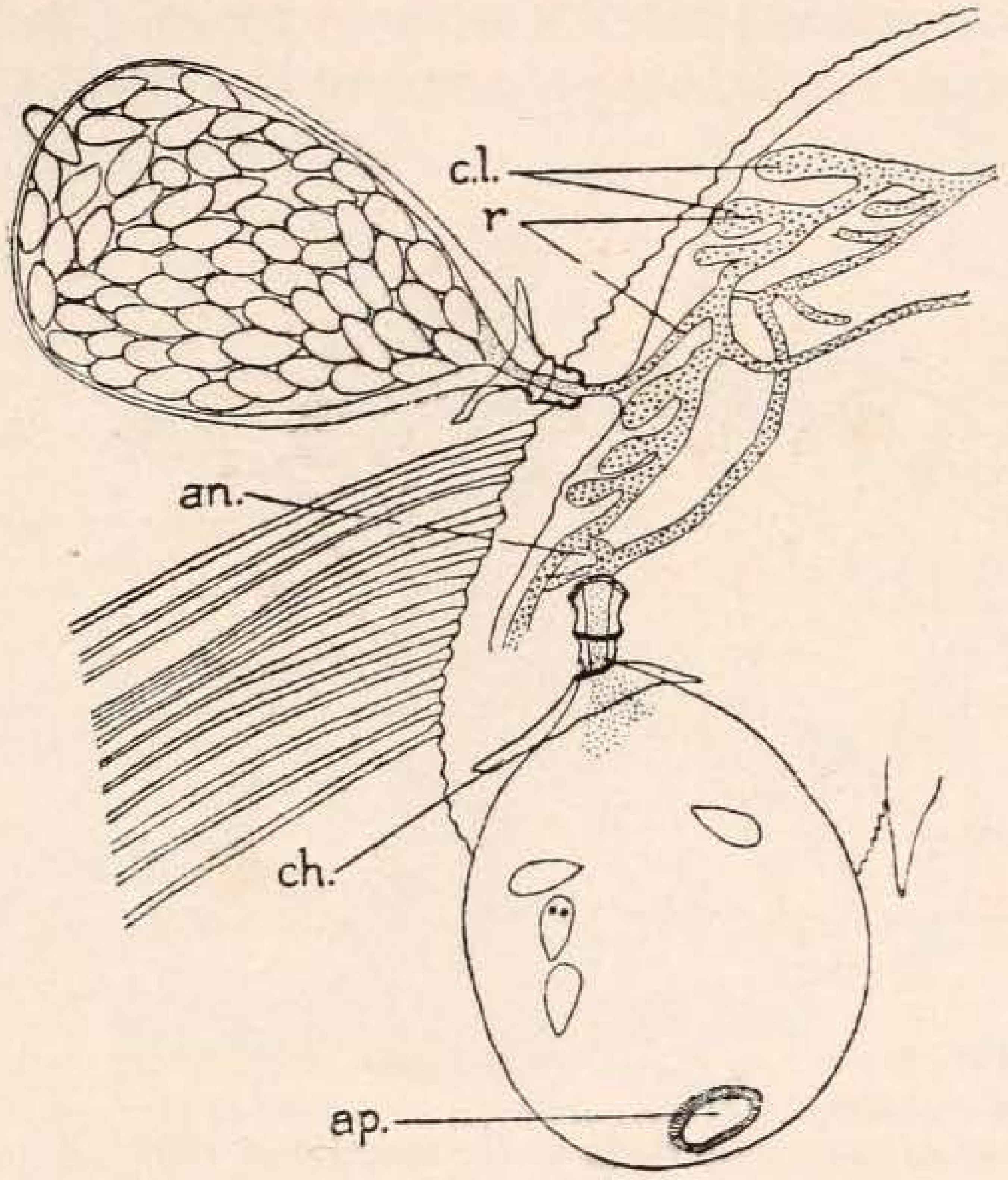

FIG. 5.

Thompsonia parasitic on *Synalpheus brucei*, showing mature external sacs springing from a tail fan of the host. One is full of mature Cypris larvæ. In the other the larvæ have mostly escaped through the apical aperture, *ap.* The root system, *r*, is remarkable for the large number of internal buds, *cl.*, none of which are advanced in development. At *an.* anastomosis of two branches may be seen. The external sacs have recently undergone a moult and the remnant of the chitinous envelope, *ch.*, is seen around the peduncle. Fixed in Flemming's fluid. X35.

It will be well now to consider the terminal swellings of the rootlets (text-figure 4B). These are formed by the development of the external syncytial layer as well as the enlargement of the lacuna within. The external layer increases in thickness and the nuclei become much more numerous, migrating superficially, taking up a position with their long axes at right angles to the border. In fact, the tissue tends to assume a regular epithelial structure. Internally the protoplasm contains numerous yolk globules of various sizes and nuclei are rare and sparse. The interior lacuna is occupied by a dense mass of small rounded cellules of equal size which will give rise to the egg cells and nutritive cells of the external sac.

The whole structure is in fact a developing external sac. By the increase in size of the structure it comes into close contact with the chitinous cuticle, so that if the Alpheid were to moult it would emerge to the exterior. It is well known, of course, that *Sacculina* prevents its host from moulting. But some time ago I pointed out (**7**) that hermit crabs infected by *Peltogaster* still moult frequently and now it is to be recorded that, although the root system of *Thompsonia* is almost as extensive as that of *Sacculina* and the great number of external sacs must require a large and constant supply of nourishment, yet no check appears to be placed on the moulting function of the host. The number of moults observed was, it is true, only two or three, but this was due to the difficulty experienced in keeping *Synalpheus* in captivity and to the short time of observation, and I do not doubt that the moulting of infected specimens is a normal and frequent phenomenon.

Not only, then, is the whole number of existing external sacs budded off from one root system, but provision is made for replacing these when they have functioned. A necessary condition for securing this replacement is that the host should continue to moult. Further consideration will be given to the whole phenomenon after the sections dealing with the external sacs and the development of the egg cells. At present I wish to point out that the root system has the remarkable power of regenerating external sacs and producing germ cells throughout the whole period of its existence.

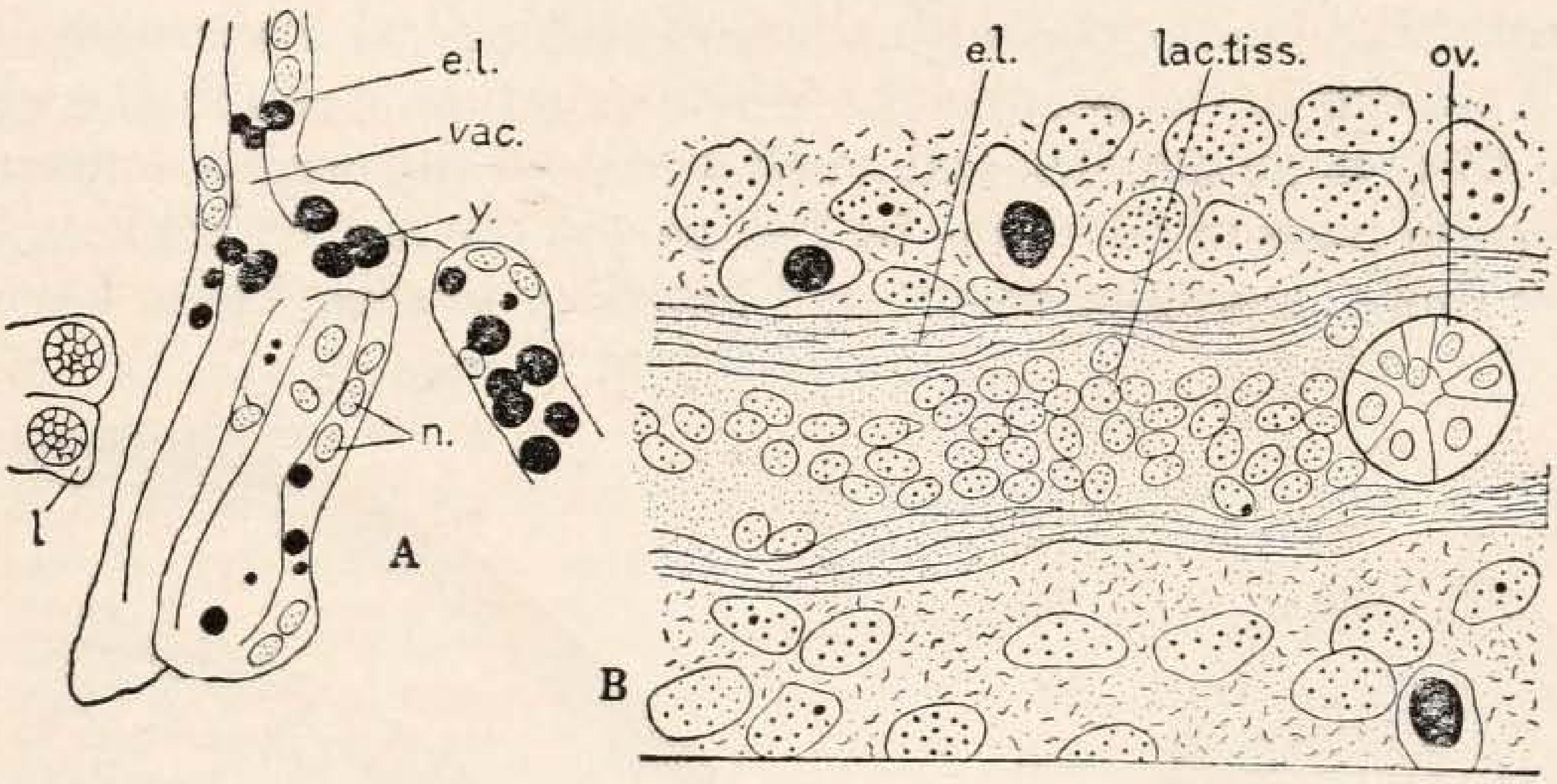

FIG. 6.

A. Roots of central system, showing external layer, *e. l.;* with nuclei, *n.;* lacunar space, *lac.;* yolk globules, *y.* ×660.

B. Root of peripheral system running through a pleuron of *Synalpheus*. This shows the non-nucleated external layer, the lacunar tissue, *lac. tiss.*, and a developing egg, *ov.* ×660. Fixed in corrosive sublimate and stained with borax-carmine.

If the distribution of the external sacs (which must follow that of the root system) is studied in a series of individuals it is seen to vary considerably. In some hosts they are confined to the abdominal swimmerets, but in the majority they are also present anteriorly on the thoracic limbs and posteriorly on the tail-fans and telson. In the former lightly infected individuals the root system has, we may suppose, been established for a comparatively short period, while in the latter class the root system has had time to spread throughout the whole body of the host. From the fact that the external sacs appear at first only on abdominal and never on thoracic appendages alone, we may safely conclude that the internal stage of *Thompsonia* fixes and grows in the abdomen of the host, as is the case in *Sacculina* and probably the other members of the Rhizocephala.

THE STRUCTURE OF THE EXTERNAL SACS.

It has already been pointed out that the external sacs are rounded or cylindrical bodies attached to the host by a peduncle and varying in length from 0.5 to 1.0 mm. in the parasite of *Synalpheus*, attaining to 3 mm. in that of *Thalamita*. The smaller forms are immature, the larger are occupied by larvæ ready to hatch. The external sacs are probably homologous with those of the typical Rhizocephala, but differ from this in the simplicity of their structure, a simplicity which is due to their large number and small size. Of the organs contained in the visceral mass of *Sacculina* or *Peltogaster*, the nerve ganglion, reproductive ducts, muscular tissue, and probably too the testis, have been lost.

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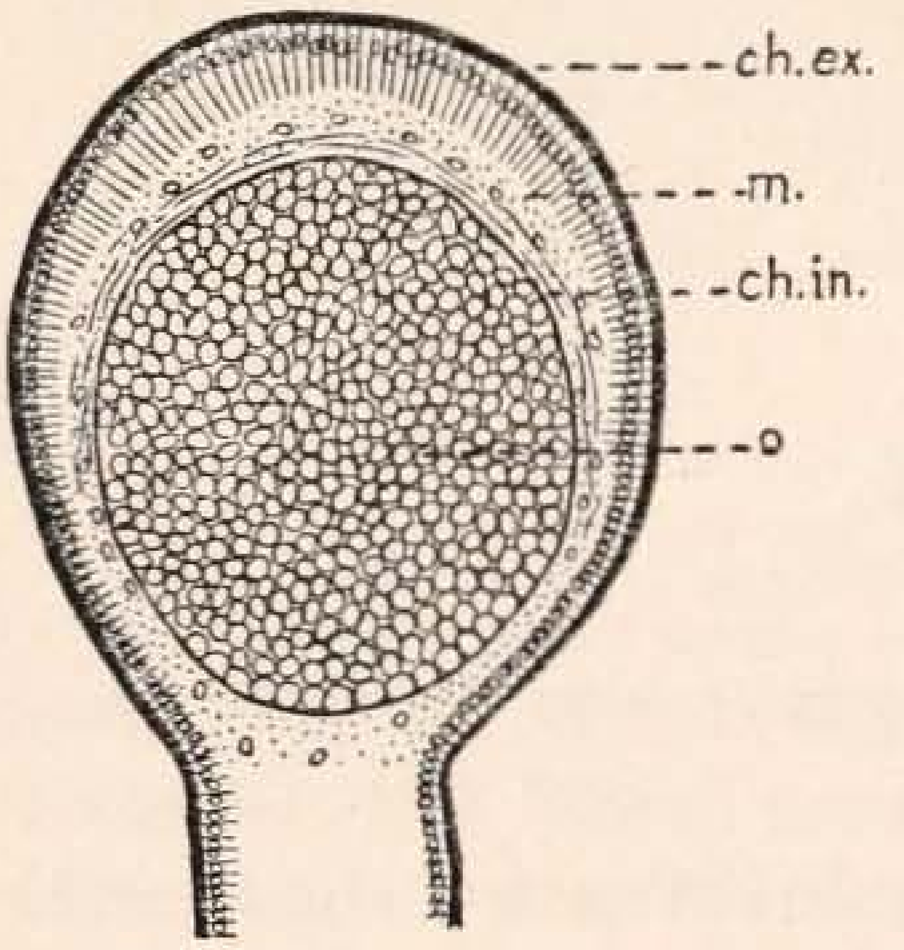

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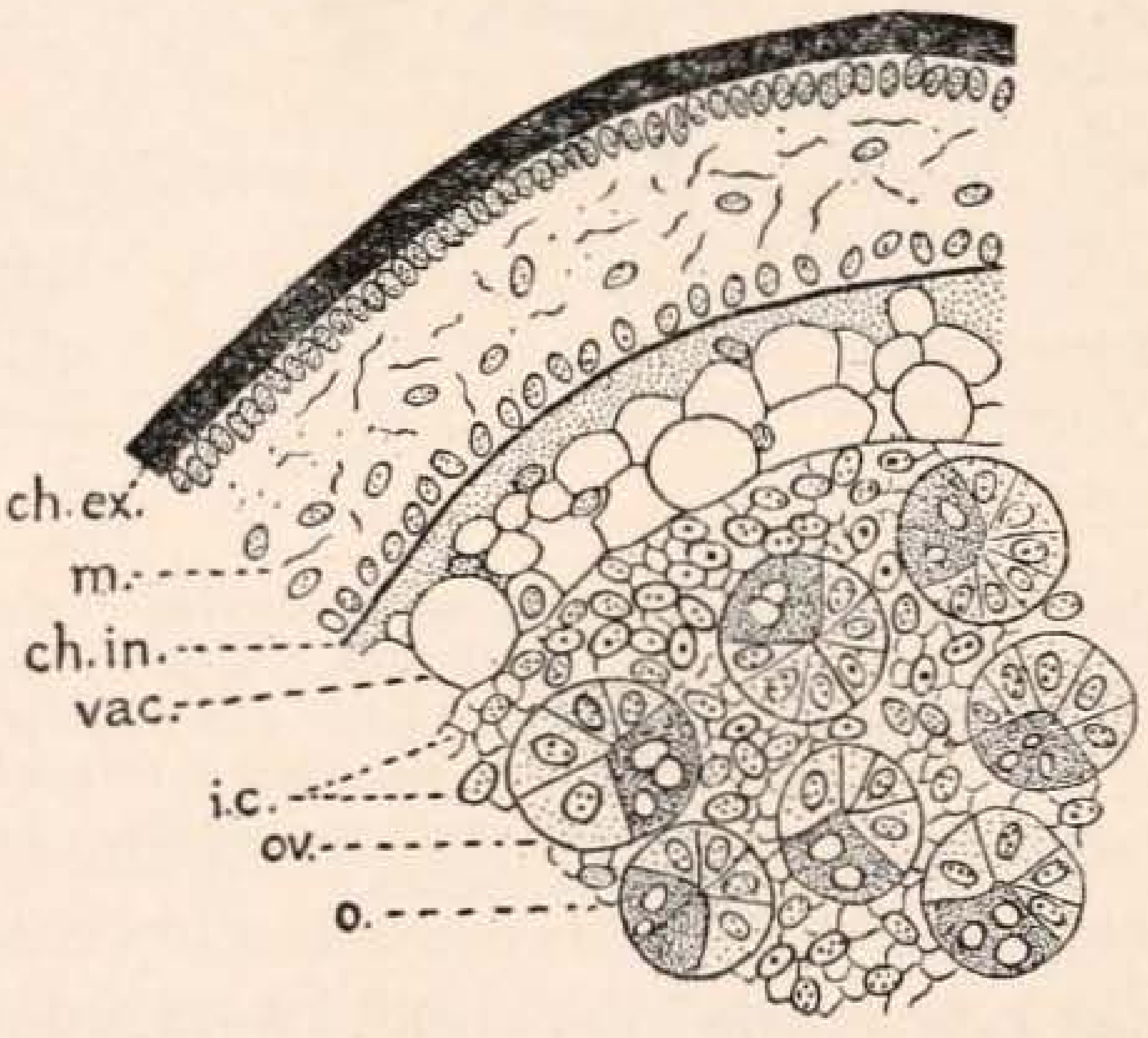

FIG. 7.—Young external sac of *Thompsonia;* whole preparation to show general appearance of mantle and ovary. ×60.

FIG. 8.—Portion of transverse section of a more advanced external sac. ×240. *m.*, mantle; *ch. ex.*, external layer of chitin; *ch. in.*, internal layer; *vac.*, vacuolated external layer of visceral mass; *o.*, ovary, with *ov.*, developing eggs, and *i.c.*, interstitial cells.

Coutière states that the external sacs of *Thylacoplethus* show the following typical Rhizocephalan structures: "Un *manteau* à double paroi, dans lequel est suspendue une *masse viscérale* et qui porte une ouverture cloacale." With this general summary I am in agreement. Häfele, on the other hand, does not appear to recognise any homology between the external layer of tissue (äussere Gewebeschicht) and the *mantle* of other Rhizocephala, or between the internal body (internale Gewebeschicht and Ovarium) and the *visceral mass*. There is, however, no definite *mantle cavity* between the mantle and the visceral mass, for the latter fills up all the internal space. The so-called mantle cavities which are described by Coutière and Häfele and figured by the latter author are, in my opinion, merely artifacts. In many of my own sections the shrinkage of the visceral mass due to unequal fixation has been followed by the appearance of a space between the former organ and the mantle, but in others the preservation is sufficiently good to show the true state of affairs. The thick external cuticle of the mantle prevents the proper penetration of reagents and on this account it is easy to make mistakes.

The *mantle* consists, in my material, of a syncytium in which the nuclei are mainly concentrated on the external and internal borders. This is due to the fact that there is secretion of chitin on these two surfaces forming an outer and inner investment of the mantle. The nuclei of the outer layer are more crowded and numerous in correlation with the greater thickness of the chitin here. The chitin of the internal boundary is exceedingly delicate, but it is only the presence of such a structure which enables us to homologise the outer part of the external sac with the mantle,* in the absence of a mantle cavity. Between the two thickly nucleated layers there is a mesh-work of protoplasm with a few scattered nuclei.

The visceral mass consists of an investing layer of vacuolated tissue with scattered nuclei (=innere Gewebeschicht of Häfele) which does not appear to take part in the secretion of the inner layer of chitin (*vac.*) and a central mass, densely packed with nuclei, in which the ova arise (*ov.*). This central mass was called the *ovary* by Häfele.

But distally to the ovary there is a second region where proliferation of nuclei takes place, but no egg cells arise. This is described by Häfele as a testis because the cells are rather similar to the spermatogonia of other Rhizocephala and many of them are in course of division. No spermatozoa are seen at any stage examined and an inspection of Häfele's figures does not inspire much confidence in his conclusion that *Thompsonia* is hermaphrodite. The active division of the nuclei in this region is accounted for by its apical position, which makes it a centre of proliferation. Growth proceeds throughout the development of the ova, until the larvæ are ready to hatch, and Häfele states that this organ has disappeared by that time. Certain large cells, with nuclei four to five times as great as those of the surrounding cells, seem to me to be clearly egg cells rather retarded in development, and their occurrence here shows that the apical portion of the visceral mass is not substantially different from the rest, but contains a larger amount of embryonic tissue.

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*The roots, mantle, and visceral mass of *Thompsonia* form a syncytium without any cell boundaries whatever, and it is not correct to speak of layers of cells, as Coutière and Häfele have done. This point is specially emphasised by Coutière.

So far as my own experience goes there is no sign of any organ which can be called a testis nor of spermatozoa wandering through the tissues. I think that probably *Thompsonia* is to be placed with *Sylon* and *Mycetomorpha* as Rhizocephala which have substituted parthenogenesis for hermaphroditism.

Coutière also seems to refer to this organ in speaking of a distally situated growing point. I must confess myself unable to understand a good deal of his description without the aid of figures. His conception of the life-history of *Thompsonia,* moreover, leads him to see in the visceral mass the abdomen of the Cypris larva and explain the proliferation here by the laws of growth observed in Annelids and Crustacean larvæ.

DEVELOPMENT.

The account which I give of the development of *Thompsonia* is very incomplete, for the material in my possession illustrates only a number of isolated stages. I have not been able to gather any information about the maturation of the egg.

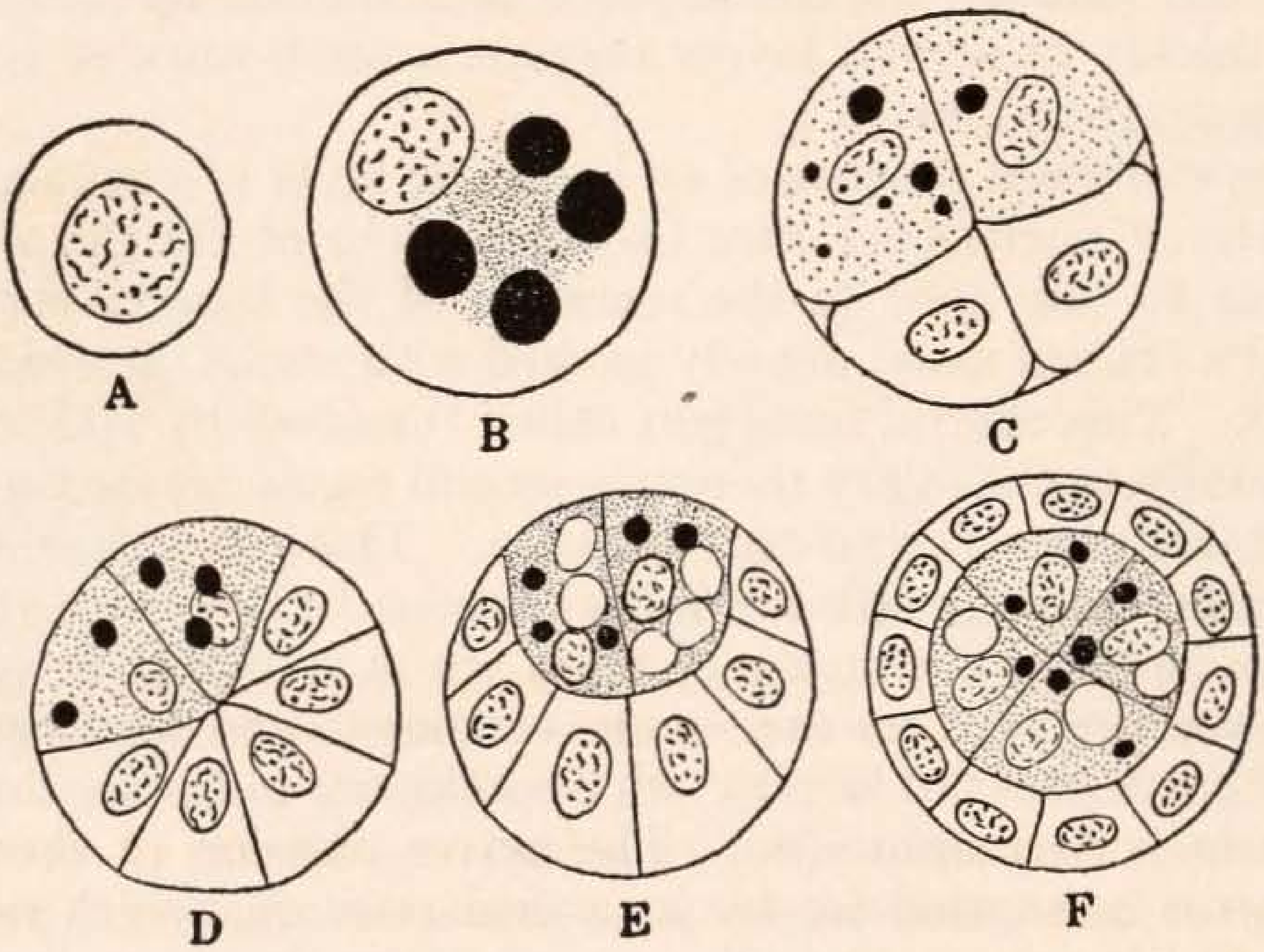

FIG. 9.—Developing eggs of *Thompsonia.* ×1000.

A. Young egg cell.
B. Oocyte nucleus has come to lie excentrically owing to the development of yolk (in black globules).
C. Four-cell stage: two micromeres (unshaded) and two macromeres (shaded) containing the yolk.
D. Beginning of gastrulation; micromeres have divided; macromeres undivided.
E. Development of gastrulation; appearance of vacuoles in the protoplasm of the macromeres.
F. Gastrulation complete; macromeres have divided once, so there are now four cells; more generally there seem to be three.

In the youngest external sacs the visceral mass is occupied by small cells of uniform size. Amongst these there soon become differentiated young oogonia which are rather larger than the remaining interstitial cells (text-figure 9A). These latter, when teased out from the living parasite, take up amœboid forms. In the oocyte stage the germ cells increase in size and yolk globules accumulate within them. In the internal buds this substance is confined to the external layer, but in the external sacs it occurs within both the visceral mass and mantle. The interstitial cells contain it and very possibly transfer it as required to the developing eggs.

When the oocyte attains its full size the nucleus lines on one side with the yolk granules occupying the largest part (text-figure 9B). They vary in number and are very unequal in size, but there are generally three or four large ones. The egg is very unlike that of *Sacculina* with its numerous equal-sized globules, which seem to occupy the whole space

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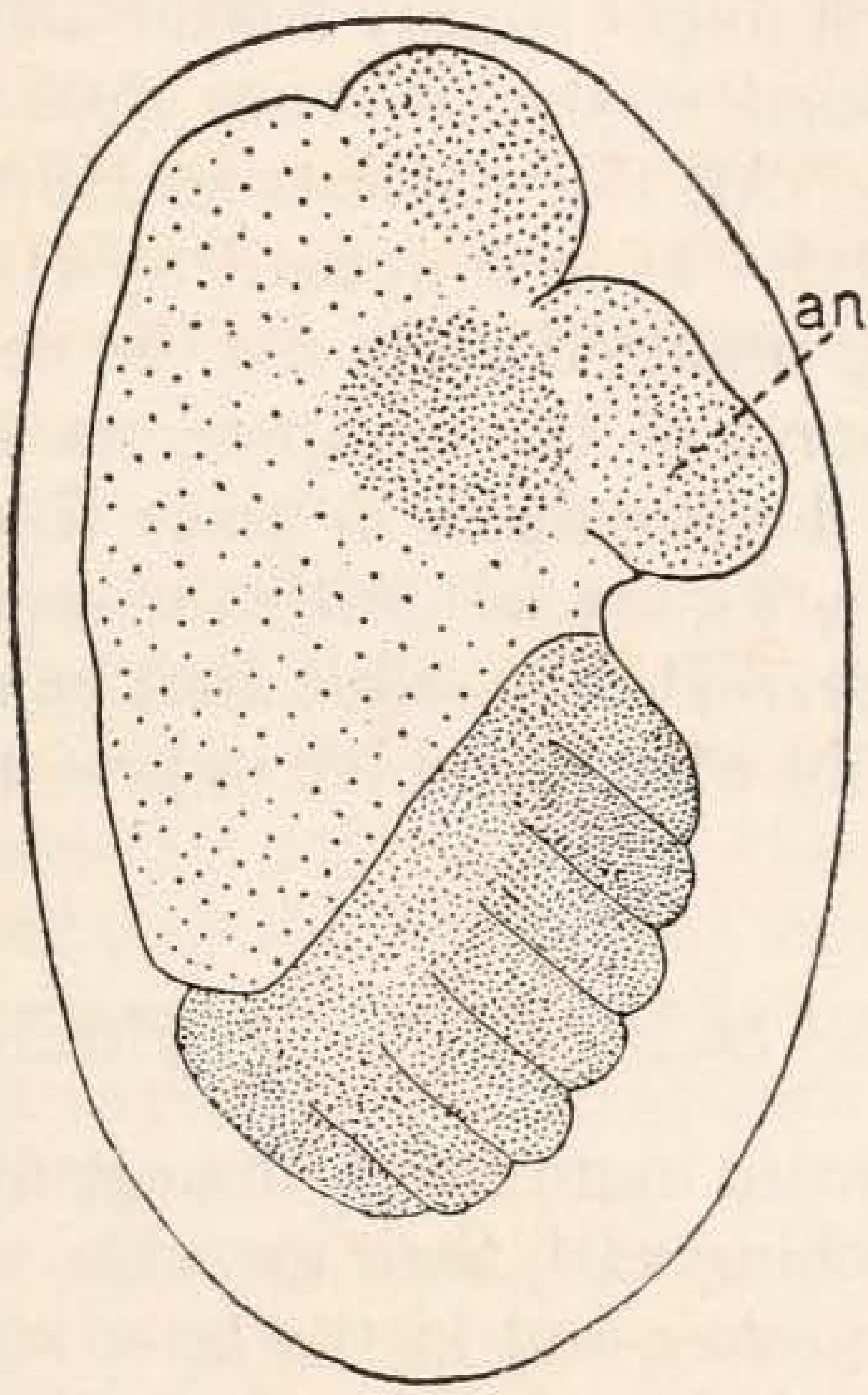

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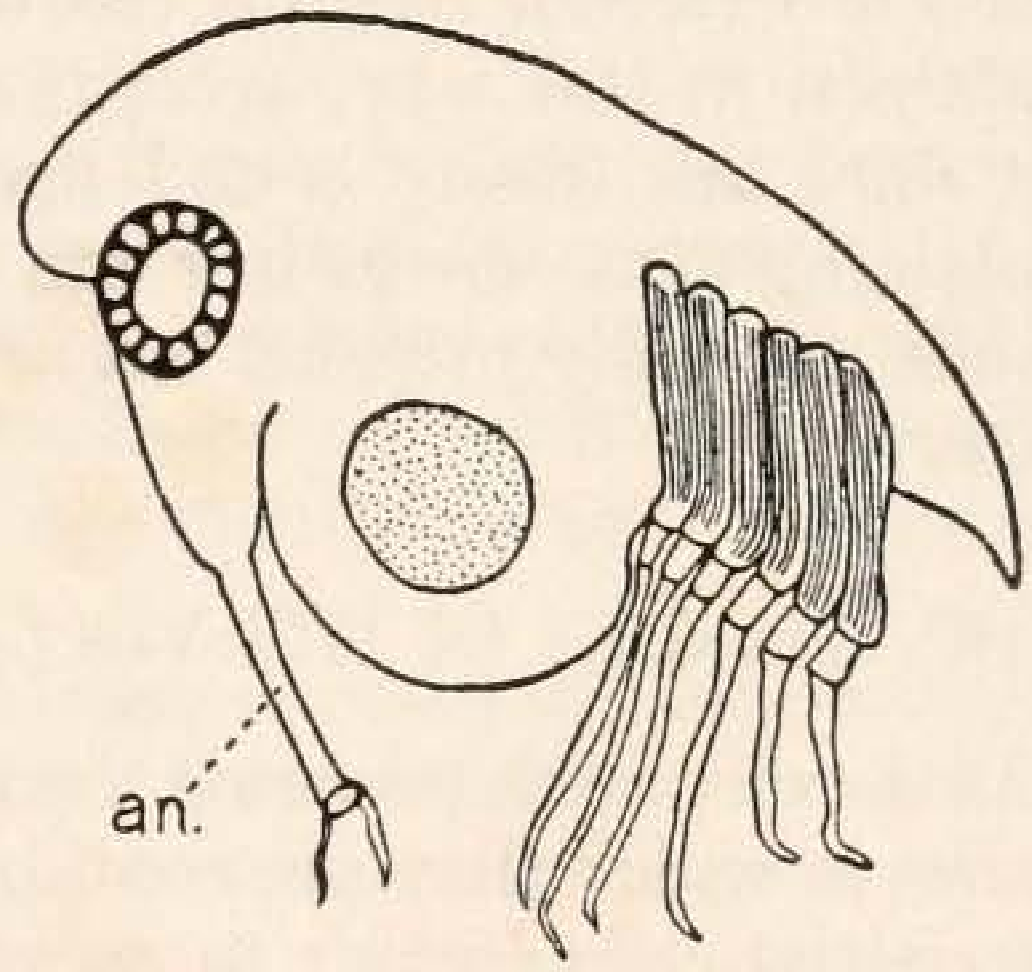

FIG. 10.—"Pro-Cypris" larva of *Thompsonia* from *Thalamita* in egg-membrane. ×375.
FIG. 11.—Cypris larva of *Thompsonia* from *Synalpheus*. The dotted area in the ventral part of the body contains reserve materials. *an.*, antenna. ×470.

within the egg membrane. While, moreover, the egg of *Sacculina* is comparatively large, 600 to 800 μ in diameter, that of *Thompsonia* measures only about 34 μ.

Segmentation commences unequally, a micromere and a macromere with all the yolk being formed. Both micromere and macromere take part in the second (text-figure 9C) and probably also in the third division, but after this the yolk-containing cells cease to divide. The continued division of those without yolk leads to their rapid extension over the yolked cells and gastrulation (text-figure 9 D, E, F) thus takes place by epibole.

Beyond the gastrula I have not been able to trace development. The next stage observed is comparatively far advanced, showing a single pair of rudimentary processes, probably representing the antennæ. I am not able to say whether any stage resembling the Nauplius is passed through within the egg membranes, but think it is unlikely.

I figure here a "pro-Cypris" stage (text-figure 10) where the typical form of the Cypris has been attained, but the secretion of chitin has only just commenced and so the appendages have not assumed their articulate form. The embryonic antennæ are much larger in size than their ultimate development would lead one to expect.

The Cypris larva (text-figure 11) has rather a broad, squat form compared to that of other Rhizocephala. As Häfele has pointed out, it is very much reduced in organisation. The antennæ appear to lack the "appendices sensoriels," which in *Sacculina* are used for anchoring the larvæ to the hairs of the host. The distal article of the antenna is very small and the cement glands which might supply a secretion for fixation were not seen in the larvæ examined, so that it is not clear how attachment is effected in the first place. All these points in Häfele's description are borne out by my material. It is supposed by Häfele that attachment takes place on a freshly moulted crab, for the occurrence of external sacs on the hairless parts of the carapace must be explained in this way, according to the development in place theory; but since this theory is no longer tenable, we are left with the onus of explaining attachment in some other way. It is possible that cement glands are really present, but are seen only with difficulty in preserved material.

THE CHANGES IN THE VISCERAL MASS DURING DEVELOPMENT.

As development proceeds the larvæ take up more room, the egg membranes in which they are contained stretching with their growth. The interstitial cells appear to decrease in number and in the later stages the interior of the visceral mass consists of a mosaic of developing embryos, all in contact with small numbers of interstitial cells in the gaps between the egg shells. The mantle, too, as the result of the pressure of the embryos, becomes a very thin layer of tissue.

There is, however, a definite organ in the centre of the visceral mass which makes its appearance at this stage and retains its individuality until the larvæ hatch. This is a long thin process, the continuation of the peduncular tissue, and it is hardly to be doubted that its function is to supply nourishment to the developing eggs. (It is very well figured in Häfele, l. c., Taf. 2, Fig. 14, *schw.*) Coutière says, in reference to it, that it represents the whole visceral mass; he regards the developing eggs as now occupying the "mantle cavity" (cavitè incubatrice), while the ovarian epithelium has entirely disappeared. As stated above, the mantle cavity has no real existence in *Thompsonia*, and in young specimens it is not simply the matter of an ovarian epithelium, but the ovary occupies almost the whole of the visceral mass.

It is interesting, however, to compare this organ with the so-called "spadix" in the sporosacs of the Hydromedusæ. Here we have an exceedingly degenerate form of the medusa, with the germ cells lying between a single layer of ectodermal cells and the endodermal core. This latter is the "spadix" and it forms a tube which may be greatly elongated and even branched, wandering in the midst of the generative cells. In the general simplification of structure it is thus elaborated, no doubt, to supply nourishment to the developing eggs. But the organ described in *Thompsonia* is by no means so definite as this.

THE LIBERATION OF THE CYPRIS LARVÆ.

In Coutière's first note upon *Thylacoplethus* it is clearly stated that a cloacal aperture is present, which is, however, closed by "le paroi externe du manteau," by which I understand that the protoplasmic part of the mantle is penetrated by an aperture, but the chitinous envelope is entirely continuous. He believes that the embryos are liberated by a moult. Häfele, however, denies the existence of a cloacal aperture in the mantle of those species of *Thompsonia* which came under his notice. In *T. japonica* he states that the larvæ are finally freed by a longitudinal splitting of the chitinous envelope (l. c., Taf. 1, Fig. 1). But in a second unnamed species every external sac possesses a genital pore—that is, an opening in the chitinous envelope closed by a lid which falls away at the appropriate time. The agency of a moult is not required.

An investigation of my own material leads to conclusions in harmony with those of Coutière. In one example a number of the external sacs were more or less empty. All these had lost their chitinous envelope, save for a frayed collar round the peduncle. A small aperture was situated at the apex of the sac in the mantle and this gave a definite outlet for the embryos. This is represented in text-figure 5. The aperture must, however, make its appearance at a late phase of development; for, although it is such a regular and definite feature here, no signs of such an organ occur in any other specimens in my possession.

It seems likely that the description which Häfele gives of the larvæ of *T. japonica* escaping by means of an irregular rent in the chitin is an observation of an accidental case. With regard to the definite lid observed in another species, this may constitute a true specific distinction.

THE FORMATION OF NEW EXTERNAL SACS.

When the Cypris larvæ have all escaped nothing is left but a hollow sac (cf. text-figure 5). As the visceral mass thus disintegrates with the progress of the development of the larvæ, the question naturally arises whether the existence of the parasite is terminated at the birth of the first brood of larvæ. Häfele concluded that this was so.* But, as I have mentioned above, this question was answered in the opposite sense by observation of the moulting of an infected host. On September 30 an Alpheid was collected which bore large external sacs, containing Cypris larvæ, nearly all situated on the abdominal appendages. It was isolated and the next day was found to have moulted, the external sacs of course being carried away with the cast skin, which was preserved. Three days after this the host was examined to see whether any recurrence of external parasitic structures could be noted. A number of pink bodies much smaller than any observed hitherto, but with the characteristic structure of the external sac, were found on the abdominal appendages. One of these was cut off and, after being examined alive, was fixed carefully. I give here two figures comparing the old external sacs on the cast skin and the new on the appendage after moulting (text-figure 12); they show that the distribution is roughly similar, but in no case are the positions identical. The new

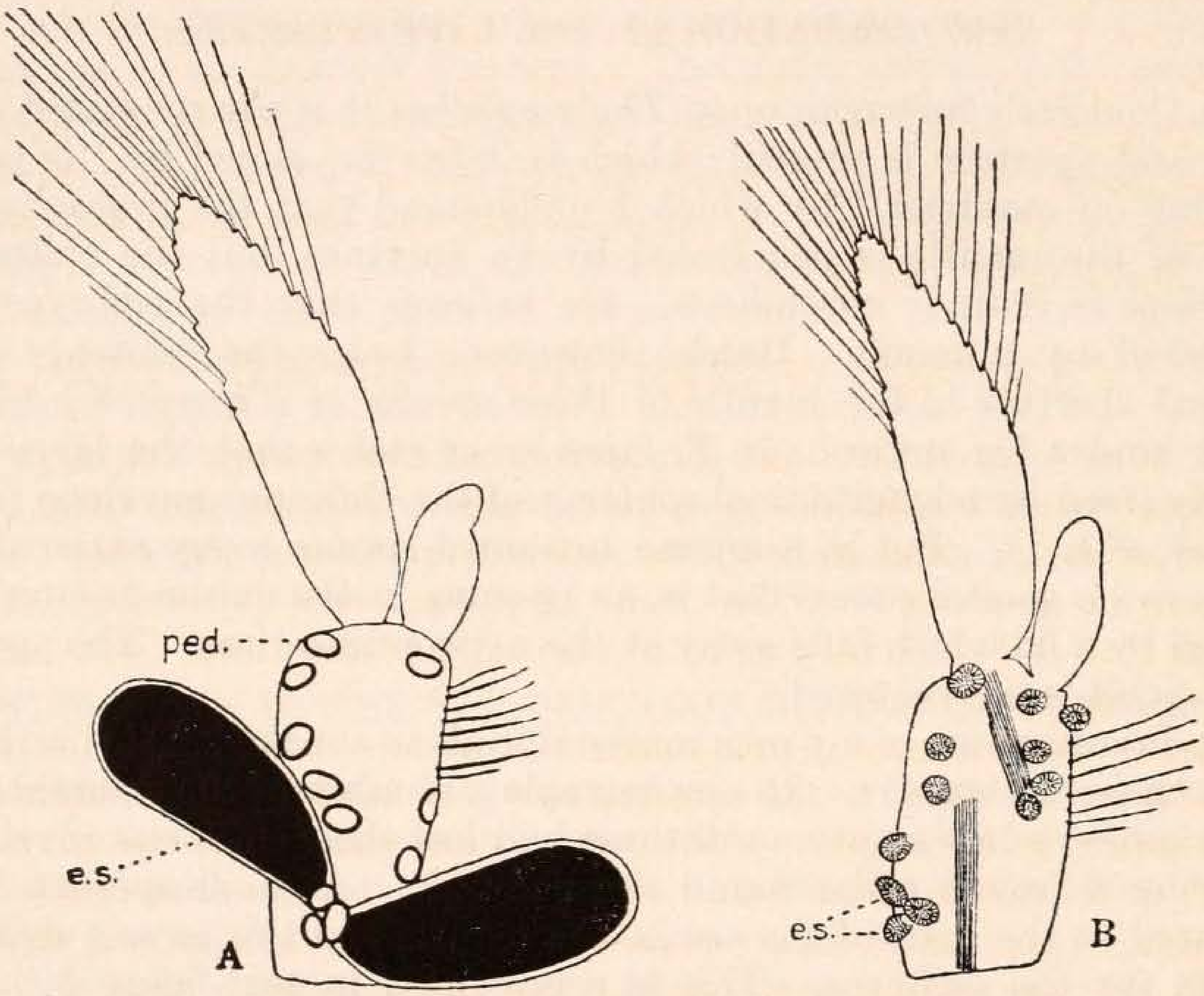

FIG. 12.—First abdominal appendage (right hand side) of *Synalpheus brucei* bearing external sacs of *Thompsonia*. ×28.

A. Cast skin showing external sacs (*e. s.*) containing nearly mature larvæ. Only two sacs are still present, the others having been accidentally detached, but the round black rings (*ped.*) indicate their position.

B. The same appendage 3 days after moulting, showing the new crop of external sacs.

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*"Diese Reduktion der Organe hängt offenbardamit zusammen, dass die Parasiten nur einmal fähig sind, Nachkömmen zu produzieren, wie aus den Verhalten des Ovariums und Hodens geschlossen werden kann."

sacs, then, evidently originate from the internal club-shaped processes of the root system; the rootlets which supplied the old external sacs do not regenerate new ones at once.

Clearly, then, successive crops of sacs containing the reproductive organs are produced by the root system. It would seem likely that the period of development of the parasite has been adjusted to correspond to the time elapsing between moults of the host. This theory is supported by the fact that in the case cited above the external sacs contained advanced larvæ at the time of moulting. I imagine that the disturbance connected with capture and change of conditions hastened the moult, which otherwise might not have occurred until the larvæ were liberated. If the correspondence does not exist, or is only partial, an immense waste must go on; for surely the moult of the host and consequent disconnection from the root system will suspend the development of the parasite and interfere with the mechanism for securing the liberation of the larvæ.

DEVELOPMENT OF GERM CELLS IN THE ROOT SYSTEM.

I have pointed out that the peripheral root system contains in its lacunar space multitudes of minute cells, which, in the formation of internal buds, migrate into the interior and form the ovary of the future external sac. At first they all appear exactly similar, but it is clear that only a small proportion actually become ova, the remainder being interstitial cells. We do not know how the germ cells are stimulated to simultaneous development, but whatever stimulus it is that so acts is not confined to the external sacs, but is also felt throughout the peripheral root system; for when this is examined in a specimen with well-developed external sacs there are seen, among the cellules of the lacunar space, much larger bodies corresponding in size and structure with the segmenting eggs found in the external sacs. One of these is figured here (text-figure 8, *ov.*). These eggs, for such they undoubtedly are, are not so numerous as those concentrated in the external sacs, but they are widely diffused throughout the peripheral system. They develop until gastrulation begins, but how much further than that I do not know. They certainly do not produce larvæ; yet the early segmentation seems to be normal and the egg is surrounded by a chitinous shell. In one of my preparations the egg appeared to break up at a later stage and the blastomeres to separate, but this was indicated only indistinctly. The existence of these bodies in the root system is exceedingly interesting and the problem of their fate is important.

I have not observed whether the stages of development of the eggs in the external sacs and in the root system correspond exactly.

THE SOCIAL FORMS OF PELTOGASTER AND THOMPSONIA COMPARED.

"*Peltogaster socialis* . . . is remarkable for the fact that it is never found solitary, but always infests a single host in numbers varying between 4 and 30, the usual number being about 20 . . . The numerous parasites affixed to each host are always at very much the same stage of development, so that the infection by so many individuals must have taken place at the same time. There is a certain mystery to be solved here, because the parasite in general is so rare that its occurrence, when it does occur in such large numbers on a single host, must either mean a most peculiar gregarious habit in the Cypris larvæ or else we must look for some quite different explanation. The explanation which occurred to me was that the numerous individuals on a single host are really the product of a single Cypris larva by a process of budding from the endoparasitic central tumour and its root system. Although this would mean an unique process in Crustacea, namely, the production of a true colony by budding, there is nothing inherently improbable in the hypothesis, if we take into account the peculiar nature of the development of the Rhizocephala, *i. e.*, the assumption in the middle of the developmental history of an embryonic condition.

"There is also a further fact which made me expect to find such a process of budding. Delage, in his memoir, makes mention (p. 665) of finding in the central tumour of a *Sacculina interna* two cellular masses, representing the future visceral mass and mantle, instead of one, and he wonders whether it is possible for a single tumour ever to give rise to two Sacculinæ; but he dismisses the idea partly because his preparation was a poor one and partly because this hypothesis is contrary to the general facts of development.

"Now, in the course of my investigations on *Sacculina interna*, I have found incontestable evidence on two occasions that Delage's first opinion is perfectly correct, and that occasionally two Sacculinæ may begin to form a single central tumour; but whether two such Sacculinæ ever come to maturity I am unable to say. One of these specimens is shown in plate 6, fig. 10. It is here seen that two mantle and visceral masses are developing opposite one another in a single central tumour, which must of course have been produced from a single Cypris larva.

"There is therefore a tendency towards a kind of polyembryony or budding of the 'nucleus' of the central tumour in *Sacculina*, and this led me to suspect that possibly in *Peltogaster socialis*, and in such a genus as *Thylacoplethus* (Coutière), in which the parasite is present to the number of about a hundred, this process of budding has become normal and permanent.

"According to this view it should be possible to prove that the root systems of the apparently separate individuals of *P. socialis* on the same host are all in connection; I was therefore at pains to investigate this subject. To my great disappointment I was able to prove that each individual has a separate root system at no point in continuity with that of another individual. Furthermore, in one instance I was so fortunate as to come across a crab infected with *Peltogaster socialis*, the individuals of which were still internal and at a very early stage in development, and even at this early stage there is no continuity between the tumours and root systems of separate individuals. Plate 6, fig. 9, is a section taken through two central tumours of *P. socialis* . . . The hypothesis, therefore, that the individuals of *P. socialis* are produced by budding from a single tumour receives no confirmation so far from the investigation of facts, but I do not yet altogether give up the hypothesis. It may well prove that the slitting up of a single central tumour into the rudiments of several individuals takes place at a still earlier stage, before any differentiation of the tumour has occurred, possibly soon after the entrance of the embryonic cells of the Cypris larva. The final test of this hypothesis must, however, be left to the future, for someone who has the opportunity of studying either this species or some such form as *Thylacoplethus*, where material is abundant."*

I have given this quotation from Smith in full because I feel certain of the general correctness of his suggestion that where "numerous individuals on a single host"† occur in the Rhizocephala they are really produced from a single Cypris larva by a process of budding. It is amply proved in *Thompsonia,* I claim, by the evidence here put forward, even though I have not been able to describe the endoparasitic stages; and in *Peltogaster socialis,* with which the passage I quote is specially concerned, I feel confident that a similar phenomenon takes place.

It is perfectly certain, however, that the details of the budding process differ in the two genera. Smith has shown in *P. socialis,* there are, in the endoparasitic stage, separate central tumours (the *anlagen* of the visceral mass) and separate root systems belonging to them. He suggests that division of the original embryo may even take place before there has been any differentiation. Thus early division and consequent development of separate embryos, each with a separate central tumour and root system, are probably characteristic of the budding process in *P. socialis.* In *Thompsonia* the parasitic organism is at all stages continuous within the body of the host and consists of a single root system which is established first, and a large number of reproductive sacs which are budded off and become external at a later phase. Their number and late and recurrent appearance are characteristic of *Thompsonia* and correlated with a degenerate structure.

It will be of interest in connection with this discussion to give a small series of drawings of a social Rhizocephalan very similar to *Peltogaster socialis* and, I think, identical with the form from Japan described by Krüger as a new genus and species (*Peltogasterella socialis*). In 1911, while enjoying the delightful hospitality of Professor Trevor Kincaid at the Puget Sound Marine Biological Laboratory at Friday Harbour, I collected a number of individuals of the hermit crab, *Pagurus alaskensis* heavily infected by this form. Plate 2 represents the parasite at three widely different periods of growth, but in each case all the individuals are of uniform size, and, it can hardly be doubted, of the same age too. The only alternative to a theory of budding is that of simultaneous fixation of the Cypris larvæ. This theory indeed sup-

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*Smith, l. c., pp. 57–58.

†This does not apply to all the numerous instances where a crab bears two or three *Sacculinæ* or a hermit crab more than one *Peltogaster.* Far more commonly these must be cases of successive infections.

poses, as Smith remarks, "a most peculiar gregarious habit in the larvæ," and when we remember that marine larvæ are dependent for distribution, so far as we know, on chance vagaries of current rather than an internal migratory instinct, I for one can not suppose that so many larvæ should share a common path to their intended host and achieve such remarkable success in fixation. It is true that Delage, experimenting on the development of *Sacculina*, found that of a brood of Cypris larvæ, confined in a small aquarium in company with a crab, large numbers were found attached to the carapace of the crab; but this was certainly due to the stillness of the water in the aquarium and the small space in which the thousands of larvæ were confined, conditions which would hardly be repeated in nature. The fact that two Sacculinæ are occasionally, and even three rarely, found on a single host shows that contemporaneous infection does take place, but it also shows, I think, its comparative infrequency.

I regret that I can not throw further light on the question of the continuity of the root systems of adjacent parasites, for I think Geoffrey Smith's statement requires confirmation. The time at my disposal was short and material came into my hands only early in my visit, so I did not preserve it carefully for histological study. Nor was I able either to make the search I had intended for the *Peltogaster interna* stage. But the whole life history is worthy of an exhaustive study by some worker on the Pacific coast having access to this rich source of material.

THE EVOLUTION OF THOMPSONIA.

If a budding process is actually proved to exist in *Peltogaster* and *Peltogasterella* it helps us to understand how such a form as *Thompsonia* has risen. When once the continuity of the root system in *Thompsonia* is demonstrated, it becomes impossible to regard it as a primitive representative of the group; it must, on the other hand, be admitted to be the most specialised of all. The root system is undoubtedly a new development unrepresented in the typical Cirripede; but in the course of endoparasitic development in *Sacculina* it appears before the central tumour, which in its complete development as external sac may still be said to show something of Cirripede structure. But the retardation of the appearance of the external sacs here foreshadowed reaches its climax in *Thompsonia*. There is here still further exaltation of the root system at their expense, for not only do the roots fulfil their nutritive functions, but they also produce germ cells. The root system is, in point of fact, the organism and the external sacs are merely externally placed ovaries, organs of a wholly transient nature.

It is hardly possible to consider *Thompsonia* as a direct descendant of *Peltogaster socialis*, but the former genus may well have had an ancestor with many external sacs of normal Rhizocephalan type. A likely scheme of evolution is the following:

The typical Rhizocephalan with single external sac and single root system.

↓

Rhizocephalan with single root system but several external sacs of normal structure.

↓ ↓

Peltogaster socialis.
Separate external sacs and root systems.

Thompsonia.
A single root system and many externa sacs of simple structure.

In this remarkable life-history we find many phenomena which could hardly have been expected in so high a phylum as the Arthropoda. The analogy with the Fungi is strikingly shown in the mycelium-like root-system, producing its singular asexual reproductive organs, which are not dissimilar to the sporangia of a form like *Mucor*. A more convincing parallel may be drawn with a lower animal phylum, the Cœlenterata, where typical Hydromedusan forms, like *Obelia* and *Podocoryne*, produce medusa buds with a complex structure and germ cells differentiated *in situ*; while there are other genera, like *Eudendrium* and *Aglaophenia*, in which the medusoid individuals are entirely degenerate, with the simplest structure, and the germ cells are formed in the cœnosarc and migrate thence into the medusoids. If *Sacculina* and *Peltogaster* correspond roughly to the former class, *Thompsonia* occupies a place similar to that of the latter.

THOMPSONIA AND THYLACOPLETHUS.

When Coutière established his genus *Thylacoplethus* he remarked that in form it approaches *Thompsonia globosa* Kossmann:

> "Mais il doit en être séparé génériquement, même avant toute comparaison de la structure interne; *Thompsonia* a été trouvée fixée sur les pattes d'un Crabe (*Melia tesselata* Latr. provenant des Philippines), c'est-a-dire sur un Crustacé tres éloigné des Alphées dans la systématique, et d'autre part *Thylacoplethus* offre le premier exemple d'un Rhizocéphale aussi completement gregaire."

In spite of the very incomplete description of Kossmann's parasite, Häfele is almost certainly correct in identifying the Japanese form described by him as *Thompsonia*. There is only one serious discrepancy to be explained. In the type *T. globosa* only two external sacs were found upon the original host, while *T. japonica* is as "gregarious" as Coutière's *Thylacoplethus*. This is not a point, however, which weighs with me at all, for I know how easily these sacs are detached. There were probably a larger number present at the time of capture. The hosts were in both cases brachyurous Decapods and in both cases the parasites were attached to the thoracic legs. It seems, however, that *Thompsonia* is not like the other genera of Rhizocephala, the occurrence of which is confined in each case within a very narrow division of the Decapods, but enjoys a very wide diversity of hospitality; for Krüger reports that not only does *T. japonica* parasitise Brachyura, but is even found upon a hermit crab (*Pagurus striatus*). The two points, then, upon which Coutière lays such great stress are shown to be without importance by later work.

Why, then, did Häfele not recognise the identity of *Thompsonia* and *Thylacoplethus?* His negative decision rests upon points of difference in structure, but he makes some reservation owing to the unsatisfactory nature of Coutière's unillustrated account. I will quote his concluding sentence:

> "Gerade aber der Umstand, dass Coutière von einem 'Manteau à double paroi chitineux dans lequel est suspendue une masse viscérale, et qui porte une ouverture cloacale' spricht, lässt mich mit ziemlichen Sicherheit vermuten, dass in *Thylacoplethus* eine ganz andere Gattung vorliegt."

I am at a loss to understand why Häfele did not find an inner layer of chitin (the internal boundary of the mantle), but I think it will be found to exist in *T. globosa* when better preserved material is examined. With regard to the existence or non-existence of a cloacal aperture, this apparent difference is due to the fact that the organ appears only at a very late stage in development. But in any case I hardly think that, in view of the obvious agreement in structure and development, there could be any reason for separating generically *Thompsonia* (as described by Häfele) and the forms parasitic on Alpheids (as described by Coutière and myself). My own observations fail to reveal any difference between the parasites of Brachyura and Alpheids and an examination of the figures given by Häfele for *Thompsonia globosa* (for stages which the parasite of *Thalamita* does not show) and comparison with sections of corresponding stages in the Alpheid parasites show an essential similarity.

There is one point to which I refer further in the next section in Coutière's description of *Thylacoplethus*, but may be briefly mentioned here. It is the occurrence of parasites on the sternum and not on the appendages of the host. But this difference can hardly be conceived to be of generic value.

AMENDED DIAGNOSIS OF GENUS.

Thompsonia Kossmann (= *Thylacoplethus* Coutière).

A colonial Rhizocephalan infecting various Decapod Crustacea. Root system diffuse, widely distributed in body of host, sending branches into thoracic and abdominal appendages, which give off numerous sacs containing reproductive cells and becoming external at a moult of the host. These *external sacs* consist of a mantle and visceral mass without an intervening mantle cavity: mantle thin and devoid of muscle fibres. Visceral mass contains ovary only without generative ducts, testis, or nerve ganglion. Development probably parthenogenetic. Nauplius stage omitted from life-history, larvæ liberated at Cypris stage, after disintegration of the visceral mass, through apical cloacal aperture which appears in the mantle at a late stage. Moulting of host not prevented.

I will quote here the original description of Kossmann (**6**, Taf. v, Fig. II *a*):

"Die *Thompsonia globosa* entbehrt einer Mantelöffnung. Dagegen besitzt sie einen ausserordentlich langen Rüssell, welcher etwa in der Mitte seiner Länge einen Ring verdickter Cuticula zeigt. Der Körper des untersuchten Thieres war gänzlich reducirt, die Bruthöhle aber angefüllt mit Larven des Cypris stadiums, welche zwei Augen besassen. Die grösse des Thiers war sehr gering: 1.8 mm. Länge incl. des Rüssels zu 0.75 mm. Breite. Die beiden Exemplare nach welchen die obige lückenhafte Beschreibung gemacht ist, sassen beide, nicht am Abdomen, sondern an den Beinen einer *Melia tresselata*. Fundort, Aibukit, Palaos."

THE SPECIES OF THOMPSONIA.

The following is a list of the species which have been described up to the present:

	Host.	Place.	Lenth of external sac.
Thompsonia globosa Kossm....	Melia tessellata.....	Aibukit Pelews...	1.8 mm.
Thompsonia (Thylacoplethus) edwardsi Cout.	Alpheus edwardsi....	Thursday Island, Torres Straits.	
Thompsonia (Thylacoplethus) heurteli Cout.	Alpheus macrochirus	Fernando Veloso..	4.5 mm.
Thompsonia (Thylacoplethus) sp.	Alpheus avarus......	Torres Straits....	1 mm. (young).
Thompsonia japonica Häfele..	Pilumnus sp........ Pagurus striatus.....	Japan........... Japan.	2 mm. elongated.
Thompsonia affinis Krüger....	Diptychus sp.......	Japan...........	1 mm. round.

This list does not include the parasite mentioned by Spence Bate as occurring on *Alpheus digitatus* from Fiji. It appears to be a species of *Thompsonia*.

I next give a tabular statement of the forms of *Thompsonia* which I have seen myself and the characters in which they differ:

Species on which the forms occur.	Localities.	Differences in characteristics.
Synalpheus brucei...	Murray Island, Torres Straits..	External sac, pear-shaped, pink, 1 mm. long. Cypris.
Actæa ruppellii.....	South Africa..................	External sac, pear-shaped to round, 1 mm. long.
Thalamita prymna..	Murray Island, Torres Straits..	External sac, elongate, lemon-yellow, 3 mm. long. Cypris.

It is, I think, very difficult to establish specific distinctions until more material of *Thompsonia* has been collected and compared. At present one can not say how far the character of the host affects such superficial characters as size, shape, and colour. I think that in the three forms which I have examined we very possibly have three distinct species, but I refrain from burdening systematic zoology with fresh names when we know so little about the validity of those already given.

One point in Coutière's description of *Thylacoplethus* may have an important bearing on the systematic question. In the three Alpheids which he examined the parasites were, he says, situated on "les quatres premiers pléosternites, qui se montrent soulevés en un large bourrelet transversal." And he contrasts this with the form, certainly very near and probably identical,* which Spence Bate mentions and figures in the *Challenger* monograph on the Decapoda, occurring to the number of 30 individuals at the base of the abdominal appendages of *Alpheus malleodigitatus* from Fiji. The parasites which I describe from *Synalpheus* are also confined to the appendages and are therefore, if I read Coutière's account aright, much more like the *Challenger* form than are those of the French investigator. It is possible that a section of the genus is characterised by the occurrence of the external sacs on the sternum rather than on the appendages.

THE INFLUENCE OF THE PARASITE ON THE HOST.

So far as my material goes, the effect of the parasite upon the host is negligible. The gonad does not diminish in size and in some cases at least does not cease to function. One female Alpheid which I collected had both fertilised eggs and parasites upon her abdominal appendages. This was probably an exceptional case.

The secondary sexual characters do not undergo any change. The specimen of *Thalamita prymna* was a heavily parasitised male, but the abdomen showed no broadening, assumption of female appendages, or diminution of copulatory appendages. In the Alpheid *Synalpheus brucei* the abdominal appendages do not differ in the two sexes and the female is to be distinguished from the male only by the greater width of the abdomen and better development of the pleura. This character is not affected by the parasite.

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*Spence Bate did not think that his parasite was related to *Sacculina* because the embryo exhibited no Crustacean affinities. Development must have been at a very early stage; the general appearance and position are so unmistakably those of *Thompsonia*.

SUMMARY.

(1) The root system of *Thompsonia* is continuous throughout the body of the host, whatever the number or stage of development of the external sacs may be.

(2) Where they penetrate the appendages the roots contain fewer yolk globules and the lacunar space is filled with germ cells. Besides the external sacs, there are a number of terminal swellings in the tissue of the appendages. These are similar in structure to the external sacs and become external at a subsequent moult of the host.

(3) The external sacs consist of a mantle with an external and internal cuticular investment and a visceral mass mainly occupied by the ovary. No mantle cavity is found between the mantle and visceral mass.

(4) There is no testis, development being in all probability parthenogenetic. The egg is lightly yolked and gastrulation takes place by epibole. The Nauplius stage is omitted from the life history, the young hatching at the Cypris stage.

(5) During development the visceral mass disintegrates so that at the time of hatching the mantle contains a great number of Cypris larvæ ready to emerge. An apical perforation is made in the mantle, and on the moult of the cuticle a way is thus opened to the exterior for the larvæ.

(6) The escape of the larvæ is contemporaneous with or soon followed by a moult of the host. The empty shells of external sacs are carried away with the cast skin, and the terminal swellings of the root system emerge as a new crop of external sacs.

(7) Development of the germ cells in the lacunar tissue of the roots may take place *in situ* as well as in the external sacs, but it does not apparently proceed very far.

(8) The large number of external sacs in both *Thompsonia* and *Peltogaster socialis* is accounted for by a process of internal budding from a single original larva.

(9) *Thompsonia* is not a primitive Rhizocephalan, but a very specialised form.

(10) The genus *Thylacoplethus* Coutière is synonymous with *Thompsonia* Kossmann.

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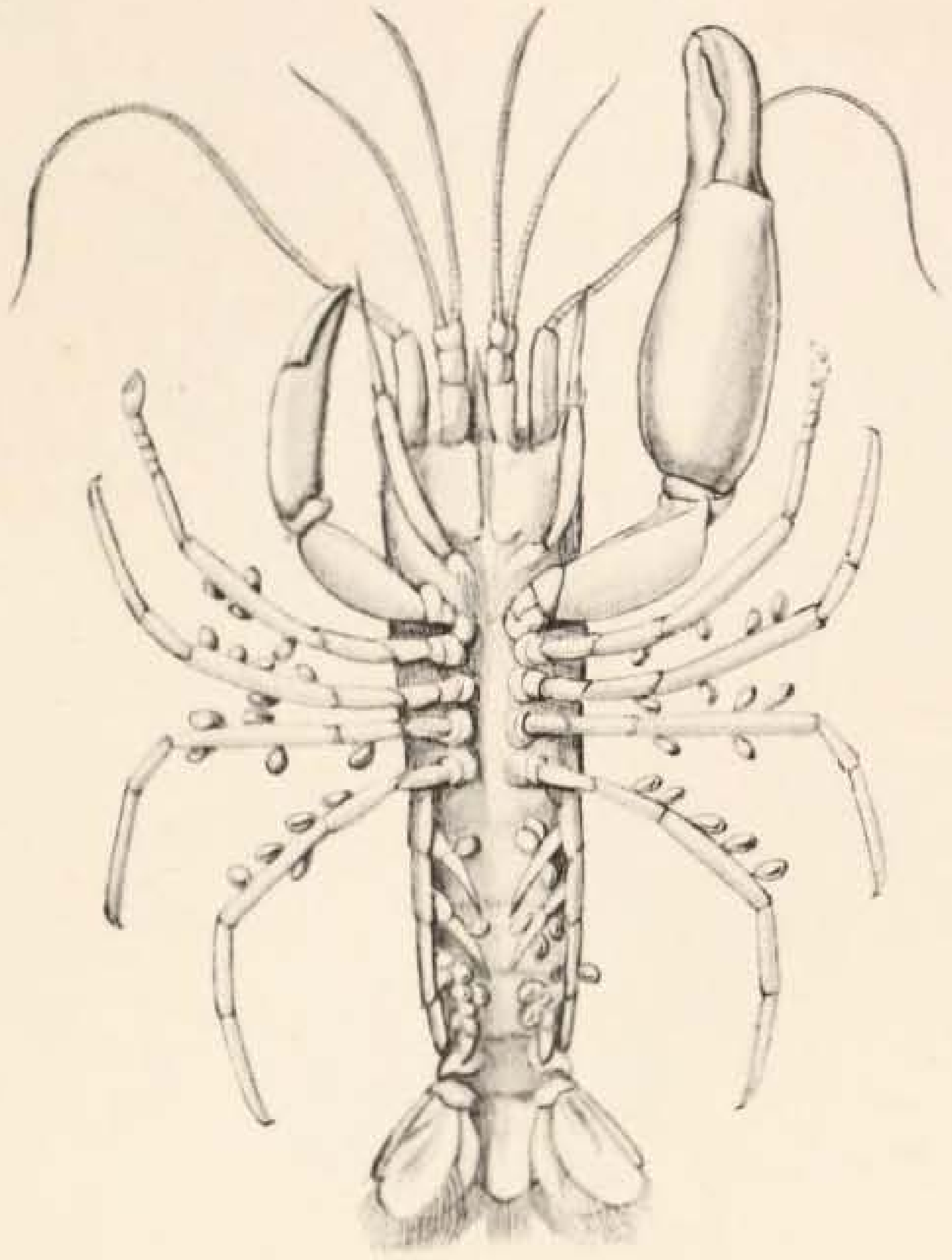

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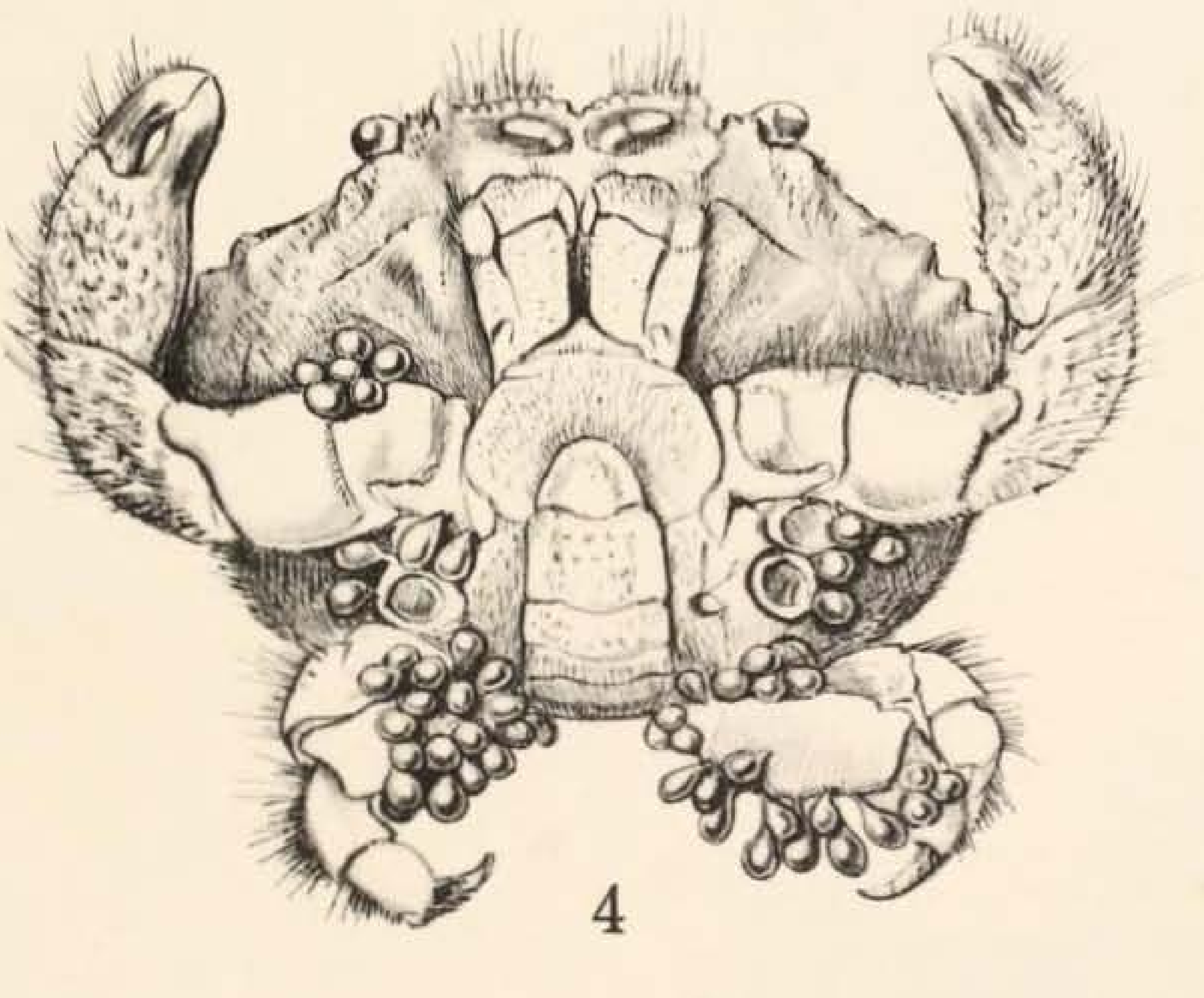

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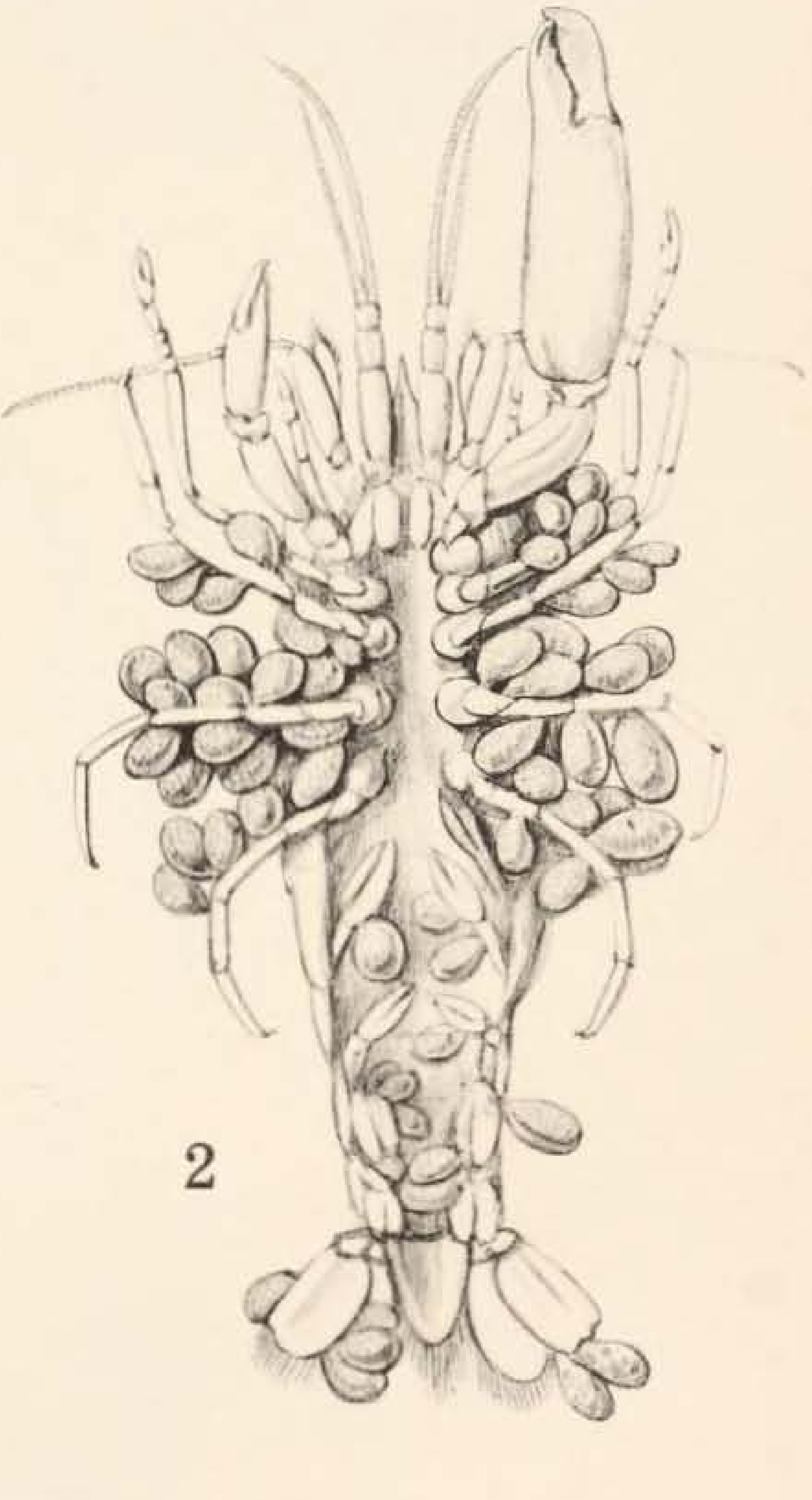

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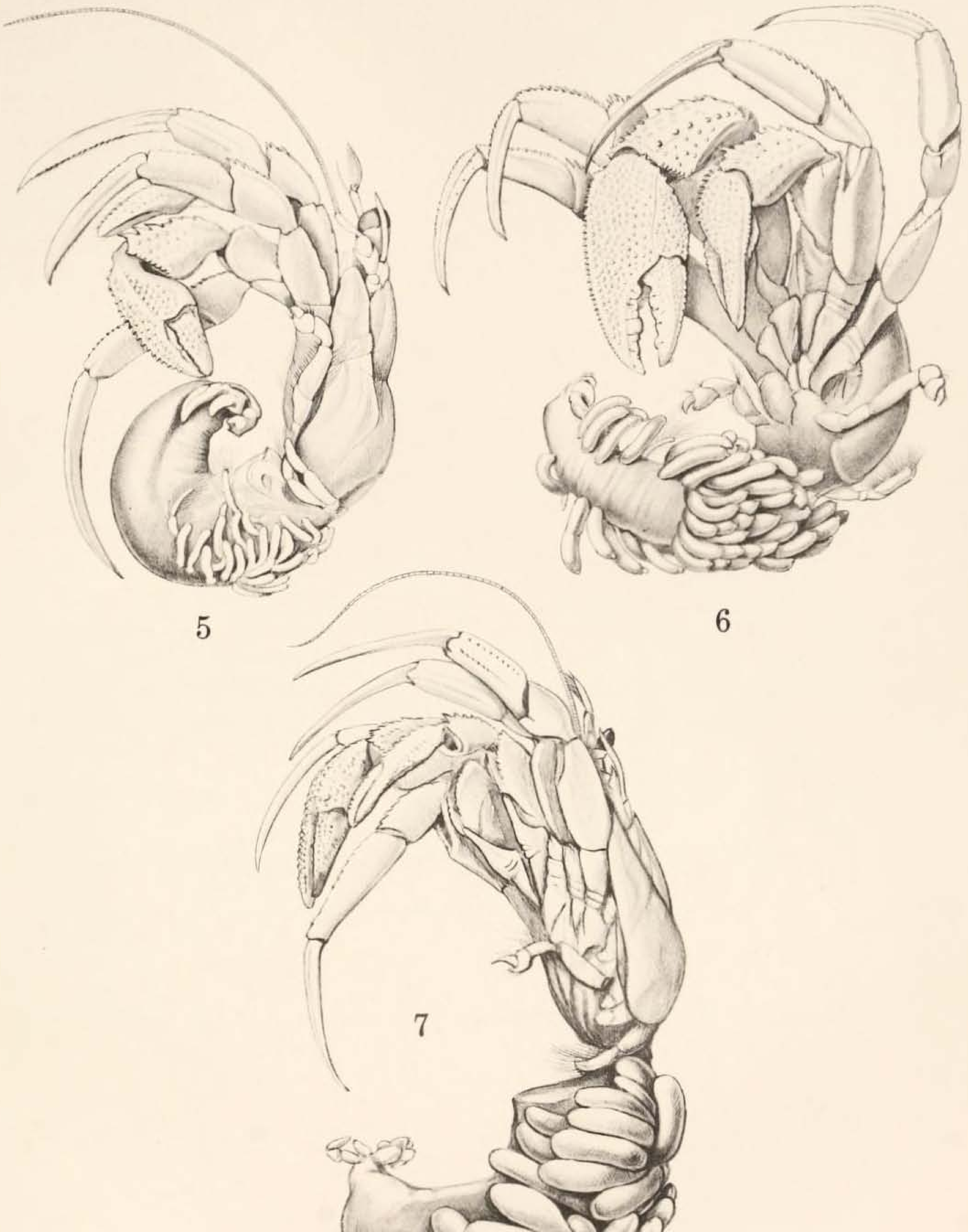
Fig. 1. Thompsonia on Synalpheus brucei. Young external sacs on the abdominal and thoracic appendages. x 3.

Fig. 2. The same at a later stage. The external sacs now contain Cypris larvæ which are roughly indicated within. x 3.

Fig. 3. Thompsonia on Thalamita prymna. To show the very large number of external sacs occurring on this specimen. Natural size.

Fig. 4. Thompsonia on Actæa ruppellii. External sacs pear-shaped. x 2.

The first three specimens figured are from Murray Island, the fourth from South Africa.



Peltogasterella socialis, Krüger.

Figs. 5, 6, and 7. Stages in growth of the external sacs of Peltogasterella socialis, on Pagurus alaskensis. x 2. Friday Harbour, San Juan Archipelago, State of Washington, U. S. A.