FAUNA UND FLORA

DES GOLFES VON NEAPEL

UND DER

ANGRENZENDEN MEERES-ABSCHNITTE.

HERAUSGEGEBEN

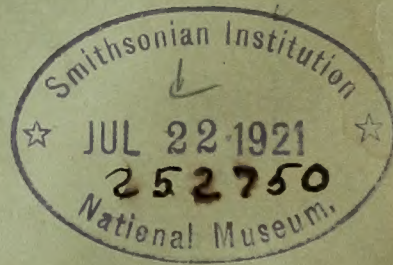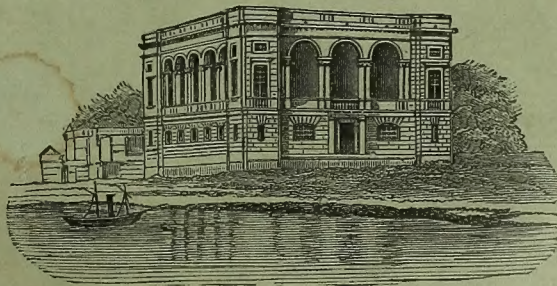#### VON DER

ZOOLOGISCHEN STATION ZU NEAPEL.

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29. MONOGRAPHIE:

"RHIZOCEPHALA"

BY

GEOFFREY SMITH, B. A. OXFORD.

MIT 24 FIGUREN IM TEXT UND 8 TAFELN.

BERLIN

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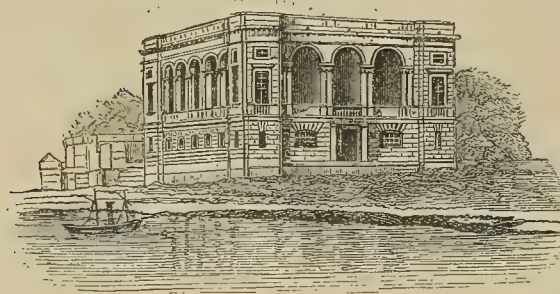
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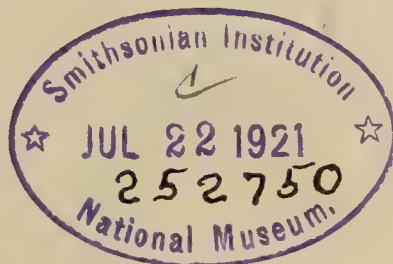## GEOFFREY SMITH, B. A. OXFORD.

WITH 24 TEXTFIGURES AND 8 PLATES.

HERAUSGEGEBEN

VON DER

ZOOLOGISCHEN STATION ZU NEAPEL.

BERLIN

Preface.

The group of parasitic Cirripedes monographed in this book has engaged the attention of many celebrated naturalists since the time of CAVOLINI, and in comparatively recent years has formed the subject of a keenly contested controversy: it may therefore seem a bold step for an unknown writer to enter the field with a monograph which to many will seem to affect the pretension without attaining the reality of completeness.

But I cannot disguise from myself, and I have neither the wish nor the power to disguise from other people, the many respects in which my work not only falls short of completeness but has been entirely baffled by difficulties of observation and reasoning; and perhaps the best plea I can put forward for avoiding a too harsh criticism is that my very lack of completeness and finality is in part due to the many curious facts which my work has partially brought to light but which will require future independent investigations to fully clear up.

Not to mention a number of observers who have laid the basis of our knowledge of the Rhizocephala, we owe most perhaps to the two contemporary French naturalists, Professors DELAGE and GIARD, to the former for his work on the anatomy and life-history of *Sacculina carcini*, and to the latter for his interesting observations on the effect of the parasites on their hosts. It is a matter of regret that these two authors are unable to agree upon many fundamental questions in this subject, but I trust that the record of my observations made under a deep sense of obligation to their work, may, without escaping their criticism, engage their impartial consideration.

There remains for me in this preface the duty of acknowledging the support of institutions and the generosity of friends, without whose help I could not have undertaken this work.

The observations recorded in this book extend over a space of nearly three years, and were made for the most part at the Zoological Station of Naples, during my occupancy of the Oxford Biological Scholarship for two years, and of the British Association Table for one year.

To Professor DOHRN I am more deeply indebted than I can well express for the continuous support which he has given me in my work, and for the many suggestions which he has offered relatively to the morphology of my group.

To the whole staff of the Zoological Station and particularly to Professor MAYER under whose province my work especially came, I am deeply obliged for their friendly attention to my needs.

Of the many friends and acquaintances who have helped me I would mention especially Dr. H. J. HANSEN, who, during my visit to Kjöbenhavn, introduced me to the riches of the collection under his charge, and put many rare specimens at my disposal, the value of which to my work has been very great. Dr. W. CALMAN, of the British Museum, has not only assisted my examination of the specimens under his charge, but has materially helped me in acquiring what I believe are just views of the morphological relationship of the Rhizocephala to normal Cirripedes. To Dr. DUNCKER I am indebted for specimens and manuscript notes which are considered in the proper place, while Mr. PUNNETT kindly gave me two specimens of *Anelasma squalicola* which have been of great use to me, Mr. CROSSLAND some interesting specimens from the Red Sea, and Prof. D'ARCY THOMPSON a specimen of the rare form *Sylon*.

New College, Oxford, August 1906.

Contents.

Chapter 1.

Bibliography and General Morphology.

1. Bibliography.

In reviewing our progress in knowledge of the animals which form the subject of this monograph, I will only refer to the most important papers previous to 1884, because DELAGE in his memoir on *Sacculina* (**14**) published in that year has not only given a very complete bibliography but also a spirited critique of many of the authors cited. Moreover at the end of each chapter in the body of this book, a special bibliography is given with reference to each particular branch of our subject.

I am pleased to think that the study of the Rhizocephala began in Naples in 1787, when CAVOLINI (**1**) published his volume "Sulla generazione dei Pesci e dei Granchi". Although his view of the adult *Sacculina* as a morbid growth produced by the crab to surround a deposit of the eggs of a parasite is only of historic interest, we may admire the fortune and merit of the Neapolitan naturalist in recognizing the Crustaceous nature of the parasite through its Nauplius larvae, and also in discovering the Cryptoniscus larva of a parasite of the *Sacculina*, which he rightly referred to the Isopoda, under the name *Oniscus squilliformis*. His work was ignored till 1854, and unsurpassed till 1862.

The correct reference of *Sacculina* to the Cirripedes is due to J. V. THOMPSON (**2**) in 1836, but he did not greatly add to our knowledge of the group.

In 1858 and 1862 ANDERSON (**3** and **5**) made the distinct advance of recognizing the method of nourishment by an internal root system in both *Peltogaster* and *Sacculina*; and in 1861 LILLJEBORG (**4**) made some anatomical observations of real merit, and discovered a degenerate Cypris male in *Peltogaster* fixed at the mantle opening, without however recognizing the meaning or importance of his discovery.

I pass to the papers of FRITZ MÜLLER (**6** and **7**) in 1862 and 1863 which constitute a real advance, for besides elucidating the main features in the anatomy of the adult, he care-

fully describes the Nauplius and Cypris stages, and also places Lilljeborg's discovery of the larval males, whose nature he rightly surmises, upon a firm basis.

In 1873 and 1874 appeared a series of papers by Giard (**8, 11** and **12**) and Kossmann (**9** and **10**), whose chief merit appears to me to be the recognition of the orientation of the body and the position of the mesentery as furnishing the clue to the inter-relationship of the parasites. But I cannot accept a deal of Kossmann's systematic work, and there is no trace of a suspicion in the work of either Kossmann or Giard of the complicated life-history subsequently discovered by Delage.

In 1875 Dohrn (**13**) in his well known essay on Vertebrate descent advanced the view, which despite Delage's arguments I believe to be correct, that the Rhizocephala are fixed to their hosts by a part of the body corresponding to the stalk of the Cirripedia. This view, based on a comparison of the Rhizocephala with *Anelasma*, might belong, according to the rules of priority to Kossmann (**10**), who admits that he owed to Professor Dohrn the inspiration to study *Anelasma* and the possession of his material for the study. His possession of the theory, however, is not so secure; for in his first paper (**9** p. 34) he announces, and in his second (**10** p. 11) reaffirms the discovery of a tube in *Sacculina hians*, running from the ring of attachment (Rüssel) and opening in the mantle cavity, which he takes to be the remnant of the gut, an interpretation which, if it were real, would be quite disastrous to his theory that the ring of attachment is homologous to the stalk of the Cirripedes, and would confirm the previously accepted view that the ring of attachment equals the mouth.

But this theory of the relationship of *Anelasma* to the Rhizocephala, which appears to be suddenly revealed in Kossmann's paper, was accurately sketched by Lilljeborg (**4** p. 82), thirteen years previously. The Norwegian naturalist's essay is written in French, but this can hardly account for Kossmann's neglect of it.

In 1884 Delage's monograph (**14**) appeared containing a very complete exposition of the anatomy and life-history of *Sacculina carcini* (Thompson). In this extremely interesting work the author makes most important additions to our knowledge of the general anatomy, describing the nervous system for the first time; but the discovery which attracted the wondering attention of all naturalists was the method of fixation of the Cypris larva upon an hair on any part of the host's body, except on the ventral surface of the abdomen where the adult *Sacculina* is situated, the migration of the cells of the larva into the crab's body where they establish the system of roots, and the subsequent appearance upon the lower part of the crab's intestine of the Sacculina interna which afterwards becomes evaginated as the adolescent Sacculina externa. Delage observed in numerous cases the fixation of the Cypris larvae and their subsequent transformation leading to the so-called Kentrogon stage, but he did not observe the actual passage of the cells into the crab's body, because the larvae under his observation died soon after the assumption of what he terms the Kentrogon stage. There is therefore a lacuna in Delage's account of the life history between the fixation of the Cypris larva and the appearance of the parasite within the body of the crab, fixed upon the intestine roughly

at the point where the adult *Sacculina* is definitely attached. DELAGE fills in this lacuna by the very just inference that the cells of the Cypris larva, after reaching the blood system of the crab wander through the body establishing the root system, and finally, on reaching the intestine at the junction of thorax and abdomen, form the body of the Sacculina interna which he found at various stages of development in this position.

Before DELAGE's discovery it must be remarked that no one knew that the parasite passed through an internal stage at all. It was generally supposed (e. g. KOSSMANN) that the Cypris larva fixed itself upon the abdomen of the crab and became transformed in situ into the adult animal. GIARD in fact suggested that he had seen the parasite in process of development at this point, a pretended discovery which wasted a great deal of DELAGE's time, so we are told, and drew from him a decidedly caustic criticism. (Loc. cit. p. 557.)

Besides observations on the fixation and internal stages, DELAGE rediscovered the larval males of FRITZ MÜLLER, and affirmed that they are always present to the number of 1—12 attached to the mantle-opening of Sacculinae which have recently become external. He never succeeded in observing more than the dead cuticle of these larvae, a failure shared by all previous observers. But DELAGE, from their invariable occurrence, utterly repudiates GIARD's suggestion that they are only ordinary larvae fixed there by accident, and he accepts MÜLLER's interpretation of them as larval males. Finally, with regard to the effect of the parasite on the host, DELAGE criticises unfavourably the suggestions of previous authors, dismisses, curiously enough, GIARD's observation as to the sterility of the host effected by the parasite, and states that the chief effect is that the crab is inhibited in its growth and prevented from moulting.

In this short review we have only touched on controversial questions and have not pretended to give a complete summary of DELAGE's masterly memoir, to which further reference will frequently be made. DELAGE's account of the fixation and internal parasitism of *Sacculina* has been generally accepted and incorporated in all the standard text-books, but there has been one dissentient, loudly dissentient, voice. Professor GIARD (**16**) in 1886 published a note in the Comptes Rendus entitled "Sur l'orientation de la Sacculine". He here finds fault with DELAGE's explication of the asymmetry of the adult *Sacculina* and reaffirms his own, with the criticism that DELAGE's view is influenced by his preconceived idea that the position of fixation of the Cypris larva cannot affect the symmetry of the adult. He suggests that HESSE in 1866 had seen and recognised Sacculinae internae and that all the world had seen them as well as DELAGE: he next denies that *Sacculina* is ever really internal, and supposes that it only appeared so to DELAGE owing to his brutal method of tearing out the intestine of the crab: finally he records his conviction that the fixation of the Cypris larvae described by DELAGE is purely abnormal and that the true method of fixation is local upon the spot where the parasite becomes adult. The only new observation of fact which GIARD makes in this critical note (it is used as an argument against DELAGE) is that *Sacculina neglecta* only infects the female of *Inachus scorpio*, a statement which he withdraws in a subsequent note. In this succeeding note (**18**) GIARD makes his first observation upon the highly interesting phenomenon

of parasitic castration, the discovery of which is due to him. Reference to his valuable papers and to others on this subject are given in the special Bibliography at the end of Chapter 5, and in that Chapter my researches founded on his work are described.

DELAGE (**17**) replied to GIARD's criticism, and in answer to the latter's accusation of entertaining preconceived ideas as to the fixation of the larvae, remarks, "J'ai fait fixer des milliers de Cypris. Toutes se sont attachées aux pattes, au thorax, etc. aucune à la face ventrale de l'abdomen; d'où je conclus que la fixation n'a pas lieu sous l'abdomen. M. GIARD n'a jamais vu la fixation, pas plus à l'abdomen qu'ailleurs, et il conclut que c'est à l'abdomen que se fixent les Cypris. Lequel de nous juge d'après des idées préconçues?"

In 1888 HOEK (**19**) published an account of a new species of *Sylon*, and the following year GIARD (**20**) in commenting on this species uses the fact that the basilar membrane is separated from the intestinal wall by a thick muscular mass as an argument against the indefinitely localized fixation advocated by DELAGE for *Sacculina*. He further states that *Sacculina* "garde constamment, comme je l'ai indiqué, ses rapports avec l'extérieur", and this we take to be a denial of the occurrence of Sacculina interna.

In 1891 GIARD (**21**) comments upon certain Ascothoracica, and introduces a discussion upon the genus *Sphaerothylacus* which lives in colonies fixed to the branchial chamber of Ascidians. GIARD holds that *Sphaerothylacus* is a link between Ascothoracida and Rhizocephala, and concludes — "la seule connaissance de ce type intéressant suffit à démolir le roman échafaudé par DELAGE avec une mise en scène qui a pu en s'imposer à beaucoup de zoologistes. Nous aurons occasion de revenir prochainement sur cette gigantesque mystification".

In 1898 SCHIMKEWITSCH (**22**) gives an account of the discovery by PEKARSKY of an endoparasite stage in the life-history of *Peltogaster* corresponding to DELAGE's Sacculina interna.

In 1900 DELAGE (**23**) states that he found a young crab at Roscoff with a Kentrogon larva attached to a hair on one of its legs, and when the crab moulted he preserved the integument with the remains of the Kentrogon on it. Some months later, a Sacculina interna appeared upon the crab's intestine.

In 1901 DUBOSCQ (**24**) investigated the spermatogenesis of *Sacculina carcini* and remarks in a footnote: "Le stade de *Sacculina* interne n'est pas niable. Des coupes seriées montrent qu'il n'y a, d'abord aucun rapport, même de contiguité entre la jeune Sacculine et l'épithélium externe du crabe".

In 1902 COUTIÈRE (**25**) published a series of notes on a most interesting gregarious parasite of the Alpheidae for which he has created the generic name *Thylacoplethus*. The author considers that since the roots of the parasites are confined to a limited area round the intestine, this parasite does not pass through an internal stage similar to that described by DELAGE for *Sacculina carcini*.

I have now summarised the chief papers which bear upon the controversy as to the fixation and endoparasitism of the Rhizocephala. The position which GIARD originally took up on the appearance of DELAGE's work and from which he has never withdrawn, has naturally

had an influence in throwing doubt upon this subject, but from a mere consideration of the literature it is clear that neither GIARD's position nor the doubt diffused from it are justified. From my own observations recorded in chapter 4 of this book, I am forced to the conclusion that DELAGE's account of the life-history of *Sacculina* is in its main outlines perfectly correct, the two fundamental postulates of DELAGE's account, (1) that *Sacculina* passes through an entirely endoparasitic stage, and (2) that it enters the body of the host at some point other than that at which it is finally affixed in the adult state, being confirmed in detail.

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12. —— ——, Sur l'éthologie de la *Sacculina carcini*. ibid. Tome 79 p. 24 1874.
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25. **Coutière**, A., Sur un type nouveau de Rhizocephale. in: C. R. Acad. Sc. Paris Tome 134 p. 913 and 1452 1902 and in: C. R. Soc. Biol. Paris Tome 54 p. 447, 625 and 724 1902.

2. General Morphology.

The Rhizocephala, excluding certain doubtful forms which have been held to be linked with them, are a compact group of parasites comprising a few genera, all of which exhibit a similar organization and habit of life. All the known genera except one, are parasites of Decapod Crustacea; the Macrura, Anomura and Brachyura being all liable to the attacks of special kinds: the one exception is the curious genus *Duplorbis*, found by Dr. H. J. HANSEN in a collection from Greenland and described for the first time in this work, which infects the Isopod, *Calathura brachiata*.

The parasites are most frequently solitary, a single individual infesting each host; there are however gregarious species such as *Peltogaster socialis* and *Thylacoplethus* which are never solitary, and even in the typically solitary forms it very frequently occurs that two or more individuals of the parasite are found on one and the same host.

In the adult state the Rhizocephala are partly ectoparasitic and partly endoparasitic, the body consisting of two portions, an external sac containing the reproductive, muscular and nervous organs, and an internal system of ramifying roots which absorb the nourishment from the internal juices of the host. All the species, however, whose life-histories are known, pass through a most elaborate metamorphosis before achieving this stage, being at first free-swimming larvae and subsequently passing through a completely endoparasitic stage in the body of the host.

The external sac-like portion of the adult body frequently takes up the position on the host which is normally occupied by the brood of eggs, and the colour and appearance of this sac is frequently assimilated to the colour and appearance of the eggs, conspicuously in *Peltogaster* (Plate 1 fig. 8). Moreover since the parasite in the majority of cases has the remarkable property of calling forth the development of female characteristics in the male host, this position of the parasite is almost always of advantage, because even when it is situated on a male host it is frequently protected by the development of those structures of the host's body which are intended to safeguard the eggs. These facts and the general appearance of the various parasites on their hosts are illustrated on Plate 1.

The Rhizocephala are known from almost all seas and at all latitudes from the Arctic circle to the tropics, but the best known species come from the North Sea, from the English and French Coasts and the Mediterranean.

The morphology of our group might be treated in a purely descriptive method, but the anatomy of *Sacculina* has already been elucidated by DELAGE (**14**) with detailed correctness, and in the systematic part of this work full diagnoses of the genera are given; we will therefore here introduce a series of salient anatomical facts as evidence of phylogenetic relationship, remembering that although every phylogenetic system is to a certain extent arbitrary, the mind desires an ordered system and the imagination is aroused in endeavouring to reconstruct the

past. We will therefore consider the comparative anatomy of the Rhizocephala with refer-ence to two problems, firstly what is the relationship of the Rhizocephala to other Crustacea, secondly what is the relationship inter se of the different forms of Rhizocephala. The partial solution of these problems will bear a practical importance since it will enable us to determine a rational orientation of the body of these imperfectly understood animals.

A. The Relationship of Rhizocephala to other Crustacea.

An examination of the characters of an adult, without limbs or gut and with the ner-vous system reduced to a single ganglion, might leave us in doubt not only of the order of Crustacea to which the Rhizocephala should be referred, but even as to their Crustacean affi-nities at all: we are however able from the distinctive features of their free-swimming larvae to fix the Rhizocephala as a suborder of the Cirripedia. The shape of the Nauplius with its frontal horns (Plate 4 figs. 17 and 18) and the passage through a Cypris stage (Plate 4 fig. 19), characteristic of Cirripedes, are sufficient for the argument. It may nevertheless be borne in mind that the Nauplius and Cypris larvae of the Rhizocephala differ from those of all other Cirripedes in the invariable absence of a gut, but this peculiarity is correlated with the sub-sequent endoparasitic development. The endoparasitic stage which follows the free-swimming Cypris stage throws a great difficulty in the way of interpreting the adult anatomy, for this endoparasitic stage practically amounts to the resumption of an embryonic state in which all continuity with the organs and orientation of the Cypris larva is lost. The adult parasite is evolved from a little mass of undifferentiated embryonic cells which are passed from the body of the Cypris into the body-cavity of the host and after a period of wandering and growth become differentiated into the two essential portions of the adult body, namely the root system which remains inside the host, and the sac-like external portion which is thrust out of the host's body and comes to maturity ectoparasitically. It is this external sac-like portion which carries all the essential adult organs and which we must attempt to homologise in some manner with the adult Cirripede body, but the discontinuous method of development of this body from the Cypris larva precludes the possibility of founding our homologies on an em-bryonic basis.

We are therefore compelled to seek in the comparative relations of the adult anatomy itself for some clue as to the orientation and homology of the body relatively to other Cirripedes.

To illustrate the adult structure of our group I choose *Peltogaster*, because for reasons that will be given later, this genus may be considered to retain the simplest and most typical organization of the Rhizocephala.

The Root system of *Peltogaster* does not concern us; it forms a compact green mass in the abdomen of the infected Hermit-crab, taking up the position of the gonad. The roots communicate with the external portion of the body at the chitinous ring which affixes the

latter to the abdomen of the host; the method of communication between the root system and the external portion of the body is shown in transverse section on Plate 6 fig. 6, which passes through the chitinous ring: the tissues of the host are distinguished by the red tint.

The external sac-like portion of a *Peltogaster* with which we are now concerned is of a vivid red colour and of an irregular cylindrical shape (Plate 1 fig. 8); anatomically it consists of two chief parts: an external mantle, which surrounds a visceral mass.
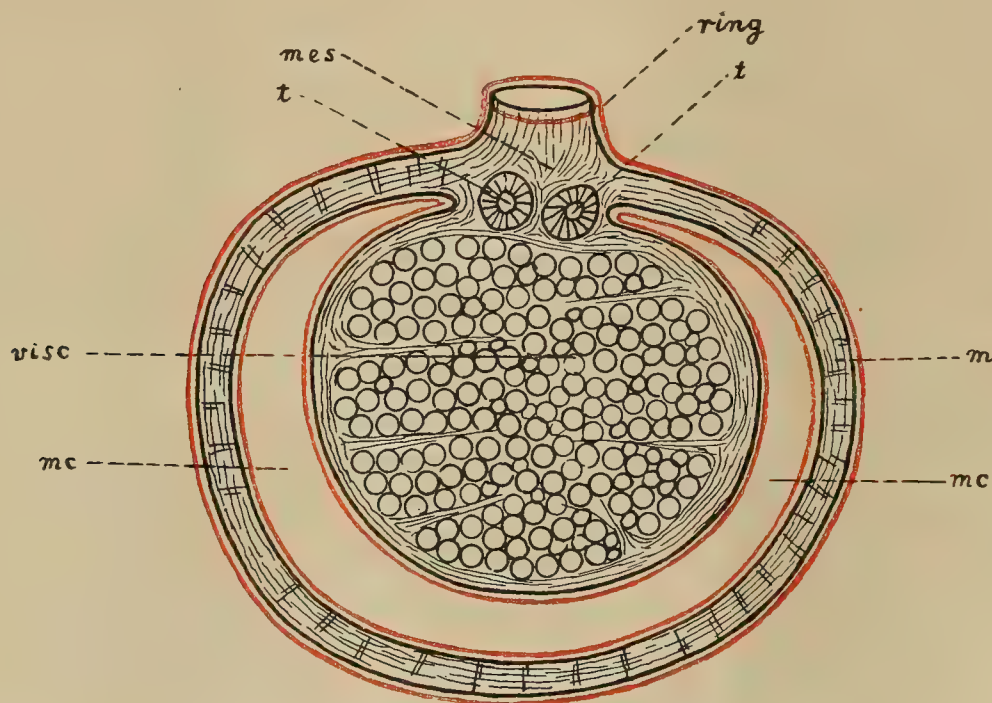
Text fig. 1.

As seen in the diagrammatic transverse section (Text fig. 1) between the mantle (*m*) and the visceral mass (*visc*) there is a cavity, the mantle cavity or brood pouch (*mc*): this cavity extends all round the visceral mass, except along the surface apposed to the abdomen of the host; here the visceral mass is broadly attached to the mantle cavity by means of a mesentery (*mes*) which runs in the long axis of the body, and is pierced in the centre by the ring of attachment (*ring*). The mantle externally and the whole of the mantle cavity internally is lined with chitin (coloured red in diagram); the mantle is provided with circular and longitudinal muscles, and so also is the visceral mass.

Besides the muscular and connective tissues of the mantle and visceral mass, *Peltogaster* is provided with several organs, the relative positions of which are of great importance.

At the end of the body pointing to the head of the host is the mantle opening (*op*), often misnamed the cloaca; this opening, which serves for the aeration of the brood pouch and for the emission of the Nauplius young, is provided with a sphincter muscle, and its lower lip is attached to an extremity of the mesentery. In the diagrammatic longitudinal section of *Peltogaster* shown in Text figure 2, the mantle opening is seen (*op*), the mesentery (*mes*) is indicated by the horizontal lines at the base of the figure, and at the junction of mesentery and visceral mass are shown the nervous ganglion (*gn*), and the openings of the oviduct (*ovd*)

and vas deferens (*vd*) of one side, the latter two organs being bilateral, but the ganglion median and unpaired. The testes (*t*) are small tubes lying in the mesentery, while the ovaries (*ov*) occupy the main bulk of the visceral mass. Such are the main outlines of the anatomy of
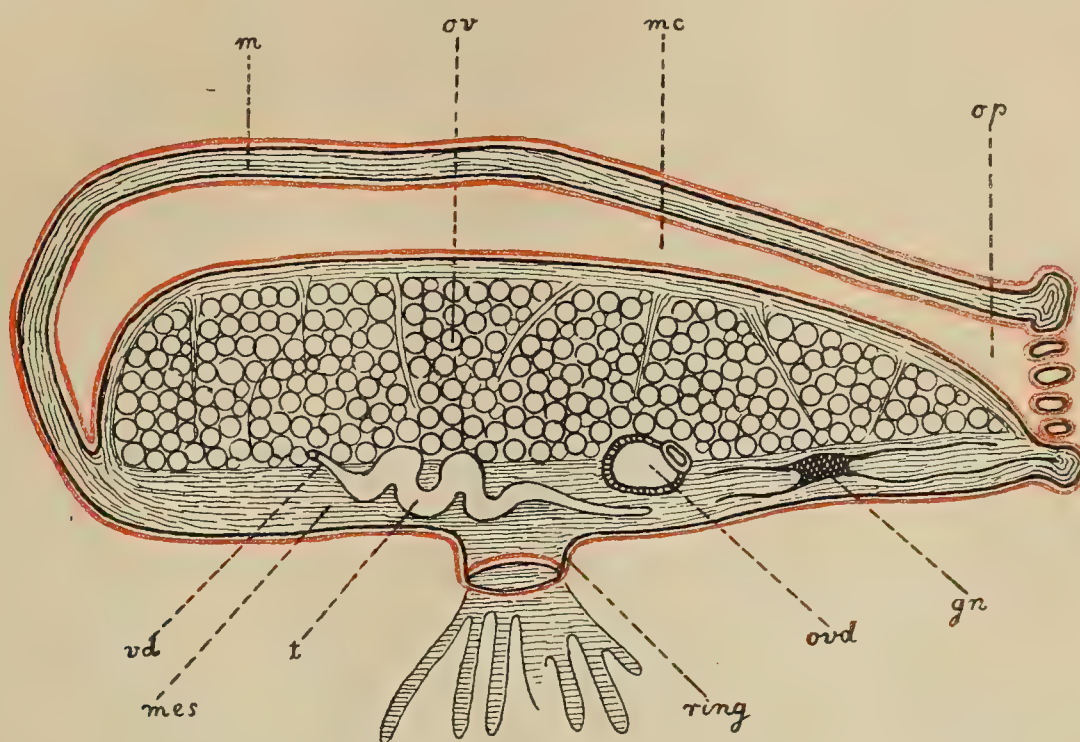
Text fig. 2.
Ideal longitudinal section passing a little to one side of middle line.

Peltogaster, and this essential organization is followed out with various complications in the other genera of Rhizocephala.

The proximity of the ganglion to the mantle opening, and the position of the oviducts between the ganglion and the vasa deferentia, give us the clue to the orientation of the body relatively to normal Cirripedes. In Text fig. 3 B is represented a diagrammatic longitudinal
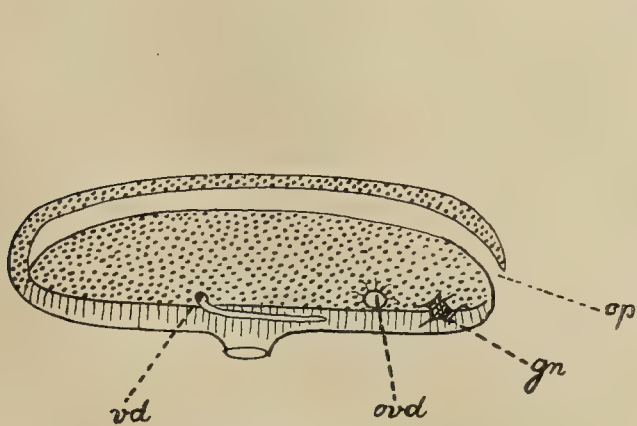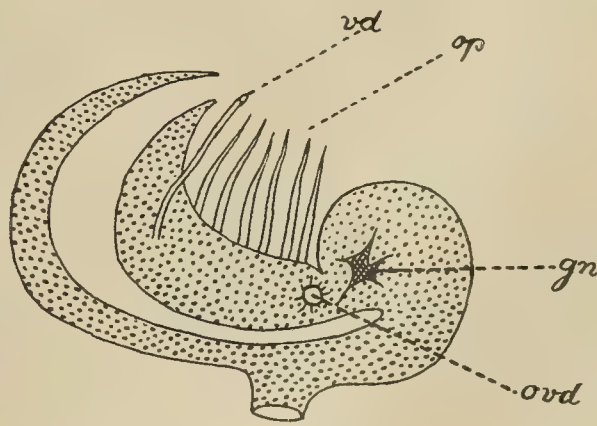
Text fig. 3 A.   Text fig. 3 B.

section through a typical Cirripede, and here the essential relations of brain (*gn*), oviduct (*ovd*) and vas deferens (*vd*) are shown to be the same as those in *Peltogaster* represented in Text fig. 3 A; the peculiarly anterior position of the oviducts in normal Cirripedes being reproduced in *Pelto-gaster*. The relations of the mantle in our typical Cirripede and in *Peltogaster* are seen to differ

considerably, but it must be remembered that the dorsal fold in Cirripedes which cuts off the body from the mantle is developmentally a late modification, the Cypris larva possessing a median dorsal attachment of the bivalve carapace to the body, which we may take to represent the mesentery of *Peltogaster*.   Obliterating therefore the fold along the dorsal middle line in our typical Cirripede and apposing the posterior edge of the mantle towards the head so as to form a small anterior mantle opening, we obtain the essential relations of *Peltogaster* in all respects.   This morphological comparison, which was suggested to me by Dr. CALMAN, appears so satisfactory that on the strength of it we may proceed to fix the orientation of *Peltogaster*, and by implication of the Rhizocephala in general.

Clearly the long axis of the mesentery fixes the antero-posterior axis, and the anterior pole is occupied by the mantle opening.   The mesentery is situated on the dorsal surface, and the ring of attachment is homologous to the stalk or peduncle of the Cirripedes. The ganglion, situated anteriorly and dorsally, corresponds to the brain of the Cirripedia.

The morphological interpretation here offered is different to that of DELAGE (**14**, p. 699 and 700), who relying on the fact that a single ganglion is present, considers that the body of the Rhizocephala represents merely the head of a normal Cirripede, and since the ganglion of *Sacculina* is developed from a portion of the mantle and the visceral mass near the mesentery, he regards the mesenterial surface as ventral, because the nervous system is always developed ventrally in Crustacea.   But we may object that the ganglion is developed laterally and not in the line of the mesentery (see p. 53), and in answer to the first proposition we know that the nervous system of the males of *Scalpellum*, whose bodies certainly represent the whole body of a Cirripede, is reduced to a supraoesophageal ganglion and a single thoracic ganglion: I am therefore not inclined to sacrifice the general comparison of the body of the Rhizocephala to that of an ordinary Cirripede for the reasons urged by DELAGE.

Definite connecting links between the Rhizocephala and the other orders of Cirripedia have not been hitherto shown, in my opinion, to exist: though GIARD (**21**) contends that the parasite *Sphaerothylacus*, described by SLUITER (Über einen in Ascidien schmarotzenden Wurzelkrebs. in: Nat. Tijd. Nederl. Indië Batavia Deel 43) from the gill of a Cynthiad Ascidian, is an intermediate form between the Ascothoracica and Rhizocephala.   The presence in this animal of a well developed gut and its infection of an Ascidian, both of which characters are utterly unknown among Rhizocephala, may make us sceptical in accepting this little known genus as a connecting link, but it is at least interesting to perceive how the whole Cirripede body can be represented by an oval sac without limbs or sense organs as the result of a parasitic mode of life.

Another genus which has been suggested as belonging to the primitive Rhizocephala is *Sarcotaces*, described by HJORT (Zur Anatomie und Entwicklungsgeschichte einer im Fleisch von Fischen schmarotzenden Crustacée. in: Vid. Selsk. Skrifter Christiania 1895), but here again the presence of a gut, the nature of the host, and the imperfect characterisation of the animal, precludes our acceptance of it at present.

In *Anelasma squalicola*, a Pedunculate Cirripede, parasitic on the Selachian genus *Spinax*, an important resemblance to the Rhizocephala is found in the possession of a root system, springing from the region of fixation, which penetrates into the flesh of the shark and probably serves to nourish the parasite, since the cirri and mouth-parts show marked signs of degeneration. The gut although it appears to be usually devoid of food does not show any distinct signs of degeneration.

The root system of *Anelasma* which springs from the whole surface of the greatly swollen peduncle and ramifies in the tissues of the host, bears an extraordinary resemblance to that of the Rhizocephala, both in general appearance and minute structure. On Plate 2 fig. 3 is presented an optical section through some roots of *Anelasma squalicola*, with which the Fig. 2 on Plate 3, representing some roots of *Sacculina*, should be compared. In both cases we have an external chitinous investment (*ch*), beneath which lies a regular epithelium (*ep*), while the interior of the roots is occupied by a lacunar tissue of branching vacuolated cells (*lac*). The lacunar cells of the Rhizocephala are less filamentous and more pronouncedly vacuolated than in *Anelasma*.

In the Rhizocephala the lacunar tissue of the roots is continuous through the ring of attachment with the connective tissues of the mantle and visceral mass.

Similarly, the roots of *Anelasma* are connected with a ramifying lacunar tissue in the Peduncle which surrounds the ovary, in the manner shown on Plate 2 fig. 4 *lac*. This lacunar tissue is largely developed throughout the *Anelasma* body, and through it the nourishment absorbed by the roots may be distributed to all the organs besides the ovary.

There is moreover a very peculiar fact relative to the ovary in *Anelasma* which has not, to my knowledge, been described in any other Cirripede, and may very possibly be connected with the method of nourishment by roots. At the edges of the ovary it can be seen that certain ova have migrated out of the ovary and are beginning to degenerate, the nuclei becoming swollen and irregular in shape and diffusing their chromatin into the surrounding cytoplasm (Plate 2 fig. 4 *ov.deg*). These degenerating ova can be traced from the edges of the ovary right into the substance of the mantle, whither they must have actively migrated; and all through the substance of the mantle, even at the points most remote from the ovary, these wandering ova can be observed in large quantities at various stages of degeneration. A section through part of the mantle is shown in Fig. 5 Plate 2, where some of the degenerate ova are shown in a high-power drawing, from which it is seen that the nucleus may break up into several pieces in one ovum. It must be remarked that this phenomenon is quite different to the normal distribution of the ovary into the mantle which occurs in many Cirripedes; it appears that here, owing to the surplus of nourishment supplied to the ovary and peduncle by the root system, certain of the ova actively migrate into the tissues of the body to serve as nourishment. It seems, therefore, certain that the chief method of nourishment in *Anelasma* is by means of the root system, either directly or indirectly by these ova.

Since on purely anatomical grounds we are convinced that the ring of attachment of the Rhizocephala equals the stalk of the Cirripedes it is highly suggestive to find a normal Pedunculate Cirripede which is on the way to convert the stalk into a similar organ of nutrition with a root system branching out if it. It is however more than probable that the actual resemblance of *Anelasma* to the Rhizocephala is due to convergence, for *Anelasma* is a fairly typical genus of the Pedunculata in all other respects.

The parasite of the isopod *Calathura*, which I have named *Duplorbis*, will have to be taken account of in dealing with the phylogeny of the Rhizocephala, but the discussion of this genus will be introduced more appropriately after dealing with the endoparasitic stages of development, since its structure throws light more especially on the derivation of the endo-parasitism of the Rhizocephala. For further remarks, therefore, on the general relationships and derivation of the Rhizocephala the reader is referred to chapter 4 p. 58.

After this preliminary survey of the organization of our group we may turn to a more detailed comparison of the various genera, which will reveal to us many interesting deviations both in structure and symmetry.

B. The inter-relationship of the Genera of Rhizocephala.

The Rhizocephala, as far as our present knowledge extends, comprise the twelve genera *Duplorbis*, *Clistosaccus*, *Peltogaster*, *Parthenopea*, *Sylon*, *Sacculina*, *Heterosaccus*, *Lernaeodiscus*, *Triangulus*, *Thompsonia*, *Apeltes* and *Thylacoplethus*. Of these *Duplorbis*, *Heterosaccus* and *Triangulus* are described for the first time in this work; but I must consider the anatomy of *Clistosaccus*, *Sylon* and *Lernaeodiscus* as hitherto imperfectly known. The three genera *Thompsonia*, *Apeltes* and *Thylacoplethus* are too slightly characterised to be included in this discussion.

The other nine genera may be separated from one another chiefly by the condition of the mesentery and the symmetry of the body relatively to that of the host, and a considera-tion of the variations of these characters, combined with that of the general anatomy, may lead us to the conclusion that *Peltogaster* preserves the most generalized condition, and that the characters, especially those of asymmetry, of the other genera, with the exceptions of *Clistosaccus*, *Duplorbis* and *Sylon*, are modifications of a primitively *Peltogaster*-like structure and symmetry. In developing this thesis I am only extending the original idea of GIARD (**12** and **16**) applied relatively to *Peltogaster* and *Sacculina*.

The anatomy of *Peltogaster* has been sketched in the first part of this section. I base my view of its generalized nature upon the compact, simply branching root system, the un-branched and simple oviducts whose walls are not complicated into an elaborate colleteric gland as in the other genera, and upon a feature in the endoparasitic development which consists in the entire absence of a perisomatic cavity, a characteristic organ of *Sacculina* (see p. 51); but chiefly upon the simple symmetrical relation to its host.

Peltogaster is parasitic on the Hermit-crabs, and is affixed to the dorso-lateral surface

of the left side of the abdomen, with the antero-posterior axis elongated in the same direction as that of its host, as shown in Text fig. 4; the parasite is curved in correspondence to the curvature of the crab's abdomen; and the paired organs of the *Peltogaster*, viz.: the vasa deferentia and oviducts, are symmetrically disposed about the long axis of the mesentery, the genital openings on the morphological left side of the *Peltogaster* (actual right in Figure 4) being slightly
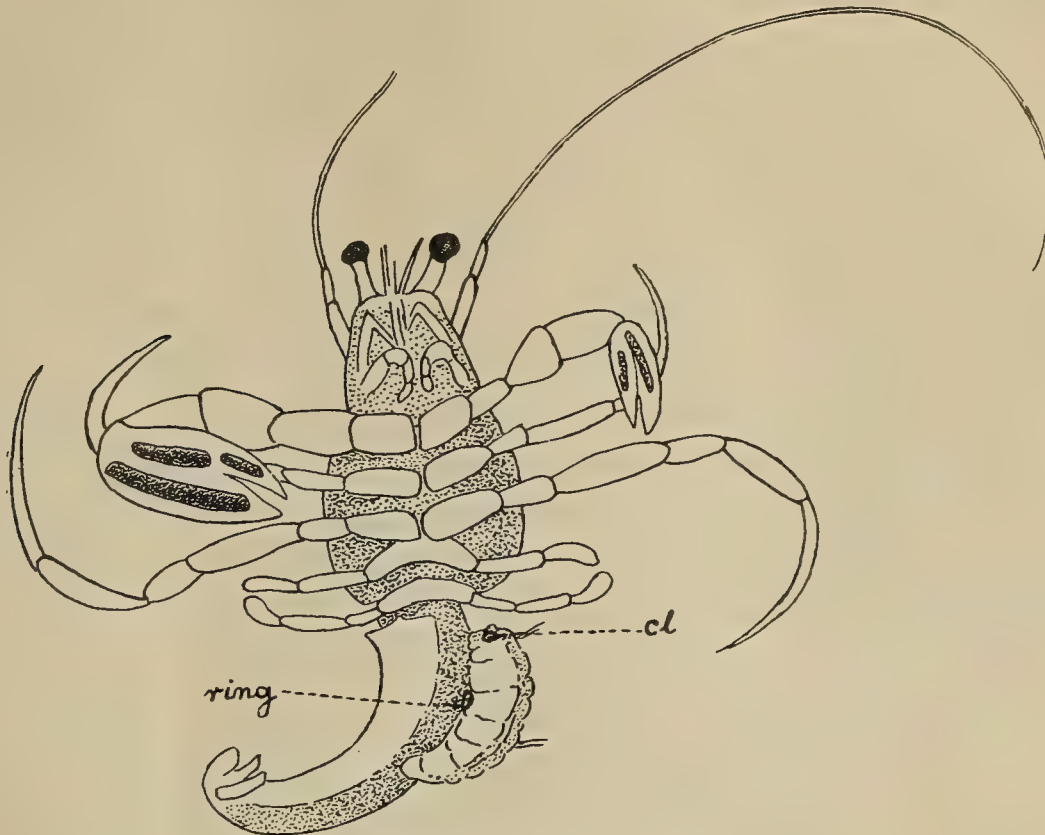
Text fig. 4.

in advance of those on the right (see Text fig. 5 A). The symmetry of the body is in fact in complete and constant accord with the symmetry of the host.

Now all the other genera of Rhizocephala, leaving aside *Duplorbis*, *Clistosaccus* and *Sylon*, are parasitic on the orders of symmetrical Decapoda, and the peculiar feature of their organization is that they all exhibit a constant asymmetry relatively to their hosts, while the genera *Lernaeodiscus* and *Triangulus* are not only asymmetrical relatively to their hosts but are in themselves highly asymmetrical animals. That the position of a parasite on its host should be irregularly asymmetrical and indefinite is natural, but that a whole group should be asymmetrical in a constant and fixed manner calls for some explanation.

Bearing in mind that these genera in their general organization show a greater degree of complication than *Peltogaster*, for instance in the root system and in the branching colleteric gland, we infer that they owe their peculiar symmetrical relations to their descent from a *Peltogaster*-like form which was parasitic on the asymmetrical Hermit-crabs, and that the act of shifting from a dorso-lateral position on the Hermit-crab's abdomen to a ventro-median position on the abdomen of the symmetrical crabs has led to a distortion of the original bilateral symmetry of the *Peltogaster* form. Because if we imagine the *Peltogaster* in Text Figure 4 simply

shifting its position onto the ventro-median line of a symmetrical crab, the mantle opening would be situated in the most disadvantageous position, namely at the immediate junction of thorax and abdomen, where the flexure of the host's body would not admit of free passage through the mantle opening. Now this is exactly what has been avoided in all Rhizocephala by an alteration of the symmetry of the body relatively to the crab, and in some cases by the assumption of a definite asymmetry in the body itself.

It appears that this has been effected in two ways, one method producing the genera *Parthenopea*, *Sacculina* and *Heterosaccus*, the other method producing the curious asymmetry of *Lernaeodiscus* and *Triangulus*.

In the first of these two groups the body has been simply as it were rotated on its peduncle or ring of attachment so as to bring the mantle opening from the anterior position of *Peltogaster* to a lateral or posterior position, and concomitantly the ring of attachment has shifted from the middle of the mesentery to its posterior extremity. The first stage in the process is represented by *Parthenopea* (Plate 1 fig. 7) a parasite found on the ventral surface of the thorax of the Macrurous genus *Callianassa*. The appearance and anatomy of this form strongly recalls *Peltogaster*; as in *Peltogaster* the root system is green and the external part of the body is red, but the roots are more diffusely branched and the oviduct is slightly complicated into a branched colleteric gland.
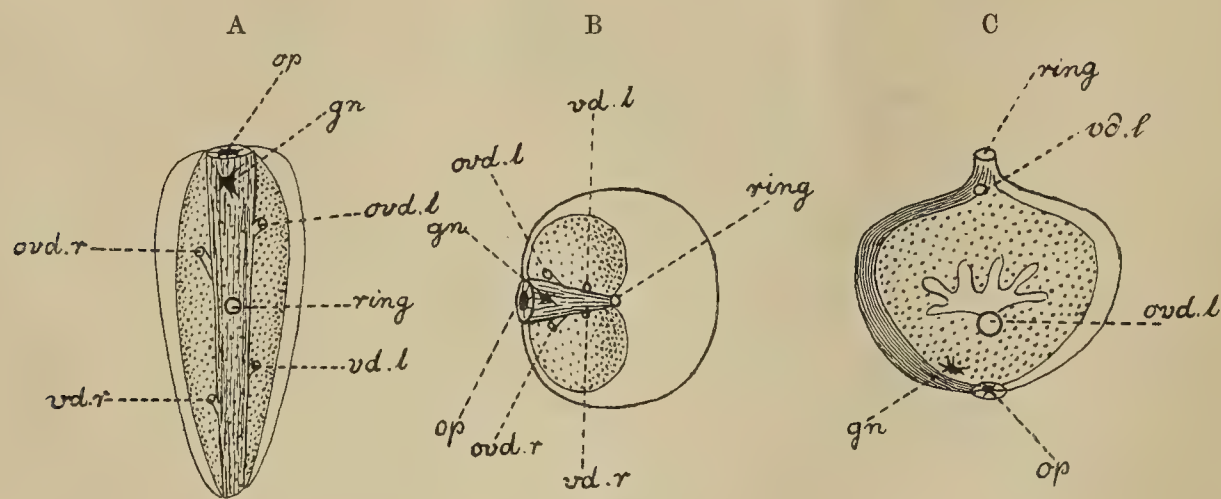
Text fig. 5.

The external part of the body is more or less spherical, and the mantle opening is situated laterally relatively to the host, being either on the right or left side. The long axis of the mesentery, which stretches from the ring of attachment to the mantle opening is vertical to the long axis of the host, so that the length of the mesentery is only seen in a lateral view of the host. The genital openings are situated symmetrically about the mesentery (Text fig. 5 B).

Parthenopea, intermediate in its anatomical characters between *Peltogaster* and *Sacculina*, and with its axis of symmetry shifted onto a vertical and lateral position on the ventral surface of its symmetrical host, gives the clue to the condition found in *Sacculina*.

Sacculina occurs on the Brachyura; it is fixed usually near the junction of thorax and abdomen, and when the tail of the crab is held apposed to the thorax, as in the normal position, the mantle opening points forward toward the head of the host and is situated roughly in the middle line. But the apparent symmetry of the body relatively to the host is spurious, for the long axis of the mesentery runs on the morphologically right side of the crab (Text fig. 6 *mes*) passing from ring of attachment to mantle-opening (*cl*), and the genital openings
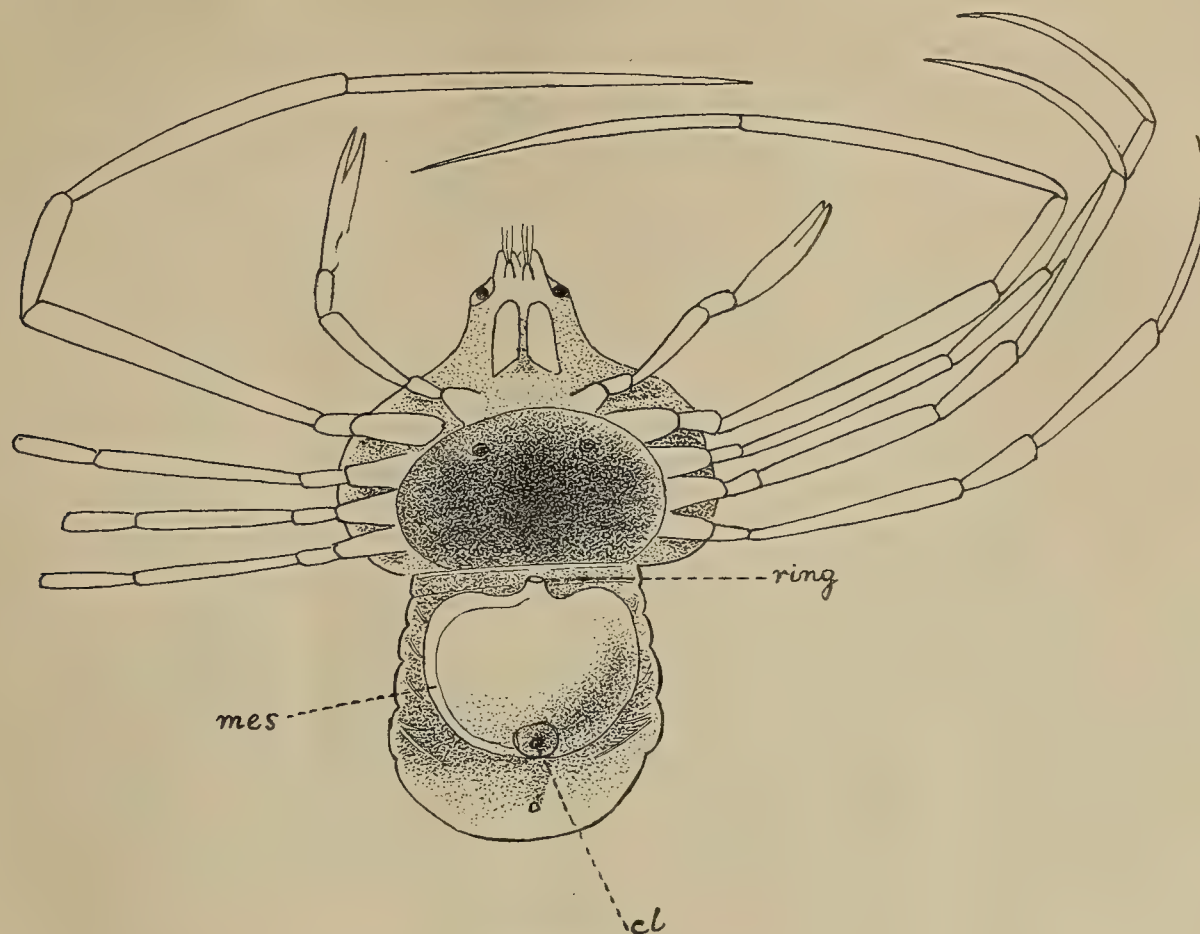
Text fig. 6.

are disposed to right and left of the mesentery (only the left-hand openings being exposed in Fig. 5 C), so that the axis of symmetry of the *Sacculina* is horizontal to that of the host. This condition is easily derived from that in *Parthenopea* (Fig. 5 B) by simply pulling the mantle opening (*op*) posteriorly, and at the same time flattening the body laterally, a process that might naturally result from the position of the parasite under the tail of the Brachyurous host.

The genus *Heterosaccus* differs from *Sacculina* merely in the fact of the mesentery being confined to the region of the ring of attachment, and not stretching down to the mantle opening; the rest of the organs are disposed exactly as in *Sacculina*.

We now turn to the second group containing the genera *Lernaeodiscus* and *Triangulus*. These are both parasitic on symmetrical Anomurous genera, namely *Porcellana*, *Galathea* and *Munida*. In *Lernaeodiscus* the mesentery has the form of a broad hinge clasping the visceral mass in the middle line, the acute angle of the hinge being pierced by the ring of attachment (Plate 7 figs. 33 and 34). Regarding the mesenterial surface of the body as the dorsal surface,

we may say that in *Lernaeodiscus* this surface is greatly elongated and laterally extended, and shows an immense curvature, owing to the antero-posterior compression of the body. Since the mesentery and mantle opening are both situated in the middle line relatively to the crab, the body has the appearance of bilateral symmetry; but this is deceptive, as the peculiar positions of the genital openings show. These are situated in an asymmetrical position, the vas deferens and oviduct of one side opening on the anterior hinge of the mesentery, those of the other side on the posterior hinge (Plate 7 figs. 33 and 34). The condition of *Lernaeodiscus* can very simply be derived from that of *Peltogaster* by first slipping the latter, without altering its symmetry relatively to the host, onto the median ventral line. We than take the *Peltogaster* and without twisting its axis bend the anterior portion of the body lying in front of the ring of attachment outwards towards the posterior pole. In this manner the mesentery will become bent into an hinge as in *Lernaeodiscus*, and the mantle opening will face towards the posterior pole of the host instead of anteriorly as in *Peltogaster*. Now with regard to the
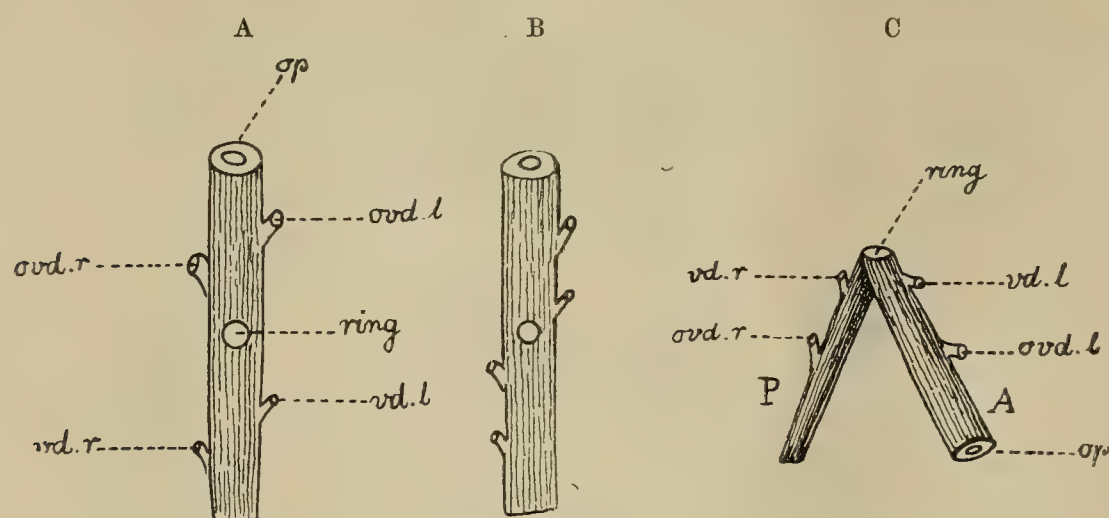
Text fig. 7.

asymmetry of the genital openings: it has been already noted that in *Peltogaster* the openings on one side are always slightly in advance of the other side. We may illustrate this diagrammatically by Text fig. 7 A which represents the mesentery of *Peltogaster* viewed ventrally with the genital openings upon it, those of the morphologically left side being in advance of those on the right.

If we exaggerate this condition as shown in Text fig. 7 B, the bending of the mesentery into an hinge at the ring of attachment will have the result of carrying the openings of the morphologically left side onto the anterior hinge of the mesentery (*A*), and those of the right side onto the posterior hinge (*P*), as shown in Text fig. 7 C, and this is exactly the condition of *Lernaeodiscus*.

The allied genus *Triangulus* differs from *Lernaeodiscus* in much the same way as *Heterosaccus* differs from *Sacculina*, namely in the suppression of part of the mesentery. In *Triangulus* the anterior arm of the hinged mesentery, namely that arm which should connect the

ring of attachment to the mantle opening is absent, but the genital openings, although slightly shifted, have the same asymmetrical position as in *Lernaeodiscus*.

In the above manner, namely by the supposition of their twofold descent from a *Peltogaster*-like form, I would account for the curious fact that these genera of Rhizocephala, although parasitic on symmetrical crabs, exhibit a constant and definite type of asymmetry relatively to their hosts.

We have still to assign a position to the remaining three genera *Duplorbis*, *Clistosaccus* and *Sylon*. The genera which we have considered all agree closely in their general anatomy, but these three genera show striking differences. *Duplorbis* possesses so many peculiar features as almost to justify its removal to a separate sub-class. *Clistosaccus* does not possess a mantle opening, at any rate when adult, while *Sylon* has two; *Clistosaccus* has a single median testis, and *Sylon* does not possess a testis at all, as I have determined on four specimens by means of serial sections. Both *Sylon* and *Clistosaccus* have a median unpaired oviduct. The chief peculiarity of *Duplorbis* consists in its method of attachment to its host and the apparent absence of a root system, but this form will be fully discussed at the end of Chapter 4 p. 60.

In regard to symmetry, *Duplorbis*, which is highly peculiar in being parasitic on the Isopod *Calathura*, is immensely laterally elongated, so that the actual long axis of the body is at right angles to the morphological antero-posterior long axis. The position on the ventral surface of the host is indefinitely oblique (Plate 8 fig. 9).

Clistosaccus (Plate 8 figs. 5—8) is, like *Peltogaster*, a parasite of the Hermit-crabs; its position on the host is also the same as in *Peltogaster*. *Sylon* (Plate 8 figs. 1—4) is parasitic on the Shrimps, and is the single genus of the Rhizocephala, parasitic on a symmetrical host, which exhibits a simple symmetrical relation to it. The mesentery runs in the middle line from the ring of attachment to the double mantle opening, the antero-posterior axis coinciding with that of the Shrimp.

Combined with these morphological differences which separate *Duplorbis*, *Clistosaccus* and *Sylon* from the other genera, we find striking differences in the sexual relations, a subject which will be treated fully in Chapter 2. *Peltogaster*, *Sacculina*, *Lernaeodiscus* and the allied genera are structurally hermaphrodite, the testes showing a peculiar kind of degeneration of certain cells. Complemental males in these genera, when present, are entirely degenerate, and do not develope beyond the Cypris stage. In *Clistosaccus*, *Duplorbis* and *Sylon* we have three different modes of reproduction. In *Clistosaccus*, which is structurally hermaphrodite, the testis shows no signs of degeneration at all and is crammed with sperm at maturity; in *Duplorbis*, bodies which may possibly be interpreted as fully developed complemental males containing masses of sperm may be present in the mantle cavity and serve for fertilization; in *Sylon*, the animal is structurally female, and since there is no evidence of the occurrence of males, we must presume that parthenogenesis occurs.

To summarise all the foregoing facts in tabular form we may construct a kind of genealogical scheme, as follows, taking a hypothetical *Peltogaster*-like ancestor as the central form

from which the other genera appear to radiate, but I must remain doubtful as to the true positions of *Duplorbis*, *Clistosaccus* and *Sylon*. When the life-history and anatomy of *Duplorbis* are better known it may be found necessary to remove it to a separate class, but the remaining genera certainly constitute a natural group.
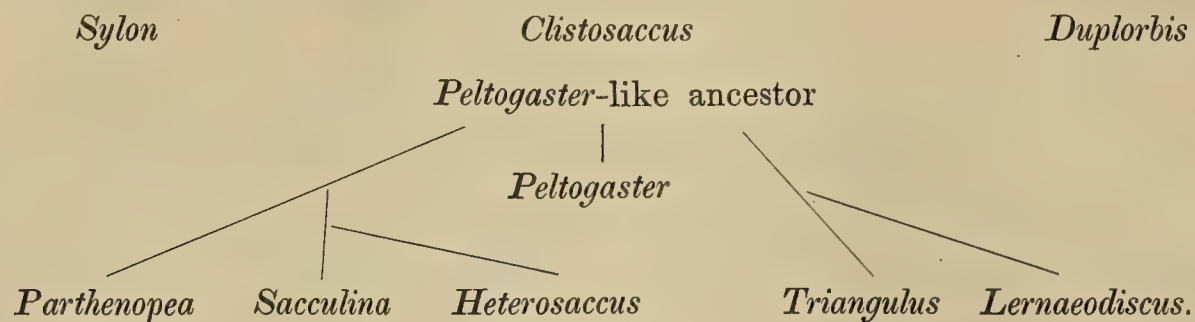
In the above account only the essential features of the different genera have been touched upon; a more exhaustive diagnosis will be found in the Systematic part, Chapter 7.

Chapter 2.

The Sexual Organization of the Rhizocephala.

In this chapter we will deal in detail with the sexual organization of our group, concerning which many points have been left obscure by previous observers. The Rhizocephala as a group are hermaphrodites, but unlike most hermaphrodites and unlike almost all Cirripedes, they possess no means of cross-fertilization. Thus even in those species, such as *P. sulcatus*, which occur gregariously on the same host, no organ is present for conveying the spermatozoa from one individual to another, and this as a matter of fact never does occur, while the majority of Rhizocephala are solitary, and cross-fertilization is impossible.

On the other hand evidence has been produced by several authors, especially FRITZ MÜLLER (5) and DELAGE (9), for the existence of complemental males such as are known to exist among certain Pedunculata, and they have supposed that cross-fertilization, at any rate during some stages of the animal's existence is effected by them, but this has never been confirmed by actual observation. The interest of this question is considerable, owing to its bearing on the principles which govern the evolution of sex, and especially the laws which determine the self- or cross-fertilization of hermaphrodites; I need not therefore apologize for going into considerable detail in describing the observations I have made on this subject.

Before entering into this description I will shortly state the nature of the problem before us, and indicate the solution at which I have arrived. DELAGE (9 p. 546—549) has clearly brought out the fact that in *Sacculina*, at the same time as the internal epithelium of the mantle secretes a chitinous investment, the vasa deferentia of the testes do the same, so that they become blocked by a plug of chitin which is continuous with the chitinous investment of the mantle. When this is the case it is impossible for the spermatozoa in the testes to escape into the mantle-cavity and to fertilize the eggs, but this is normally made possible by the mantle and the vasa deferentia undergoing a moult immediately before the maturing eggs are shed into the mantle-cavity, so that when this happens a free passage is left for the spermatozoa to gain access to the eggs. But in DELAGE's opinion, this moult does not take place previously to the expulsion of the first batch of eggs into the mantle cavity, so that

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for this first batch some other method of fertilization must occur. This other method of fertilization DELAGE supposed to be derived from the complemental males.

These complemental males, which to all appearances are identical with the ordinary Cypris larvae of *Sacculina*, were found by DELAGE to be almost invariably present, in numbers varying from two to fourteen, fixed round the mantle-opening of very young Sacculinae which had only just become external. They were never found at subsequent stages of the growth of *Sacculina*; DELAGE therefore concluded that their function was to fertilize the first batch of eggs. This batch of eggs is, in the species studied by DELAGE, not mature until about a month after the fixation of the Cypris larvae round the mantle opening; these larvae must therefore in DELAGE's opinion, either go through some transformation inside the mantle cavity of the Sacculina, or else deposit their spermatozoa in the mantle cavity to wait for the maturation of the eggs. Neither FRITZ MÜLLER nor DELAGE ever succeeded in seeing more than the dead external cuticle of these so-called larval males, so that the manner of fertilization, if it occurs, is really involved in mystery.

Now with regard to the ordinary fertilization of the succeeding broods in *Sacculina* it is not easy to be certain from DELAGE's account, for although there is nothing to prevent the spermatozoa from escaping from the testes into the mantle cavity, it is difficult to see how they reach the eggs, because the latter, according to DELAGE, as they pass through the oviducts are surrounded by a solid chitinous investment which would effectually prevent the spermatozoa from reaching them. DELAGE supposes therefore that fertilization takes place either in the ovary or oviduct, but exactly how this occurs has never been observed.

The answer to these questions which will be supported in the following pages is shortly as follows. The presence of Cypris larvae, from one to nineteen in number, fixed round the mantle opening of quite young Sacculinae externae (see Plate 6 fig. 11) has been found by me, as by DELAGE, to be almost invariable. In the Sacculina of *Inachus scorpio* I have calculated that they were present in varying numbers in about ninety per cent of the several hundred young Sacculinae examined by me.

The idea, brought forward by GIARD (7), therefore, that their presence is purely accidental cannot be accepted, and in view of the common occurrence of complemental males in certain genera of Cirripedes in an exactly analogous position, namely at the mantle opening, I can hardly question that their interpretation by MÜLLER and DELAGE as complemental males is correct. Now with regard to their function. After studying these larvae in numerous instances, both living and immediately after death, I have determined that they never produce spermatozoa, that their cell-contents are doomed to degeneration, and never enter the mantle cavity of the Sacculina, and that the fertilization of the first batch of eggs is effected by the spermatozoa of the hermaphrodite itself, as in all succeeding broods.

For the fertilization of the first batch of eggs both in *Sacculina* and *Peltogaster* there is always a passage left free for the escape of the spermatozoa into the mantle cavity, and furthermore DELAGE was mistaken in regarding the investment of the eggs, derived from the

passage through the colleteric glands, as solid and chitinous; it is in reality at first glutinous and permeable by the spermatozoa, and only subsequently hardens.

Self-fertilization then in *Sacculina* and *Peltogaster* is the invariable rule, while the Cypris larvae that fix themselves round the mantle are no longer functional. It is however just possible that in *Duplorbis*, the parasite of *Calathura*, functional males may be present in the mantle cavity, the parasite itself being female. This may also be the case in *Sylon* which is structurally female and not hermaphrodite, but reproduction here may be parthenogenetic as there is no evidence of the occurrence of males.

We now turn to the detailed proof of these conclusions and at the end I will attempt to give an explanation of the state of affairs, especially of the nature of the degenerate males. The subject will be divided under the following headings —

1. The testes of the Hermaphrodites.
2. The moulting of the mantle-cavity and of the vasa deferentia and the passage of the ova into the mantle-cavity.
3. The maturation and fertilization of the ova.
4. The complemental males.
5. The sexual nature of *Sylon*.
6. General discussion.

1. The testes of the Hermaphrodites.
(Plate 2 figs. 6—14 and Plate 8 figs. 7 and 8.)

In our general sketch of the morphology in Chapter 1, we dealt with the position of the paired testes in the various genera: it will therefore suffice here to recall the fact that the testes are always situated at the junction of visceral mass and mesentery, and that their paired openings into the mantle cavity are on the mesentery in the morphologically posterior region of the body. In *Clistosaccus* there is only one testis and it differs considerable in structure from that of the other forms; in *Sylon* there are no testes present, so that this genus and *Duplorbis*, whose sexual nature is problematical, will be reserved for a special section.

We will consider first the testes of *Sacculina*, *Peltogaster* and the allied genera, and then that of *Clistosaccus*.

The structure of the testes and the process of spermatogenesis was described by DELAGE (**9**), but he wrote at a time when these matters were but little understood: it remained therefore for DUBOSCQ (**13**) to give a correct account of the matter, with which I am in complete agreement.

We are not concerned here with the first appearance of the testes in organogeny, which is described on p. 51, but with their evolution during the adolescence of the parasites.

The chief regions of the testis are already differentiated to some extent as soon as the parasite becomes external; it is then possible to distinguish in each testis three regions, (1) the vas deferens, (2) the true germinal region, (3) the region of degenerate hypertrophy.

The latter two regions are differently situated in *Sacculina* and *Peltogaster* (Text figs. 8 and 9).
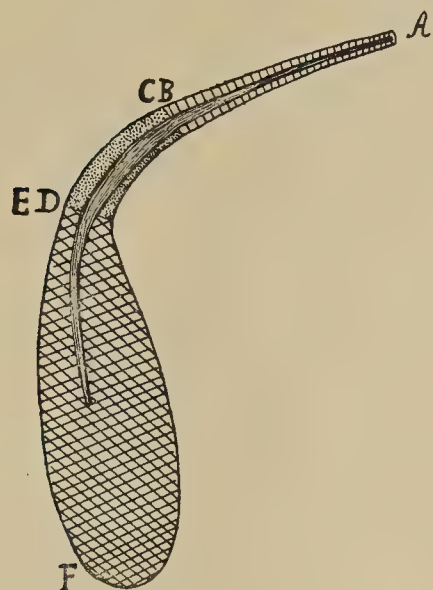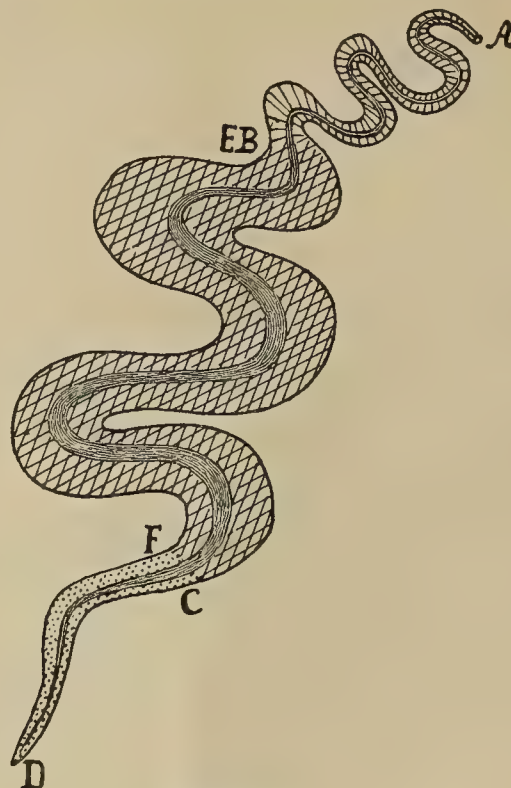
Text fig. 8.   Text fig. 9.

In *Sacculina* (Text figure 8) the germinal region, *D-C* in the figure, is situated between the vas deferens *A-B* and the region of hypertrophy *E-F*, while in *Peltogaster* (Text figure 9) the germinal region, *C-D*, is situated at the extremity of the testis. The lumen of the testis in young *Sacculina* does not penetrate to the distal extremity, but in *Peltogaster* it does so.

In both cases spermatozoa are only produced by the limited germinal region *D-C*, while the cells which compose the region of hypertrophy *E-F* undergo a series of transformations which end in their disintegration. Thus the greater part of the testes undergoes degeneration while only a comparatively small part gives rise to spermatozoa. In consequence it happens that the testes are never at any time full of spermatozoa, the latter being produced in very sparing quantities during the whole life of the parasite.

The histological changes which take place in the cells of the testes are illustrated in the series of sections on Plate 2 figs. 6—14.

In the germinal region of a young parasite the cells surrounding the central lumen have the character shown in figures 6 and 7. Figure 6 refers to *Sacculina*, figure 7 is a lower power drawing of *Peltogaster*. The cells of the germinal epithelium (*gm*) divide by mitosis and give rise to a number of smaller primary spermatocytes (*sp*), which fall into the lumen of the tube. This process takes place when the parasite has been external for three or four days.

Meantime the cells of the region of hypertrophy (figs. 8, 9, 10, d) are proceeding on their course of degeneration. These cells are derived from a germinal epithelium in all points similar to that of the true germinal region. But they rapidly take on a very different character, losing the conspicuous nucleolus and growing to a large size (fig. 8 *Sacculina* and fig. 9 *Peltogaster*). They divide by amitosis, mitoses never being observed in this region. A further stage in their degeneration is shown in figure 10 Plate 2. The greatly enlarged nuclei, crowded with chromatin, are beginning to fall out of their cell bodies, leaving large honeycombed spaces in the testis wall. A stage in which this process has gone further is shown for *Peltogaster* in figure 11, where the testes wall has assumed a truly honeycombed structure owing to the degeneration of the cells composing it. A section through the hypertrophied region of an old *Peltogaster* is shown in figure 11a.

When this process of degeneration has reached a certain stage the spermatocytes which have been derived from the germinal region and have fallen into the lumen are carried to the region of hypertrophy, and there lying in the honeycombed walls reach their maturity. In *Sacculina* they must pass backwards: and when the transformations of the hypertrophied region have reached a certain stage, a number of spermatocytes (sp) in various stages of development can be observed lining the cavity of the testis side by side with the degenerate cells (d_2 fig. 12). In *Peltogaster* the spermatocytes must pass forward to reach the region of hypertrophy, but they often become mature in the germinal region itself.

The spermatozoa are derived from the spermatocytes by the ordinary two divisions, the details of which I have not worked out owing to the small size of the cells and the crowding of the chromosomes. The transformation of the spermatid into the spermatozoon is shown in fig. 7a Plate 2. The spermatid is at first an oval shaped body composed almost entirely of chromatic substance. It gradually elongates but retains for some time a thickening somewhere along its length, often at an extremity, so that it then appears to possess a true head and tail, but in reality the nucleus is drawn out into a thread along the whole length of the threadlike body. In the mature spermatozoon no trace of this thickening is left and the filamentous body is composed wholly of an immensely elongated nucleus surrounded by a thin hardly distinguishable cytoplasmic pellicle which may be continued beyond the nucleus as a true tail. The centrosome is not distinguishable for certain, though a highly refringent granule can sometimes be distinguished at one extremity, and we shall see that it is equally hard to distinguish, as far as my observation goes, even after the spermatozoon has entered the egg in fertilization. We may compare these spermatozoa and their method of derivation with those figured on Plate 8 fig. 8. In *Clistosaccus* (fig. 8) the young spermatids (spd) have crescent shaped nuclei which gradually elongate to form the filamentous spermatozoa. In the complemental males of *Scalpellum vulgare* (Plate 8 fig. 21) we see essentially similar changes.

Reviewing the evolution of the testes in *Sacculina* and *Peltogaster* the most interesting feature is the economy practised in the production of spermatozoa. Thus in both forms only a small part of the testes produces spermatozoa, the greater part undergoing a peculiar kind

of hypertrophied degeneration. In this manner only a very small quantity of spermatozoa are produced at a time. This is also the case in all the closely allied genera, e. g. *Parthenopea*, *Lernaeodiscus* and *Heterosaccus*.

The only genus in which this is not the case is *Clistosaccus*, where the whole length of the single testis may produce spermatozoa, and where no signs of hypertrophied degeneration are visible, the whole length of the testes having the appearance shown in figures 8 and 9 Plate 8. It is possible here that a compensation has been brought about by the development of only a single testis. I must admit however that the single testis of this animal produces more sperm than the two testes in any other species.

Another connected feature in the spermatogenesis of the Rhizocephala is its strictly rhythmical nature, so that ripe spermatozoa are never to be found in the testes except immediately before the ova of the various batches are ready to be fertilized.

Furthermore, at any rate in *Sacculina*, it appears that only one testis usually functions at a time, i. e. contains ripe spermatozoa, an observation originally made by DELAGE, and confirmed by DUBOSCQ and myself.

In all these means for securing an economy in the production of spermatozoa we see an adaptation incident on self-fertilization. If we compare the Rhizocephala in this respect with other Cirripedes in which the hermaphrodites habitually cross-fertilize one another, it is at once apparent that in the latter an immensely greater mass of spermatozoa is produced, and that none of the germinal cells undergo the hypertrophied degeneration which renders sterile the greater number of the cells of the testis in the Rhizocephala: and this is all the more striking because in the production of eggs the Rhizocephala are far more prolific than any other Cirripedia. But since their eggs are fertilized, as we shall see, by the sperm of the same individual which produces them, there is no possibility of a loss of spermatozoa through the accidents that may accompany cross-fertilization, and in this manner we can understand the possibility of this great economy in the production of sperm being practised.

2. The moulting of the mantle-cavity and of the vas deferens and the passage of the ova into the mantle-cavity.

We have now to explain the manner in which the spermatozoa, when they are mature are brought into contact with the eggs, and fertilization effected.

The mantle both externally and internally is lined with chitin, and the chitinous investment of the mantle-cavity internally is continued into the lining of the vasa deferentia.

In *Peltogaster* when the animal moults the whole chitinous investment of the exterior surface of the body, of the interior surface of the mantle-cavity and of the vasa deferentia may be cast off as one continuous sheet at the same time. Often in *Peltogaster* and probably

always in *Sacculina* the external chitinous investment and the lining of the mantle-cavity and vasa deferentia are cast off separately, a rupture taking place at the mantle-opening.

The moulting of the mantle-cavity and of the vasa deferentia always occurs soon after the nauplii in the mantle-cavity have been set free, and immediately before the new brood of eggs is passed into the mantle-cavity for fertilization. The interval between the emission of the nauplii of one brood and the deposition of the eggs of the next brood varies in length according to the species, and also according to the physiological condition of the individual. DELAGE observed this interval in *Sacculina carcini* to be about four days, while I have found it in *Sacculina neglecta* to be usually less than twenty-four hours. In *Peltogaster curvatus* four or six days usually elapse before the mantle-cavity moults and receives its new brood of eggs.

The moulting of the mantle-cavity between the emission of the nauplii of one brood and the passage of the eggs of the next brood from the ovary into the mantle-cavity, serves two purposes: in the first place it cleanses the mantle-cavity of the débris left from the last brood of embryos, and secondly it removes the chitinous plug from the vasa deferentia which would otherwise block the way for the entrance of the spermatozoa into the mantle-cavity. The effectual method in which the vas deferens may be blocked by this chitinous plug is shown in Plate 2 fig. 13 which represents a section through the opening of the vas deferens in *Parthenopea*.

In *Sacculina*, moreover, the moult serves another purpose, for in this form special chitinous hooks or retinacula are present on the internal surface of the mantle-cavity for holding the egg-tubes fast, and the moulting of the mantle-cavity after the liberation of one brood of nauplii is necessary to expose the new chitinous lining with its fresh set of retinacula on it.

The foregoing account applies to the preparations for the fertilization of all the batches of eggs except the first.

But previously to the entrance of the first batch of eggs into the mantle-cavity the latter has been empty, and as a matter of fact no moult takes place immediately before the passage of the eggs. But the necessity for this is obviated by the fact that during the early stages in growth preceding the maturation of the first brood of eggs, the chitin lining the internal surface of the mantle and of the vasa deferentia never attains to sufficient thickness to occlude the openings of the vasa deferentia into the mantle-cavity. I have proved on numerous occasions in *Sacculina neglecta* that at, and immediately after, the moment when the first brood of eggs is passed into the mantle-cavity, the chitinous lining of the mantle-cavity and of the vasa deferentia was exceedingly thin, and left a free passage for the spermatozoa to reach the eggs in the mantle-cavity, a passage which they had evidently availed themselves of, as the testes were devoid of spermatozoa, which were found lying among the eggs in the mantle-cavity.

It is therefore equally possible for self-fertilization to occur in the first brood of eggs as in the succeeding broods, and in fact it always does occur.

We have now to describe the manner in which the eggs are passed into the mantle-cavity and the adaptations connected with the process.

We will take as typical the case of a brood of eggs subsequent to the first in *Peltogaster*. The nauplii of the preceding brood are expelled from the mantle-cavity through the mantle-opening by the rhythmical contractions of the muscular mantle. For some time after the emptying of the mantle-cavity the mantle-opening remains widely gaping, and, by the continued contractions of the mantle, water is pumped in and out of the cavity. After a time, varying according to conditions, as has been previously stated, the moult of the mantle externally and of the mantle-cavity internally, together with the plugs of the vasa deferentia, takes place. Immediately after this the sphincter of the mantle-opening becomes tightly shut but the mantle continues to contract rhythmically and strongly. And now the eggs lying in the greatly distended visceral mass are forced by the muscular contractions of the mantle and of the visceral mass first into the colleteric glands of either side and so into the mantle-cavity. As they pass through the colleteric glands they are surrounded by the slime secreted there. In *Sacculina* the colleteric glands are greatly branched, each branch corresponding to a diverticulum of the ovary. It thus happens that the eggs of *Sacculina* are thrust out into the mantle-cavity conglomerated into definite tubiform masses, but the slime which glues the eggs together is glutinous and not solid as DELAGE supposed. In *Peltogaster* the colleteric glands being simple the eggs are passed into the mantle-cavity in an irregular mass.

For at least nine or ten hours the active contractions of the mantle continue in *Peltogaster* (not so actively in *Sacculina*), the mantle-opening remaining tightly shut. In this period the processes of maturation and fertilization are completed and the segmentation stages are initiated, and gradually the slime surrounding the eggs begins to solidify attaching them to the lining of the mantle-cavity, a process which is further secured in *Sacculina* by means of the retinacula. When this process is complete the mantle-opening relaxes and the muscular contractions of the mantle quiet down into the slow rhythmical pumping action which serves for the aeration of the developing embryos in the mantle-cavity.

As to the manner in which the spermatozoa pass down the vas deferens into the mantle-cavity I imagine that this is accomplished by the active vibratile movements of which they are capable; but they may also be assisted by the muscular contractions of the body. They never appear to reach the mantle-cavity until the eggs have been there for some hours; when they do reach the eggs the sphincter of the mantle-opening is of course tightly shut so that eggs and spermatozoa are shaken up together by the contractions of the mantle in a completely closed cavity.

In all these facts, together with the fact of the production of ripe sperm only at the period immediately before the maturation of the eggs, we see a series of adaptations, which both for the first and for all the succeeding batches of eggs are intended to ensure self-fertilization with the greatest amount of economy and efficacy.

3. The maturation and fertilization of the ova.
(Plate 3 figs. 1—22.).

The processes of maturation which take place immediately before and for some time after the extrusion of the ova into the mantle-cavity, cannot be followed in the living ova, partly because of the obscurity caused by the yolk, and partly because the eggs apparently will not develop when taken out of the mantle-cavity. My observations therefore are all made on fixed and stained material (fixation in corrosive and acetic, staining with borax-carmine, iron-haematoxylin etc.). There is however little or no danger of error in following the series of changes because the eggs of one and the same brood are often at a slightly different stage of maturation, though substantially the same; and by observing the eggs in the act of being extruded into the mantle-cavity and then preserving the various batches at different periods after this extrusion, a chronological series is obtained.

The chronological order of events in *Peltogaster curvatus* is roughly as follows, but much individual variation apparently pertains.

Stage	Hours after extrusion into mantle-cavity.
1st polar spindle to formation of 1st polar body	1—3 hours
2nd polar spindle and formation of 2nd polar body	2—5 hours
Fertilization and migration of pronuclei	3—7 hours.

We will now describe in detail these processes in *Peltogaster curvatus*.

The first maturation spindle of the ovum (sp_1) is formed while the latter is still in the ovary, lying amid the germinal epithelium and immature ova at various stages of growth (Plate 3 fig. 1). The spindle is at first directed with its long axis parallel to the surface of the egg. The chromosomes which are at first irregularly scattered along the spindle, show signs of the typical tetrad formation as exhibited in Plate 3 fig. 2, but when they are arranged in the equatorial plate the tetrad arrangement is no longer visible and it is possible to count between twelve and fourteen dumb-bell shaped chromosomes (figs. 3 and 3 a). At about the period when the spindle begins to rotate the maturing eggs are expelled into the mantle-cavity, passing through the colleteric glands on either side of the body. As soon as the eggs have passed into the mantle-cavity the spindle is found to have rotated so that its long axis is at right angles to the egg-surface (figs. 4 and 4 a). In figures 5 and 5 a Plate 3 a transverse section is shown through the spindle.

The spindle now passes into telophase and the first polar body is extruded, the second polar spindle being immediately formed without any reconstitution of the nucleus (fig. 6). A view of the equatorial plate of the second maturation spindle is given in the drawing of the whole preparation (fig. 7). Fourteen chromosomes are visible.

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In figures 7 a and 8 are given two drawings of some eggs which were extracted from the mantle-cavity at this stage and kept for a quarter of an hour in sea water. The result was taht the second polar spindle was broken down and the chromosomes scattered so as to make them much easier to count. Fig. 7 a is a whole view showing the first polar body (*pb1*) and 14 single chromosomes; figs. 8 and 8 a represent sections showing apparently 12 chromosomes many of which have the appearance of dyads.

The second spindle may often travel some distance away from the first polar body as shown in fig. 9 Plate 3.

The telophase of the second spindle is shown in fig. 9 a, and the formation of the second polar body (*pb2*) is indicated.

By this time the first polar body (*pb1*) has been extruded far out of the egg and is seen upon the membrane which surrounds the egg at this period. The exact nature of this membrane I cannot explain but it appears to be formed at the time of fertilization. At this point fertilization occurs, and the entrance of the spermatozoon is the signal for a change in the distribution of cytoplasm and yolk in the egg. Hitherto there has been no concentration of cytoplasm at any particular region, but now a wedge of cytoplasm is formed immediately beneath the point where the polar bodies have been extruded and including the newly entered spermatozoon and the egg pronucleus (fig. 10).

The male and female pronucleus are at first clearly distinguishable from one another as shown in figure 10. In the male pronucleus we can still distinguish the immensely elongated chromatic strand of the spermatozoon, but this rapidly breaks up into small granules, the nuclear membrane becomes more spherical, and the chromatin becomes finally agglomerated into a nucleolus, and the male and female pronuclei are indistinguishable in appearance. Neither in the recently entered spermatozoon nor in the male pronucleus can a trace of centrosome or sphere be as yet distinguished.

The cytoplasmic wedge with the two pronuclei now passes to the centre of the egg (fig. 11) while on the periphery we can recognize the second polar body (*pb2*) brightly staining and lying within the egg membrane, and in favourable cases the first polar body (*pb1*) lying outside the egg membrane and rapidly fading from view. After this stage the first polar body is no longer visible in preparations, but the second polar body can be easily seen even after segmentation has begun. The fact of the rapid disappearance of the first polar body for a long time deceived me into suspecting parthenogenesis, and the difficulty of getting the fertilization stages, which are so rapidly passed through, confirmed me in this error.

As the pronuclei pass to the centre of the egg they increase greatly in size and their chromatin becomes more diffuse, and now they proceed rapidly to pass again to the periphery of the egg together with the cytoplasm which surrounds them (figs. 12 and 13).

They always arrive at the periphery at the same point from which they started namely immediately beneath the second polar body. In figures 14 and 15 the pronuclei are shown after regaining the periphery and increasing greatly in size.

The pronuclei are often markedly lobed and this lobation may lead, as in the instance figured on Plate 3 fig. 16, to the apparent presence of three pronuclei in the egg. So far there has been no trace of an aster in the egg, but now this appears between the nuclei, as shown in Plate 3 fig. 17, but its exact mode of origin is uncertain. Probably it emerges from the male pronucleus. The aster divides and forms an amphiaster round the two pronuclei whose membranes have begun to fade and in certain instances to coalesce (fig. 18).

In the next stage (fig. 19) we see the fully constituted first segmentation spindle at the periphery of the egg with the chromosomes arranged in the equatorial plate. The second polar body ($pb2$) is clearly distinguishable beneath the egg membrane.

Sections through the first segmentation spindle (metaphase figs. 20 and 20 a, telophase 21 and 21 a) give the chromatic number 24—28, i. e. twice the number which appeared in the maturation phases.

An interesting feature in the telophase of the first segmentation division (fig. 22) is that the daughter nuclei are reconstituted at first not as single nuclei but as a number of smaller bodies, each body containing a chromosome, which subsequently fuse to form the single nucleus of either hemisphere.

Such are the detailed processes of maturation and self-fertilization which occur in all the batches of eggs, whether first or subsequent, in *Peltogaster curvatus*; and essentially the same processes have been found to occur in *Sacculina neglecta* and *Parthenopea subterranea*, and I do not doubt that they also occur in *Lernaeodiscus*, *Triangulus*, *Heterosaccus* and *Clistosaccus*.

4. The complemental males.
(Plate 6 figs. 11—15.)

A. In *Sacculina* and *Peltogaster*.

We have shown so far that self-fertilization is the invariable rule in those Rhizocephala hitherto considered: what then is the function of the so-called complemental males in these animals? LILLJEBORG (4) was the first to observe, but FRITZ MÜLLER (5) was the first to make serious comments on this subject, and he found in young specimens of *Peltogaster socialis* that there might be present a varying number of Cypris larvae fixed round the mantle-opening. When he observed these larvae they were always dead and consisted of the mere chitinous cuticle, but he judged from their position and from the analogy of other Cirripedes that they were complemental males.

DELAGE (9) extended these observations to *Sacculina carcini*, but never saw the larvae alive. My observations have been made on *Sacculina neglecta* and are as follows.

In about ninety per cent of the youngest Sacculinae externae, measuring from 1—3 mm in breadth, a number of Cypris larvae varying from 1—19, have been found fixed round the

mantle-opening. The mantle-opening of a young *Sacculina* which carried fourteen of these larvae is figured on Plate 6 fig. 11.

An examination of the external characters of these larvae showed them to be identical in every detail with the ordinary Cypris larvae of *Sacculina neglecta*. We are therefore not dealing with an extraneous parasite, but with Cypris larvae derived from other specimens of *Sacculina neglecta* which, after spending a period of free existence, have sought out a young external parasite of their own species and have fixed themselves on it at the mantle-opening.

The larvae are not simply attached to the mantle-opening but lie underneath a chitinous investment of the mantle in the manner shown in fig. 14 Plate 2 ♂ and in fig. 12 Plate 6.

This chitinous investment is continuous all over the external surface of the young *Sacculina* and completely blocks up the mantle-opening (fig. 12 Plate 6 *cl*). It has however a free edge near the peduncle of attachment, and it is here and here only that the Cypris larvae can enter into the chitinous pocket to attain to the position in which they are found fixed. I have on several occasions observed the Cypris larvae immediately after entering beneath the free edge of the chitinous investment and before attaining to the region of the mantle-opening.

This chitinous investment, forming a cul-de-sac round the mantle-opening is only present for a few days in very young Sacculinae, being thrown off at the first moult, and after this period the Cypris larvae are never to be observed again on the Sacculinae.

It is not easy to obtain living specimens of these Cypris larvae, because immediately after fixation round the mantle-opening the degenerative processes set in which we will now describe.

If we examine either in an whole preparation or in serial sections one of these larvae either before it has reached the mantle-opening or immediately afterwards we find that the anterior region of the thorax in front of the legs is occupied almost entirely by a mass of cells with conspicuous nucleoli (Plate 6 figs. 13 and 14 *em*). These cells are arranged in the thorax in two laterally paired masses so that a transverse section through the middle of the Cypris gives the appearance shown in fig. 14 Plate 6. But these lateral masses are continuous with one another anteriorly and posteriorly so that an horizontal section, as in fig. 13, shows the cephalothorax surrounded by a ring of these cells.

If we compare these larvae with the ordinary Cypris larvae which I have found fixed on the thorax of *Inachus scorpio* about to infect the crab, we find that they are identical in all respects, and that in the latter we find the same arrangement of cells in the thorax, these cells being the so-called "embryonic cells" which are passed through the antenna in the manner originally described by DELAGE, to infect the crab. Not only are they identical in arrangement but in every histological detail (see Plate 4 fig. 20 and Plate 5 figs. 3, 4, 6).

Now if we study the contents of one of these larvae a little time after fixation at the mantle-opening we may obtain the appearance shown in figs. 12 and 15 Plate 6. The "embryonic cells" have drawn together into a compact mass and are beginning to pass into the antenna by which the Cypris is fixed, exactly in the same manner which occurs in ordinary Cypris

larvae which are in process of infecting a crab, except that no special chitinous investment is formed round the embryonic cells to produce the Kentrogon stage.

And now one of two things may happen; either the antenna splits and the embryonic cells pass out into the pocket round the mantle-opening where they may frequently be found in the act of degeneration, or else they remain in the Cypris body and disintegrate there.

In only one instance have I observed a case in which the mass of embryonic cells, owing to the antenna of the Cypris being deeply imbedded in the substance of the mantle, had passed within the chitinous plug occluding the mantle-opening and lay in the folds of the mantle round the opening.

After repeated attempts to find any other explanation of the matter, I have unwillingly adopted the conclusion that these Cypris larvae and their contents are in all cases doomed to degeneration and that they no longer play any part in the propagation of their species. We may scrutinise the mantle-cavity and mantle and the whole body of Sacculinae between the period of fixation of the Cypris larvae round the mantle-opening and the maturity of the first brood of eggs, a period of about three weeks in *Sacculina neglecta*, but there is never a trace either of spermatozoa or of the embryonic cells to be found. If those cells really play any part in furnishing spermatozoa for the fertilization of the first brood of eggs it is inconceivable that one should not be able to detect them somewhere. For they cannot be lying scattered about in the mantle-cavity, since the latter is being continually washed out with water, and moreover when the embryonic cells leave the Cypris larvae, on the occasions when they do succeed in this, they are far from being spermatozoa and would have to go through numerous divisions and changes. Finally we have seen that as a matter of fact the spermatozoa which fertilize the first brood of eggs are derived from the testes of the hermaphrodite, and that when they do reach the mantle-cavity there is not the least difficulty in detecting them. Why then should we suppose that the embryonic cells of the Cypris larvae, which are in so many cases actually seen to degenerate, can give rise to spermatozoa which remain invisible for three weeks and are only to be detected at the moment of fertilization?

It is my conviction, then, after examining these larvae living and in process of degeneration on numerons occasions, and after searching in vain for any trace of their products in young Sacculinae between the period of fixation of the so-called complemental males and the fertilization of the eggs of the first brood, that they represent in a certain sense a degenerate sex, but the explanation of their true nature and persistent presence despite their uselessness will be deferred until the end of the chapter.

B. In *Duplorbis calathurae* (?).
(Plate 8 figs. 14, 18, 19.)

I have now to describe the remarkable bodies found in the mantle-cavity of *Duplorbis calathurae*, the species discovered by Dr. H. J. HANSEN on the Isopod *Calathura brachiata* from Greenland. These bodies are of an admittedly problematic nature, since there has been no

oportunity of tracing their genesis or development, but it is possible that they give a clue to the question of the complemental males in the other Rhizocephala.

These bodies are figured on Plate 8 figs. 14 ♂, 18, and 19, and their position relatively to the other parts of the body is shown in Text fig. 24. I have examined them in two specimens of *Duplorbis* by means of serial sections; in one specimen two bodies were present, one at each end of the mantle-cavity, while in the other specimen I could only observe one, but it is possible that I missed the other owing to the imperfection of this specimen. The possibly paired regularity of their position speaks against their being complemental males, but their relation to the other parts of the body, namely as two sacs invested by chitin and lying attached to the internal chitinous investment of the mantle-cavity among the eggs, discontinuous from the other tissues of the parasite, speaks in favour of this interpretation. Besides their thick chitinous coat (Plate 8 fig. 18 *ch*) they consist simply of cells in process of spermatogenesis, the ripe spermatozoa being identical in appearance with those of other Rhizocephala (fig. 19). The large cells with conspicuous nucleoli, which I interpret as spermatogonia, are very similar in appearance to the "embryonic cells" we have described in the degenerate males of *Sacculina*: it appears to me possible therefore that these bodies are derived from functional males which have succeeded in passing their embryonic cells into the mantle-cavity in the manner in which the Cypris larvae of *Sacculina* evidently attempt to do, and that certains of these cells have secreted a chitinous coat while others have proceeded to form spermatozoa.

If we compare these bodies with the complemental males of *Scalpellum vulgare*, a section through one of which is given on Plate 8 fig. 20, we may be struck by the essential similarity of the two, though the males of *Scalpellum* show a much higher grade of organization in the presence of muscles and a rudimentary mantle (*mc*).

Supposing that these bodies in *Duplorbis* are really males and not very peculiarly situated testes, this animal would be a female with functional dwarf males as is the case among Cirripedes in *Scalpellum ornatum* and *velutinum*, *Ibla quadrivalvis* and the whole order of Abdominalia.

5. The sexual nature of Sylon.

We have now discussed the sexual nature of all the forms of Rhizocephala concerning which evidence is forthcoming, except *Sylon*, the little known parasite of *Hippolyte* and allied shrimps.

As pointed out in Chapter 7, this animal was originally studied by Michael Sars (**6**), but an accurate account of its anatomy was first given by Hoek (**10**). I have had the opportunity through the kindness of Dr. H. J. Hansen of Kjöbenhavn and of Professor D'Arcy Thompson in Glasgow, of studying four specimens by means of serial sections, and I disagree with Dr. Hoek's account in only one particular, but that is of fundamental importance and concerns

the presence or absence of a testis. I gather that Dr. HOEK studied two specimens of *Sylon* by means of sections, and in only one of them could he detect anything that "might be interpreted as a testis", so that from his account I suppose that he himself is not confident of the presence of this organ. His figure of the body which he interprets as perhaps a testis does not very closely resemble a section through the testis of any other Rhizocephala. In the four specimens studied by me no trace of a testis was to be seen; and since the four specimens were at different stages of maturity, and in one the eggs were nearly ready for fertilization, it is almost impossible that I should have entirely missed this organ.

I am therefore convinced that *Sylon* is structurally female and not hermaphrodite, and its method of reproduction must be either parthenogenetic or else by means of dwarf males. Since no one has ever seen a trace of these males, we may expect that parthenogenesis will be found to occur in this form.

In the gregarious parasite *Thylacoplethus*, found on Australasian Alpheidae by COUTIÈRE (**14**), no mention is made of the presence of a testis: it is therefore probable that this form must be associated with *Sylon* in its manner of reproduction.

An investigation of the manner of propagation of these forms would give highly interesting results, and material for the study of *Sylon* should not be very difficult to obtain for a Norwegian or Danish naturalist.

6. General discussion.

To recapitulate the detailed evidence which has now been given — the Rhizocephala, with the exception of *Sylon* and perhaps *Thylacoplethus* and *Duplorbis*, are hermaphrodites in which reproduction is carried on by a continuous round of self-fertilization. Degenerate complemental males may be present, but these no longer play any part in fertilization. *Sylon* (and perhaps we may add *Thylacoplethus* and *Duplorbis*) is structurally female, and reproduction is carried on either by separate males or parthenogenetically.

It is perhaps of interest to establish the unbroken occurrence of self-fertilization in a large group of related genera, and to study the interesting adaptations connected with the process, especially the remarkable economy in the production of sperm effected by the hypertrophied degeneration of the greater number of the male germinal cells. The occurrence of perpetual self-fertilization, in any extensive group of animals or plants, has rarely been proved to occur, and in view of the striking contrivances for effecting cross-fertilization in the great majority of animals and plants, it is always mysterious how any group can withstand the evil consequences which are inferred to result from continuous in-breeding. The existence of such a group as the Rhizocephala, which are among the most dominant and prolific Crustacea, is certainly paradoxical especially when we consider that self-fertilization in other Cirripedes is

unknown, save perhaps in *Pollicipes* and such a form as *Balanus perforatus*; but here, as GRUVEL has pointed out (**15** p. 431), cross-fertilization may be effected by means of giant wandering spermatozoa.

The capacity for self-fertilization (see **2** and **3**) appears to arise in an animal or plant as though by a capricious chance; thus scattered among the genera of certain groups of plants, especially the Orchids, we may find single species as for instance *Ophrys apifera*, which have given up the process of cross-fertilization for which they were evidently originally intended, and have taken to continuous self-fertilization without apparent damage; while in DARWIN's classical experiments on the effects of cross- and self-fertilization in plants, the self-fertile varieties of plants which are generally adapted for cross-fertilization, e. g. races of *Mimulus luteus*, *Nicotiana* and *Reseda*, appeared to arise by the merest caprice.

We can only in our ignorance suppose that certain ancestral varieties of the Rhizocephala were by chance self-fertile, and that owing to their being solitary parasites, this method of propagation was perpetuated by natural selection as being the only one suited to the conditions of the animal's lives. But this does not in the least explain how the evil effects of self-fertilization are obviated, or what these evil effects really are.

But not only have the Rhizocephala adopted perpetual self-fertilization, but they have done so when a means of cross-fertilization was apparently at hand, namely by the complemental males. We must now attempt to give some explanatory account of these organisms.

In order to do so it is necessary to consider shortly the sexual variations of the Cirripedia in general, since the Rhizocephala are evidently derived from some ancestral form common to the rest of the Cirripedia.

The majority of the Cirripedia, i. e. the majority of the Pedunculata, and all the Operculata are simple cross-fertilizing hermaphrodites: in the Abdominalia and Ascothoracica, the sexes are separate, but it is in certain Pedunculate forms that the most interesting conditions are found. As originally pointed out by DARWIN (**1**), and confirmed by HOEK (**8**) and GRUVEL (**11** and **15**), there are two main variations of the ordinary plan; firstly we may have hermaphrodites to which complemental males are attached as in *Scalpellum vulgare*, the majority of the species of *Scalpellum*, and *Ibla cumingii*; or else females to which small males, resembling complemental males more or less, are attached as in *Scalpellum velutinum* and *ornatum* and *Ibla quadrivalvis*.

The ordinary view of these variations, the view adopted by the authors cited, is that they have been derived from the ordinary hermaphrodite condition found in most Pedunculata, and that we are witnessing in them stages in the secondary separation of the sexes from the hermaphrodite state.

The occurrence of complemental males in a degenerate condition in the Rhizocephala is a serious, if not fatal, objection to this view, because we must suppose that the Rhizocephala are an ancient group of animals and that they diverged from the other Cirripedes at a remote period: if then the complemental males are a progressive stage in the secondary

separation of the sexes, how strange must it appear to find them in an ancient group of Cirripedes in a degenerate condition!

I am also unable to look upon the presence of complemental males in such a form as *Scalpellum vulgare*, as a progressive differentiation of the sexes, because the hermaphrodite individuals of *Scalpellum vulgare* are perfectly capable of, and do indeed effect, cross-fertilization, and the particular use of the minute complemental males is very difficult to understand. I am inclined to regard them far more as approaching the rudimentary condition actually found in the Rhizocephala.

I would suggest that the explanation of the whole matter must be sought in the fundamental nature of secondary hermaphroditism, i. e. an hermaphroditism which has been imposed on an originally dioecious organism as we must certainly suppose the original ancestors of the Cirripedia were.

In Chapter 5 of this book, in the light of which the present discussion must be read, certain evidences drawn from the phenomena of parasitic castration are put forward to show that in all cases of secondary hermaphroditism, the hermaphrodite state is imposed on the male organism and on the male organism alone, the female being incapable of assuming this condition. I am therefore led to look upon the ordinary hermaphrodite Cirripedes as simply representing the male sex, the female having been suppressed, and the occurrence of complemental males in an arrested condition of development as in *Scalpellum*, or in a degenerate state as in the Rhizocephala, is due to the peculiar condition of protandric hermaphroditism through which the animals at some time have passed.

According to my view, the most primitive condition is exhibited in such forms as *S. velutinum*, *I. quadrivalvis*, and the Abdominalia, in which the male sex becomes mature while still in a semi-embryonic condition and is affixed to the female. This male sex, in the subsequent evolution of the group, next became hermaphrodite, and instead of always fixing on the females began to start an independent life, though the old habit of fixing on other individuals was kept up by those larvae which happened to find either a female or an adult hermaphrodite on which to fix. With the extinction of the whole female sex, whose use in propagation would be precarious, the larvae which happened to find other individuals to fix on, would still do this, but it would be not upon females but always upon adult protandric hermaphrodites, the larvae themselves being potentially protandric hermaphrodites, but in the cases where they became fixed to other individuals not developing beyond the male state. This I take to be the actual case in *Scalpellum vulgare* etc., the so-called complemental males being in reality protandric hermaphrodites like all the other individuals, but arrested in development owing to their peculiar position on the hermaphrodites. Exceedingly suggestive in this connection is the fact that in *Scalpellum Peroni* the complemental males do show a trace of incipient hermaphroditism as remarked by GRUVEL (**15** p. 152).

Now if we compare this idea with what actually happens in the only other group of hermaphrodite Crustacea, namely the Epicarida or parasitic Isopoda, we find that it is in

perfect agreement. In the whole group of Epicarida, as brought out by BONNIER (**12**), and as I have confirmed for the Cryptoniscinae (see Chapter 6) all the individuals are at first larval males which, when young, crawl upon the adult parasites and fertilize them, and then fix themselves to their hosts and themselves develope into females. All the individuals are, in fact, protandric hermaphrodites.

Applying the same idea to the Rhizocephala, we regard the degenerate Cypris males as of exactly the same nature as the Cypris larvae which develope into the adult hermaphrodites, but owing to the position which they have taken up they are arrested in development. Their presence in this position is a reminiscence of a state through which the Rhizocephala have passed, exactly similar to the Epicarida, in which larval males (being potential hermaphrodites) fertilized adult females (also potential hermaphrodites), but owing to the acquisition of self-fertilization and the simultaneous ripening of the male and female sexual products, their instinct for fixing, while still larvae, on other hermaphrodites is rendered useless. But we can understand in some sense why this instinct has not been eliminated, because all the larvae, being essentially males in derivation, must have possessed it, and the damage which its retention does to the species is probably small, as only comparatively few larvae out of the myriads produced ever find their way to the mantle-opening of a young parasite, instead of fixing on a crab and infecting it. If we suppose however that the Cypris larvae fixed round the mantle-opening really represent individuals of a true male sex quite separate from the hermaphrodite individuals, then we must also suppose that a great number of larvae, probably about half, are produced in every generation which are from the first doomed to uselessness, whether they find young parasites to fix themselves onto or not, and this would be a solecism in the whole field of nature.

There is also an additional factor which may help to explain the retention of this masculine instinct, and that is the essentially gregarious nature of most Cirripedes, which we also see exhibited in several forms of Rhizocephala. It seems to me highly probable that this gregarious instinct has been derived from the originally masculine instinct which led the Cypris larvae to fix themselves upon an adult member of their own species whether female or hermaphrodite, and was subsequently slightly modified so as to lead the Cypris larvae to fix near other individuals instead of on them. (We may note in passing that Cirripede colonies are built up by larvae fixing on an object which already holds specimens at various stages of growth, and not merely by the simultaneous fixation of a number of larvae on the same spot. The larvae also show a preference for fixing on the peduncle of the adult individuals.)

The essential instinct, then, has always remained the same, and results in the occasional fixation of a Cypris actually in its orginal position, adapted for fertilizing the individual on which it is fixed, and under these circumstances it leads to arrested development and the production of complemental males.

To recapitulate — the complemental males in Cirripedes are in reality potential hermaphrodites like the other individuals, which have been arrested in their development owing to

their taking up a position on other individuals of the same species. They do this, not as a special adaptation for securing cross-fertilization, but owing to the retention of an instinct which is no longer of any essential use to the species, except in so far as it lies at the basis of the gregarious habit. This instinct was derived in the following way: the Cirripedes were originally dioecious, the male being fixed upon the female, as in *Scalpellum velutinum*, the Abdominalia etc. The male sex then acquired protandric hermaphroditism, the female sex being suppressed and fertilization occurring much as in the Epicarida, namely by the larvae (functionally males) fixing on the adult hermaphrodites (functionally females). Then a shifting of the time of sexual maturity occurred, the male and female products maturing at the same time in the adult state, and in the majority of forms the instinct of fixation on the hermaphrodites for fertilization possessed by the larvae was entirely given up and converted into a general gregarious instinct instead. But in certain forms, viz. those with so-called complemental males, the instinct still remains in the larvae more or less in its original state, and this results in the fact that when they meet with an adult hermaphrodite at the proper stage of development they fix themselves on it in the old position and are arrested in their development, so as to appear as true males and not hermaphrodites as they really are.

Finally there is nothing, either in the external or internal structure of the Cypris larvae that fix themselves round the mantle-openings of Sacculinae, to make us suppose that they differ from the ordinary Cypris larvae which affix themselves to crabs, in any other respect than in the fact of their falling victims to a misguided instinct which all the larvae equally possess. By following these lines of argument is it possible to obtain an explanation of two of the most noteworthy characteristics of Cirripedes, firstly their gregarious habits, and secondly their remarkable sexual variations together with the retention of an instinct long after it has ceased to subserve its original function. But the full weight of the argument can only be appreciated when the fundamental nature of hermaphroditism, as exposed in Chapter 5, has been fully grasped and accepted.

In contemplating this abortive male instinct and the curious results to which it leads, I see in it another confirmation of the principles enunciated by the illustrious discoverer of complemental males in Cirripedes, who first taught us completely that sublime aspect of Nature which looks only to the preservation of the species and ignores the safety of the individual.

And I do not think that we need be incredulous of the possible persistence of dangerous and obsolete instincts, capable as we are of recognizing, if not in ourselves, at least in other persons, the insistent development of instincts and habilitudes which, whatever may have been their use in that state of nature to which they and certain theorists would rapidly reconvert us, are inconsistent with the fulfillment of that destiny which civilization or reason may persuade us to be ours.

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Chapter 3.

Embryonic development and Larval Stages.

1. Embryonic development (To Nauplius Stage).

Peltogaster curvatus (Kossmann).

(Plate 4.)

The whole of the embryonic development to the Nauplius stage is passed through in the maternal mantle-cavity.

We have already seen, p. 29, that the first segmentation division takes place at the periphery of the egg, and that at first the two daughter nuclei resulting from the division are split up into a number of chromomeres. These separate bodies rapidly fuse to constitute an ordinary nucleus; the furrow spreads till it cleaves the egg into two equal parts, and so we obtain the two-cell stage figured (Plate 4 fig. 1). In a section through the upper hemisphere the two nuclei are seen reconstituted (fig. 2). These two nuclei now divide simultaneously, and a furrow, at right angles to the first, cleaves each cell into two. Thus is reached the four-cell stage (Plate 4 fig. 3), a section through the upper hemisphere being shown in Plate 4 fig. 4. So far the cleavage has been regular, total and equal, but at this point irregularities occur.

I may mention at this point the researches of P. Abric on the cleavage of the egg of *Sacculina carcini*. This had already been described by E. van Beneden (**1**), but Abric (**3**) undertakes to correct this author in some points. Thus he finds that in the first two divisions the daughter nuclei differ in size at first, a micromere being as it were budded off from a macromere; the two products are however quickly equalised in size. The author also calls attention to the frequent irregularities in the order of segmentation of the first few cells. With regard to the inequality in size of the products of the first swo segmentation divisions, I am unable to confirm Abric's observation for *Sacculina*, and I do not think that it is to be observed in *Peltogaster*.

After the 4-cell stage the cleavage does not affect the yolk, and the cells at the animal pole go on rapidly dividing in all directions so as to form a continuous blastoderm over the egg (Plate 4 figs. 5 and 6).

Soon after the blastoderm is complete an invagination begins at the equator of the egg (fig. 7) and soon a complete little bag is formed (fig. 8); this is the gastrula stage. That a very perfect gastrulation should occur in this manner is of high interest, because neither in the Nauplius nor in any later stage of the life history is there any trace of gut or endoderm to be observed. Soon after the gastrulation is complete the cells which form the endoderm bag break apart and lie in the middle of the yolk (fig. 9). Here they remain for a short time, but they rapidly begin to degenerate, and though they may be observed lying in the yolk after the rudiments of the limbs have begun to be formed (Plate 4 fig. 11), after this stage no sign of them can be detected. The perfect gastrulation, which also occurs in the embryogeny of *Sacculina*, is therefore merely an ancestral rudiment and has no relation, that we can see, to the present requirements of the animal, which does not develope a functional gut at any period of its existence.

The rudiments of the future Nauplius are first laid down as two lateral proliferations of the blastoderm which soon become segmented in the manner shown in fig. 10. The first antennal segment remains continuous with the acron after the second antennal and mandibular segments have been completely divided off. The blastoderm in the dorsal and ventral regions remains one cell thick at present. A horizontal section at this stage (fig. 11) shows that the segmental proliferations are solid and many cell-layers thick. In the next stage (Plate 4 fig. 12), another continuous unsegmented proliferation of the blastoderm has occurred in the ventral middle line (*VP*); this ventral plate ends abruptly, at a little below the egg's equator, in a transverse furrow, which gives the young Nauplius its characteristic shape. At the posterior pole of the egg certain large cells with conspicuous nucleoli have begun to differentiate (*Th*), which are the rudiments of the thorax of the future Cypris. The blastoderm on the dorsal surface is still one cell thick. The first antenna is from the first uniramous, the 2nd antenna and mandible are already bifurcated. The rudiments of the frontal horns are marked out by some conspicuous cells (*Fh*).

Plate 4 fig. 13 is a ventral view of a slightly later stage in which all these structures can again be observed. The horizontal section drawn in fig. 14 shows some interesting internal structures: the section passing through the ventral plate and the appendages. At the base of the second antenna are to be observed two little vesicles (*Ves*) which I take to represent the antennal gland characteristic of entomostracan Nauplii. They appear to be entirely closed and I cannot determine if they are developed from the ectoderm or mesoderm. Lying just posteriorly to them are a pair of skeletogenous elements (*sk*) which serve as attachments for the muscles which move the limbs. The large cells of the thoracic rudiment (*Th*) are also shown. In the transverse section (fig. 15) at this stage we again see the vesicle of one side and the paired skeletogenous elements from which muscles (*musc*) pass dorsally. The transverse

section (fig. 16) is taken through the extreme anterior end of the head and on the right side is seen one of the Frontal glands. These glands are of a true cellular nature, and not as DELAGE supposed non-cellular accretions.

The Nauplius with the structure described is now soon ready to be hatched out of the mantle-cavity.

2. Larval Stages and Fixation.

The free swimming Nauplius of *Sacculina carcini* has been minutely described by DELAGE (**2**) and since the Nauplii of *Sacculina neglecta* and *S. benedeni* agree with his description and figures in every detail, I will only refer the reader to Plate 4 fig. 17, which depicts the Nauplius of *Sacculina neglecta* from the ventral view. DELAGE points out that the newly-hatched Nauplii appear under two forms, a round and a long form; but this is only due to the long forms having already accomplished a moult on hatching. This is also true of *Sacculina neglecta*, our figure being taken from a long-shaped larva.

Plate 4 fig. 18 depicts the Nauplius larva of *Peltogaster curvatus*.

The transformation of the Nauplius into the Cypris has been described with the minutest detail by DELAGE, and he also gives instructions for rearing the larvae.

His account of the larval stages and of the fixation are the most elaborate and careful parts of his memoir, and since my own observations on this subject have been far from successful (see Note p. 44), I cannot do better than follow his account, only adding confirmatory remarks of my own where I am able to do so.

The Nauplius of *Sacculina* undergoes four moults in five days in order to achieve the Cypris stage. These moults do not effect any change in structure until the last moult which discloses the fully formed Cypris.

The Cypris larva of *Sacculina neglecta* is figured in our Plate 4 fig. 19; it resembles in all points the Cypris of *Sacculina carcini*. The cephalothorax bears a pair of antennae furnished with hooks, and also a pair of H-shaped "chitinous tendons" which are very conspicuous. There is a conspicuous pigmented eye, and a pair of glands on each side, the four openings of which are shown in the figure. Posteriorly the large cells in the thorax of the Nauplius have given rise to six pairs of biramous thoracic limbs; the abdomen is exceedingly small and rudimentary. Beside these organs there is a mass of cells, which DELAGE calls the ovary, but which for reasons that will be given, I prefer to call the "embryonic cells", situated as paired lateral masses on either side of the cephalothorax (*Em* Plate 4 fig. 19). These embryonic cells of a lately fixed Cypris, found upon the dorsal surface of the carapace of *Inachus scorpio*, are shown in horizontal section in fig. 20. They are derived from the mass of mesodermal cells situated in a similar position in the Nauplius larvae (*Em* Plate 4 figs. 17
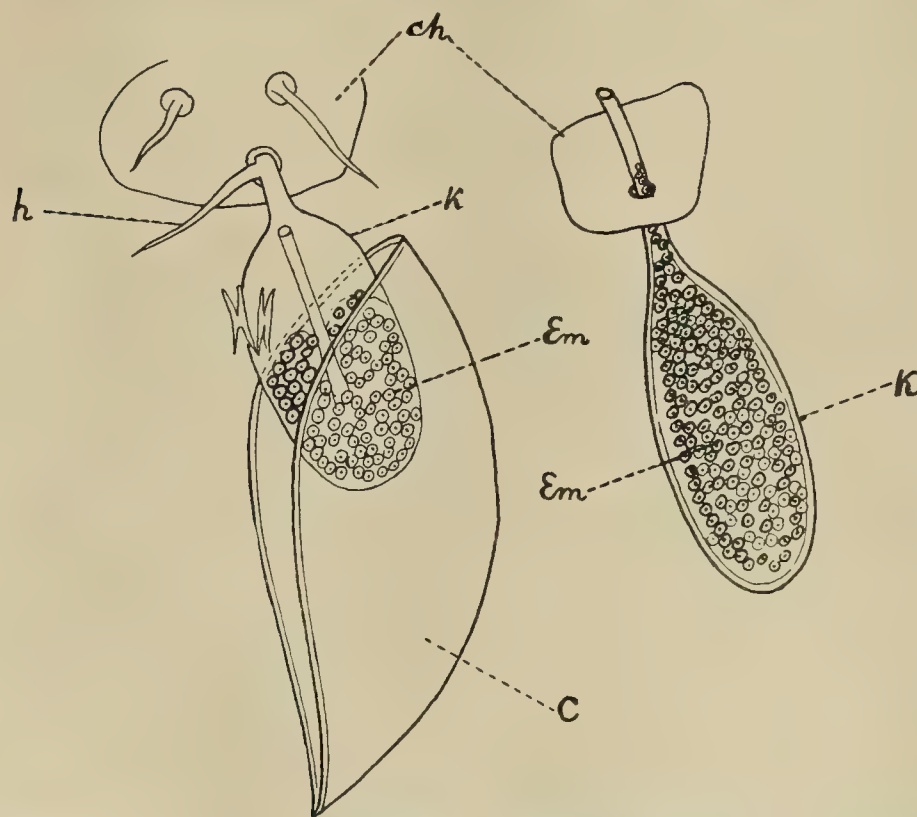
and 18). In our figure the chitinous investment of the embryonic cells (*ch* fig. 20), which will become the coat of the Kentrogon is clearly shown.

The Cypris larva spends a free and active existence for four days, and it is then ready to fix itself on the host.

DELAGE who has observed the fixation of the Cypris larva on *Carcinus maenas* on numerous occasions, states that fixation occurs at any point on the surface of the body or the appendages, except on the under surface of the abdomen where the adult Sacculina is evaginated. The Cypris fixes itself by the hook on its antenna to a hair of the crab. I have found Cypris larvae on two occasions upon the dorsal surface of the carapace of *Inachus scorpio*.

It cannot be disputed therefore that the Cypris larva may fix itself at almost any point of the body of its host; and after fixation it undergoes a series of changes which evidently have for their object the insertion of part of the cellular contents of the Cypris into the host.

These changes, as described by DELAGE, are shortly as follows: The thoracic appendages and abdomen are amputated and cast off, and a chitinous investment is formed round the mass of embryonic cells. The shell of the Cypris is thrown away, and the Kentrogon larva is left affixed to the base of the crab's hair. The base of the hair is penetrated by a chitinous tube of the Kentrogon larva which pushes into the sheath of the antenna, and the "embryonic cells" pass through this tube into the body of the crab.

These processes are illustrated in the Text figs. 10 and 11.

Text figs. 10 and 11. *c* = carapace of Cypris. *Em* = embryonic cells. *k* = kentrogon. *ch* = chitinous surface of crab. *h* = hair.

It appears to me that two questions present themselves with relation to the history of the fixation of the Cypris in *Sacculina* as described by DELAGE; firstly is this method of fixation the normal method by which the Sacculina gains an entrance into the body of the crab, and secondly of what nature are the cells which enter into the crab's body?

It appears to me that the definitive answer to these questions can only be given by studying the Sacculina soon after its entrance into the crab's body. This will be done in the next chapter, and we shall find that with regard to the first question, the youngest internal Sacculinae found must have entered the crab at some point other than the position of evagination of the adult body, in other words, most probably in the manner described by DELAGE;

and secondly that the cells of the Kentrogon which enter the body are all alike and undifferentiated, and not, as DELAGE suggested, already differentiated into ectoderm, ovary and other mesodermal cellular elements. It is for this reason that I have dropped DELAGE's terms of ovary, ectoderm etc. and substituted that of "embryonic cells" for the cellular elements of the Cypris that enter the crab and give rise to the whole of the adult Sacculina. The "ovary" and indeed all the organs of the adult Sacculina are subsequent differentiations of the embryonic cells, after they have entered the crab and begun to attain to the definitive position of the adult parasite.

To the proof of these points we now turn; but a word must be said with relation to the fixation in other forms of Rhizocephala. In *Sacculina* the fixation may be quite indefinite; at any rate the subsequent history will show us that it does not normally take place on the underside of the abdomen where the adult Sacculina is situated. But in *Peltogaster* and perhaps in other forms, it is possible that the fixation of the larva may take place in a position near the point of evagination of the adult. For in the youngest internal stages of *Peltogaster* which I have found, before the roots have attained any size and before any differentiation of the other organs, the parasite was already situated in the abdomen of its host very much in the definitive position of the adult.

The question of the fixation indeed, whether definite or indefinite in position, assumes a subordinate interest: the point which will be proved in the next chapter is that DELAGE was perfectly correct in his idea of the discontinuity in the development from the Cypris to the adult; in fact that this discontinuity is even more complete than he supposed and may be best described as a kind of alternation of generations. Furthermore we will confirm DELAGE in his statement that the passage from the Cypris to the adult is effected through stages which are completely endoparasitic.

It has been a great disappointment to me not to be able to follow out the processes of fixation as described so completely by DELAGE, and I do not doubt that this failure will be made much of by DELAGE's opponents; but the unprejudiced reader will be as little inclined as I am to disbelieve DELAGE's minute and exhaustive account of these processes when he perceives that the earliest endoparasitic stages in *Sacculina*, to be described in the next chapter, are perfectly in accord with DELAGE's account of the fixation and utterly inconsistent with any other method of fixation which has been suggested, or, as far as I can see, can be imagined.

I trust therefore that my failure in this matter, although it may be legitimately used as a serious reproach against me, will not be employed in the service of obscurantist criticism which too long has shrouded this question.

Note. — My failure to obtain the Cypris larvae of the Rhizocephala, by rearing the Nauplii, requires some explanation. DELAGE has given a description of the method by which he obtained the Cypris, and I have naturally followed his methods with great care, but without success. He found that it was necessary to choose Sacculinae of a purple colour in which the Nauplii were nearly ready to be hatched out, to wait for the emission of the larvae, and then to keep them in a vessel of water without current or aeration. Under favourable circumstances the Nauplii should change into Cypris larvae in four days, and the Cypris should be ready to fix on the Sacculinae at the end of four more days of free existence. The chief source of failure, according to DELAGE, consists in not obtaining a normal emission of the Nauplii from the brood-pouch of the parent.

Following DELAGE's directions I have obtained on more than a hundred occasions the emission of the Nauplii of *Sacculina neglecta*, *S. benedeni* and *Peltogaster curvatus*, but although the larvae have been kept alive for as long as seven days they have never changed into Cypris, unhealthy signs being sooner or later always apparent in them.

The Nauplii of *Peltogaster* and of *Sacculina* behave very differently, those of *Peltogaster* being feebly heliotropic and strongly negatively geotropic, those of *Sacculina* beeing strongly heliotropic and without any marked reaction to gravity. The rearing of the Nauplii of *Peltogaster*, without some special apparatus which has not yet been devised for marine larvae, is really hopeless, as the larvae soon reach the surface film of the water, and the presence of any motion in the water to disturb the surface film is fatal.

With *Sacculina* it is easy to keep the Nauplii alive for a long time, and I am unable to state the cause of my failure to obtain the Cypris. I have observed that the Nauplii of *Sacculina benedeni* live longer than those of *S. neglecta*, perhaps owing to the host of *S. benedeni*, viz. *Pachygrapsus marmoratus*, being a littoral form and therefore exposed to more varying conditions in a state of nature, but as *S. benedeni* is not very common at Naples I have not been able to obtain it in sufficient quantities for performing a successful experiment, large quantities of material being essential for success, as DELAGE has repeatedly insisted. The form on which DELAGE worked was *S. carcini*, the parasite of *Carcinus maenas*; and the fact that this race of *Sacculina* is parasitic on a littoral species of crab and is exceedingly common at Roscoff, may account in some measure for DELAGE's success.

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Chapter 4.

The Endoparasitic Development of the Rhizocephala.

Contents.

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1. The History and Development of Sacculina interna.

Those who have read DELAGE's memoir (**1**) and have followed the subsequent contro-versy on the internal parasitism of *Sacculina* will remember that DELAGE describes no stage between the indefinitely located fixation of the Cypris larva, and the appearance of the nearly adult body of the Sacculina at the position of evagination. At this latter stage the root system is already fully etablished; it is apparent therefore that there is a wide gap between these two stages of DELAGE. It was the existence of this gap which gave GIARD's scepticism some sort of basis. I am now able substantially to fill in that gap, and the earlier stages of the internal parasite, which I have found, completely confirm DELAGE's deduction that there is an internal stage of the life-history when the parasite is engaged in establishing the system of

roots and gradually attaining to its definitive position on the intestine of the crab at the junction of thorax and abdomen.

Before describing these early stages I wish to give some directions as to the best method of studying Sacculina interna, because, owing to the controversial nature of the subject, it is probable that some naturalists would like to satisfy themselves as to the truth of my statements.

Since it is impossible in the great majority of cases to foresee which crabs contain a Sacculina interna by mere inspection, it is advisable to attempt the study only where the parasite is known to be very common. At Roscoff, according to DELAGE, *Sacculina carcini* is very common, and *Sacculina neglecta* at Naples has been found by me to infect about an eighth of the whole population of *Inachus scorpio*. The following directions apply to *Sacculina neglecta* at Naples.

The first thing for the investigator to do is to thoroughly familiarize himself with the living appearance of the roots of the Sacculina, so that he can at once recognize and distinguish these roots from all the tissues of the crab. This can be accomplished by the examination of the roots of an adult Sacculina externa. A large collection should then be made of the crabs not bearing Sacculinae externae, but these crabs should be taken from an area where Sacculinae externae are common. The most promising time of the year is the late autumn and winter, and for preference young crabs of 5—16 millimeters carapace length should be selected. The thorax of each crab, freshly killed, is now removed and pieces of the liver surrounding the posterior part of the intestine are carefully removed and examined under a fairly low power.

If Sacculina roots are recognized the crab is infected with a Sacculina interna, and the whole intestine should be very carefully removed and preserved.

The central tumour containing the body of *Sacculina* at some stage of development will be found attached to the intestine somewhere in the neighbourhood of the unpaired diverticulum which springs from the intestine where the latter passes from the thorax into the abdomen (see Plate 5 fig. 10 a). The only satisfactory way of studying the organization of Sacculina interna is by serial sections. If Sacculina roots are not recognized clinging to the liver, in any particular crab, two alternatives are possible: either the crab is uninfected or else the Sacculina interna is very young and has not yet established its system of roots.

Carefully separate the liver tubes from the intestine along its whole length and examine with a lens if there is anything clinging to the intestine on its upper portion immediately below the stomach, or on its middle portion. If any body can be detected remove the whole intestine along its whole length and examine this body under a low power. In some cases blood clots and vessels are attached to the intestine which must not be mistaken for the young Sacculina. In this manner after the dissection of a hundred crabs or so, one or two Sacculinae internae will be found loosely attached to the upper or middle portion of the intestine with a few short roots beginning to grow out into the surrounding tissues, but

with no sign of any roots on the lower part of the intestine where the adult Sacculina will appear. The histological examination of the youngest of these Sacculinae will disclose the fact that at present no differentiation of organs has appeared, but that the whole body consists of a hollow plate drawn out into short processes and composed of a number of large embryonic cells, many of which are undergoing mitosis. With these few directions which doubtless the individual investigator will improve as his experience in the matter accumulates, I pass to the description of these youngest stages of all before the Sacculina has reached its definitive position. Plate 5 fig. 2 represents a young Sacculina interna (*sac*) on the upper part of the host's intestine, far removed from the definitive position of the adult parasite (*x*).

A. Sacculina interna migrans.
(Plate 5 figs. 1—9.)

It appears to me probable that when the "embryonic cells" of the Kentrogon have entered the haemocoel of the crab at any point, they are passively carried about until they reach the space surrounding the upper part of the intestine just below the stomach. They then become applied to the intestine in this region and begin to throw out roots and at the same time to grow down the intestine towards the definitive position of the adult. DELAGE supposed that directly after inoculation the cells began to grow and establish roots, the motion of the Sacculina in the crab being from the start purely due to growth. My reason for disagreeing with him is that the young Sacculinae internae which I have found attached to the upper portion of the intestine (see Plate 5 figs. 1 and 2) have not exhibited as far as I could observe an elongated root leading to the point of inoculation, and moreover since I have found in every case observed that the Sacculina first becomes attached to the upper part of the intestine and then grows downward, it is difficult to see why, if the Sacculina begins to establish its root system from the first, it should always take this roundabout course to reach its final position near the unpaired diverticulum of the gut.

It appears to be, highly probable that the normal course of development is always as I have described, namely that the "embryonic cells" of the Cypris larva, after entering the crab at any point, are first carried to the upper part of the gut near the stomach, and then grow downwards to the definite position of the adult, spreading out the root system meantime in all directions; but it may well be that in abnormal cases the growth may proceed from some other situation.

However this may be, the youngest stages of Sacculina interna, which I have found, have been always attached near or actually on the intestine at its upper portion immediately below the paired diverticula which spring from the gut just below the stomach. Two such Sacculinae are figured from the life in Plate 5 figs. 1 and 2.

The gut of the crab in this region is separated from the external epithelium of the crab by liver diverticula and blood spaces, and of course it is nowhere near the place where

the adolescent Sacculina is evaginated (*x*). The discovery of these early stages is therefore irreconcilable with Giard's theory of local fixation and development, at any rate in Sacculina.

The body at this stage is composed of an hollow plate which sends out processes, the future roots, many of which are bifurcated and in the act of ramifying. Histologically the structure is very simple; the essential facts are shown in Plate 5 figs. 3 and 4. The walls of the plate are composed of large cells with nuclei which either have a conspicuous nucleolus or else are in mitosis. The external wall has a layer of chitin; the wall which clings to the intestine is naked, and the internal cells of this wall may be drawn out into amoeboid processes. The structure of the central tumour (Plate 5 fig. 3 *ct.cav*) is the same as that of the roots (*r*) and at this stage there is no sign of a differentiated ovary or organ of any kind.

This latter fact is of the highest importance, and will be given its due prominence when we consider the general nature of the development of the Rhizocephala (p. 59).

In the next stages of development the parasite continues to throw out roots, while, as a result of the growth of the whole, the part attached to the intestine begins to grow along the surface of the latter towards its definitive position near the unpaired diverticulum (Plate 5 figs. 5 and 8). As it grows the roots become histologically differentiated into an external epithelium and an internal mass of spider cells (Plate 5 fig. 18). During its passage, also, the organs of the adult Sacculina first appear as a little mass or "nucleus" (figs. 5 and 8 *n*) of cells at the posterior border of the growing parasite, that is to say at the border which approaches most nearly and will soonest reach the definitive position (*x*).

It is exceedingly difficult to say exactly how this "nucleus" or rudiment of the adult Sacculina body arises. In the youngest stage at which I have been able to recognize it, it has the appearance in section shown in Plate 5 fig. 6. This section is through the parasite figured in fig. 5. The "nucleus" (*n*) is seen to consist of a mass of small cells surrounded by a small hollow sac (*bc*). The whole is enclosed within the walls of the central tumour, which is composed as before of large nucleolated cells. In the cavity surrounding the "nucleus" are other small cells identical with the spider cells found in the roots (*sp*).

Delage believed that this "nucleus" of cells was already differentiated in the Cypris larva and that the sac surrounding it (*bc*) is formed by an invagination of the wall of the central tumour. It has been shown that in the earlier stages of Sacculina interna migrans the small cells composing the "nucleus" do not exist as such, the only cells present being the large "embryonic cells". Delage was in fact deceived when he called the cells of the Cypris which pass into the crab "an ovary"; those cells become the large embryonic cells which give rise to the whole mass of the Sacculina. The "nucleus" therefore is a subsequent differentiation of these embryonic cells. With regard to the formation of the sac surrounding the nucleus, I am in two minds. Delage believes that it is formed by an invagination from the wall of the central tumour and he gives in support of this theory his fig. 36. Now I have found a similar stage in which the sac (*bc*) is in continuity with the central tumour wall (Plate 5 fig. 7),

but this stage is later than that represented in my fig. 6 where not only is there no continuity, but the cells composing the sac are very small like those of the "nucleus" and utterly unlike the large cells of the wall of the central tumour. I think it probable that the sac is hollowed out in situ from the cells forming the rim of the "nucleus", but I do not wish to be dogmatic and the matter is of minor importance.

By the time the central tumour with its "nucleus" has reached the region round the unpaired diverticulum, the "nucleus" has enlarged, the surrounding sac is more clearly visible and the spider cells in the tumour have increased in number and become more filamentous. The epithelial cells composing the walls of the tumour and of the roots have increased greatly in number and are becoming somewhat smaller. The roots already have a wide distribution. We now pass to the differentiation of the organs of the Sacculina which takes place after the latter has reached its definitive position shown in Plate 5 fig. 10a. The whole of the Sacculina is of course still entirely inside the body of the crab, the continuity of the abdominal epithelium and chitin of the crab being easily demonstrable in serial sections (e.g. Plate 5 fig. 10).

B. Sacculina interna.   Organogeny and Evagination.
(Plate 5 figs. 9—18.)

The organogeny of Sacculina interna has been described by DELAGE and with almost all his description I am in agreement, but with regard to the formation of the mantle and of the perisomatic space I entirely disagree with him. I am surprised that our accounts of the formation of these two organs should be so entirely different, because it is evident that in all other points of anatomy and development *Sacculina neglecta* and *Sacculina carcini* are practically identical. But I am not in these respects satisfied with DELAGE's account, because the figures on which he bases it are to my mind not at all convincing, and one figure, which should be the crucial one, is drawn from a confessedly abnormal specimen (DELAGE's figure 38). We both agree in starting from the stage figured in Plate 5 fig. 7 of this work, and in DELAGE's figure 37. We both agree in reaching a stage in which the visceral mass of the developing Sacculina is enveloped by two sacs, an inner one the mantle cavity or brood pouch, and an outer one the perisomatic space, but as to how these two sacs are formed we are in irreconcilable disagreement.

According to DELAGE the mantle sac (*bc*) is formed by delamination from the inner wall of the original investing sac (*pc*), the cavity of this latter sac forming the cavity of the perisomatic space. This view is presented in the Diagrams in Text fig. 12.

According to me the original investing sac (Plate 5, *bc* in figs. 6 and 7) remains unaltered as the mantle cavity or brood pouch, while the perisomatic cavity is formed by a separate invagination of the wall of the central tumour. This view is presented in the Diagrams Text fig. 13.

These diagrams (Text fig. 13) are constructed from the actual sections drawn on Plate 5. In Figures 10 and 11 (Plate 5) the invagination to form the perisomatic space (*pc*) has just
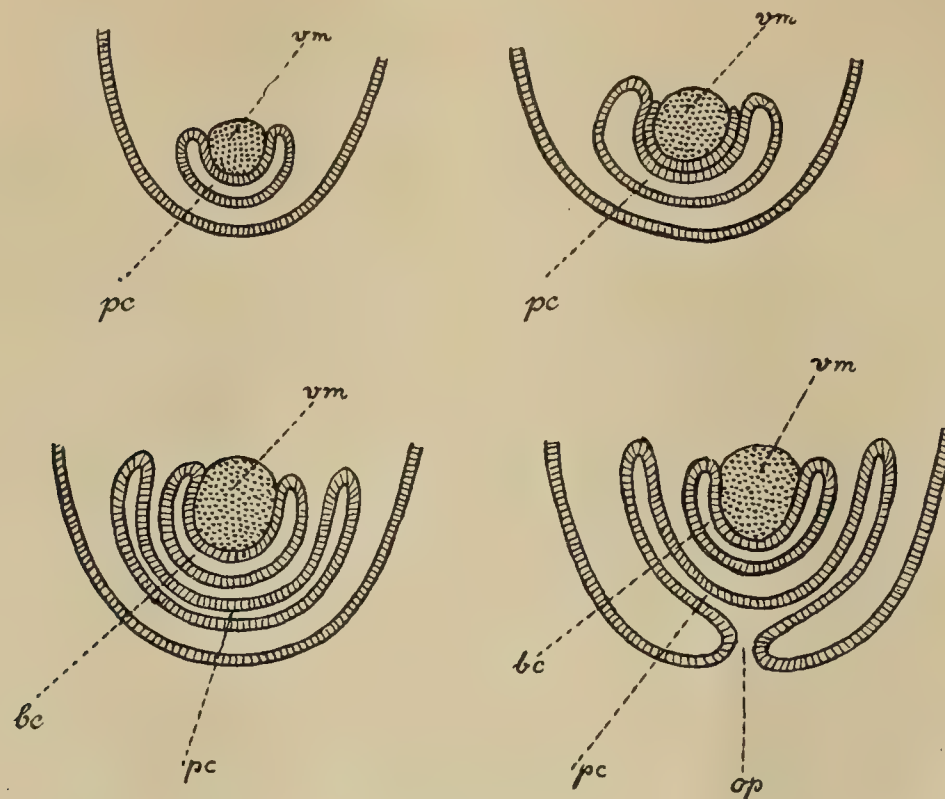
Text fig. 12.
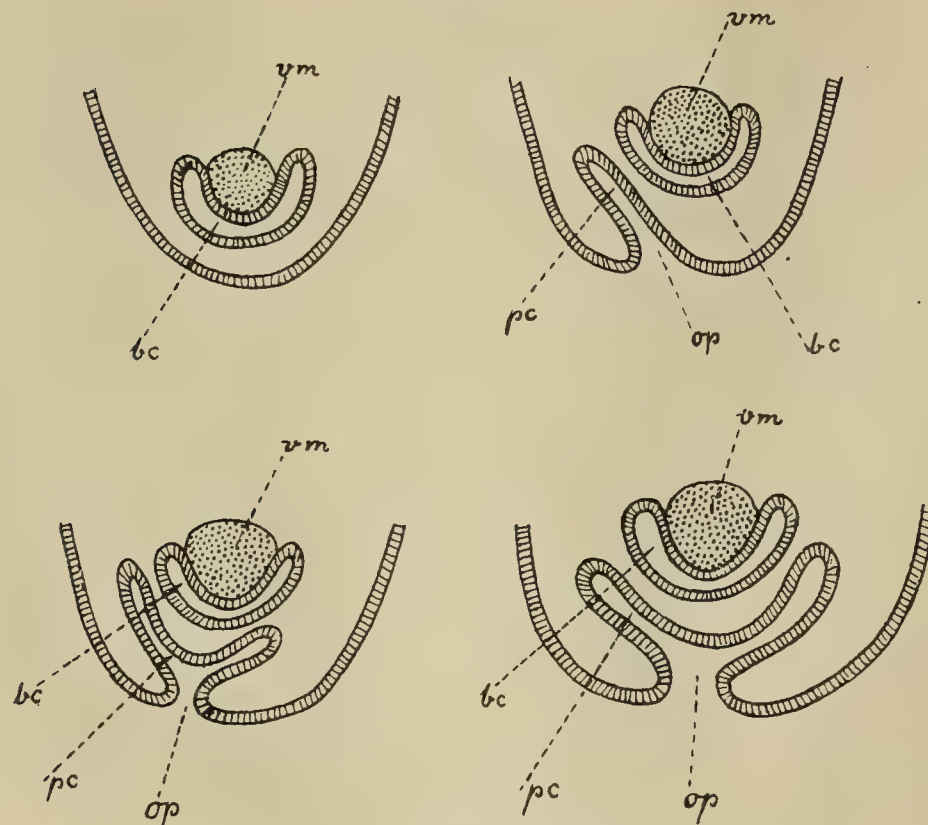
Text fig. 13.

vm = visceral mass.   *bc* = mantle cavity.   *pc* = perisomatic cavity.   *op* = opening of perisomatic cavity.

begun.   It always begins in the same place namely between the visceral mass of the Sacculina and the intestine of the crab, and at the posterior part of the central tumour.   The cells

composing the wall of the central tumour in this region of invagination take on a more definitely epithelial character. In figs. 12 and 13 (Plate 5) the invagination has proceeded further, and an arm is beginning to enclose the Sacculina's visceral mass on its outer side. In Plate 5 fig. 14 the perisomatic space (*pc*) is completely formed and surrounds the visceral mass and the mantle cavity altogether. All this time the walls of the inner cavity, i. e. the mantle cavity or brood pouch (*bc*), have remained unaltered and have taken no part in the formation of the perisomatic cavity, which has been formed entirely from the wall of the central tumour by an invagination proceeding more rapidly in the region lying between the Sacculina and the crab's intestine. DELAGE makes his perisomatic cavity at first closed and then opening secondarily (Text fig. 12); according to me the perisomatic space is open from the beginning.

During the formation of the perisomatic space or cavity, the rest of the organogeny has been proceeding. The first organ to appear, besides the brood-pouch, is the ovary (*ov* Plate 5). This is distinguishable as a large mass of cells surrounded by a membrane; it is bilobed so that in many of the sections there appear to be two bodies, as in Plate 8 figs. 12 and 13, but where a section passes through either one of the lobes or the intermediate portion of the ovary uniting the two lobes, the mass appears single (fig. 11). Surrounding the ovary at this stage are a mass of indifferent cells which pass insensibly into the filamentous spider-cells (*sp*) which fill the central tumour (Plate 5 figs. 11, 12 and 13).

Certain of these spider-cells intrude between the outer epithelial layer of the brood-pouch (fig. 13 *ep2*) and that layer of the central tumour which will form the inner wall of the perisomatic space (fig. 13 *ep3*). These cells form the circular musculature of the outer wall of the brood-pouch. The transverse musculature, i. e. the fibres which stretch across the thickness of the outer wall of the brood-pouch, I agree with DELAGE in deriving from the epithelial cells of the central tumour (Plate 5 fig. 13 *ep3*) and from the outer epithelial layer of the brood-pouch (fig. 13 *ep2*).

The mesentery (*mes*) is formed during the invagination of the perisomatic space. Ever since the appearance of the central "nucleus" and its investing mantle sac, a portion of the "nucleus" of cells has been left unenveloped by the mantle sac (fig. 11 *mes*). As the epithelium of the central tumour rolls in to form the perisomatic space, it unites with the cells of the central "nucleus" to form the mesentery along the line where the mantle cavity is blocked (fig. 11 *mes*).

The formation of the nervous ganglion (Plate 5 figs. 13 and 17 *gn*) takes place when the perisomatic space is nearly completed. The nervous ganglion pushes into the visceral mass from the outer epithelial layer of the mantle-sac (*bc*), opposite the extreme anterior region of the mesentery and slightly to one side of the middle line. This position will be more clearly explained on p. 53.

The testes (*t*) are not apparent until a rather late point in development. Two little pockets push in from the summit of the mantle sac to form the vasa deferentia, and grouped round them two masses of cells with rather large nuclei can be distinguished, which will give rise to the glandular portion of future testes (Plate 5 figs. 15 and 16, *t* and *dv*).

7*

Soon after, the colleteric glands of the ovary are clearly distinguishable by their regular epithelium (Plate 5 fig. 16 cg). At this stage all the adult organs are fully differentiated, the ovary ramifies greatly, and in the spaces between its lobes are seen muscle fibres and connective tissue cells. The testes are conspicuous as darkly staining bodies in the posterior part of the visceral mass. The visceral mass of the Sacculina has attained a large size, comparatively to the little "nucleus" of undifferentiated cells from which it has sprung, and it now occupies nearly the whole of the central tumour. It is still invested with the two sacs, i. e. internally the mantle sac and externally the perisomatic sac. Now the cloacal opening is formed as a rupture of the outer wall of the mantle cavity, but the opening is as yet obstructed by a chitinous plate. The body of the young Sacculina is now gradually pushed through the wide opening of the perisomatic space, and is ready for the moult of its host which will convert it from a Sacculina interna into a Sacculina externa. DELAGE has fully explained the way in which the young Sacculina becomes external and with his description I am in entire agreement. The presence of the Sacculina interna causes after a while the crab's muscular and epithelial tissue, to which it is applied, to degenerate; in consequence no chitin is secreted on the ventral surface of the abdomen which is in contact with the growing Sacculina interna. Thus when the crab moults, a round hole is left in this region rather larger than the Sacculina, and the latter, as it goes on growing, naturally protrudes through this aperture. At first there is no chitinous ring of attachment, but when the Sacculina has grown to such an extent that the peduncle, by which it is attached to the crab, completely fills up the aperture in the crab's abdomen through which the Sacculina made its egress, the chitinous ring is formed where the peduncle is in contact with the rim of the aperture.

C. Orientation of the body during Organogeny.

In the foregoing account of the organogeny I have paid no attention to the morphological orientation of the body relatively to the axes of the host. It is now necessary to explain this interesting relation.

During the early stages of organogeny, up to the formation of the perisomatic space, the morphological axes of the parasite coincide with those of the host. This fact is represented diagrammatically in Text fig. 14.

The red lines represent the intestine of the crab with its asymmetrical diverticulum which enters the intestine on the morphologically left side. The dorsal surface of the intestine is on the left of the figure, and the right hand surface is towards the reader, the left hand surface being hidden. On the ventral surface of the intestine is placed the Sacculina interna (in black).

The antero-posterior long axis of the Sacculina is given by the mesentery (mes), the anterior pole of the body being given by the nervous ganglion (gn) which is at the extremity pointing to the posterior pole of the host.

Now the long axis of the mesentery, and in consequence the morphological long axis of the Sacculina body, coincides with the morphological long axis of the crab, the organs of the Sacculina being situated symmetrically on either side of this long axis; in other words the symmetry of the Sacculina corresponds to the symmetry of the crab.

The nervous ganglion (*gn*) however is formed later in an asymmetrical position, namely slightly to the right of the middle line and just anteriorly to the extreme anterior end of the mesentery.

On general grounds, explained in Chapter 1 p. 10, I regard the mesenterial surface of the Sacculina as the dorsal, so that the nervous ganglion is formed apically and slightly laterally.
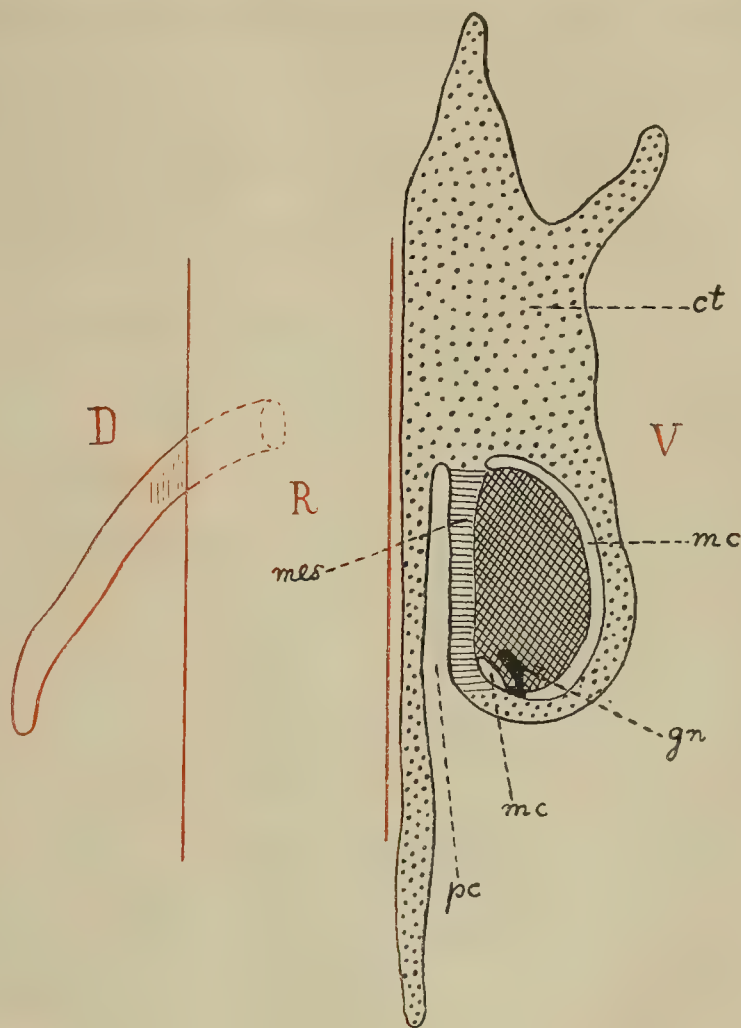
The main arm of the perisomatic in-vagination (*pc*) is pushed up between the visceral mass of the Sacculina and the ventral surface of the crab's intestine.

To summarise the morphological position of the Sacculina during the early stages of organogeny we may say that it is applied by its dorsal or mesenterial surface to the ventral surface of the host's intestine, the bilateral symmetry of its organs coinciding with that of the crab.

Now during the formation of the pe-risomatic space a rotation of the body takes place, of such a kind that the mesenterial surface of the Sacculina is pulled towards the morphological right side of the crab's intestine, forsaking its median symmetrical position.

In this manner when the Sacculina interna becomes external, its position on the crab is asymmetrical, the mesentery being situated on the morphologically right side of the crab's abdomen, and the plane of symmetry of the Sacculina being horizontal to that of the crab.

Text fig. 14.

ct = central tumour.   *mc* = mantle-cavity.   *mes* = mesentery.
pc = perisomatic cavity.   *gn* = ganglion.

I have explained in Chapter 1 how the asymmetry of *Sacculina* relatively to its host can be derived from the symmetrical condition of *Peltogaster*, and it may be now pointed out that the passage of *Sacculina* through an embryonic stage in which it is symmetrically applied to its host along its dorsal or mesenterial surface, as is the case in the adult *Peltogaster*, is strikingly confirmatory of the views developed in Chapter 1.

2. The Endoparasitic Development of Peltogaster curvatus (Kossmann).

(Plate 6 figs. 1—6.)

With the exception of a note by Schimkewitsch (**2**) no account has been given of the internal development of *Peltogaster*.

Peltogaster in its endoparasitic development follows an essentially similar course to *Sacculina*, but with certain very instructive and interesting deviations. Since this parasite is by no means so frequent as *Sacculina*, it is difficult to obtain a complete series of stages; I have been so fortunate, however, as to find several specimens at an exceedingly early stage of endoparasitic development, corresponding to that described above for *Sacculina* under the name of Sacculina interna migrans.

This stage in *Peltogaster* is figured in Plate 6 figs. 1, 2 and 3. The long stolon-like structure drawn under a low power in fig. 1 was found in all cases in the position where the roots of the adult are finally situated, namely clinging to the gonad, or to the liver near the gonad, on the left side of the body. It was situated entirely inside the body of its host with no communication or contact with the external epithelium.

I may mention here that Mr. F. A. Potts of Trinity Hall, Cambridge, in the course of his investigations on the effect of *Peltogaster* on *Eupagurus meticulosus*, has found two specimens of *Peltogaster* at this early internal stage which he handed over to me for further study.

The body, which is at this stage of a pale green colour, consists of an elongated hollow central tumour which is beginning to throw out slender roots in all directions. At present no sign of the differentiation of the mantle and visceral mass is visible: histologically the central tumour is composed of a single epithelial layer of large cells, many of which are undergoing mitosis, and the roots have an identical structure. But at the extreme anterior end (Plate 6 fig. 1 *n*) in the region where the mantle and visceral mass will soon be differentiated, the epithelium has given rise to a quantity of smaller cells which lie beneath the surface. Fig. 3 is a drawing of a whole preparation of this region. Fig. 3 a is a drawing of a root. In some of the specimens, the roots were short, but in others the growth of the roots had proceeded further and were quite unmistakably identical in structure and appearance with those of an adult *Peltogaster*, although considerably smaller. It should be observed that the roots of *Peltogaster* do not branch and subdivide, like those of *Sacculina*, but continue as long unbranched filaments even in the adult. The method of growth of *Peltogaster* is thus a little different and more simple than that of *Sacculina*, for whereas in the latter the central tumour, as it grows to its definite position, becomes broken up into a multitude of ramifying roots, in *Peltogaster* the central tumour from the earliest period, when roots are being formed, occupies pretty accurately its definitive position and from that position sends out simple unbranched roots. In an old *Peltogaster* the central tumour is no longer present as such, having broken

up into the compact green mass of filamentous roots which characterises the adult *Peltogaster*. But *Peltogaster* agrees with *Sacculina* in the essential feature that at an early stage of its endoparasitic development the body consists of a growing central tumour and roots composed of embryonic actively dividing cells, without a trace of further differentiation into the organs of the adult. The method of growth of the tumour and roots of *Peltogaster*, while differing from *Sacculina* in its greater simplicity, is highly instructive, because from it we gain a perfect confirmation of the idea which we formed as to how the young Sacculina interna passes along the intestine of its host to its definitive position. We supposed in the case of *Sacculina* that the process of growth was brought about by the central tumour as it increased in size continually throwing off roots towards the anterior region of the crab, while the tumour itself travelled in the opposite direction, namely toward the posterior part of the crab. The necessary result of this method would be that the oldest roots, i. e. the first formed, would always be further away from the central tumour and the region of differentiation of the external body than the younger roots. Now this in *Sacculina* is hard to prove because of the roots being so highly branched and complicated, but in a young Peltogaster internus it is quite easy to see that the state of things postulated by our theory is exactly the truth. Because it may be held as a safe rule that the age of a root is indicated by its length reckoned from the tip to the point where it joins the main stolon, and in Plate 6 fig. 1 which represents a typical Peltogaster internus it is seen that the roots become regularly longer and longer the further they are situated from the point (n) where the external body will be differentiated. We take this to be a certain proof of the method of growth postulated for *Sacculina* and again indicated above, namely the change of position by growth of a central tumour which leaves in its train a system of roots, the oldest of which are always further away from that part of the central tumour which has advanced furthest and which will give rise to the future external body of the parasite.

The differentiation of the mantle and visceral mass takes place, as already mentioned, at the anterior end of the central tumour (n in fig. 1). When this differentiation is still far from complete, this portion of the body acquires its deep red colour, so that the presence of a young developing *Peltogaster* at this stage can, under favourable circumstances, be recognised as a glowing red spot through the external tissues of the abdomen of its host. The differentiation of the body occurs in *Peltogaster* long before the root system has assumed its adult character, so that in this way I have been able to place the identity and nature of the young *Peltogaster*, before any differentiation of the visceral mass had occurred, with those in which it had already begun, beyond question.

The differentiation of the organs in Peltogaster internus occurs in the main similarly to that in *Sacculina*, but there is one exceedingly interesting difference which is illustrated in Plate 6 figs. 4 and 5. Here the fact is shown that no perisomatic cavity, a structure so characteristic of Sacculina interna, is formed. At a corresponding stage in *Sacculina* the perisomatic cavity would already be complete, because as figs. 4 and 5 show, all the organs

of the adult are already laid down in miniature, and fig. 4 shows that the body of the *Pelto-gaster* is already beginning to gain access to the exterior, and yet no invagination has begun to form the rudiment of a perisomatic cavity. Fig. 6 is a section through a young Pelto-gaster externus and here the method of communication of the external part of the body with the central tumour is further proof that no perisomatic cavity has been formed, because in a young Sacculina externa the ragged edges of the perisomatic cavity are always to be observed instead of the clear-cut continuity of external body and internal central tumour shown in Plate 6 fig. 6.

With regard to the rest of the organogeny of *Peltogaster* I will not enter into details, because it evidently follows the essential lines described for *Sacculina*, as may be gathered from Plate 6 fig. 5, from which also the difference in shape of the young parasite can be observed.

There is however one important consideration with regard to the manner in which Peltogaster internus becomes external. We have seen in *Sacculina* that this is always effected by a moult of the host at the critical period when the Sacculina is ready to be evaginated. Now in *Peltogaster* there is very strong evidence to show that the parasite pushes its body through the abdominal tissues of its host and so becomes external without any special moult on the part of the latter. In Plate 6 fig. 4 the young parasite is already beginning to pro-trude through the external tissues of its host's abdomen (red in figure), and this crab showed no sign of having recently undergone a moult. The fact that the Peltogaster may become evaginated from its host's body without a moult on the part of the crab has since been confirmed on several occasions by Mr. F. A. POTTS, whose investigations on the relation of parasite to host will, I understand, be shortly published.

Recapitulating the chief points in the endoparasitic development of *Peltogaster* we may state : —

1. A completely embryonic undifferentiated stage is passed through in the host's body corresponding to the youngest Sacculina interna migrans.

2. The central tumour does not so actively change its position as in *Sacculina*, after once it has begun to throw out roots; but its method of growth resembles that of *Sacculina* in that the oldest roots are always further away from the point where the external body will be differentiated.

3. No perisomatic cavity is formed.

4. The parasite probably gains to its external position independently of a moult on the part of its host.

The last three points confirm our opinion developed in Chapter 1 that *Peltogaster* is more primitive than *Sacculina*.

3. The Endoparasitic development of Peltogaster socialis, and Polyembryony in Sacculina.

It is only possible to touch lightly here on a subject which offers a very interesting field of research, but since the species in question is not at all common at Naples I am only able to give a few notes which may perhaps be of value for the future.

Peltogaster socialis, a parasite of *Eupagurus prideauxii* and *meticulosus*, 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. In Plate 6 fig. 7 I have drawn a specimen of *E. prideauxii* which carried 22 parasites. The shape of a single animal is shown in fig. 8; in anatomical characters it does not differ in any respect from the ordinary solitary kinds of *Peltogaster*.

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 larvae, 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 (1 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 Sacculinae; but he dismisses the idea, partly because his preparation was a poor one and partly because the 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 Sacculinae may begin to develope from a single central tumour; but whether two such Sacculinae 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 (see Chap. 7), this process of budding had become normal and permanent.

According to this view it should be possible to prove that the root systems of the apparently separate individuals of *Peltogaster 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* showing the mantle and visceral mass in process of formation, the whole lying entirely within the body of the crab, whose tissues are tinted red in the figure. 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 as yet altogether give up that hypothesis. It may well prove that the splitting 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.

4. The general nature of the endoparasitic development of the Rhizocephala.

The interpretation which I am bound to give of the endoparasitic development of the Rhizocephala differs, as the reader will have noticed, in an important point from that of DELAGE. He cautiously endeavours to identify in the cells of the Kentrogon, which pass into the body of the crab, the differentiated elements of the ectoderm, ovary and other mesodermal structures of the adult. But in his figure of the Kentrogon (fig. 27) these differentiated elements are not distinguishable, all the cells being of the same undifferentiated embryonic character; and in the fixed Cypris, a section of which I figure on Plate 4 fig. 20, the cells of the future Kentrogon, which will enter the crab, are seen to be undifferentiated in character (*em*).

When we pass to the earliest endoparasitic stages described in this Chapter for *Sacculina* and *Peltogaster*, which where unknown to DELAGE, we find that the body at this

stage consists of undifferentiated cellular elements, the ovary and other organs being a later differentiation from them.

It appears therefore that there is even less continuity between the structure of the Cypris and of the adult than DELAGE supposed, and that a truly embryonic undifferentiated period is interpolated in the life-history between the Cypris larva and the adult.

The embryonic cells of the Cypris and of the Kentrogon are paralleled by those cells of the Rediae of Trematodes which give rise to Cercariae, except that in the Rhizocephala only one adult is produced from a single Cypris. And yet we have seen that there is a tendency in the occasional polyembryony of *Sacculina* to simulate still further the condition of the Trematodes, and it was further suggested that the so-called gregarious forms of the Rhizocephala might be due to the production of several adults from the embryonic cells of a single Cypris. However this may be, the remarkable life history of the Rhizocephala shows an intermediate condition of a most suggestive kind between an ordinary continuous development and a true alternation of generations.

It is perhaps idle to speculate why the Rhizocephala have acquired a developmental history so utterly different from that of all other Crustacea. We may however safely suppose that the ancestors of the Rhizocephala were originally ectoparasites on other Crustacea, and that owing to the dangers to the parasites involved by the continual moulting of their hosts, they gradually acquired a partially endoparasitic habit. Hand in hand with this acquisition, an economy was practised in the division of the developmental phases into two periods, firstly the rapid establishment of the root system, and subequently the retarded differentiation of the adult organs. The chief advantage of this postponement of the differentiation of the adult organs is perhaps to be found in the prevention by this means of the parasite being interfered with by the host's moulting: for when the retarded development of the adult organs takes place and the part of the body containing the reproductive organs must be protruded from the host for the purposes of reproduction, the precocious establishment of the root system has inhibited the growth of the host, and prevents the continual moulting which would certainly interfere with the welfare of the parasite. In this manner we may perceive the usefulness of the interpolation of an endoparasitic undifferentiated state for the etablishment of the root system, but as to how the developmental processes are so shifted we are as ignorant in this case as in every other.

As far therefore as the adaptational meaning of the process is concerned, the clue appears to lie in the necessity for the parasite to overcome the dangers incident to parasitism on a Crustacean which is continually casting its skin. In *Sacculina*, which from every point of view we regard as the most highly specialized of the Rhizocephala, the adaptational relation of the parasite to the moulting of its host has reached a point of extreme delicacy. For by the time the root system has been established and the adult organs are beginning to develope in the proper situation, the growing-powers of the host have not been so completely inhibited

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as to prevent one more moult, and this moult which brings the reproductive part of the parasite to the exterior is the final growth-effort of the host, which henceforth remains without an ecdysis until the death of the parasite. In this remarkable manner the host is compelled to act in a way serviceable to its enemy.

In the next section the derivation of the endoparasitic development will be further considered.

5. The morphology of Duplorbis and the derivation of the endoparasitic development.

It seems probable that the condition and manner of fixation in *Duplorbis calathurae*, the parasite of the Isopod *Calathura brachiata* which is described in detail on pp. 120—122, may throw a considerable light on the steps by which the endoparasitic development of the other Rhizocephala has been attained.

Without entering into the details of the anatomy of this animal which will be found in the Systematic part I will here explain its apparent manner of fixation on its host, and the relation which this manner of fixation may bear to the general problem of Rhizocephalan development.

The only three specimens of *Duplorbis* so far discovered, were found by Dr. HANSEN on a single specimen of *Calathura brachiata* in the position shown on Plate 8 fig. 9. Each specimen
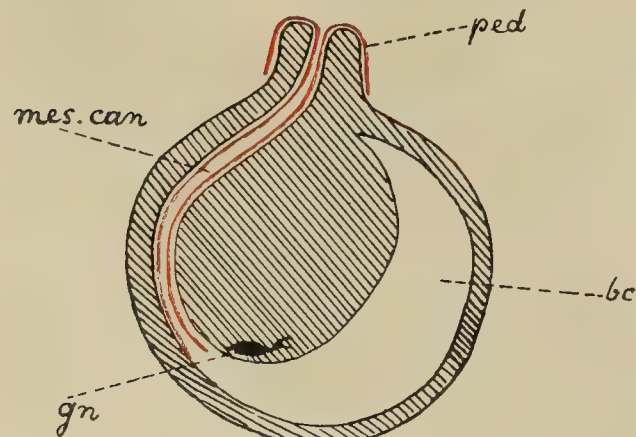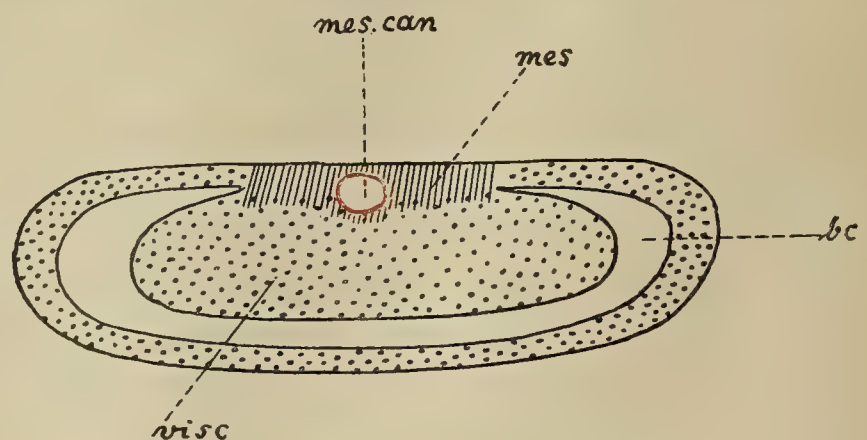
Text fig. 15.   Text fig. 16.

was fixed to the abdomen of the host by means of a peduncle which penetrated the external tissues of the abdomen. Apparently no roots are given off from this peduncle, but a tube is present opening at the top of the peduncle into the body of the host and running in the substance of the mesentery to open into the mantle cavity of the parasite. The relations of this tube, which I call the mesenteric canal, are shown in the diagrams Text figs. 15 and 16.

Text fig. 15 represents a section taken through the morphological long axis of the

body, exhibiting the mesenteric canal (*mes. can.* in red) in all its length, opening posteriorly at the summit of the peduncle (*ped*), and anteriorly into the mantle-cavity (*bc*) just behind the nervous ganglion (*gn*).

Text fig. 16 is a morphologically transverse section, and here the mesenteric canal (*mes. can*, in red) is shown as a tube lying in the mesentery (*mes*). This canal is lined throughout with chitin, which is continuous with the chitinous layer of the external surface of the body and of the internal surface of the mantle-cavity; the canal exhibits a regular epithelium, but no glandular appendages. It is surrounded by the lacunar tissue of the mesentery and evidently represents the organ by which the parasite absorbs its nutrition from the host.

A superficial interpretation of this tube might lead us to regard it as a gut, the mouth being at the summit of the peduncle and the anus at the opening into the mantle-cavity, but the reader will hardly adopt, nor would I encourage an interpretation so utterly at variance
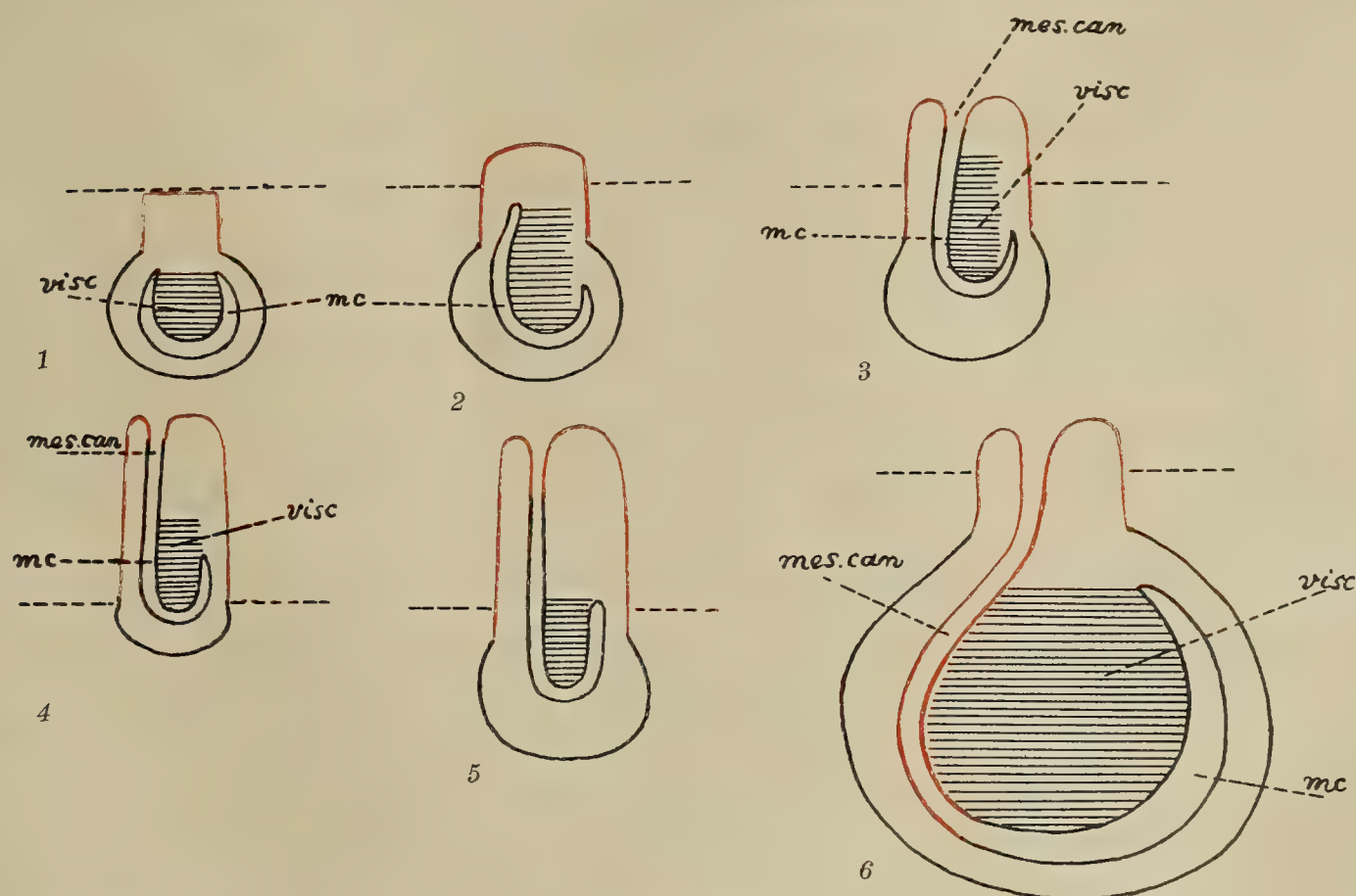
Text fig. 17.

with all we know of Cirripedes in general, and of the Rhizocephala in particular. Cirripedes do not fix themselves by the mouth, but by the antennae which become converted into the stalk, and the Rhizocephala never possess a mouth or gut even as larvae, and their fixation is always accomplished by means of the antennae as in all other Cirripedes.

What then is the morphological nature of the mesenteric canal in *Duplorbis*?

It represents, in my opinion, the invaginated stalk of an ordinary Cirripede.

We may next enquire how the stalk comes to be invaginated in this way, and in an-swering this problem we will endeavour to reconstruct the probable ontogeny of *Duplorbis*, with the help of our general knowledge of Cirripede and Rhizocephalan development.

The imaginary stages in the development of *Duplorbis* are shown in the Text figure 17.

I start from an ordinary Cirripede form, shown schematically in Text fig. 17 *1*, in which the peduncle (in red) is simply fixed to the surface of the host (broken line), and the mantle-cavity (*mc*) does not intrude into the region of the peduncle. In fig. *2* the peduncle has sunk below the surface of the host, and the mantle-cavity (*mc*) and visceral mass (*visc*) are beginning to pass into the peduncle. This condition is actually realized in *Anelasma*, the mantle-cavity in the mid-dorsal line being pushed far up into the peduncle. In fig. *3*, I imagine this process continued, the mantle-cavity continuing to push up into the enlarged peduncle and dragging with it the organs of the visceral mass (*visc*). Meantime the invagination of the mantle in the mid-dorsal line will have fused with the top of the peduncle to form the be-ginning of the mesenteric canal (*mes.can*).

In fig. *4*, is represented a further stage in which the mantle-cavity with all the organs of the visceral mass (*visc*) have passed right into the greatly enlarged peduncle, so that almost the whole body lies beneath the surface of the host.

In this manner I conceive the endoparasitic habit of *Duplorbis* and phylogenetically of all the Rhizocephala to have been acquired, namely by the mantle and visceral mass gra-dually sinking into the peduncle which becomes buried in the host. If this is so, we can easily understand the process by which *Sacculina* now becomes an internal parasite, the cells of the Cypris passing through the antenna [i. e. the peduncle[1])] to gain the interior of the host.

To return to the supposititious ontogeny of *Duplorbis*; in fig. *5*, the parasite is repre-sented as beginning to pass to the exterior of the host again. This it does by being evagi-nated out of the peduncle, and in this process the mesenteric canal is formed as shown in figs. *5* and *6*. Thus the mesenteric canal (*mes.can* in fig. *6*) really represents the peduncle which has been invaginated into the body, and in so doing has pushed the parasite to the exterior. In this manner the actual condition of the adult *Duplorbis* is obtained (fig. *6*). *Duplorbis* does not apparently possess any root system; this it must have either secondarily lost, or else the root system is a secondary acquisition of the other Rhizocephala; it is very easy to see how it would arise as a system of processes springing from the edges of the peduncle buried in the host.

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[1]) Peduncle = antennae, yes; but this is only a rough statement, sufficiently exact for our purpose, but not a perfectly correct homology. The peduncle of Cirripedes = the antennae primarily + a portion of the head between and round the antennae which becomes secondarily drawn into the formation of the peduncle. Perhaps for peduncle = antennae, substitute, = antennal region.

Whether *Duplorbis* actually passes through the stages indicated can only be proved by future investigation of this genus, but the nature of its fixation and the presence of the mesenteric canal can be explained on that supposition.

Taking therefore into consideration, firstly the morphological certainty that the Rhizocephala have always affixed themselves to their hosts by means of a peduncle = the antennae (see Note p. 62), secondly that in such a form as *Anelasma* this peduncle, used as an organ of nutrition, is buried in the tissues of its host, and that the organs of the body show a tendency to be pushed up into the peduncle, thirdly that in *Sacculina* and probably all Rhizocephala the endoparasitic position is attained by the embryonic cells of the Cypris passing right through the antenna (= the peduncle) to gain the interior of the host, and fourthly that in *Duplorbis*, an undoubted though aberrant Rhizocephalon, fixation is effected by a peduncle, which through its connection by means of a tube with the mantle cavity suggests the process of invagination explained above, — taking all these facts into consideration I think that we are in a position to maintain that the manner in which the endoparasitism of the Rhizocephala has been phylogenetically acquired, consisted in the penetration of the host's body by the peduncle = the antenna, and by the organs of the body being pushed up into the peduncle so that the whole organism became an endoparasite. Simultaneously or subsequently the root system was added to make the peduncle a more efficient organ of nutrition, and as this root system became of more and more importance in the life history of the parasite it was developed earlier and earlier until finally the condition of indefinite fixation and the simulation of a process of alternate generations was acquired by the higher genera of Rhizocephala. In this manner we may perhaps gain some shadowy idea of the steps by which a process of development, perhaps the most wonderful in the whole field of embryology, has been acquired, and although I do not hold that the riddle is by any means solved, yet there is hope that the discovery and investigation of intermediate forms like *Duplorbis* may in a short time give us a satisfactory solution.

I conclude from the apparent absence of a root system in *Duplorbis* that the Cypris of this animal fixes on the host in the position where the adult parasite is situated. The most peculiar fact in the morphology of the other Rhizocephala e. g. *Sacculina*, in which the Cypris may fix at any point, is that the adult parasite, although it has lost all connection with the original organ of fixation, yet becomes finally fixed to the host by a peduncle which preserves the essential morphological relations of the Cirripede stalk, as shown in Chapter 1.

We may perhaps gain some insight into this remarkable fact by comparing it with that kind of development which GIARD has called Poecilogonie (La Poecilogonie. in: Bull. Sc. France Belg. Tome 39 1905 p. 133), in which two closely allied animals, which are almost identical in the adult state, may yet pass through totally different embryonic stages. Thus the adult Rhizocephala are comparable in all their parts with an ordinary adult Cirripede, but the two kinds of adult reach their final essential similarity after passing through

utterly different embryonic states. I am anxious to call attention to this point of view, not only because I think that by bringing the development of the Rhizocephala into relation with other classes of facts we gain a certain explanation of it, but also because I hope that Professor GIARD may be induced to regard the only account I am able to give of Rhizocephalan development as affording another instance of Poecilogonie, and not as a gigantic mystification.

List of Literature.

1. **Delage**, Y., L'évolution de la Sacculine. in: Arch. Z. Expér. (2) Tome 2 p. 417 1884.
2. **Schimkewitsch**, W., Über die Untersuchungen von J. O. PEKARSKY über die Entwickelung von *Peltogaster paguri*. in: Trav. Soc. Natural. Pétersbourg Vol. 28 p. 218 1898.

(For controversial literature see Chapter 1 pp. 2—5.)

Chapter 5.

The effect of the Parasites on their Hosts.
(With Plate 7 figs. 1—21.)

Contents.

The discovery of the phenomenon of parasitic castration is due to GIARD who in a series of valuable papers (see Bibliography p. 93) has shown that the sexual condition of a number of hosts is profoundly modified by the presence of certain parasites.

It appeared to me that by the detailed examination, both by statistics and dissection, of a few types, a more exact knowledge of this question could be obtained, and for this purpose I have chosen to study especially the effect of *Sacculina neglecta* on *Inachus scorpio*, because both host and parasite are very common at Naples, and the sexual dimorphism of *I. scorpio* is very highly marked so that any modification is easily detected. The following remarks therefore mostly apply to this particular case, and it will be seen that many new facts of importance have come to light, especially with regard to the internal condition of infected individuals. After considering in detail the case of *Inachus scorpio*, some further facts are added in reference to *Pachygrapsus marmoratus* and *Eriphia spinifrons*.

1. General effect of S. neglecta on I. scorpio.

While the parasite is internal it is difficult to calculate what effect it has on the growth of its host, but it is probable that when the system of roots is well established growth is considerably retarded. This supposition is confirmed by the fact that Sacculinae internae are more frequently found in crabs which have not moulted for some time. The parasite becomes external invariably immediately after, and as the result of, a moult on the part of its host, and from this point onward until the death of the parasite the infected crab never moults again. Infected crabs are more sluggish in their movements than uninfected specimens and they cannot resist so well the irregularities of aquarium life. After the death of the parasite the crab may recover, but the process is slow, and exceedingly few recovered crabs are met with in nature, chiefly because the life of *I. scorpio* is probably never much prolonged over two years and in consequence crabs that have passed through the disease have mostly fulfilled their term of existence. And yet the rarity of recovered crabs must in some measure be put down to the fatality of the disease, since a great many young crabs especially in autumn have external parasites and yet few survive into the succeeding summer.

2. Effect on the primary and secondary sexual characters.

It is in this respect that the most interesting effect is to be observed. In the treatment of this highly important subject I propose to divide my data under separate headings, exhibiting first (A) the effect exerted by the parasite on the secondary sexual characters: in order to do this the rate of growth and the development of the various characters in infected males and

females will be compared with these characters in uninfected individuals of either sex. Since the crab does not moult again after once the parasite has become external there is no progressive effect on the secondary sexual characters after this state has been assumed. Under the heading B the condition of the sexual gland is dealt with. In C those crabs are studied which have been so profoundly modified both externally and internally that it is difficult to assign them for certain to either sex, though, as we shall see, these crabs are almost certainly profoundly modified males. In D the highly unexpected phenomena exhibited by recovered crabs are described.

A summary of the chief results and a general discussion are reserved until certain facts relating to other forms have been considered.

A preliminary point must be settled relatively to the time at which the transformation of the secondary sexual characters occurs. The parasite becomes external, after establishing its root system in the host, by means of an ecdysis of the latter; it is at this ecdysis that the external transformation due to the parasitic castration invariably occurs, and from this point onward, owing to the inhibition of growth, the host does not moult again. In about thirty or forty cases I have observed that this moult has failed to bring the Sacculina to the exterior, so that the phenomenon was observed of the effects of parasitic castration being apparently brought about by Sacculina interna. But these cases, all of them in large crabs with thick chitinous integuments, are only peculiar exceptions easy of recognition, because the Sacculina interna was evidently at a period of development when it ought to have been evaginated. In normal cases therefore the effects of parasitic castration are revealed at the same period in the life history of the parasite, and do not alter again after that period, and it is owing to this fact that the phenomena of parasitic castration in these crabs afford us so secure and easily appreciable a means of analysing the sexual characters of infected animals, since the cause of the castration is always equivalent and the same, so that the differences in the effect must be chiefly due to differences inherent in the infected animals.

A. Effect on the secondary sexual characters.

1. Females. The normal uninfected females of *I. scorpio* occur under two sharply differentiated forms which I call adolescent and adult. The adolescent crabs (Plate 7 figs. 1 and 2) have flat and comparatively small abdomina and the abdominal appendages are short, stout, and unprovided with long hairs. This adolescent form is preserved by the female until the first brood of eggs is produced, that is at any rate till the female measures 12 millimeters in carapace length, and very frequently later, especially in winter when no reproduction is occurring.

The adult females on the other hand (Plate 7 figs. 3 and 4) have large trough-shaped abdomina with four long biramous appendages, provided with long hairs, the endopodites being furnished with exceedingly long branched hairs which carry the eggs. These appendages are

situated on the second, third, fourth and fifth segments. No intermediate state between the adolescent and adult crabs exists, i. e. the two forms are separated by a single ecdysis.

The full reproductive season begins in March in the Bay of Naples and goes on continuously till August, two broods at least being produced by every crab. The characters to which I have paid attention are the abdominal length and breadth, the length and breadth of the chela, and the abdominal appendages, since these are the characters signally different in the two sexes. These characters will be considered in relation to the carapace length which is taken as an index of general growth, since it has been determined that growth in length, breadth and depth of the carapace is practically proportional at all ages and in both sexes whether infected or uninfected.

The first character to be considered is the abdominal length; my results for the breadth are not given because they are substantially the same. Diagram 1 (p. 71) is a diagram composed from Tables 1 and 2 in the Appendix which refer to the rate of growth of uninfected and infected females respectively, in abdominal length. The Diagram is constructed by drawing a line as nearly as possible through the average or mean condition of each abdominal length associated with each particular carapace length. The black line refers to uninfected females, the red to infected females. It is seen at a glance that the black line follows a different pitch before and after 12 millimeters carapace length, and this is due to the distinction already drawn between the abdomina of adolescent and adult females. The remarkable fact disclosed by comparing this black line with the red line referring to infected females is that the result of infection has been to straighten out the curved line of growth, and this is due to the fact that the small infected females under 13 millimeters no longer appear as a rule under the adolescent type, but as adults with long broad and trough-like abdomina. This result is, I believe, highly unexpected; but the fact is beyond question.

After 13 millimeters no obvious difference can be detected between infected and uninfected females in respect to the abdomen.

The effect then of the parasitism on young females under 13 mm. is to make them prematurely assume the adult type of female abdomen. This is of great theoretical interest because it helps to preclude the possibility of interpreting the effect of the parasite as being a return to an embryonic, sexually undifferentiated condition.

The chela length and breadth is uninfluenced by the parasitism.

With regard to the abdominal appendages I have arranged five categories for infected females as follows:

1. appendages rudimentary or absent,
2. appendages much reduced (Plate 7 fig. 5),
3. endopodites only of appendages absent or much reduced,
4. endopodites slightly reduced,
5. appendages wholly unmodified.

Table 3 (Appendix p. 96) sets out, I believe with substantial truth, the effect of the parasitism upon this character in females of various sizes. From this it appears that 55 out of 245 are

unmodified; of these 40 are over 15 mm. in carapace length. That is to say about 1/10th of the crabs under 15 mm. are unmodified, while nearly 1/2 over 15 mm. are unmodified. The whole table indeed shows that the proportion of modified crabs and the degree of modification in the abdominal appendages increases as we proceed to younger and younger crabs. This holds good except in those very youngest crabs which have the adolescent type of abdomen and appendage which does not appear to be so liable to modification as the adult. To sum up, it appears that the parasitism of *Sacculina* on the secondary sexual characters of females of *Inachus scorpio* has a definite effect which chiefly consists in the reduction of the abdominal appendages, but except in this purely negative character the infected females do not show any approach to the male structure.

2. Males. There is a curious fact with regard to the growth and development of the secondary sexual characters in normal uninfected males of *I. scorpio*, which will be only touched on here, as elsewhere (see p. 90) I have treated the matter more fully. It is that during the breeding season the males appear under three chief types, firstly small males under 16 mm. with rather swollen chelae (Plate 7 fig. 8), secondly males of medium size[1]) with flat female-like chelae (Plate 7 fig. 7), and thirdly males from 20—26 mm. with enormously swollen chelae (Plate 7 fig. 6). It is true that a few medium sized crabs with swollen chelae can be found in summer which form a link between the first and third categories, but these are very rare; indeed the whole number of crabs belonging to the second category are very rare during the breeding season. The medium sized crabs with flat chelae on dissection prove to have poorly developed testes and vesiculae seminales compared to the other two kinds, and spermatogenesis is in abeyance. It appears therefore that only two categories of male crabs take part in the breeding season, differing from one another in point of size and in the development of the chelae. In winter a great number of small and medium sized crabs are met with, all with flat chelae, and exceedingly few crabs of the first and third category. The explanation of this is undoubtedly that young crabs of 13—16 mm., after taking part in the breeding season of one year, pass into a kind of non-sexual state for the winter and growing rapidly appear as fully developed males of the third category in the following spring. But it appears that the assumption of the suppressed and of the fully developed sexual states is dependent to a large

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[1]) An explanation of these medium sized crabs with flat chelae may occur to the reader in the possibility of their chelae having undergone regeneration. This explanation is however quite precluded by the following facts. 1. The chelae of the medium sized males are always symmetrical so that if they have regenerated, both chelae must have been lost at the same time. Now in more than a thousand males only ten have been found in which one chela was plainly a regenerated one, but the chance of a crab losing both chelae at once is much smaller than the chance of its losing one. 2. Why should the medium sized crabs with flat chelae always have poorly developed testes if the reduction of their chelae is simply due to accidental loss and regeneration? 3. Why should males with flat chelae and poorly developed testes occur normally in the winter when males with swollen chelae are very rare, especially as in the winter the males do not fight for the females and so are less liable to lose their chelae? 4. Why should the flat chelae be associated with males of a certain size, when breeding males, liable to the loss of chelae, are of all sizes except of this particular size with flat chelae?

extent upon some internal law of growth and not directly upon the time of year, because exceptional crabs which reach 20—26 mm. in the winter, assume the full sexual form, though uselessly, and on the other hand males which attain a medium-size in the spring pass into the non-sexual vegetative phase.

It is necessary to take these various phases into consideration, because the existence of this suppressed sexual condition in the normal history of the males renders the parasitic effect less striking than it would otherwise be. Yet it is sufficiently striking, a most pronounced effect being visible on the abdominal length and breadth, the development of the chela, and of the abdominal appendages. I will exhibit first the effect on the a b d o m i n a l l e n g t h. The black line in Diagram 2 refers to uninfected males, the red line to infected males. It will be seen at once that the average abdominal lengths associated with particular carapace lengths are in all cases more than a millimeter greater in infected than in uninfected males. But a reference to the Tables 3 and 4 in the Appendix on p. 96 gives an even more certain idea of the remarkable modification undergone by the abdomen, for here the extreme variants are noticeable, some of which have abdomina typically female in dimensions. One or two variously modified males are illustrated on Plate 7 figs. 9, 10, 11, 12, and these drawings show that the abdomen under the influence of the parasite may assume all the intermediate conditions between male and female.

To sum up with regard to the abdomen, w h e r e t h e c r a b s h o w s t h e c h a r a c t e r-istic modification, the abdomen takes on a female character to a greater or less degree, becoming long, broad and trough-like; and this occurs to an easily appreciable extent in 145 out of 224 infected males examined.

We now turn to the development of the c h e l a (Diagram 3) and the first thing to note is the characteristic deviation in the black line of growth for uninfected males between 15 and 18 mm. carapace length, due to the phenomenon of sexual suppression noted above. Despite this, the difference between the two lines for infected (red) and uninfected (black) individuals is easily discerned. The effect of the parasitism, then, is t o v e r y s e n s i b l y l e s s e n t h e swollen nature of the m a l e c h e l a a n d t o m a k e i t a p p r o x i m a t e t o t h e f l a t f e m a l e type which never exceeds 3 m i l l i m e t e r s in breadth.

In considering the a b d o m i n a l a p p e n d a g e s it must be remembered that the normal males have a pair of stout copulatory styles on the first segment, followed by a rudimentary appendage on the second segment (Plate 7 fig. 13). The effect of the parasitism is exhibited by the tapering out or complete reduction of the copulatory style and in some cases by the development of more or less rudimentary female appendages on the segments which normally bear none. I have arranged the following numerical categories:

1 = One or more female appendages present (Plate 7 fig. 11).

2 = Copulatory style rudimentary, no ♀ appendages present.

3 = Style very slender or reduced.

4 = Style slightly reduced or tapered (Plate 7 fig. 12).

5 = No modification.

Table 8 in the Appendix p. 98 shows that 96 out of 140 were modified to some extent, while 11 showed the presence of female appendages. With regard to the latter it should be noted that although these female appendages possessed by modified males are usually reduced,

Abdominal length in millimeters.
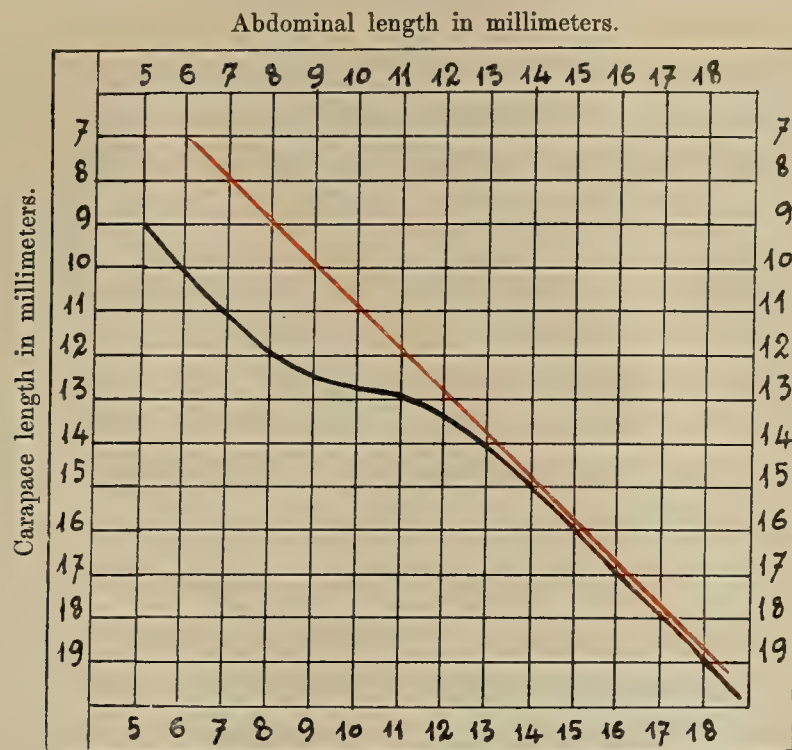
Text fig. 18. Diagram 1.
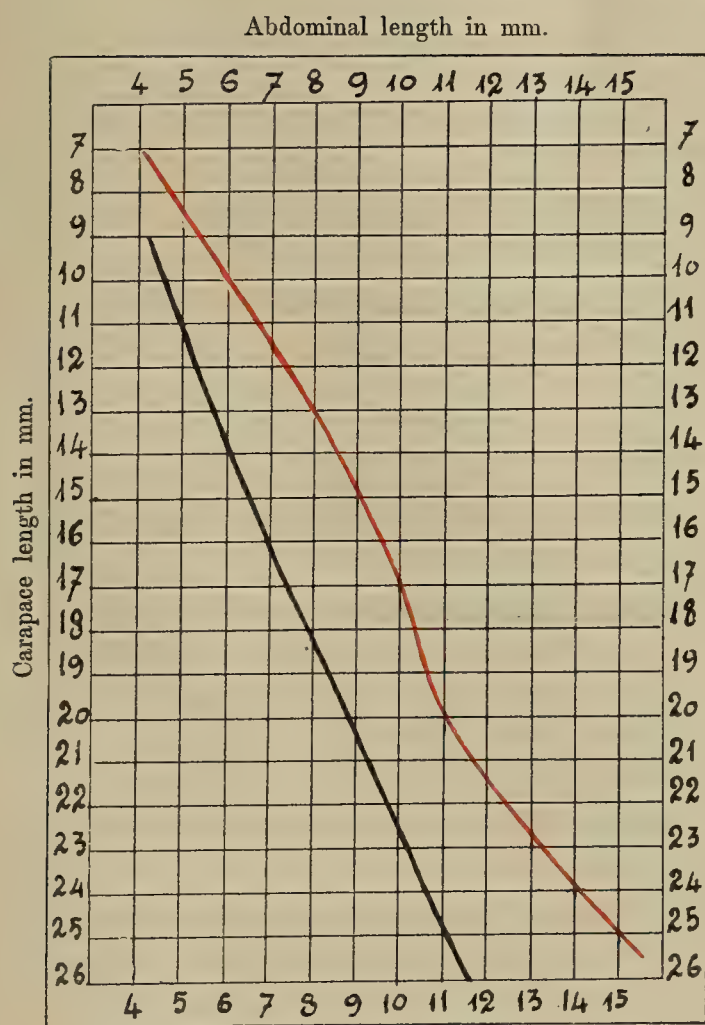
Text fig. 19. Diagram 2.

Text fig. 20. Diagram 3.

they are at the same time of the typically adult female nature, and not a return to any embryonic or ancestral condition.

To sum up the effect on the male organization of *Inachus scorpio* it is seen, that in all the secondary sexual characters the infected males become in various degrees typically female. In extreme cases where a male has assumed the chelae, abdomen and abdominal appendage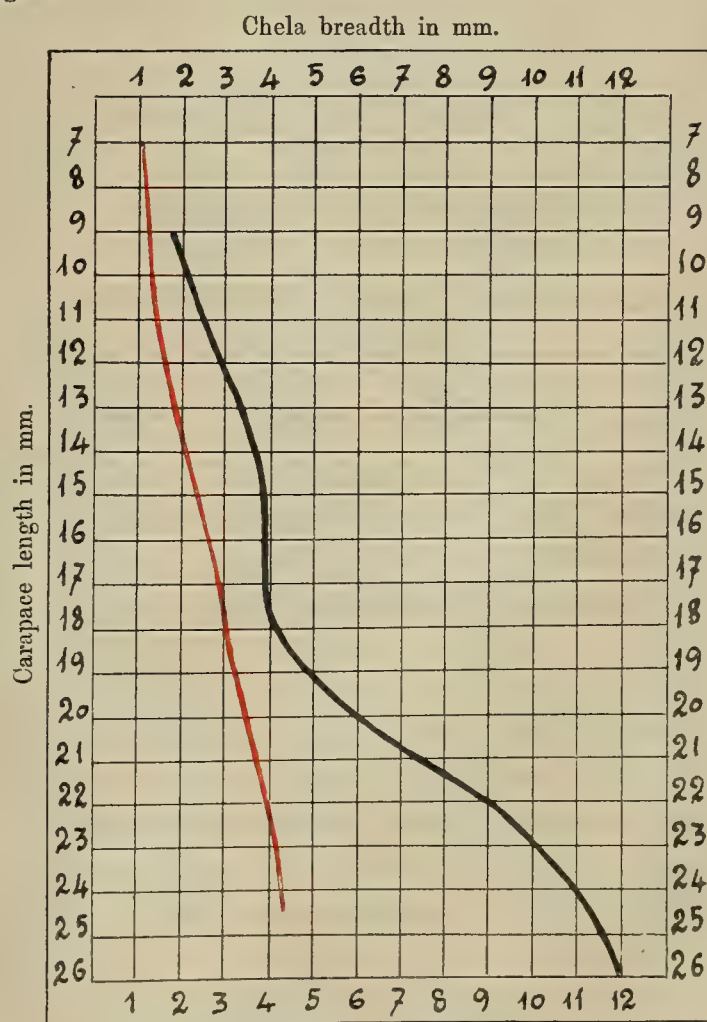s of a female we can only be sure that it is a male by the presence of a copulatory style and by the slightly smaller width of the abdomen in comparison with a typical female.

B. Effect on the primary sexual character.

By dissecting a large number of crabs (about 500 infected and 400 uninfected) it has been possible to establish that some effect is always exerted by the parasite on the gonad. But just as in the case of the secondary sexual characters, the degree of affection varies greatly; and to a certain extent, there is a correlation in one and the same animal between the degree of degredation of the gonad and of the secondary sexual characters. That this correlation is not exact would be expected from the fact that the atrophy of the gonads continues after the Sacculina has become external, whereas the secondary sexual characters do not change after this point. The effect on the gonad is most clearly perceived during the breeding-season when the females instead of having red ovaries have small white ovaries which may be either much shrunken or else in a state of actual disintegration; while the testes and vesiculae seminales of infected males are always obviously greatly reduced in comparison with those of uninfected individuals. In many cases the ovaries and testes with their ducts may be altogether absent, and this is always associated with very highly modified secondary sexual characters. At the opposite extreme we may meet with an occasional female which has actually shed its ova, which are then carried under the abdomen with the parasite, but these eggs are always few, and dissection of such a female has invariably revealed that its gonads internally are much retarded in development.

As to how the parasite brings about this reduction and in many cases final atrophy of the gonad there is a distinction between males and females. In the females the roots of the parasite may actually penetrate the epithelium of the ovary and ramify among the degenerating ova, but in the males the roots never appear to penetrate the testicular tubes. I have also good evidence to show that the actual irruption of roots into the ovary is often only a second phase in the atrophy of the gland, and that a reducing effect appears before the roots have actually penetrated into its substance. It must be concluded that the Sacculina primarily causes the reduction of the gonad by interfering with the general metabolism of the body, possibly by depositing in the body some fermentative or excretory substance, or more probably by altering its general state of nutrition. This disturbance of the general metabolism must interfere in some manner with the sexual condition of the body, but with this subject we will deal more fully at the end of the chapter.

C. Crabs of apparently doubtful sex.

I have studied altogether about 200 infected crabs which had been so completely modified both externally and internally that it was impossible at first sight to assign them with any certainty to either sex. All of them had the female type of abdomen, but all of them possessed a pair of copulatory styles in more or less perfection, and all of them had the characteristic female appendages, either perfectly or imperfectly developed (Plate 7 figs. 14, 15, 16, 17). The chela was in all cases but one of the female type. All the specimens were small, most being 9—11 mm., while only one was over 15 mm. (Plate 7 figs. 18, 19).

It appeared to me most important to determine the state of the gonads in these crabs. I was therefore not content with dissection but in numerous cases made preparations and serial sections of the whole contents of the thorax.

In the great majority of these crabs I was unable to find the least trace of a gonad, and yet in infected crabs of the same size which showed by their secondary sexual characters that they were either male or female, I never failed to detect a differentiated gonad, though often much reduced.

In three infected crabs which were externally perfect hermaphrodites, I was able to detect the presence of much reduced vesiculae seminales with exceedingly fine strands of tissue passing upward from them, which were doubtless the remains of testes. These three crabs were therefore all males, and for a variety of reasons I am forced to the conclusion that all these crabs of apparently doubtful sex are in reality highly modified males. Perhaps the most cogent reasons for this conclusion are given under the cases of *Pachygrapsus marmoratus* and *Eriphia spinifrons* further on, but a consideration of the facts in *I. scorpio* alone are sufficient almost to convince us. For it has been seen in Paragraph A that infected females, as regards the chela and the abdomen, do not in any degree approach the male form, but that infected males in both these characters and also in the presence of female appendages become assimilated in all their characters to the female form. Thus a perfect transition in every detail can be traced from undoubted males to these crabs of doubtful sex, while females, since they never assume any other male characteristic under infection, can hardly be supposed to suddenly develope the typically male copulatory styles. Further the great majority of these crabs are found in October and November, and among the whole number of infected individuals only a very small percentage can be recognised as males, the rest being either clearly female or else hermaphrodite. If therefore the latter are not really modified males, we must suppose that a very much greater percentage of females are infected than males, which is contrary to all the observations I have made on this head. Finally, since in the three cases in which the remains of a gonad could be detected, the gonad was male in structure and histological characters, though containing no sperm, I conclude that all these crabs of apparently doubtful sex are really highly modified males.

There are thus two conclusions from the study of these crabs to be specially emphasised.

Firstly, that a perfect external hermaphroditism can be associated with the entire absence of a differentiated gonad. Secondly, that the male sex, and probably the male sex alone, can be so radically modified in its sexual nature as to assume a perfect external hermaphroditism.

In the next section we describe the remarkable phenomena which accompany the recovery of these crabs from their parasitic affection.

D. The sexual condition of recovered crabs.

1. In a state of nature.

When the Sacculina has produced a certain number of broods and has finished its term of existence, it drops off, leaving a scar by which crabs that have been once infected can be easily recognised. I have found a fair number of such recovered crabs in nature, and I have artificially freed crabs of their parasites in the aquarium. The roots of the parasite remain alive for some time, but if the crab does not die, as it usually does, the roots may be resorbed to some extent after a few months. In three or four male crabs which had not undergone much external modification the testes had recovered considerably and were functional, but I have only observed one recovered female with mature ovaries.

The most important discovery I have made relating to recovered crabs is that under certain circumstances the crab regenerates a perfect hermaphrodite gland. I have found altogether 4 such crabs; they were all perfect hermaphrodites externally as well as internally, and one of them had formed oviducts and vasa deferentia, while in the other three the ducts were absent. The gland was paired, the upper portion on either side being a testis, the lower an ovary; the testis in all cases containing fully differentiated spermatozoa, and the ovary large pigmented ova, which were nearly mature. Plate 7 fig. 20 is a low-power drawing of a section of part of the ovotestis, showing two ovarian and one testicular tube. Plate 7 fig. 20 a is a section taken through the part of the gland where the testicular passed into the ovarian tubes, and it is seen that in this region one and the same tube is giving rise to ova and spermatozoa.

All these curious crabs, except one, showed unmistakable signs of having been infected with Sacculina, the characteristic chitinous ring of attachment being conspicuous on the ventral side of the abdomen, and since no kind of hermaphroditism has ever been found in *I. scorpio* apart from the effect on the external characters caused by Sacculina, we are quite safe in concluding that the sole cause of the internal hermaphroditism of these 4 crabs was the fact that their gonads had been eradicated by Sacculina and had subsequently regenerated. The gonads must first have been practically eradicated, because these crabs belong to the category in which the external characters are truly hermaphroditic (Plate 7 figs. 14—19), and it has been proved that crabs of this category never have differentiated gonads, or at most the degenerate remains of a testis (see Paragraph C).

One of these crabs as I have mentioned had no scar, indicating that a Sacculina had been there, and this crab differed from the other three in its general characters and especially in its large size. This crab is figured Plate 7 figs. 18 and 19. I do not think that there can be any doubt that this crab was once infected and that subsequently it had recovered and gone through several moults so as to lose the scar and to attain to its remarkable size. In any case the occurrence of this crab does not in the least invalidate the conclusions drawn from the other three, because it is certain in them, firstly, that they had been infected by Sacculina and had recovered, secondly that their gonads had been nearly eradicated, thirdly that they had regenerated perfect hermaphroditic gonads. That the large crab figured in figs. 18 and 19 belongs to the same category is, I think, certain from the entire absence of any approach to an hermaphrodite state in any other crab out of thousands examined, apart from the effect of Sacculina. On the other hand an approach to an hermaphrodite condition with regard to external characters is shown in a majority of infected crabs, and the perfect hermaphroditism exhibited by these recovered crabs is the natural culmination of the state.

In conclusion therefore, Crabs which have been modified externally into perfect hermaphrodites and have lost internally the differentiated gonads, if they recover, regenerate a perfect hermaphrodite gonad capable of producing mature ova and spermatozoa.

2. Crabs experimentally freed from Sacculina in Aquaria.

After perceiving the remarkable fact that infected crabs on recovery may regenerate a hermaphrodite gonad, I was anxious to test this experimentally with the especial purpose of finding out whether this regeneration only takes place in crabs of a particular category, namely in those with perfect external hermaphroditism, as appeared to be the case from the four specimens found in nature.

During the autumn and winter a large number of crabs, showing every degree of external modification from complete external hermaphroditism to the absence of all modification, were artificially freed of their parasites, and kept in Aquaria until the following summer. Unfortunately the death rate among these crabs was very large, and exceedingly few survived till the summer. Of these however not a single one of the incompletely modified crabs showed any signs in their gonads of hermaphroditism, though in some of them the gonads had evidently recuperated to a large extent; but in one of the crabs which exhibited perfect hermaphroditism externally (i. e. belonged to the crabs described in Section C), a small hermaphrodite gland was present on the left side of the thorax, consisting posteriorly of an ovary containing immature but large ova, and anteriorly of a testis containing a quantity of mature spermatozoa. The testicular tube was continuous with the ovary and at the point of junction ova and spermatozoa were lying mingled together. No ducts were present.

This crab therefore makes the fifth recovered individual with hermaphrodite gonads found so far, and like all the others it showed a perfect external hemaphroditism as well. This individual is figured in Plate 7 fig. 21. The copulatory styles (p) were very small, as were also the other appendages.

It appears therefore fairly certain that only those crabs with perfect external hermaphroditism, i. e. perfectly modified males, are capable of regenerating an hermaphrodite gland.

3. The cellular origin of the regenerated gonad.

I have spoken of the gonads of these hermaphrodites as having been practically eradicated; it is therefore natural to enquire how and from what cells the hermaphrodite gonad is regenerated. The answer to this question must be found in the condition of the gonads of those infected crabs described in Paragraph C, which were externally perfect hermaphrodites, because these crabs, on recovery, evidently furnish the material for the animals which are hermaphrodite externally and internally. I have stated in Paragraph C that in the great majority of these crabs no trace of a gonad could be detected, but that in three specimens the degenerate remains of a testis could be detected. Sections through these degenerate remains showed an entire absence of spermatozoa, the tubes being simply lined with undifferentiated germinal cells. The vesiculae seminales contained a clear fluid but no sexual elements. It can hardly be doubted therefore that the regeneration of the hermaphrodite gonad takes place from the small shreds of testicular epithelium which to a varying extent probably persist in all these crabs, but which in the majority of cases are so small and fragmentary as easily to escape detection.

3. The Case of Eriphia spinifrons.

A. The simultaneous parasitism of Entoniscidae and Rhizocephala.

In this section, through the kindness of Dr. G. Duncker, I am able to bring forward a very complete confirmation of a highly remarkable observation made originally by Fritz Müller (*Entoniscus porcellanae*, eine neue Schmarotzerassel. in: Arch. Naturg. 18. Bd. p. 10), and afterwards adopted and extended by Giard & Bonnier (Contributions à l'étude des Bopyriens. in: Trav. Inst. Z. Lille Tome 5). This observation concerns the simultaneous parasitism in a crab of an Entoniscid[1]) and a Rhizocephalon, and constitutes perhaps one of the most mysterious facts in parasitology. Fritz Müller observed that on 1000 *Porcellana* crabs there were 84 specimens of the Rhizocephalon *Lernaeodiscus porcellanae* and 49 of *Entoniscus por-*

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[1]) The Entoniscidae are a family of the Bopyrid Isopods. The parasite enters the branchial chamber of the crab and finally in the adult stage becomes invaginated into the thoracic body cavity, occupying a large space with its hugely developed ovary.

cellanae. Now if the simultaneous occurrence of *Lernaeodiscus* and *Entoniscus* on one and the same crab is simply a matter of chance we should expect only 4 crabs out of the 1000 examined to be simultaneously infected; but MÜLLER found that 21 out of the 1000 carried both *Lernaeodiscus* and *Entoniscus.*

GIARD & BONNIER (l. c.) have confirmed this observation with reference to *Portunion maenadis* and *Sacculina carcini,* parasites of *Carcinus maenas,* and to *Portunion salvatoris* and *Sacculina similis,* parasites of *Portunus arcuatus*: but the number of parasites observed in neither case was very large.

The case which is here to be described concerns the parasites of *Eriphia spinifrons,* neither of which have been hitherto described as far as I am aware. The Rhizocephalous parasite of *Eriphia spinifrons* is very similar to the parasite of *Pachygrapsus marmoratus* which KOSSMANN calls *Sacculina benedeni.* The Entoniscid parasite of *Eriphia spinifrons* has not been notified hitherto; I am unable to give a diagnosis of it since my observations on it are confined to the adult state when all specific distinctions have disappeared. The fact that *Eriphia spinifrons* is infected by a species of Entoniscid was revealed to me in a most curious way.

Dr. DUNCKER in the course of his investigations on correlation in *Eriphia spinifrons* at Naples made some incidental notes with regard to the occurrence of *Sacculina* on this species, with a view to testing GIARD's theory of parasitic castration. The facts which he elicited were of so peculiar a kind that he was led to believe that they constituted a most antagonistic piece of evidence to GIARD's theory: learning that I was specially interested in this subject he handed over his notes and some most valuable material to me, the examination of which has led to the discovery in question. Dr. DUNCKER investigated 2601 specimens of *Eriphia spinifrons* of which 63 carried external Sacculinae. Now the whole array of crabs fell into three sharply distinguished categories, namely males, females and hermaphrodite forms. The males are distinguished sharply from the females by the narrowness of the abdomen and the fact that the latter are furnished only with a pair of copulatory styles while in the female the abdomen is broader and carries four pairs of ovigerous appendages. The hermaphrodite forms belong to a compact and easily distinguished category; the abdomen is nearly as broad as in the female which it further resembles in colour and in the presence of fringing hairs, but instead of having the ovigerous appendages of the female it possesses a pair of copulatory styles. The three types of abdomen are shown in dorsal and ventral view in the Text fig. 21 *A—F* (*AD* = male, *BE* = female, *CF* = hermaphrodite).

The 66 crabs infected with Sacculina were distributed among these three categories in the following manner.

	Males	Females	Hermaphrodite
Total number	1354	1200	47
Number of crabs infected with Sacculina	16	31	16

Thus there were 16 infected males and 31 infected females which showed no modification at all, while out of 47 hermaphrodite forms only 16 were infected with Sacculina. This constituted in Dr. Duncker's opinion a strong objection to the view that the hermaphrodite form had anything to do with the presence of the Sacculina. Dr. Duncker very kindly put about twenty of the specimens of hermaphrodite form at my disposal, and on
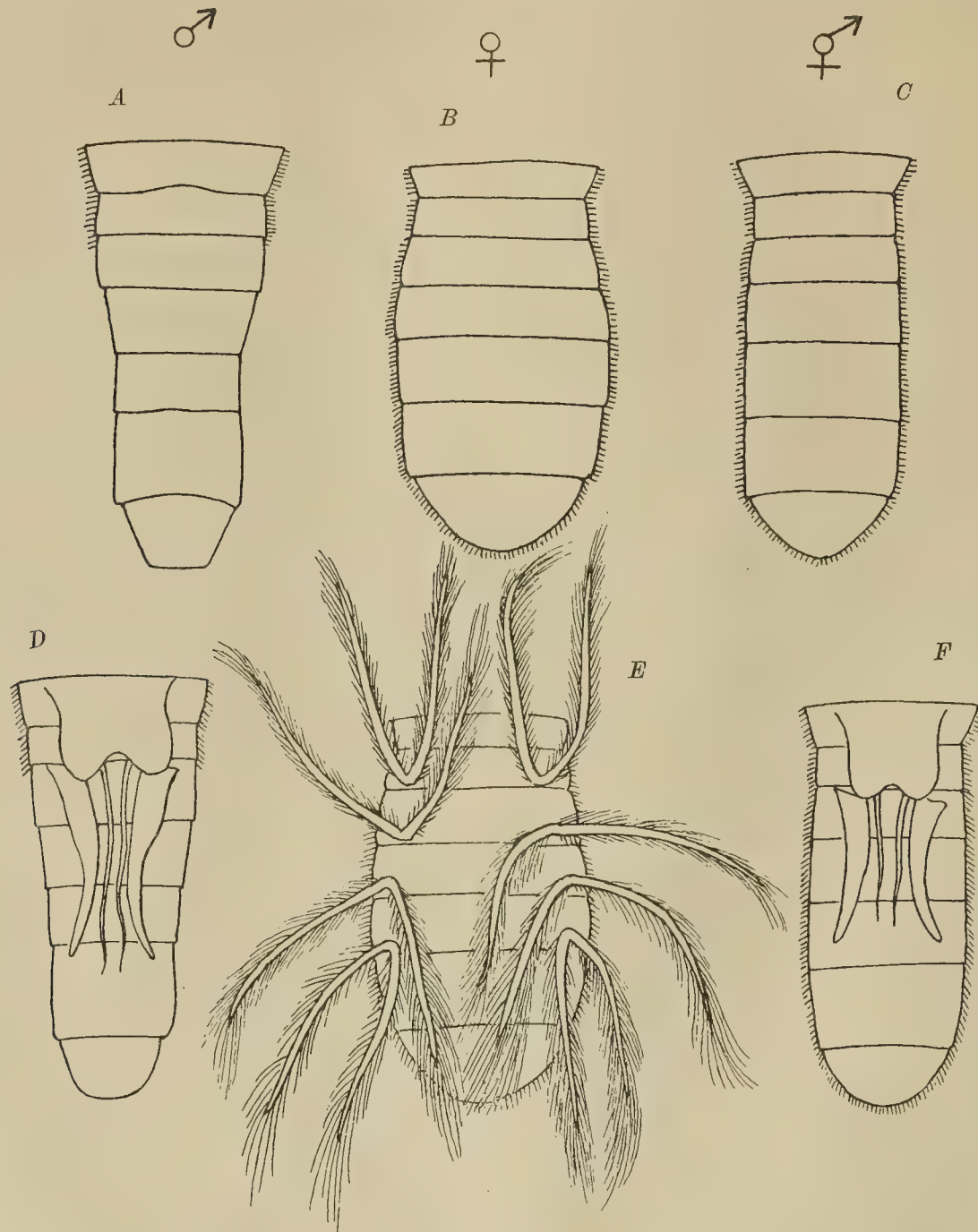
Text fig. 21.

dissecting them I found that everyone without exception contained a specimen of Entoniscus. The gonads in these specimens appeared to have totally aborted.

The fact that Entoniscus may effect the parasitic castration of its host has been known for a long time owing to the researches of Giard & Bonnier, and it appears that in this case, whereas the Sacculina has little or no power to bring about the castration, this is effected completely by the Entoniscus.

But now to return to the question of the association of Entoniscus and Sacculina on the same host.   We see from the table given above, that the fact of this association is completely brought out by Dr. DUNCKER's figures, since out of 47 crabs infected with Entoniscus 16 had also Sacculina, that is about one third, while out of 2554 males and females which were presumably without Entoniscus only 47 carried Sacculina, that is about one fifty-fourth.

I regard therefore the results of these statistics as a complete vindication of the fact that there is a marked tendency for the association of the two parasites upon the same individual host.

The explanation of this curious association given by GIARD & BONNIER is of great ingenuity.   These authors hold that the Entoniscids are derived from a group of the Cryptoniscinae like Liriopsidae (see Chapter 6 of this Monograph), which are parasites of the Rhizocephala.   The Liriopsidae, as is already known and as I have continually observed, may be fixed either on the Rhizocephala themselves or else on the body of the infected crabs near the attachment of the Rhizocephala; in the latter case they nourish themselves on the internal roots instead of on the external body of the Rhizocephala.   Now it is supposed that the Entoniscids in the course of their descent from the Liriopsidae have gradually forsaken the Rhizocephala as hosts for the crab itself, so as to finally become parasites of the Brachyura and not of the Rhizocephala.   But they still retain a trace of their old habits in showing a selective preference for crabs infested by Rhizocephala.   Whether this explanation is true or not (and it is hard to find a prettier), the fact is certain that Rhizocephala and Entoniscids are so frequently found in association on the same individual host that their simultaneous occurrence must have some definite cause other than chance; nor does it seem that they mutually benefit one another in any way, as they are not dependent on one another for nutriment and the presence of two such large parasites on one host would more likely be of disadvantage to both in this respect.   At any rate they are certainly not necessary to one another either as associates or enemies, as is proved by their generally occurring on separate hosts, and the fact of their simultaneous occurrence, merely in so great a proportion that a purely chance coincidence is ruled out, points emphatically to a rudimentary condition such as GIARD suggests, rather than to a vital organic connection between the two parasites.

I am however inclined to put forward an alternative explanation which does not involve any phylogenetic theory.   It is a well-known fact that the presence of Sacculina in a crab retards the growth and consequently diminishes the number of moults of the host.   In consequence of this, crabs which harbour a Sacculina are generally covered with various kinds of animal and vegetable growths.

Now the Entoniscid parasites of the crabs enter by way of the gills, and doubtless in the early stages of development before they have penetrated into the thoracic cavity of the crab, they would be liable to removal or injury by the constant moulting of the host.   But if an Entoniscid were to enter a crab containing a Sacculina interna which had already begun to inhibit the growth of the crab, its liability to removal and injury through the moulting of

the host would be greatly diminished, and so a greater number of Entoniscids would survive when associated with a *Sacculina*, than in crabs uninfected by *Sacculina*.

Whatever the explanation may be, the association of the two parasites is of great biological interest.

B. The nature of the parasitic castration in Eriphia spinifrons.

It is shown by Dr. Duncker's notes that Sacculina has no obvious effect[1]) on the secondary sexual characters of *Eriphia spinifrons* but that a very perfect effect is produced by a parasite belonging to the family of the Entoniscidae. This effect differs from that described for *Inachus scorpio* in that the modified crabs all belong to a homogeneous and sharply defined category which shows no gradation into the female or male condition. One partial exception to this rule was observed however, namely in a modified crab which carried a single rudimentary female appendage on one side of the abdomen.

We are therefore confronted with the same problem which occurred to us in the case of the perfect external hermaphrodites of *Inachus scorpio*, namely to determine to what sex the modified crabs originally belonged. A perfectly definite and irrefragable answer is given to this question in the next case to be examined, *Pachygrapsus marmoratus*, but in the present case the statistics strongly suggest to us that all the hermaphrodite forms are in reality modified males, as we found to be probably the case in *Inachus scorpio*. For the statistics show that unless we add the hermaphrodite forms infected by *Sacculina* to the undoubted males so infected, there is an extraordinary preponderance of infected females over infected males, i. e. more than twice as many females are infected than males, in proportion to the whole number of the two sexes found in nature. But if we add the infected hermaphrodites to the infected males the proportion of infected males and females is made about equal, and this is what we should expect from our knowledge of the method of infection of the parasite.

Although this argument is not conclusive, it is perhaps a suggestive prelude to the definite proof which is furnished in the next case to be considered.

4. The Case of Pachygrapsus marmoratus.

This crab in the Bay of Naples is very commonly infested by a species of Sacculina named by Kossmann *S. benedeni*: it also harbours a species of Entoniscid called *Grapsion Cavolinii* (Giard). Of some 200 specimens examined by me only five contained *Grapsion Cavolinii*, while about 70 had Sacculina either externally or internally. The five specimens which harboured Grapsion were also infested by Sacculina so that it is highly probable that the remarkable coincidence of these two parasites which was discovered in *Eriphia spinifrons* also

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[1]) Subsequent researches have shown that Sacculina may also exert some influence in this species without the cooperation of Entoniscus.

pertains in this crab. But into this point we need not enter here; we are concerned here with the parasitic castration of the crab effected by *Sacculina*, when not associated with a *Grapsion*. The nature of the castration in this form throws a bright light upon the phenomena which we have been discussing. In the first place the modified crabs fall into a more or less homogeneous category of the same kind as that found in the case of *Eriphia spinifrons*, and this is interesting because the parasite which is the cause of the modification is of a totally different nature in the two cases, being a Rhizocephalon in the one and an Isopod in the other case.

In the diagram Text fig. 22 are given drawings of the abdomina of an unmodified male (*B*) and female (*A*) and of the hermaphrodite form (*C*). The dimensions of the abdomen in the latter form are seen to be intermediate between the male and the female; on the under side the hermaphrodite carries a typical pair of copulatory styles, and in many instances either a complete set or a few female appendages.
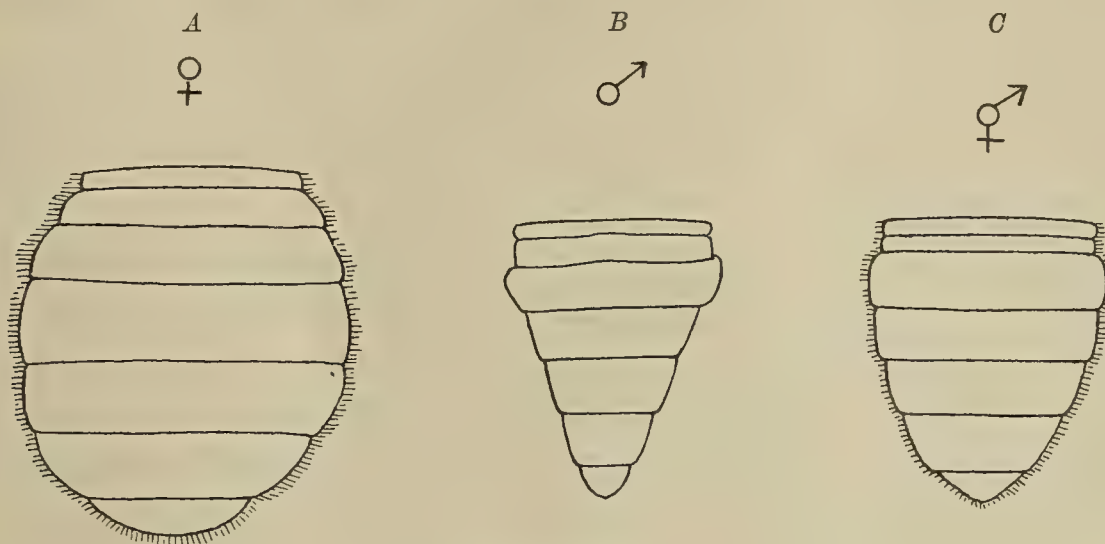
Text fig. 22.

Together with the infected hermaphrodites occur infected males and females quite unmodified in their secondary sexual characters.

The hermaphrodite forms with Sacculinae externae on dissection rarely revealed any trace of a differentiated sexual gland or ducts from which its original sex could be determined, but in those cases in which the ducts remained, they were always male ducts.

Now besides the hermaphrodites with Sacculinae externae, I have found twelve specimens of the hermaphrodite form in which the Sacculina was still internal, and the dissection of all these forms revealed the presence of a vas deferens in process of degeneration, but still containing the remains of spermatophores, while in no single specimen was there any sign of female generative organs.

The case of *Pachygrapsus marmoratus*, therefore, clinches all our former arguments to the effect that the hermaphrodite form is always imposed upon the male organism and never upon the female, the latter being incapable in all the cases examined of assuming a single male characteristic.

5. General Conclusions and Summaries.

Before entering into a general discussion on the subject of parasitic castration, a summary of the chief facts now recounted will be given in order that the reader may have them concisely before his eyes. These facts will then be discussed in their relation to other evidence bearing on the problem of sexual differentiation, and finally I append a summary of the conclusions that appear to be suggested by a consideration of the whole matter.

Summary of Facts.

1. Of about 5000 specimens of *Inachus scorpio* examined, all the cases of partial or complete hermaphroditism (in all over a thousand) observed, were found in crabs which carried either Sacculina externa or interna, or else showed unmistakable signs of having been once infected by Sacculina. The only possible exception was a single perfect hermaphrodite, which probably had recovered from Sacculina and undergone several moults so as to lose the scar characteristic of recovered crabs.

2. About 70% of the males and females of *I. scorpio* infected with Sacculina showed obvious alterations in their secondary sexual characters: all the infected individuals showed an arrested development of the sexual gland in various degrees, or in certain cases perfect hermaphroditism.

3. We may therefore conclude that in *Inachus scorpio*, whenever an hermaphrodite condition of any degree is found associated with the presence of Sacculina, the latter has brought about the hermaphroditism of its host.

4. In *Eriphia spinifrons* the Sacculina does not appear to have much effect on its host: but a parasitic castration of the male is effected by a species of Entoniscid, which is usually associated with a Sacculina on the same host.

5. In *Pachygrapsus marmoratus* parasitic castration is brought about by the Sacculina. The modified hermaphrodite form is of a definite character and is clearly always derived from the male.

6. In parasitic castration by Sacculina the reduction of the gonad is brought about before the roots of the parasite actually attack that organ, though the final eradication of the gonad, especially in the female, is probably influenced by the irruption of the roots into the germinal tissues. In the case of Entoniscus however the parasite never invades the actual tissues of the gonad.

7. Infected males assume in various degrees the secondary sexual characters proper to the female: in certain cases of *I. scorpio* they do this so perfectly that the only sign that they once were males is the presence of a much reduced copulatory style.

8. The infected females have the swimmerets reduced or rudimentary: they do not however acquire any distinctively male character.

9. Infected males of *I. scorpio* which have been completely modified externally, only retaining the copulatory style to identify them as male, are found to have the gonad and its ducts so completely reduced in most cases as not to be visible either by dissection or serial sections.

10. These perfectly modified males of *I. scorpio*, if they recover sufficiently to regenerate gonads, may regenerate a perfect hermaphrodite gland capable of producing mature ova and spermatozoa.

11. There is no evidence that crabs of any other category, i. e. males or females which have been imperfectly modified externally, ever regenerate hermaphrodite gonads.

The question which presents itself at the outset is, how does the parasite effect the arrest and atrophy of the gonad? It is clear that in the phenomenon of parasitic castration the atrophy of the gonad is brought about not merely by the parasite attacking and devouring this organ: this is proved by those cases of parasitic castration where the parasite never comes into contact with the gonad at all, e. g. the case of Entoniscus, and especially that of the Bopyridae (8) where the parasite is situated in the gill of its host. There are therefore two alternatives: either the parasite introduces into the host some specific substance that attacks the gonad and causes its atrophy, or else the parasite has a general effect on the metabolism of the host which reacts upon the gonad causing it to be absorbed. There can be little doubt that the latter alternative is the true one; for if the parasitic castration is due to the introduction of a specific substance into the host, it is very curious that parasites of such totally different natures as Cirripedes, Isopods, Trematodes and Gregarines (9 and 23) should all exercise the same influence on their various hosts: but it is intelligible on the second hypothesis that all these parasites should influence the metabolism of their hosts in much the same way, and that the altered condition of the metabolism should react upon the gonad.

To this point we will return after considering another question, namely, in what relation do the secondary and primary sexual characters stand to one another? It is generally assumed from the results of ordinary castration and from observations upon diseased gonads, that the sexual gland itself either by means of an internal secretion or else by some other means, causes the development of the secondary sexual characters proper to it.

HERBST (16) in his Formative Reize has given an excellent summary and discussion of the available evidence, and he concludes that the presence of a differentiated gonad is not necessary for the first stages in the development of the secondary sexual characters, but that it is necessary for their full development. HERBST clearly brings out the contradictory nature of the evidence on the subject: and we may add a further case which has recently been published and seems to controvert the idea that there is any necessary connection between the development of the secondary and the primary sexual characters at all. KELLOGG (18) effected the complete destruction of the gonad in the larva of the silkworm before any differentiation of the gland had set in, and on rearing these larvae to the imago state found that they developed perfect secondary sexual characters, despite the entire absence of a gonad.

11*

Now in the face of this contradictory evidence let us examine the case of *Inachus scorpio* and *Sacculina*. We see here that the infected males may develope the perfect secondary sexual characters of the female without the presence of an ovary at all. The full development of the female secondary sexual characters is therefore not dependent on the presence of a differentiated ovary. But we know from the subsequent history of these males that they possess the potentiality of forming an ovary, because they are capable of regenerating an hermaphrodite gonad with mature ova. Now we also know that infected females, which have the ovaries degenerate, do not possess fully formed female secondary sexual characters. It is clear therefore that what causes the development of the female secondary sexual characters is the potentiality to form a differentiated ovary and vice versâ in the male. Now we do not know in what this potentiality lies, but if we frame some material hypothesis to account for the facts, we may safely suppose that this potentiality lies in the presence of some formative substance in the body which causes the differentiation of the primary and of the secondary sexual characters. In other words, the differential development of the secondary sexual characters is not due to the presence of a corresponding differentiated gonad, but the differential development of both primary and secondary sexual characters is due to a third common factor, which may be assumed to be the presence in the body of a sexual formative substance. This is the only theory which can account for the assumption in infected males of *I. scorpio* of the secondary sexual characters proper to the female when they do not possess an ovary, and for their subsequent development of an ovary.

In the light of this theory also all the apparently contradictory evidences from ordinary castration etc. are brought into harmony. For we suppose that the differentiation of the gonad consists in its taking up from the body the sexual formative substance; the removal of the gonad therefore after it has begun to be differentiated means the removal of a large quantity of the formative substance, and this will react on the development of the secondary sexual characters, according to the degree in which the formative substance was centred in the gonad; but the removal of the gland at a very early stage before differentiation has set in, as in KELLOGG's experiment, need not influence the development of the secondary sexual characters, because but little of the formative substance will have been removed. In any case by referring the undoubted correlation that exists between the primary and secondary sexual characters to a third factor, we explain to a large extent why this correlation appears so imperfect and erratic.

We have arrived then at a conception of sexual differentiation which points to a formative substance at work in the body causing the visible differentiation of the germinal cells into male and female, and also calling forth the development of the appropriate secondary sexual characters.

The question, therefore, that was first put as to how the parasite brings about the parasitic castration, comes to be, how does the parasite affect the sexual formative substance? We imagine this substance to be a product of the general metabolism of the body which

differs characteristically in the male and female. The presence of the parasite by interfering with the metabolism of the body prevents the normal production of the characteristic sexual substance, with the result that this substance is changed, causing in the female the atrophy of the gonad and the secondary sexual characters, in the male passing from the highly differentiated male condition to the more generalized hermaphrodite state.

The great experience of Prof. GIARD in the facts of parasitic castration, of which he was the original discoverer, gives a corresponding weight to the theoretical conclusions which he draws; it was therefore with great interest that I read a paper (12) recently published by him and courteously sent to me, in which he considers the general question, how does castration affect the secondary sexual characters of an animal. The conclusions which he draws are certainly negative, but not of less value for that reason. With perfect justice he argues against the view that the secondary sexual characters are entirely controlled in their development by a liquid substance (humorale) of the nature of a ferment circulating in the general fluids of the body. The most weighty objection which he urges against this theory is the fact that often a remarkable geometrical correlation appears to exist between the gonad and the secondary sexual characters, such that the secondary sexual characters of one side appear to be correlated with the gonad of that side alone (as for instance in many abnormally hermaphrodite Lepidoptera), or the correlation instead of being lateral may be transverse.

Since the theory that I have adopted must be placed in the category which accepts the action of a liquid substance circulating in the body, I believe that GIARD's objection must apply to this theory equally. I, moreover, fully agree with GIARD that the correlation between the primary and secondary sexual characters is not due to a specific ferment produced in the gonad: and I think that the serious objection which he urges against the general theory of specific liquids can be overcome in our theory by a little reflexion.

According to the theory which I have sketched in this section the differentiation and growth of both the primary and secondary sexual characters are due to a third common factor, namely the evolution in the body of a sexual formative substance which may be either male or female or hermaphrodite. This substance, whose presence I infer from the observations detailed in this chapter, I must also infer to be a fluid of some kind which can be distributed to all the parts of the body, including the gonad, which can be affected by sexual differentiation.

But I cannot claim that the evolution of this substance is the sole factor; the other factor must be, I think, a determinate differentiation of a certain degree which concerns the cellular elements of the body. Thus, in an hermaphrodite Ascidian for example, I regard the process of sexual differentiation as being due to two factors, firstly the evolution of the hermaphrodite sexual substance which circulates in the body and is the product of its metabolism, and which becomes divided and distributed at maturity to the male and female cells, and secondly a perhaps structural differentiation of these sexual cells of such a kind that only those in a particular position and of a particular internal structure are capable of

becoming ova under the influence of the sexual formative substance, while others are capable of becoming male cells.

In this manner I would account for the peculiar lateral or transverse correlation in gynandromorphous animals; in them also it is, I think, possible to hold that a sexual formative substance is present circulating in the whole body, which is the condition of the hermaphroditic development, but this substance affects different parts of the body in a different manner owing to a determining differentiation already present in the cells of these different parts. In the special case of gynandromorphous insects, theories have been suggested by both Boveri and Morgan (see 22) to account for such a cellular differentiation; thus Boveri suggests that in a gynandromorphous insect the spermatozoon, bearing the determination of one sex, may have united, not with the egg nucleus, but with one of the products of its first division: then supposing that the right and left sides of the body correspond to the first two blastomeres it might result that the two halves of the body would be sexually different. Morgan has suggested a slightly different but analogous interpretation.

If we admit therefore that sexual differentiation as a whole is due to two interacting factors, namely the factor of a generally distributed formative substance, and the factor of a local and specific differentiation of particular cells, we obtain what is probably an approximately true hypothesis, and moreover an hypothesis which is in excellent accord with the whole tendency of modern experimental embryology. Thus E. B. Wilson (20), in whose recent papers may be found not only the most judicious experimentation but the most critical analysis of contemporary results, has adopted a view of development which in the combination of the idea of formative stuffs and of localized germinal areas, is fundamentally similar and was indeed suggestive of our view of sexual differentiation; while the analogous position of this author in relation to the particular problem of sex as being perhaps determined primarily by the presence or absence in the germ cells of particular structural elements but being also partly a question of metabolism, exhibits the same sympathetic grasp of the just claims of both epigenetic and evolutionary ideas in embryological theory.

Returning to our special subject of parasitic castration, we must next fully discuss the remarkable and, as far as I know, hitherto unsuspected difference between the male and female sex in their reaction to their parasites. This difference, which is fully sustained by all my observations, consists in the fact that, whereas the male sex or at any rate a great number of the male sex in infected crabs can under proper conditions assume the full female characters, the female sex on the other hand cannot assume any distinctively male character under similar conditions. In this opinion I again run slightly counter to the views expressed by Giard, but I hope that in the light of the evidence produced he may modify his conclusions. It is of course undeniable that the secondary sexual characters of infected females may be in a degenerate condition, and that this degenerate condition may be an apparent approach to the male condition, but there is no secure evidence, as far as I can see, that the females under the influence of parasitic castration can assume characters distinctively and

positively male. Thus if an infected female crab, for instance, were to develope either swollen chelae or copulatory styles, it would be necessary to give up our view, but it appears most strikingly and emphatically that this is never the case. GIARD (1) has recognised this fact in *Stenorhynchus*, where he found infected individuals of the type described in this chapter as crabs of apparently doubtful sex, i. e. individuals of totally female appearence but possessing copulatory styles; these individuals he identified as highly modified males, as I do. But in other cases he appears to believe that the female sex may assume male characters, as for instance in *Andrena* infected by *Stylops* where he says "Chacun des sexes perd ainsi plus ou moins les attributs qui le caractérisent et tend à acquérir plus ou moins ceux du sexe opposé" (2 p. 15). The effect of the fungus *Ustilago* on certain kinds of *Melandrium*, has been also adduced by GIARD (6) as an instance of parasitic castration, in which the male characters are called forth in a female plant. This botanical case, however, differs essentially from all other cases of parasitic castration, and it is probable that we are dealing with a different order of phenomena. The following particulars are taken from STRASBURGER (14). The so-called female flower of *Melandrium* already possesses the rudiments of the male organization as small hooks. These hooks normally do not develope, but when the flower is attacked by *Ustilago*, the latter is particularly concentrated in the hooks which, probably in consequence of the stimulus, proceed to develope into normal anthers. The anthers however never get beyond producing the pollen mother cells, which are then destroyed by the fungus. In consequence of the development of the anther rudiments the female organization may atrophy to a certain extent. It is clear, I think, that the resemblance of this process to the parasitic castration of animals is quite spurious. The development of the rudimentary anthers is due to a local stimulus given by the *Ustilago*, and in any case it cannot be compared to a female animal giving rise to male characters, because the flower of *Melandrium* is potentially hermaphrodite already since it possesses the rudiments of anthers.

From the fact that GIARD adduces this case and from his general language, I conclude that he holds the view that there is no essential difference in the reaction of male and female animals under parasitic castration, and that the female can assume male characters in the same way that males can assume female characters.

The common view[1] of hermaphroditism as being derived from the male or female indifferently, according as the hermaphrodite resembles more closely one sex or the other, is proved to be utterly fallacious, since we know that a male crab may assume all the attributes of the female and only retain a copulatory style in a more or less degenerate state.

So striking is the apparent incapacity of the female crabs to assume a single distinctively male character, that I am tempted to think that the female sex in general really does not possess the male modification of the sexual formative substance in a latent state, whereas the male evidently does possess the female. The question, therefore, naturally arises if this conception

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[1] This view is so widely spread in biological literature that I need not give special references. In view of the facts given in this chapter it is seen to be altogether inadequate and uncritical.

of sex and of hermaphroditism can be of universal application. The most serious objection to this view is that in certain rare cases, chiefly among fowl and deer — see Herbst (**16**) and Rörig (**17**) — individuals which have actually functioned as females and which show no trace of male gonads may subsequently acquire the secondary sexual characters of the male sex, and these cases, at any rate in the case of deer, merge into those where a female with diseased or at least non-functional gonads may acquire secondary male characters. Although these cases are strong prima facie evidence in favour of the view that the female sex may normally carry the male in a latent condition, their rarity and the fact that they merge so completely into ordinary cases of hermaphroditism, may make us suspect that these apparently once normal females have been from the beginning hermaphrodites in which for some reason the male sexual formative substance did not find expression in visible characters. Another body of facts may seem fatal to our view, the facts showing that the male characters can be transmitted through the female sex, as in the case of hybrids and of parthenogenetic females which give rise to males. But a legitimate distinction can be drawn between the presence of a metabolic substance in the body capable of assuming activity under the proper stimuli, and the transmission of a sexual potentiality which may depend on some quiescent structural element incapable of activity except after the elaborate and mysterious changes which accompany the inception of a new generation.

The theory that the male sex alone normally carries the formative substance of the opposite sex receives a certain value if we apply it to those classes of animals descended from dioecious ancestors which have become secondarily hermaphrodite. In view of a number of considerations which are urged at the end of Chapter 6, it is difficult to maintain that hermaphroditism, as an apparently necessary concomitant to a fixed habit of life, can be accounted for as a mere adaptation for securing reproduction. In this chapter we have seen how a complete state of hermaphroditism can be imposed upon certain individuals of the male sex, as the result of a degenerate process initiated by the presence of a parasite, which apparently works through an affec tionof the general conditions of metabolism. In ordinary fixed hermaphrodite animals we meet with undoubtedly a peculiar condition of metabolism, and a general process of degeneration which usually affects the whole organization. It is, therefore, reasonable to suppose that the hermaphrodite state in fixed animals has been acquired by simple degeneration, imposed upon the male organism as an adaptive response to the changed conditions of metabolism incident on the fixed habit of life.

If we argue that secondarily acquired hermaphroditism is always a form of degeneration, or the passage from a higher to a less degree of metabolic specialization, it is more probable that this state has been imposed upon the male sex than upon the female, because the former is the more highly organized of the two, and for the female to acquire male characters, i. e. to become hermaphrodite, would mean an advance in organization and not a retrogression.

We arrive therefore at the unexpected, but not impossible view that animals which have become hermaphrodite through a fixed method of life, are represented merely by the

degenerate male sex, the female being entirely suppresed. The curious and unexplained protandry, which is almost invariable in all hermaphrodites, is suggestive in this connection, and the bearing of this idea on the sexual relations in Cirripedia, especially with reference to the complemental males, has been discussed in Chapter 2, pp. 33—37.

There is a final topic for discussion, namely the connection between the theory of sex here adopted and contemporary Mendelian theory. It is on many sides suggested that the so-called determination of sex may take place in the germ before developement begins, and we have already admitted, in consideration of the facts of transversely correlated hermaphroditism etc., that this is probably the case, although the facts of parasitic castration on the other hand force us to the conclusion that this "determination" is within certain limits of an elastic character. It is interesting to observe that where an attempt has been successfully made to find structural differences in the germ cells as possible indications of this early sexual differentiation, the manner of this differentiation is in harmony with the results we have obtained from the study of parasitic castration. The discoveries of HENKING, MC CLUNG, WILSON and others have shown that in many insects two kinds of spermatozoa exist differing in the constitution of their chromosomes, while the eggs are apparently all the same.

If we suppose that the two kinds of spermatozoa represent the male and female sex respectively, while the eggs are purely female, we would obtain in the process of sexual generation $1/2\, \male \female + 1/2\, \female \female$, in which the male spermatozoa united with female eggs give rise to males of really hermaphrodite constitution, while the female spermatozoa united with female eggs give rise to females of pure female constitution.

It is obvious that this interpretation is in strict agreement with the main conclusion brought out in this chapter, viz. that males are potentially hermaphrodites, while females are incapable of assuming the male characters. It is doubtful, however, whether this particular "Mendelian" interpretation can be applied generally, because in some animals, e. g. the Bee, it appears that the egg by itself is male and only becomes female through fertilization, while in many Cladocera and Aphids females give rise parthenogenetically to males.

It appears therefore that the primary mechanism of sex determination may be variously distributed in the germ cells, but this need not affect the conclusions drawn from our side of the question, namely from the reaction of a metabolic sexual substance to varying conditions in the organism. The possible connection of this substance with particular chromosomes in the germ cells is at present outside the scope of experiment.

The above discussion may be summarised in the following sentences:

Summary of conclusions.

1. The differentiation of the secondary sexual characters is not essentially dependent on the presence of a differentiated gonad, but the differentiation of both primary and secondary sexual characters is due to the evolution in the body of a third factor, which we may call a sexual formative substance.

2. Sexual differentiation, both primary and secondary, is not entirely due to the action of the sexual formative substance, but rather to the interaction of this substance with the predetermined properties of localized and self-differentiating cells.

3. The effect of parasitic castration is due to a fundamental alteration in the metabolic conditions of the body which reacts on the sexual formative substance, causing simple degeneration in the female, and degeneration with hermaphroditism either partial or complete in the male.

4. All secondary hermaphroditism, both sporadic and normal, may have been imposed solely on the male sex, the female sex being incapable of assuming hermaphroditic characters, either primary or secondary.

6. Special reference of the phenomena of Parasitic Castration to High and Low Dimorphism.

The principle of High and Low dimorphism has for long been known to affect the sexual development of the males of a number of Arthropods, such as *Forficula* and the Lamellicorn beetles. (For literature of the subject see my paper, High and Low Dimorphism. in: Mitth. Z. Stat. Neapel 17. Bd. 1905 p. 312.) It consists essentially in a quantitative relation between the general size of the males of a species and the degree of development of their secondary sexual characters, such that the larger males exhibit these characters developed to a disproportionately greater degree relatively to their size than the smaller males. Combined with this quantitative ratio we frequently find that the males of these species fall into two more or less sharply defined categories, namely large high males and small low males, the intermediate condition being very sparsely represented. This phenomenon is most clearly to be recognised in animals, like Insects, which do not grow after the attainment of maturity; in these cases I have termed the type of High and Low Dimorphism which may occur as definitive; but as I have shown in the paper referred to above and as explained on p. 69 of this chapter, the essential principle of high and low dimorphism may be exhibited in species which go on growing after the attainment of maturity; in these cases I have termed the type of dimorphism facultative. Facultative high and low dimorphism results, in such a species as *Inachus scorpio*, from the fact that the males become mature under the "low" form while still quite small, and that before attaining to the "high" condition they have to pass through an intermediate period of active growth in which the sexual development, both primary and secondary, is greatly suppressed and the males then appear as the "middle" males. The high, middle and low types of male in *I. scorpio* are figured on Plate 7 figs. 6, 7 and 8. The result of this process is that during the breeding season, the breeding males are sharply defined into high and low forms, as in the cases of definitive high and low dimorphism. (I may mention

here that an essentially similar process, namely the passage of particular males from sexual activity with well developed secondary sexual characters to a condition of sexual suppression has been previously observed by Faxon in *Cambarus* (Ann. Mag. N. H. (5) Vol. 13 1884), an observation which escaped my notice.)

It appears to me certain that the two phenomena of definitive and facultative dimorphism are essentially due to the same cause, namely to the antagonism that exists between the functional activity of the sexual organs and growth of the body as a whole in the male sex. It must be borne in mind that this antagonism appears to result in the phenomena of high and low dimorphism only in the male sex. An explanation of this peculiar relation in the male sex between sexual activity and growth is, I think, obtained by a consideration of the results arrived at from our study of the phenomena of Parasitic Castration, and also from certain other facts which I will introduce later.

In Parasitic Castration we have found that the male reacts to the presence of the parasite by producing in its body an hermaphroditic substance as opposed to a male substance, and as a result of this the testes become greatly reduced or even disappear and the secondary sexual characters take on a female character. The reason for this behaviour is, I think, to be found in the adaptive regulation of the metabolism so brought about, in order that the animal may withstand better the attack of its parasite. This adaptive regulation consists in the production of at least a partially female condition of metabolism as opposed to a wholly male condition, the female condition being (to use the terminology of Geddes and Thompson, Evolution of Sex. in: Internat. Sc. Series) preponderantly anabolic or conservative, as opposed to the katabolic male condition, and by this change from a katabolic to a more anabolic condition the animal can withstand better the drain on its system occasioned by the parasite. Now in the phenomenon of high and low dimorphism an exactly parallel state of things occurs. The male in order to grow must suppress the male condition of its metabolism and call into activity the female or anabolic condition or substance, which from the facts of Parasitic Castration we believe every male to possess in a latent state. The result of this is that we get the suppressed sexual condition (really a semi-hermaphrodite condition) in the middle-males of species, such as *I. scorpio*, which exhibit facultative high and low dimorphism, while in species with definitive high and low dimorphism we get the condition of sexual suppression i. e. semi-hermaphroditism relegated to a purely larval state, i. e. in certain individuals, perhaps partly owing to external conditions of nutrition, sexual maturity is put off (high males), while in others it is hastened on (low males).

I have recently come upon a most convincing piece of evidence to show that in the condition of sexual suppression, characteristic of high and low dimorphism, we are really dealing with a semi-hermaphrodite state exactly parallel to the condition called forth in infected males by Parasitic Castration. This evidence is derived by a reexamination which I have made this year of the sexual condition in *Orchestia deshayesii* and *gammarellus*, the common Sand Hoppers.

NEBESKI (Amphipoda Adriatica. in: Arb. Z. Inst. Wien 3. Bd. p. 134) originally found that in a large proportion of the males of *Orchestia gammarellus* immature ova are present in the anterior region of the testes, which however never come to maturity.

DELLA VALLE (Gammarini. in: Fauna Flora Golf. Neapel 20. Monogr. 1893) in trying to confirm NEBESKI's observations throws some doubt on their validity, as he remarks that he has never found the ova in fully developed males but only in occasional males which have failed to develope complete male characters.

The discrepancy between these two results is so striking that I determined to look into the matter, and the solution of the difficulty, though not yet complete, has been of some interest. In the bays of Naples and of Pozzuoli both *O. deshayesii* and *O. gammarellus* are very common, but during the winter months they lie hidden under stones and refuse and require some looking for. During the months December-March I have collected very numerous specimens of *O. deshayesii*, and on dissecting them I found that more than half the males, whether fully developed or not and of all sizes, exhibited the ova in their testes. It is clear therefore that DELLA VALLE cannot have examined *O. deshayesii* at Naples during the winter months, and that during the summer months, when O. deshayesii breeds, the fully developed males lose these ova[1]).

Now in confirmation of this, I have found that *O. gammarellus* at certain places, e. g. Cenito along the Posillipo shore, breeds during the winter months, and that during these months the males never possess the ova in their testes, but at other places, e. g. Torregaveta, I have found *O. gammarellus* at the same time of year which were not breeding (no females being found with eggs) and a large proportion of the males here had ova in the testes.

The result is this then, that the males of these species, when breeding is not going on, assume a semi-hermaphrodite condition of a quite indubitable kind which must evidently bear some relation to the metabolic conditions in the body, as the ova always degenerate and a true functional hermaphrodite Sand Hopper has, I believe, never been found. The particular metabolic condition which calls forth the production of these ova is, I think, clearly that condition of adaptive anabolism which we have studied in the infected males under Parasitic Castration, and in the middle males or males of suppressed sexuality under High and Low Dimorphism.

The remarkable manner in which all these facts fit together, presenting us with a theory of the nature of male organization, its essential difference to the female and in what this difference lies, and of the relation which subsists between male sexuality and the general growth and nutrition of the body, may give us some hope that the nature of Sex, that problem which lies at the very basis of organic life change, is open to the methods of scientific analysis.

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[1]) This inference has been subsequently confirmed.

Since this chapter was in great part written, Mr. F. A. Potts of Trinity Hall, Cambridge has studied at Naples the effect of *Peltogaster* on *Eupagurus meticulosus*. His results, which will shortly be published, are in their main features strikingly confirmatory of my own on *Sacculina*, but in many exceedingly interesting features the hermit-crabs show a divergent kind of reaction to their parasites to that which I have found in the spider crabs. By his permission I may state that infected male hermit-crabs assume in various degrees the secondary sexual characters of females, whereas the modification which females may undergo can be interpreted as a mere arrest of development and not in any way as a definite acquisition of male characters. He is therefore of the same opinion as myself that the females are incapable of assuming any definitely male character under the influence of parasitic castration.

In a large proportion of infected males the reduced testes contain a number of small ova, while in infected females no sign of spermatozoa is ever found.

This important discovery is completely in accord with the recovered male crabs found by me exhibiting an hermaphrodite gonad, except that in the hermit-crabs the ova are produced in the testes before the *Peltogaster* is got rid of and the crab has begun to recover; in other words the reaction of the gonad occurs precociously.

I have chosen out two of the most important results from Mr. Potts' work which are directly confirmatory of my conclusions, but for many other points of almost equal importance a reference must be made to his full paper, which will shortly appear in the Quarterly Journal of Microscopical Science.

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Appendix.

In this appendix are given a series of correlation tables, setting out in full the data for determining the effect of *Sacculina neglecta* on *Inachus scorpio*. All the measurements are given in millimeters, and all the tables are arranged in the same way. The following explanation of the arrangement of Table 1 can be applied to all. In the extreme left hand vertical column the figures 9 to 19 refer to carapace length in millimeters. In the top horizontal column the figures 5—19 refer to abdominal length in millimeters. The figures in the interior of the table give the numbers of crabs found with each particular measurement of carapace and abdomen indicated in the left hand vertical and top horizontal column. Thus there were 26 crabs measuring 13 mm in abdominal length and 14 mm in carapace length. In the right hand vertical column and the bottom horizontal column are given the total number of crabs exhibiting each carapace length (vertical column) and each abdominal length (horizontal column). In the extreme right hand corner is given the total number of crabs used for making the table, viz. 295.

Table 1. Uninfected females. Abdominal length.

Abdominal length in mm.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Totals
9	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
10	6	9	6	—	—	—	—	—	—	—	—	—	—	—	—	21
11	—	3	18	—	—	—	—	—	—	—	—	—	—	—	—	21
12	—	—	9	9	—	—	—	1	—	—	—	—	—	—	—	19
13	—	—	—	3	2	1	1	5	8	—	—	—	—	—	—	20
14	—	—	—	—	1	—	—	1	26	12	—	—	—	—	—	40
15	—	—	—	—	—	—	—	—	6	28	22	—	—	—	—	56
16	—	—	—	—	—	—	—	—	—	3	37	12	—	—	—	52
17	—	—	—	—	—	—	—	—	—	—	4	28	13	—	—	45
18	—	—	—	—	—	—	—	—	—	—	1	4	8	1	—	14
19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Totals	12	12	33	12	3	1	1	7	40	43	64	44	21	1	1	295

Carapace length in mm.

Table 2. Infected Females. Abdominal length.

Abdominal length in mm.

		5	6	7	8	9	10	11	12	13	14	15	16	17	18	Totals
	7	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
	8	1	—	3	—	—	—	—	—	—	—	—	—	—	—	4
	9	2	—	2	1	1	—	—	—	—	—	—	—	—	—	6
	10	—	1	—	2	12	1	—	—	—	—	—	—	—	—	16
Carapace length in mm.	11	—	2	3	2	3	22	3	—	—	—	—	—	—	—	35
	12	—	—	4	4	0	2	11	1	—	—	—	—	—	—	22
	13	—	—	—	2	1	1	2	15	7	1	—	—	—	—	29
	14	—	—	—	—	—	—	2	7	22	5	—	—	—	—	36
	15	—	—	—	—	—	1	—	—	4	30	8	—	—	—	43
	16	—	—	—	—	—	—	—	—	—	7	20	5	—	—	32
	17	—	—	—	—	—	—	—	—	—	—	6	10	2	—	18
	18	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2
	19	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Totals		3	4	12	11	17	27	18	23	33	43	34	16	3	2	246

Table 3. Infected Females. Appendages.

Appendage categories.

		1	2	3	4	5	Totals
	7	—	1	—	—	—	1
	8	—	—	1	2	1	4
	9	—	—	3	1	2	6
	10	2	4	5	4	1	16
Carapace length in mm.	11	5	8	18	2	2	35
	12	2	5	11	4	0	22
	13	2	8	14	2	3	29
	14	2	8	17	4	6	37
	15	—	4	17	5	15	41
	16	—	5	8	8	11	32
	17	—	2	2	2	12	18
	18	—	—	1	—	1	2
	19	—	—	1	—	1	2
Totals		13	45	98	34	55	245

Note. For appendage categories see p. 68.

Table 4. Uninfected Males. Abdominal length.

Abdominal length in mm.

		4	5	6	7	8	9	10	11	Totals
	9	2	—	—	—	—	—	—	—	2
	10	4	8	—	—	—	—	—	—	12
	11	—	21	1	—	—	—	—	—	22
	12	—	22	20	—	—	—	—	—	42
	13	—	2	51	1	—	—	—	—	54
	14	—	1	33	6	—	—	—	—	40
	15	—	—	3	18	—	—	—	—	21
Carapace length in mm.	16	—	—	—	22	2	—	—	—	24
	17	—	—	1	7	11	—	—	—	19
	18	—	—	—	1	8	1	—	—	10
	19	—	—	—	—	14	3	—	—	17
	20	—	—	—	—	3	11	—	—	14
	21	—	—	—	—	—	15	11	1	27
	22	—	—	—	—	—	10	16	1	27
	23	—	—	—	—	—	1	9	2	12
	24	—	—	—	—	—	—	5	7	12
	25	—	—	—	—	—	—	2	2	4
	26	—	—	—	—	—	—	—	1	1
Totals		6	54	109	55	38	41	43	14	360

Table 5. Infected Males. Abdominal length in mm.

Carapace length in mm.	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Totals
7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
8	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
9	—	3	—	—	—	—	—	—	—	—	—	—	—	—	3
10	—	—	1	1	1	—	—	—	—	—	—	—	—	—	3
11	—	8	1	2	3	2	2	—	—	—	—	—	—	—	18
12	—	4	6	1	1	1	5	4	1	—	—	—	—	—	23
13	—	—	4	1	3	3	4	4	—	—	—	—	—	—	19
14	—	—	6	2	1	2	4	7	2	—	—	—	—	—	24
15	—	—	—	10	2	—	1	3	2	—	—	—	—	—	18
16	—	—	—	6	3	1	—	1	1	1	2	—	—	—	15
17	—	—	—	1	5	4	—	—	4	5	—	1	—	—	20
18	—	—	—	—	6	2	—	4	4	2	1	1	1	—	21
19	—	—	—	—	4	3	1	1	—	2	1	—	—	—	12
20	—	—	—	—	—	4	1	1	—	2	4	—	—	—	12
21	—	—	—	—	—	1	—	1	3	4	3	2	—	—	14
22	—	—	—	—	—	—	—	1	1	1	3	3	1	2	12
23	—	—	—	1	—	—	—	—	—	2	3	—	—	1	7
24	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Totals	1	15	18	25	30	23	18	27	17	19	17	8	2	3	224

Table 6. Uninfected Males. Chela breadth in mm.

Carapace length in mm.	1	2	3	4	5	6	7	8	9	10	11	12	Totals
9	2	—	—	—	—	—	—	—	—	—	—	—	2
10	8	3	1	—	—	—	—	—	—	—	—	—	12
11	1	18	3	—	—	—	—	—	—	—	—	—	22
12	—	23	22	—	—	—	—	—	—	—	—	—	45
13	—	12	39	10	—	—	—	—	—	—	—	—	61
14	—	4	20	24	1	—	—	—	—	—	—	—	49
15	—	2	3	26	7	—	—	—	—	—	—	—	38
16	—	5	11	4	6	4	—	—	—	—	—	—	30
17	—	—	15	4	6	2	—	—	—	—	—	—	27
18	—	—	10	7	—	2	4	—	—	—	—	—	23
19	—	—	5	9	—	2	6	3	—	—	—	—	25
20	—	—	2	6	1	—	2	12	—	—	—	—	23
21	—	—	—	—	—	1	1	17	12	4	—	—	35
22	—	—	—	—	—	—	—	3	25	13	1	—	42
23	—	—	—	—	—	—	—	—	7	14	3	—	24
24	—	—	—	—	—	—	—	—	2	12	8	1	23
25	—	—	—	—	—	—	—	—	—	2	5	3	10
26	—	—	—	—	—	—	—	—	—	1	1	3	5
Totals	11	67	131	90	21	11	13	35	46	46	18	7	496

Table 7. Infected Males. Chela breadth.

Chela breadth in mm.

Carapace length in mm.	1	2	3	4	5	6	7	8	9	10	Totals
7	1	—	—	—	—	—	—	—	—	—	1
8	1	—	—	—	—	—	—	—	—	—	1
9	3	—	—	—	—	—	—	—	—	—	3
10	3	—	—	—	—	—	—	—	—	—	3
11	13	5	—	—	—	—	—	—	—	—	18
12	16	5	1	—	—	—	—	—	—	—	22
13	5	12	1	—	—	—	—	—	—	—	18
14	—	21	3	—	—	—	—	—	—	—	24
15	—	16	2	1	—	—	—	—	—	—	19
16	—	13	2	—	—	—	—	—	—	—	15
17	—	11	2	—	1	—	—	—	—	—	14
18	—	5	15	—	—	1	1	—	—	—	22
19	—	—	7	—	2	1	1	1	—	—	12
20	—	—	5	3	2	—	—	2	—	—	12
21	—	—	5	7	1	—	—	1	—	—	14
22	—	—	3	7	1	—	—	1	—	—	12
23	—	—	—	5	1	—	—	—	—	1	7
24	—	—	—	1	—	—	—	—	—	—	1
Totals	42	88	46	24	8	2	2	5	0	1	218

Table 8. Infected Males.

Appendage categories.

Carapace length in mm.	1	2	3	4	5	Totals
7	—	—	—	—	1	1
8	1	—	—	—	—	1
9	—	—	2	—	1	3
10	2	—	—	1	—	3
11	3	1	2	3	6	15
12	1	3	5	3	2	14
13	—	—	9	3	4	16
14	2	2	8	1	4	17
15	—	—	3	2	3	8
16	1	1	1	—	1	4
17	—	—	2	5	3	10
18	1	2	5	—	4	12
19	—	1	2	1	4	8
20	—	—	2	—	6	8
21	—	—	3	4	2	9
22	—	—	3	1	2	6
23	—	—	2	2	1	5
Totals	11	10	49	26	44	140

Note. For appendage categories s. p. 70.

Chapter 6.

Parasites of the Parasites.

1. Introduction.

The Rhizocephala, while inflicting the most wide spread damage on various species of Decapoda, are themselves subject to the attacks of an highly interesting group of parasites belonging to the family Liriopsidae. The Liriopsidae, according to the classification given by Bonnier in his monograph (5) belong to the suborder Cryptoniscinae of the Isopodan order Epicarida, the other suborder being the Bopyrinae. Bonnier gives a list of the Liriopsidae hitherto described with the Rhizocephala which they infest, and it appears probable that every well distinguished species of Rhizocephala has a specific Liriopsid which lives upon it. The Liriopsid is fixed by its mouth either on some part of the Rhizocephalon or it may be attached to the crab itself near the point of attachment of the Rhizocephalon, in which case it draws its nourishment from the roots instead of from the external body of the latter. In the curious form *Zeuxo alphei* which Kossmann (3) found fixed to the head of an *Alpheus*, the relation between Liriopsid and Rhizocephalon is problematical, but it is possible that the *Zeuxo* is here also essentially a parasite of the Rhizocephalon, whose roots may penetrate into the head of the *Alpheus*. The Liriopsid which I have been able to study in some detail is *Danalia curvata* (Fraisse) a parasite of *Sacculina neglecta*, itself the parasite of *Inachus scorpio*.

On Plate 1 fig. 4, a life-sized drawing of a young male *I. scorpio* is given, which carried two mature specimens of *D. curvata* fixed upon a *Sacculina*. This figure exemplifies very well the great mass of parasites with which this crab is sometimes burdened. On Plate 7 fig. 30 I have sketched a female crab which carried on the underside of its abdomen a remarkable assemblage of parasites, namely two Sacculinae and one *D. curvata*, while on the under side of the latter could be distinguished two minute larval males of *D. curvata* in the act of fertilizing the mature parasite.

Of 350 *Inachus scorpio* taken at random during the spring which were infested with

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Sacculina, 50 bore also either one or two specimens of *D. curvata*, fixed either on the *Saccu-lina* or on the abdomen of the crab near the point of attachment of the *Sacculina*. Several crabs have been found with small *D. curvata* on them which showed no external trace of a *Sacculina*, but all these crabs on dissection proved to be infected with Sacculina interna; it appears therefore that the larvae of the Liriopsid have some means of finding out crabs that are infected with *Sacculina* before the latter appear in the external world. It may be that a sense of smell directs them in these cases.

I may mention here a species of *Danalia*, which I have named *D. ypsilon* (see fig. 32 Plate 7) and which is found upon *Galathea dispersa*. This species of *Galathea* is also fre-quently infected by a Rhizocephalous parasite, *Lernaeodiscus galatheae* (see fig. 31 Plate 7) but curiously enough the adult forms of *Danalia* and *Lernaeodiscus* have never been found by me upon the same individual host, nor have I been able to prove by the presence of roots that the specimens infected with *Danalia ypsilon* have once carried a *Lernaeodiscus* or are in-fected with a still internal *Lernaeodiscus*. It is highly probable therefore that in this case the *Danalia* has secondarily become a true parasite of the *Galathea*, instead of the *Lernaeodiscus.*

Besides the species mentioned in Bonnier's work, Hansen (**6**) has described the Crypto-niscid larvae of a number of forms from the Plankton Expedition of 1889, and in his work can be found the most accurate description of the external anatomy of these larvae in exis-tence. The author adopts a different classification to that of Bonnier; in his subfamily Cryptoniscinae he includes all the parasites of the Cirripedia as well as those of the Ostracoda (Bonnier's Cyproniscidae), and of the Isopoda and Amphipoda (Bonnier's Cabiropsidae). That this classification may prove correct is highly probable, but since we are only concerned here with the parasites of the Rhizocephala, it is more convenient to adopt the more exclusive classification of Bonnier.

In comparing the larvae of Cryptoniscinae figured by Hansen (**6**) with the larvae of *Danalia curvata*, it will be seen that our larvae (Plate 1 fig. 23) in the characters of the head and of the basal portion of the first antenna correspond most closely to Hansen's *Cryptoniscus* B, but in our larvae the terminal joint of the sixth pair of thoracic legs is much elongated and not that of the seventh, as in Hansen's type.

The chief subject of interest with regard to these parasites, besides their association with the Rhizocephala, is their method of reproduction, because, being solitary fixed parasites, some special method of cross-fertilization might be expected. The following paragraphs will elucidate this problem, which has been erroneously conceived hitherto.

Fraisse (**1**) has given the only detailed account of the life-history of the Liriopsidae, and although his work is in many respects of value, he made the misleading error of describing the sexual gland of the Cryptoniscus larva as a diverticulum of the gut, while the spermatheca of the adult is considered as a gill. Furthermore an altogether illusory testis is described in the so-called larval males, which does not exist.

Fraisse conceived that the Cryptoniscus larvae are already at the free-swimming stage

differentiated males and females, that fertilization takes place in this free-swimming larval stage, and that the fertilized female Cryptoniscus larvae fix themselves on the Rhizocephala and develope into the adult females, while the larval males die without further development. This is an entire misconception. All the Cryptoniscus larvae are hermaphrodites which at first, while they are free swimming, perform the function of males, depositing their copious sperm into the spermathecae of the fixed adults: these free-swimming larvae, after functioning as males, fix themselves to a Rhizocephalon and henceforth function as females. We have in fact a perfect instance of protandric hermaphroditism with cross-fertilization: and this is in accord with what we know of all the Epicarida (see BONNIER **5**). In the literature on the Liriopsidae (references to which will be found in BONNIER's book) continual mention is made of larval males; this is perfectly correct but it must be borne in mind that these larval males are only protandric hermaphrodites which will subsequently develope into the adult female parasites.

To the proof of this we now turn.

2. Life History of D. curvata.
(Plate 7 figs. 22—30.)

The larvae, after being hatched out of the body of the parent, go through a series of changes in the free-swimming state which I have not followed, and then assume the Cryptoniscus form which is figured on Plate 7 figs. 22 and 23. With the external form of this larva we need not further concern ourselves, as it is already well known, but a careful elucidation of its sexual nature is necessary. The larvae at this stage have been found crawling upon the surface of the body of *Sacculina neglecta* or upon *Inachus scorpio* near the point of attachment of the *Sacculina*: and in a few cases I have found Cryptoniscus larvae crawling upon an adult *Danalia curvata* which they were no doubt in the act of fertilizing. The sexual nature of these larvae, whether found upon *Sacculina*, *Inachus* or *Danalia*, is always the same; they are all hermaphrodites in which the testes are already mature and the ovary immature. The hermaphrodite gland is a large paired structure lying in the anterior dorsal part of the body (fig. 22 Plate 7 *ov* and *t*). A section through the middle of the body and the hermaphrodite gland is shown in fig. 24 Plate 7. The gland in this region is a large testis which always contains a quantity of spermatozoa. The spermatozoa are rod-like organisms of the form shown in Fig. 24a. At the ventral internal border of the testis is a group of cells (*n*) some of which are large, vacuolated and with conspicuous nucleoli, while others are still small. These cells are a part of the testis and their function is to absorb the remains of that organ after fixation when it is no longer of use. I call these the "phagocytic cells". At the extreme anterior end of the gland a very small ovary is visible (*ov* fig. 22).

These larvae then are all **functionally males**, but those that are fixed to *Sacculina* or *Inachus*, as opposed to those which are crawling on adult *Danalia*, have ceased to function as males and have already begun to develope into females. All the larvae, however, examined by me which had recently attached themselves to the host, still contained some sperm, and in several cases a great quantity of sperm was still present.

Plate 7 fig. 25 is a transverse section through the body of a Cryptoniscus larva which has already become fixed to a *Sacculina*. The testis is seen to still contain some sperm, but it is now mostly composed of a coagulated fluid. The phagocytic cells (*n*) are seen to be in the act of absorbing this fluid, which in their neighbourhood is being converted into drops of liquid that are engulphed into the cell-bodies.

In the anterior region of the sexual gland, a section through which is shown in Fig. 26, the developing ovaries (*ov*) are seen as two caps of small cells on the dorsal surface, lying above the most anteriorly placed phagocytic cells.

The parasite now loses all trace of its early male nature, and has the form shown in figs. 27 and 27a. The proboscis (*pr*), which has greatly elongated, is fixed far into the tissues of the host. The gut is sack-like and greatly swollen. A conspicuous heart (*h*) is seen pulsating in the posterior region. The ovaries (*ov*) lie on the dorsal surface as narrow strips, while laterally the phagocytic cells (*n*) are seen as refringent masses. Fig. 27a Plate 7 is an optical section of a whole preparation, which shows very clearly the relations of the various parts, especially the hugely developed phagocytes. A transverse section through the body at this stage is shown in Fig. 28, in which the ovaries are clearly shown, and also the phagocytic cells (*n*) with darkly staining cytoplasm and degenerating nuclei. These phagocytes, after performing their function of absorbing the remains of the testis, do not appear to fill any further rôle in the economy of the animal. At first they increase greatly in size and in number by amitosis, but as soon as the fixed parasite begins to grow large, degenerative processes rapidly set in. The cytoplasm becomes loaded with chromatic granules derived from the degenerating nucleus, and in the adult parasite the remains of the phagocytic cells are seen as darkly staining rings of protoplasm from which all trace of a nucleus has disappeared, leaving a clear hollow in the centre (*n* Fig. 29). I am inclined to notice a close parallel between these phagocytic cells and the hypertrophied cells of the testes of the Rhizocephala described in Chapter 2. That the germinal cells of the testes of two such widely separate hermaphroditic forms should undergo similar processes of degeneration, is highly suggestive.

The rest of the life history is taken up, firstly, in the rapid growth of the **ovaries**, which, absorbing the nutriment from the inflated gut, come to fill up the whole of the body cavity, and secondly in the act of fertilization. The **spermathecae**, which FRAISSE (**1**) described as gills, are present in the adult as two pairs of ramifying organs on the ventral surface with their external openings protected by chitinous appendages. They are each composed of two parts, a part opening to the exterior lined with a regular epithelium, and an internal lacunar portion in which the spermatozoa after coition may be found lodged. Fig. 29 Plate 7

is a transverse section through an adolescent parasite in the region of the posterior pair of spermathecae. The openings (*op*) of the latter can be seen protected by the chitinous armature (*ch*), while dorsally the receptacles of the spermathecae (*sp. th*) are seen with groups of spermatozoa in them. A high power drawing (fig. 29a) of these spermatozoa reveals their complete identity with the spermatozoa found in the testes of the Cryptoniscus larvae (fig. 24a).

Such is the history of the reproductive processes in *Danalia curvata*, a history which brings these forms into complete agreement with the rest of the Epicarida, and also with such Isopods as *Anilocra* etc. whose protandric hermaphroditism has been proved by P. MAYER (2).

Professor CAULLERY has drawn my attention to a paper by MESNIL and himself (7) in which the life history of *Hemioniscus balani*, parasitic on *Balanus balanoides*, is very fully described. The hermaphroditism of this animal agrees perfectly with the description we have just given for *Danalia*. The authors describe the formation of a peculiar brood-pouch in the adult female, which, if it occurs in the Liriopsidae, has been missed by myself and previous observers.

3. On the Hermaphroditism of Fixed Animals.

A survey of all living beings will disclose to us that the state of hermaphroditism is closely correlated with a fixed habit of life. In the vegetable world fixation is the rule and hermaphroditism is by far the commonest condition, but it is in the animal kingdom that the special proofs of this contention are forthcoming. For if we consider the special groups which belong to free-living orders of creatures but have themselves adopted a fixed habit, we perceive at once that all these groups exhibit hermaphroditism to a very great extent. To take a few instances, the Cirripedes among Entomostraca, the Epicarida and Cymothoidae among Isopoda, and the Ascidians among Chordata may be mentioned. There is plainly then some causal connection between hermaphroditism and a fixed habit; but what is this connection? The most obvious answer to this question is that an animal which is fixed in one place and cannot meet with other individuals of its species can only fertilize itself and hence it has had to develope both ova and spermatozoa. But this answer must certainly be rejected, because wherever hermaphroditism is found the most elaborate means are almost invariably present for ensuring cross-fertilization, either by means of special males or else by the wide-spread occurrence of protandry, while among plants the adaptations for securing cross-fertilization are so remarkable as to need no comment. It is true that in many plants and in a few animals self-fertilization or autogamy does occur normally, but these cases are so few in comparison to the elaborate devices for securing cross-fertilization that it is necessary to regard these cases as something special and not as constituting the normal con-

dition for hermaphrodites in general. Why then are fixed animals so commonly hermaphrodites? It has been suggested that by each animal being first a male and then a female a greater percentage of eggs can be fertilized, but this supposed advantage on examination is seen to be illusory in those hermaphrodites which ripen their male and female generative products at different times, and these are by far the majority. In fact unless mutual fertilization of hermaphrodites in pairs can occur, as it may occur in the earthworm, the chances of fertilization are not any greater in an hermaphrodite than in a dioecious species. Protandric hermaphroditism therefore from this point of view is merely a violation of the principle of economy of labour and has no particular advantage that we can see. It has been already stated that in *Danalia curvata* a special apparatus of phagocytic cells is present for the sole purpose of absorbing the remains of the testes of the Cryptoniscus larva, and in a large majority of cases it was found that the testes after fixation on the host contained a large quantity of sperm which could not be of any use for the propagation of the species, and this fact certainly points to a disharmony in the sexual organization of the animal. So far then we have been unsuccessful in finding an adaptive meaning in the hermaphroditism of fixed animals, and it is difficult to suggest any other alternative. It appears on the contrary that the hermaphrodite state is one from the natural implication of which, i. e. the implication of self-fertilization, all hermaphrodites take special precautions to escape. It may be mentioned parenthetically that MAUPAS in his study of the Reproduction of Nematodes (4) was equally unable to find an adaptive meaning in the secondarily developed hermaphroditism of certain species, because in these forms he was able to prove that actually fewer eggs were fertilized than would have been the case if the normal cross-fertilization of ordinary females by males had been retained.

In Chapter 5 of this Monograph I am able to prove that a perfectly developed hermaphrodite condition may be called forth in a normally dioecious animal through the influence of the conditions of life, in this case through a fundamental alteration of the metabolic conditions effected by the presence of a parasite.

In view of this fact, and taking into consideration the extreme difficulty experienced in attempting to account for hermaphroditism as a special reproductive adaptation, we may adopt the view that the hermaphroditism of fixed animals has followed as a necessary result of the conditions of their life, and not as a special adaptation for securing the increased propagation of the species. How the state of fixation has effected this change in the reproductive system we can only vaguely guess, but it may be pointed out that fixation necessarily implies a very uniform and passive condition of life, and that it also implies a degenerative return to a simpler and less highly differentiated organization in general, and in this process the reproductive system seems to have been involved. According to this view the hermaphroditism of fixed animals is regarded as a degenerative state called into being as the result of an immobile inactive existence in which all complicated differentiation does as a matter of fact tend to be lost. Whatever may be the cause of the ordinary differentiation

into separate sexes, it is manifestly bound up in the majority of animals with widely different habits of life, so that the males and females of most species fill a different rôle in the economy of their species with regard to almost every vital function besides that of reproduction. In fixed animals which are by the fact of their fixation destined to a more or less dull routine of existence in which the vital functions have only to perform a few stereotyped duties, this elaborate differentiation of the sexes has been lost. In this manner we may look upon the hermaphroditism of fixed animals as part of the general degeneration which they have manifestly undergone in all other respects.

Without entering further here into a subject which formed the chief theme of the last chapter, I would emphasise that point of view which regards the sexual organization of every animal not merely as an adaptive means of propagation, but also as a regulation of the metabolic activities in the animal itself, irrespective of the production of a new generation. The phenomena of sex are so intimately bound up with those of assimilation, growth and differentiation, that we cannot hope to gain any complete explanation of their variations in different animals by simply regarding them as a mechanism for ensuring the production of young, while ignoring their relation to the metabolic activity of the body which exhibits them.

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Chapter 7.

Systematic guide to the genera and species of Rhizocephala, with anatomical diagnoses.

The difficulty which besets this subject is very great, because the simple structure of the adults does not offer any characteristic features by which the different species of the various genera can be sharply distinguished. The Nauplius and Cypris larvae, from which something might be hoped, do not as a matter of fact help us out: thus the Nauplius and Cypris of the so-called *Sacculina neglecta*, parasitic on *Inachus scorpio*, are, as far as I can make out, identical in structure with those of *Sacculina carcini*, parasitic on *Carcinus maenas*, and if we unite these species together as one, the rest of the so-called species of *Sacculina* must be given up. The shape of the adult body has been commonly used as a specific criterion, but this is greatly influenced by the shape of the host's body which varies with sex and age.

Another obvious criterion is the fact that the Rhizocephala infest special hosts, and the question arises whether any absolutely general rule can be laid down that each species of parasite only infests a single species as host, and never by any chance infests an host of a different species. Of course by artificially applying this rule, the systematic definition of the Rhizocephala would be immensely simplified though greatly elongated, since it would be only necessary to invent a new name for each parasite found on a distinct species of host. But it is easy to convince oneself that this method would be most highly artificial, because it would involve giving several specific names to forms which in all stages of their existence are quite inseparable by any structural detail. To take an instance, the species of *Peltogaster* which is fairly common at Naples, *P. curvatus* (Kossmann), is found occasionally on *Eupagurus prideauxii* (Leach) and much more commonly on *E. meticulosus* (Roux). I can find no means of distinguishing the parasites on these two hosts, and since they occur together on the same ground there can be little doubt that the specimens found occasionally on *E. prideauxii* are really of the same species as those commonly found on *E. meticulosus*. It is curious that the parasite should be more frequent on *E. meticulosus* because this hermit-crab is much rarer

than *E. prideauxii*. It is to be observed, however, that the shells in which *E. meticulosus* lives are very often destitute of an anenome, and never have such large anenomes as *E. prideauxii*; and it is probable that this would favour the fixation of the Cypris larva on *E. meticulosus*. But perhaps there is a more recondite reason.

As a further instance of one species of *Peltogaster* infesting more than one species of host, *P. sulcatus* (Lillj.) may be mentioned which is found at Naples indifferently on *E. prideauxii* and *E. meticulosus*; nor can I distinguish the Neapolitan forms from those found on various Norwegian Pagurids.

From these considerations and from many more that could be given, the rigid application of the rule that a special species of parasite is always attached to a special species of host is impossible.

The method I have followed in dealing with the numerous so-called species of *Sacculina*, will, I expect, be adversely criticised by many systematists, but after several attempts to discern constant specific differences between several forms that have been given distinct names, I have come to the conclusion that all the forms of *Sacculina* are only races of one true species, which may be called *Sacculina carcini* (Thompson). The present state of the systematics of this genus is most unsatisfactory; the majority of so-called species are simply characterized by the host on which they were found, or at most the external shape of the body is described, an utterly worthless character which varies with the age of the parasite and the nature, age, and sex of the host. The only attempt at a diagnosis of certain forms is made by KOSSMANN (**11**) who combines an use of a number of characters, such as the rugosity of the mantle, and the shape of the body, which I believe to be quite worthless, with a few anatomical differences scattered here and there among the species, which, even when they are not purely imaginary, always betray a lack of systematic tact. Thus he separates *Sacculina hians* from other species, largely on the ground that it possesses a tube in the visceral mass running from the ring of attachment and opening in the mantle-cavity, which he takes for the representative of the gut; a character, which if it were not imaginary, would suffice to remove *Sacculina hians*, not only from the genus *Sacculina*, but from the suborder Rhizocephala. From KOSSMANN's figure and description I suppose his *Sacculina hians* to be a form of *Heterosaccus*, and the tube which he took for the gut is merely a lacunar space underneath the ring of attachment, which needless to say does not open into the mantle-cavity and has nothing at all to do with a gut. Another species, *Sacculina papilio*, on his own showing, is manifestly a species of *Lernaeodiscus*: and although KOSSMANN has an inkling of this in supposing it to be an intermediate form between *Sacculina* and *Lernaeodiscus*, an examination of its anatomy would have shown the impossibility of retaining it in the genus *Sacculina*. The exposition of these grave errors is sufficient to throw doubt on the whole of KOSSMANN's systematic work.

I have examined the microscopic characters of the mantle, both externally and internally, and of the retinacula in the Neapolitan forms of *Sacculina*, without being able to find constant differences of specific value.

Sacculina is distributed all over the world, and the systematist in Norway who finds a small specimen on a northern Spider-crab may smile when he is asked to believe that it is the same species as a large form on the Mediterranean *Eriphia* or on a tropical crab, but he must remember that the distribution of *Sacculina* from the Arctic circle to the Tropics is perfectly continuous into various depths, and that intermediate forms can be found between all shapes and sizes. I do not however wish to dogmatise and to hold rigidly to the theory that there is only one species of *Sacculina*, but I do wish to make a practical protest against the method that has hitherto been followed, namely that of picking up a specimen of *Sacculina* on a new host and giving it a new name without attempting to point out characters of specific value that separate it from other forms. This otiose practise is not only idle but positively mischievous, because it has led in a number of cases to the neglect of real anatomical characters and to the confusion of specimens of *Sacculina* with those of *Lernaeodiscus* and other genera, which resemble *Sacculina* only in outward appearance.

That there may exist distinct races of *Sacculina* adapted to live as parasites only on particular species of Brachyura is highly probable, but until a scheme of classification based on anatomical distinctions is proposed, it appears to me idle to give separate names to these races.

In dealing with the genus *Sacculina* I have reproduced for purposes of reference the names that have been given to the parasites of various crabs.

The genera *Thompsonia*, *Apeltes* and *Thylacoplethus* I have been unable to examine myself, and I remain in doubt as to many of their characters.

Order: **Rhizocephala** (MÜLLER **6**).
(= **Suctoria** [LILLJEBORG **4**] = **Kentrogonidae** [DELAGE **16**].)

Diagnosis. Degenerate Cirripedes, parasitic on Crustacea, passing through a Nauplius and Cypris stage: fixation on the host occurring at the end of Cypris stage. The Cypris assumes the Kentrogon stage and infests the host's body with a little mass of undifferentiated embryonic cells, which now go through a period of endoparasitic life, multiplying to form a central tumour and a root system. The part of the adult body which becomes external is differentiated from the central tumour, while the roots remain inside the host and supply the parasite with nourishment.

The evaginated, external part of the body consists of a mantle, surrounding a visceral mass, the two being joined along the dorsal surface by a mesentery. The nervous system is reduced to a single ganglion, which lies dorsally and anteriorly. The body is fixed to the host by a peduncle and ring of attachment, homologous to the stalk of the Cirripedia. Alimentary canal degenerates immediately after formation by invagination in the embryo. Adult, hermaphrodite or female (*Sylon*), complemental males degenerate or perhaps functional (*Duplorbis*).

Genus **Peltogaster** (RATHKE [2]).

Diagnosis. External body of adult red or purple.

Roots green, compact, non-ramifying and without lagenae.

Mantle and visceral mass highly muscular.

Mantle-opening situated anteriorly relatively to host. Mesentery fleshy, running in long axis of body on surface of fixation, parallel to long axis of host.

Body irregularly cylindrical, uncompressed.

Ring of attachment pierces the middle of mesentery.

Colleteric glands paired and simple.

Testes paired and showing partial degeneration.

Genital openings of morphologically left side in advance of those on right.

Nauplius with much elongated frontal horns.

Endoparasitic development without active migration of central tumour and without formation of perisomatic space.

Larval males not developing beyond Cypris stage. Parasitic on Decapoda Anomala.

P. paguri (RATHKE [2]). Hosts, *Eupagurus bernhardus*, also *Pagurus pubescens, chiracanthus* and *cuanensis* according to LILLJEBORG, from Danish, Norwegian and Greenlandic seas.

Body bright red and roots conspicuous green, mantle being constricted by circular muscles. Nauplius without pigment in eye. Solitary or in couples.

P. curvatus (KOSSMANN [12]). Hosts, *Eupagurus prideauxii* (Leach) and *E. meticulosus* (Roux) from Naples.

Anatomically identical with *P. paguri*, but never attains to the size of the largest specimens of *P. paguri*.

P. philippinensis (KOSSMANN [11]), host not named, from Philippine Islands, and *P. rodriguezii* (FRAISSE [14]) on *Clibanarius misanthropus* (Risso) from Balearic Islands, are undistinguishable by any characters from *P. paguri*.

P. purpureus (MÜLLER [6]). Host not named, from Brazil. Distinguished only by purple colour of external body. Solitary.

P. sulcatus (LILLJEBORG [4]). Hosts, *Pagurus cuanensis* and *chiracanthus* from Danish and Norwegian seas, and *Ligella gracilis* and *affinis* from Valparaiso. *P. microstoma* (Lillj.), on *P. chiracanthus* and *laevis* from Norway. *P. longissimus* (KOSSMANN [12]) on *E. prideauxii* and *E. meticulosus* (mihi) from Naples. *P. albidus* (HESSE [8]), host not named, from French coasts, *P. socialis* (MÜLLER [6]) on *Pagurus* sp.?, from Brazil.

Body pale pink, roots almost colourless. Mantle unconstricted by circular muscles, body very long and cylindrical.

Nauplius with conspicuous pigment in eye. Gregarious and never solitary.

Remarks. Among all the various names that have been given only two represent true species to a certainty, namely *P. paguri* and *P. sulcatus*. It is interesting to note that both these species have an enormous distribution, from the Arctic circle to Brazil. None are known from great depths.

The anatomy and the biology of the Neapolitan race of *P. curvatus* has been the subject of so many of the observations in this book that I need not go further into it here.

Genus **Parthenopea** (Kossmann [12]).

Diagnosis.   External body of adult red.

Roots green, widely distributed and branching, without lagenae.

Mantle and visceral mass muscular.

Mantle-opening situated laterally, relatively to host.

Mesentery rather thick, short, running in the actual shortest axis of the body and vertical to long axis of host.

Body roughly spherical, slightly compressed antero-posteriorly.

Ring of attachment situated at posterior end of mesentery.

Colleteric glands paired, slightly branched.

Testes paired, showing slight partial degeneration.

Nauplius without frontal horns (Kossmann).

Endoparasitic development unknown.

Larval males not observed.

Parasitic on *Callianassa* (and *Gebia*).   Solitary.

P. subterranea (Kossmann [12]). Hosts, *Callianassa subterranea* and according to Giard (20) *Gebia stellata*, Naples. Since this is the only species, the diagnosis for the genus gives the characters of the species.

Remarks.   Dr. Lo Bianco informs me that this parasite was formerly exceedingly common at Naples, but that it is now becoming gradually extinct. He has however been able to furnish me with several specimens.

Genus **Sacculina** (Thompson [1]).

Diagnosis.   External body of adult yellow when Nauplius larvae in brood-pouch are immature, purplish when they are mature.

Roots yellow, very widely distributed even into the appendages and highly branching, with lagenae.   (For lagenae see Note on p. 113.)

Mantle and visceral mass muscular.

Mantle-opening situated posteriorly, relatively to host.

Mesentery very thin, running in a curve on the right side of the parasite relatively to the host, horizontally to long axis of host.

Body much compressed laterally.

Ring of attachment situated at posterior end of mesentery.

Colleteric glands paired, highly branched.

Egg tubes attached to mantle by retinacula (see Note on p. 113).

Testes paired, showing degenerative signs.

Nauplius with somewhat elongated frontal horns.

Endoparasitic development with active migration of central tumour and with formation of perisomatic space.

Larval males of common occurrence, not developing beyond Cypris stage.

Parasitic on Decapoda Brachyura.

S. carcini (Thompson [1]). Host of type specimens *Carcinus maenas*, from North Sea, St. George's Channel, Plymouth, Roscoff, Danish and Norwegian waters.

Characters of species those of genus.

Remarks. I append a list of all the hosts of *S. carcini* known to me, and the names given to the parasites, arranged according to geographical distribution.

North Sea, Channel and Bay of Biscay.

Host	Name of Parasite	Locality
Carcinus maenas	*S. carcini* (Thomp.)	Littoral, widely distributed, very common at Roscoff
Platycarcinus pagurus	*S. triangulus* (Anderson [7])	Firth of Forth, Bretagne
Portunus holsatus	*S. andersoni* (Giard [24])	Wimereux
P. pusillus		Devonshire
P. marmoreus	*S. belli* (Giard [24])	Wimereux
Platyonychus latipes	*S. betencourti* (Giard [24])	Wimereux
Herbstia nodosa	*S. herbstiae* (Hesse [8])	France
Pisa gibsii	*S. gibsii* (Hesse [8])	France
Stenorhynchus phalangium	*S. fraissei* (Giard [19])	Concarneau
	S. phalangi (Hoek [13])	Heligoland
Hyas coarctatus		Danish waters, very common, 10½ fthms.
		Danish waters
H. aranea	*S. inflata* (Leuckart [5])	Heligoland
Inachus dorsettensis		Danish waters, 9½ fthms.
Lispognathus thompsoni (Norm.)		North Sea, Lat. 49°25 N., 12°20 W. 1180—1275 meters

Mediterranean.

Host	Name of Parasite	Locality
Portunus corrugatus	*S. corrugatus* (GIARD)	Naples, 15 meters
P. pusillus		Naples, 15 meters
Pachygrapsus marmoratus	*S. benedeni* (KOSSMANN [12])	Naples, Littoral
Pisa armata	*S. pisae* (HOEK [13])	Naples, 25—30 meters
Gonoplax rhomboides		Naples, 100 meters or more
Eriphia spinifrons		Naples, Littoral
Inachus scorpio	*S. neglecta* (FRAISSE [14])	Naples, 15 meters
Stenorhynchus phalangium		Naples, 15 meters
Heterograpsus lucasii		Spain

Red Sea.

Host	Name of Parasite	Locality
Xantho exaratus	(KOSSMANN [11])	
Actaea granulata	(Crossland)	Suez, 5 fthms.
Chlorodopsis areolata	(Crossland)	Shabuk, stony reef edge

Oriental Waters.

Host	Name of Parasite	Locality
Eriphia laevimana	*S. rotundata* (MIERS [15])	Malaysia
Nectocarcinus integrifrons	(HASWELL [23])	Australia
Thalamita sima	(HASWELL [23])	Australia
Thalamita sp.		Siam
Melissa fragaria	(GERSTAECKER, BRONN's K. & O.	China
Neptunus sp.	Bd. 5 p. 566)	Siam
Chlorodius niger		Trincomalee

Philippine Islands (by KOSSMANN [11]).

Host	Name of Parasite	Locality
Atergatis floridus	*S. corculum*	
Portunus sp.	*S. dentata*	
Lambrus turriger	*S. bursa pastoris*	
Pisa triquetra	*S. pilosa*	
Cancer savignyi	*S. crucifera*	
(*Porcellana* sp.)	(*S. papilio*)	(see *Lernaeodiscus papilio*)

Host	Name of Parasite	Locality
Chlorodius areolatus	S. *pomum*	
Macrophthalmus sp.	S. *alas*	
Grapsus strigosus	S. *flexuosa*	
Myra fugax	S. *captiva*	
Lupa sp.	S. *carinata*	
Pilumnus ursulus	S. *cartieri*	
Lupa sp.	S. *bipunctata*	
Cancer sp.	S. *exarcuata*	
Thalamita sp.	S. *margaritifera*	
(*Thalamita* sp.)	(S. *hians*)	(see *Heterosaccus hians*)
Lambrus haplonotus	S. *cavolinii*	

Gulf of Mexico — West Indies.

Host	Name of Parasite	Locality
Panopoeus harbitii	S. *panopoei* (GISSLER [17])	Tampa, G. of Mexico.
Pilumnus sp.		Venezuela and West Indies.

Remarks. I need not add here any anatomical remarks, since the parasite of *Carcinus maenas* has been minutely treated by DELAGE, and that of *Inachus scorpio* forms the subject of many observations in this book.

As far as is known *Sacculina* infests about 50 different species of Brachyura, scattered all over the world and at all temperatures. It is not however known to enter the arctic circle. The only form coming from really deep water is the parasite of *Lispognathus Thompsoni* (Norman) (1180—1275 meters) which was shown to me by Dr. H. J. HANSEN in Kjöbenhavn. Otherwise the parasites may infest truly littoral crabs, or else in shallow water up to 100 meters.

Note. In the diagnosis of the genus *Sacculina*, the lagenae of the roots are mentioned and also the retinacula which attach the egg-tubes to the mantle. DELAGE (16 pp. 450 and 529) has described these organs and to his description I have nothing to add. With regard to the function of the lagenae I have been unable to establish their excretory nature. A root of *Sacculina neglecta* with a lagena is figured on Plate 2 fig. 1.

Genus **Heterosaccus.**

Diagnosis. Similar to *Sacculina*, save that the mesentery is confined to the surface of the visceral mass immediately round the ring of attachment, and does not stretch to the mantle opening.

Mantle opening, in consequence, widely gaping.

Parasitic on Brachyura. Solitary.

H. hians. Host, *Charybdis (Goniohellenus) ornata* (M. Edw.), from Suez Canal 5 fathoms (CROSSLAND).

Remarks. I think it probable that KOSSMANN's species *Sacculina hians* parasitic on *Thalamita* sp. from the Philippine Islands belongs here.

Three specimens were sent to me by Mr. CROSSLAND from the Red Sea, two of them being fixed on the same host.

Although the structure is so similar to that of *Sacculina*, I am bound to give generic value to a distinct difference in the disposition of the mesentery.

I was unable to determine the position of the nervous ganglion.

Genus **Lernaeodiscus** (MÜLLER [6]).

(See Plate 7 figs. 31, 33, 34.)

Diagnosis. External body of adult yellow.

Roots yellow, widely distributed and ramifying, without lagenae.

Mantle and visceral mass muscular, mantle expanded laterally into well-marked lappets (Plate 7 fig. 31).

Mantle opening situated posteriorly and mesially relatively to host (Plate 7 fig. 33).

Mesentery very broad and long, running in an hinge round an immense dorsal curvature, long axis in same direction as long axis of host (Plate 7 figs. 33 and 34).

Body compressed antero-posteriorly, dorsal surface being much elongated and curved.

Ring of attachment pierces middle of mesentery, at angle of dorsal curvature.

Colleteric glands paired and branched.

Testes paired, showing degenerative signs.

Genital openings of morphologically left side situated on anterior hinge of mesentery, those of right side on posterior hinge (Plate 7 figs. 33 and 34).

Nauplius with somewhat elongated and curved frontal horns.

Endoparasitic development unknown.

Larval males not observed.

Parasitic on symmetrical Decapoda Anomura.

L. porcellanae (MÜLLER [6]). Host, *Porcellana* sp. from Brazil. Visceral mass purplish; lappets of mantle very conspicuous and indented.

L. galatheae. Hosts, *Galathea dispersa* at Naples, *Galathea intermedia* from Norway. Visceral mass yellow; lappets of mantle inconspicuous and irregular. Anterior hinge of mesentery not very wide.

L. strigosae. Host, *Galathea strigosa* from Naples. Visceral mass yellow; lappets of mantle inconspicuous. Anterior hinge of mesentery very wide. Much larger than *L. galatheae.*

L. papilio (= Kossmann's [11] *Sacculina papilio*). Host, *Porcellana* sp., Philippine Islands. Impossible to diagnose from description, but resembles *L. galatheae*, and certainly belongs to this genus.

Remarks. Relying on the position of the mesentery, the lateral expansions of the mantle, and the nature of the host, I have placed all these forms in Müller's genus *Lernaeo-discus*, but the main features of the anatomy from which the diagnosis of the genus is made, are drawn from a careful study of *L. galatheae* alone, which is fairly common at Naples.

Müller in his description of *L. porcellanae* gives no clue to the exact position of the genital openings on which so much depends.

Genus **Triangulus.**

Diagnosis. Resembles *Lernaeodiscus*, save that the anterior hinge of the mesentery is absent, and the ring of attachment appears to have shifted posteriorly into the middle of the posterior hinge.

The genital openings have concomitantly shifted, and are situated in an highly asymmetrical position at the anterior edge of the mesentery.

Mantle opening often situated asymmetrically relatively to long axis of host.

Parasitic on symmetrical Decapoda Anomura.

T. munidae. Hosts, *Munida bamffica* from Norway, shallow water, and *Munida tenuimana*, about 500 fathoms.

Diagnosis of species that of genus.

Remarks. I have only been able to examine macroscopically two specimens, so that I could not observe the nervous system, nor the minute characters of the genital system.

The parasite is plainly closely allied to *Lernaeo-discus*, but, as in the case of *Heterosaccus* and *Sacculina*, I must treat the important difference in the mesentery as of generic value. I insert here a diagram to illustrate what I conceive to be the anatomical relations of the different parts of the body.

The parasite is viewed by transparency from the anterior dorsal face, i. e. the face in *Lernaeodiscus* which carries the anterior hinge of the mesentery. Consequently we only see the mesentery (*mes*) at its free anterior edge here, the rest being on the under surface of the visceral mass (*visc*). The ring of attachment (*ring*) is shown by transparency in the middle of the mesentery on the under or morphologically posterior surface of the visceral mass.

Text fig. 23.

15*
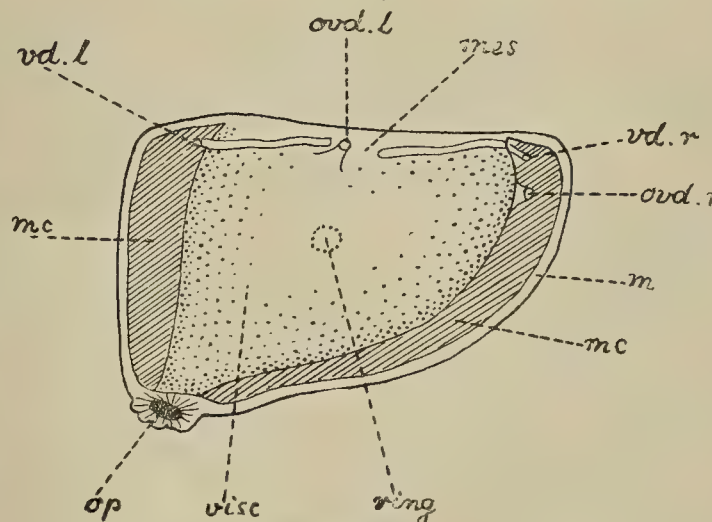
The genital openings of each side are distributed asymmetrically about the anterior free edge of the mesentery, those on the left side (*vd.l* and *ovd.l*) being on the morphologically anterior face of the visceral mass, those of the right side (*vd.r* and *ovd.r*) being on the posterior face, i. e. the face hidden in the diagram.

Genus **Sylon** (Kröyer [3]).

(See Plate 8 figs. 1—4.)

Diagnosis. External body of adult yellow.

Roots yellow, widely distributed, branching, without lagenae.

Mantle and visceral mass muscular, mantle smooth.

Mantle opening paired, situated anteriorly relatively to host (Plate 8 fig. 2).

Mesentery rather narrow, and very short, running mesially and in the same axis as long axis of host (Plate 8 fig. 2).

Body egg-shaped, dorsal surface greatly shortened and ventral surface enlarged with highly marked ventral curvature.

Ring of attachment situated at posterior end of mesentery.

Colleteric gland median, unpaired, and highly branched (Plate 8 fig. 3).

Testes absent.

Nauplius not known.

Endoparasitic development unknown.

Larval males unknown.

Parasitic on Decapoda Macrura.

S. hippolytes (Kröyer). Characters of species those of genus. I append a list of hosts, names given to the parasites, and the names of the observers, believing, however, that no anatomical distinctions exist to justify the creation of more than one species.

Host	Name of Parasite	Observer
Hippolyte pusiola	*S. hippolytis* (Kröyer) = *S. Schneideri* (Hoek [21]) Norway	Schneider, Weber, Hoek Smith
Pandalus brevirostris	*S. pandali* (Kröyer) Norway	M. Sars
Hippolyte incerta	Norway	Hoek
H. polaris	*S. danielsseni* (Giard [22]) Norway	Sabine
H. securifrons	*S. sarsi* (Giard [22]) Norway and Greenland	M. Sars
H. spinus	*S. Challengeri* (Hoek [21]) Nova Scotia and Greenland	Hoek and Smith
Hymenodora glacialis	*S. hymenodorae* (Sars [18])	G. Sars
Hippolyte fabricii	Frederikshav	Smith
Hippolyte brevirostris		
Pandalus Danae	Puget Sound	Calman (25)
Sclerocrangon munitus		

Remarks. *Sylon* appears to be a characteristically northern genus, its head quarters being apparently in the Norwegian and Greenlandic Seas, while extending south as far as Puget Sound on the American coast.

This genus has been studied by MICHAEL SARS (**10**) and later by HOEK (**21**). SARS wrote before the anatomy of the Rhizocephala was well understood, and his views are very incorrect, as he takes the eggs in the mantle cavity for the ovary, the whole visceral mass for a testis, the colleteric gland for the apex of the testis, and the two mantle openings viewed from inside as the openings of the vasa deferentia.

HOEK's views are far more correct, and I disagree with only one part of his description, though that is of fundamental importance, and relates to the presence or absence of a testis. I judge from HOEK's statement that he himself is not over confident of the nature of the body which he figures as a testis, for he says: "only in one of the specimens did I observe anything that could be considered as a testis" p. 926, and I must confess that his figure of this organ does not resemble the testis of any other Rhizocephala.

I have prepared serial sections through the visceral mass of four specimens of *Sylon*, kindly put at my disposal by Dr. H. J. HANSEN of Kjöbenhavn and by Professor D'ARCY THOMPSON of Dublin; two of these specimens were in excellent preservation and gave a perfect series of sections, while the other two were sufficiently good to serve as valuable checks. In none of them was a trace of testis to be observed, and I could hardly miss this organ now after studying it in the most various forms of Rhizocephala both by dissection and sections for about two years. I am therefore confident that *Sylon* is structurally a female and not a hermaphrodite and I feel justified in drawing the conclusions on this head given in Chapter 2 of this work. I would also say a word on the nervous system of this genus; the ganglion, situated normally near the mesentery and in close proximity to the mantle openings, is very much larger proportionately to the rest of the body, and the nuclei of the cells preserve their staining capacity far more than in other Rhizocephala. (See Plate 8 fig. 4 *gn.*)

I have been able to confirm both by observations on the whole animal and by sections the presence of two small mantle openings, as shown in Plate 8 fig. 4, in place of the unpaired opening usually found in Rhizocephala.

Genus **Clistosaccus** (LILLJEBORG [**4**]).
(See Plate 8 figs. 5—8.)

Diagnosis.   External body of adult red.

Roots colourless (?), compact.

Mantle and visceral mass highly muscular, mantle smooth and unconstricted.

Mantle opening absent.

Mesentery very thin, running in long axis of body on surface of fixation, parallel to long axis of host.

Body irregularly oblong, uncompressed.

Ring of attachment pierces mesentery near the anterior end, is very wide and disc-like. (Plate 8 fig. 5.)

Colleteric gland median, unpaired, highly branched. (Plate 8 fig. 6.)

Testis median, unpaired, showing no signs of degeneration. (Plate 8 figs. 7—8.)

Nauplius unknown.

Endoparasitic development unknown.

Larval males unknown.

Parasitic on Decapoda Anomala (Paguridae).

C. paguri (LILLJEBORG [4]). Hosts, *Eupagurus bernhardus* from Bohuslän by LILLJEBORG, *E. bernhardus* from Kattegat and *E. pubescens* from Boreal Seas seen by myself at Kjöbenhavn.

Remarks. Through the kindness of Dr. H. J. HANSEN I was enabled to examine several specimens of this hitherto almost unknown genus, and to satisfy myself as to the chief points in its anatomy. The parasite has the appearance of a *Peltogaster*, being fixed in a similar position on the Hermit-Crab's abdomen; it is usually solitary, but two or three specimens may be present on one host. Its internal anatomy however differs greatly from that of *Peltogaster*, as shown by the diagnosis given for the genus.

The most interesting feature in its structure is the presence of a single testis, enormously developed and showing no signs of the degenerative hypertrophy of its cells as in all other Rhizocephala. I have already called attention to this feature in Chapter 2 and referred the reader to the transverse sections on Plate 8 figs. 7 and 8.

The colleteric gland (Plate 8 figs. 5 and 6) is situated at the anterior end of the visceral mass.

Owing perhaps to the imperfection of my series of sections towards the extreme anterior edge of the visceral mass I could not observe the nervous system.

I also did not observe an opening of the testes into the mantle cavity, and it appears to me more than probable that the eggs are fertilized in the ovary before passing through the colleteric gland.

The absence of a mantle opening makes it probable that only one brood of eggs is produced, as the escape of the first brood must be effected by a rupture of the body wall.

Genera of Uncertain Position.
Genus **Duplorbis.**
(See Plate 8 figs. 9—19.)

Provisionary Diagnosis. External body of adult red.

Roots apparently absent; attachment to host by means of a tube running in the middle line of the mesentery and opening into mantle cavity.

Mantle and visceral mass not muscular, mantle smooth.

Mantle opening in adult absent.

Mesentery rather broad, running in shortest axis of body, irregularly and obliquely to the long axis of host.

Body cylindrical, immensely laterally expanded so that the axis running from right to left at right angles to the morphological long axis is the actual long axis of the body.

Ring of attachment at posterior end of mesentery.

Colleteric glands paired, forming two conspicuous discs on the surface of the visceral mass.

Nauplius unknown.

Endoparasitic development unknown.

Bodies of doubtful meaning but possibly complemental males, fully developed and containing spermatozoa, may be present in the mantle cavity.

Parasitic on Isopoda (Anthuridae).

D. calathurae. Host, *Calathura brachiata* from Greenland, Forsblads Fjord, 50 fathoms. Diagnosis of species that of genus.

The discovery of this highly interesting but in some respects problematical genus is due to Dr. H. J. HANSEN of Kjöbenhavn who noticed the three parasites on the Isopod and, believing them to belong to the Rhizocephala, put two out of the three specimens at my disposal. The investigation of these two specimens both by dissection and serial sections has left no doubt in my mind that we are dealing with an aberrant and probably primitive type of Rhizocephala, but the complete justification of this belief can only be reached by a study of the developmental phases through which the animal passes.

The three specimens found by Dr. HANSEN and figured on Plate 8 fig. 9 were attached to the ventral surface of their host and lay comfortably protected by the folds of the marsupium.

The reasons for considering this species a member of the Rhizocephala are as follows — (1) It is clearly a Crustacean, from the presence of chitin lining all the epithelial surfaces. (2) It must be a Cirripede owing to the character of the spermatozoa (Plate 8 fig. 19), which are filamentous bodies staining along their whole length and identical in all respects with the spermatozoa of the Rhizocephala. (3) The numerous special resemblances to the Rhizocephala besides the fact of its infecting a Crustacean are found in the presence of a visceral mass containing the ovaries and surrounded by a mantle; the nervous system reduced to a single ganglion and situated near the anterior extremity of the mesentery, the presence of two oviducts modified into colleteric glands, the character of the ova which in all their stages are identical in appearance with those of the Rhizocephala. The only fundamental difference to the Rhizocephala is found in the apparent absence of a root system and the method of fixation

by means of a tube opening at the point of fixation into the host and running through the mesentery in the middle line to open into the mantle cavity (*mes.can.* Plate 8 figs. 10, 12, 16, 17 and Text figure 24). I regard this tube which is evidently of purely ectodermal origin and is lined throughout with chitin as representing the invaginated stalk of an ordinary Cirripede, and its probable method of formation and its bearing on the general problem of Rhizocephalan development has been considered at length on pp. 61 and 62.

I will now give a description of the anatomy of *Duplorbis* which with the help of the figures on Plate 8 (figs. 9—19) and of the Text fig. 24 may lay a basis for a more complete investigation of this important genus.

In an undissected specimen, represented in two views in Figs. 10 and 11 Plate 8, we can recognize the following parts, firstly, the visceral mass (*visc*) lying enveloped by the mantle (*m*), secondly, a linear streak (*mes.can*) can be observed starting from the stalk of attachment (*st*) and running about half way round the body in its shortest circumference. This is the mesenteric canal. In the anterior region where the mesenteric canal ceases, shown in Figure 11, two large discs can be seen lying within the mantle on the visceral mass, these are the two colleteric glands (*coll*). The position of the mesentery and the fact that the nervous ganglion (*gn* Text fig. 24) is situated between the two colleteric glands, just in front of the opening of the mesenteric canal into the mantle cavity, give us the clue to the orientation of the body. The morphological antero-posterior axis runs in the actual shortest axis of the body, i. e. through the mesenteric canal, the stalk being at the posterior pole; and the surface carrying the mesenteric canal is, of course, the dorsal surface. The body is therefore immensely laterally expanded.

The gross anatomy can be studied by means of the ideal horizontal section given in Text fig. 24.

The red outlines here indicate the chitinous investments. We see that at the ring or stalk the external chitinous investment of the mantle and the external epithelium are invaginated and become continuous with the lining of the mesenteric canal (*mes.can*) which opens into the mantle cavity (*mc*) just behind the nervous ganglion (*gn*), and at the anterior edge of the mesentery (*mes*).

The two oviducts or colleteric glands (*ovd.l.*, *ovd.r.*) can be seen on either side of the ganglion, and at either end of the mantle cavity the two bodies are shown described in Chapter 2, which contain spermatozoa and are either complemental males or else very peculiarly placed testes (♂).

The mesentery (*mes*) represented in the Text fig. 24 by the slanting lines is laterally expanded, extending posteriorly to the region of the stalk of attachment and anteriorly to the opening of the mesenteric canal which runs in its substance.

Passing to the minuter structure, the sections on Plate 8 figs. 12 and 14 instruct us that the mantle (*m*) consists merely of an epithelium which secretes a chitinous membrane, muscles and connective tissue being entirely absent. The surface of the visceral mass is

similarly constituted as shown in figs. 12 and 13. This entire absence of muscles constitutes an important difference to the other Rhizocephala.

We must next remark the great poverty of lacunar and connective tissue in the visceral mass, comparatively to other Rhizocephala. That part of the visceral mass which is not occupied by the ovaries contains merely a coagulated fluid (fig. 12 *visc*). The only position in which lacunar tissue is well developed is in the mesentery immediately surrounding the

Text fig. 24.
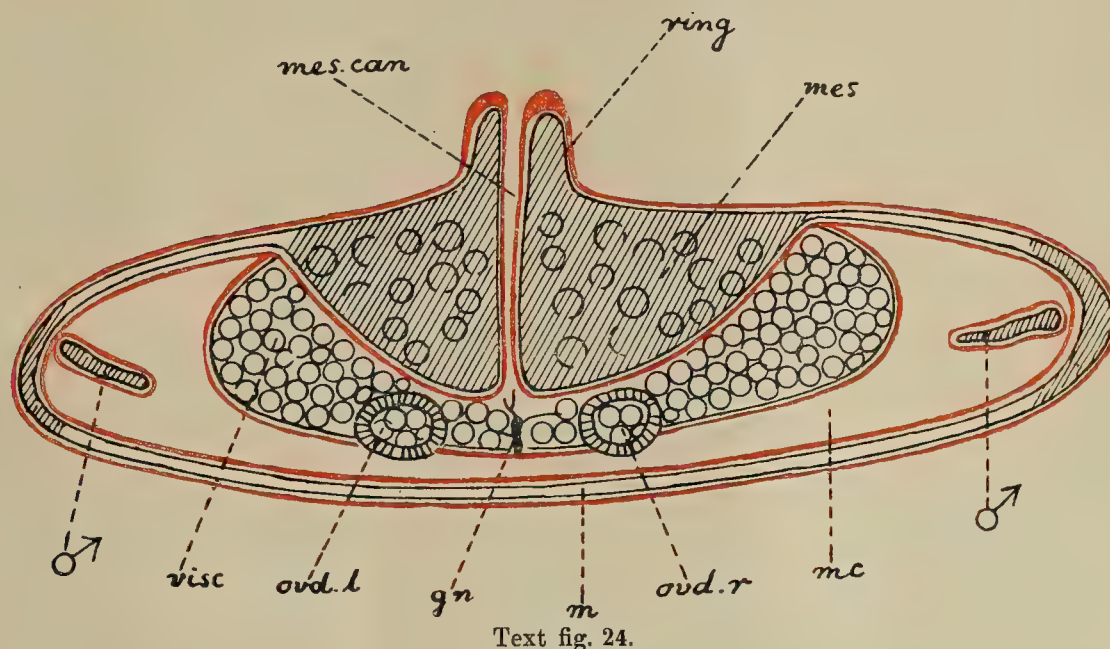
mesenteric canal (figs. 12, 15, 16 and 17 *lac*). I take this peculiar restriction of lacunar tissue to be connected with the absence of a root system and the method of nourishment by the mesenteric canal.

The structure of the mesenteric canal is indicated in figs. 12, 15, 16, 17 *mes.can.* It is lined internally by a layer of chitin continuous through the whole canal, passing posteriorly at the stalk into the external chitinous investment of the body and anteriorly into the internal chitinous investment of the mantle cavity. Externally to the chitin is an ectodermal epithelium of columnar cells, shown in longitudinal section in fig. 15, and in transverse section in fig. 16. Surrounding this epithelium is the lacunar tissue (*lac*). The posterior opening of the mesenteric canal at the end of the stalk is shown in transverse section in fig. 17.

The minute structure of the ovaries which are two in number is exactly similar to that in other Rhizocephala (fig. 13 *ov.*); we have an ovarian epithelium externally and within a large number of eggs in various stages of development.

The colleteric glands have the histological character shown in fig. 13 *coll*; the cells are highly columnar and the nuclei have their chromatin dispersed in granules. They do not differ greatly from the simple colleteric glands of such a genus as *Peltogaster*, save in their position as external discs on the surface of the visceral mass.

The nervous ganglion (fig. 12 *gn*) is large and well developed, the nuclei staining rather conspicuously as in *Sylon*.

The two bodies which I interpret as possibly complemental males have been minutely considered in Chapter 2 pp. 31, 32. Figs. 14, 18 and 19 on Plate 13 refer to them.

Genus **Apeltes** (LILLJEBORG [4]).

LILLJEBORG founds this genus for a single specimen taken on *Eupagurus bernhardus* from Bohuslän. It resembles *Clistosaccus* in its large discoidal ring of attachment and in the apparent possession of a single testis which has however two vasa deferentia. The mantle moreover has an opening anteriorly, and also according to the description a posterior opening.

The nature and position of this parasite can hardly be correctly adjudged at present.

Genus **Thompsonia** (KOSSMANN [11]).

KOSSMANN has formed this genus for a parasite found by SEMPER attached to the leg of a *Melia tesselata* from Aibukil, Palaos. The only characters given are the great length of the peduncle of attachment and the presence in the mantle cavity of larvae in the Cypris stage. The latter character is very interesting and is confirmed by SEMPER himself who gives a figure of the Cypris.

Further investigation of this genus is much needed.

Genus **Thylacoplethus** (COUTIÈRE [26]).

This is an highly interesting genus found gregariously, about an hundred on each host, upon specimens of *Alpheus* from the Australasian seas.

The root system is described as not extending far into the tissues of the hosts; but since no mention is made either of a mesentery or of a testis in COUTIÈRE's description it is impossible to judge of the affinities of this genus.

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Explanation of Plates.

Plate 1.

Parasites and hosts.

All figures natural size.

Fig. 1. Low male of *Inachus scorpio*. Ventral view.

Fig. 2. Female of *Inachus scorpio*. Ventral view.

Fig. 3. Male of *Inachus scorpio* with a *Sacculina neglecta* on it. The abdomen and chelae of the host are intermediate in character between those of an ordinary male and female. Ventral view.

Fig. 4. Male of *Inachus scorpio*, carrying on its abdomen two specimens of *Danalia curvata*, and a small *Sacculina neglecta* (dark yellow). Ventral view.

Fig. 5. Male of *Pachygrapsus marmoratus* with *Sacculina benedeni*. The abdomen of host is intermediate between male and female in its dimensions. Ventral view.

Fig. 6. Female of *Eriphia spinifrons* with *Sacculina eriphiae*. The Sacculina assumes a purplish tinge owing to the brood of larvae being ready to hatch out. Ventral view.

Fig. 7. *Callianassa subterranea* with *Parthenopea subterranea* on its abdomen. The furrow shown on the parasite indicates the position of the mesentery. Viewed from left side.

Fig. 8. *Eupagurus prideauxii* with *Peltogaster curvatus*. The green colouring of the crab's abdomen is due to the roots of the parasite shining through. From left side.

Fig. 9. *Eupagurus meticulosus* with specimens of *Peltogaster socialis* on its abdomen. From left side.

Pl. 1.

Plate 2.

Anelasma and *Sacculina*.

b.c brood cavity. *ch* chitin. *ch.pd* chitin of peduncle. *ch.pl* chitinous plug of vas deferens. *cn* connective tissue sheath of testes. *d* hypertrophied germinal cells. d^2 Later stages in degeneration of *d*. *ec* ectoderm. *ep* epithelium. *gm* germinal epithelium. *l* lumen of testis. *lag* lagena. *lac* lacunar tissue. *musc* muscle. *ov* ovary. *ov.deg* degenerate ova. *pigm* pigment. *r* root. *s* spermatozoa. *sp* spermatocytes. *t* testis. *vd* vas deferens. *vd.op* opening of vas deferens. ♂ complemental males.

Fig. 1. Section through a piece of ovary of *Inachus scorpio*, into which a root of *Sacculina* has penetrated. The root exhibits a lagena (*lag*) at its extremity. Degenerating ova (*ov*) are seen in the ovary. × 650.

Fig. 2. Optical section of a root-branch of *Sacculina*. × 50.

Fig. 3. Optical section of roots of *Anelasma squalicola*. The roots are shown springing from the surface of the peduncle (*ch.pd*), the chitin of the latter being pushed out to form the chitinous investment of the roots (*ch*). × 50.

Fig. 4. Part of a section through the peduncle of *Anelasma squalicola*, from the surface of which a root is seen to spring (*r*). In the interior of the peduncle the ovary is shown (*ov*), at the borders of which ova (*ov.deg*) are beginning to migrate into the lacunar tissue (*lac*). × 40.

Fig. 5. Section through a piece of the mantle of *Anelasma squalicola* showing the migrated ova (*ov.deg*) in process of degeneration. × 80.

Fig. 6. Transverse section through anterior region of testis of young *Sacculina neglecta*. × 865.

Fig. 7. Longitudinal section through the middle region of the testis of *Peltogaster curvatus*. × 435.

Fig. 7a. Spermatozoa of *Peltogaster curvatus*. × 865.

Fig. 8. Transverse section through posterior region of testis of young *Sacculina neglecta*. × 865.

Fig. 9. Transverse section through middle region of testis of *Peltogaster curvatus*. × 435.

Fig. 10. Transverse section through posterior region of testis of older *Sacculina neglecta*. × 865.

Fig. 11. Longitudinal section through the middle region of the testis of an old *Peltogaster curvatus*. × 435.

Fig. 11a. Longitudinal section through wall of testis of old *Peltogaster curvatus*. × 435.

Fig. 12. Transverse section through posterior region of testis of an adolescent *Sacculina neglecta*. × 435.

Fig. 13. Section through the vas deferens of *Parthenopea subterranea*. × 234.

Fig. 14. Transverse section through young *Sacculina neglecta* externa with complemental males (♂). × 93.

Pl. 2.

1

11

11a

5

14

Pl. 2.
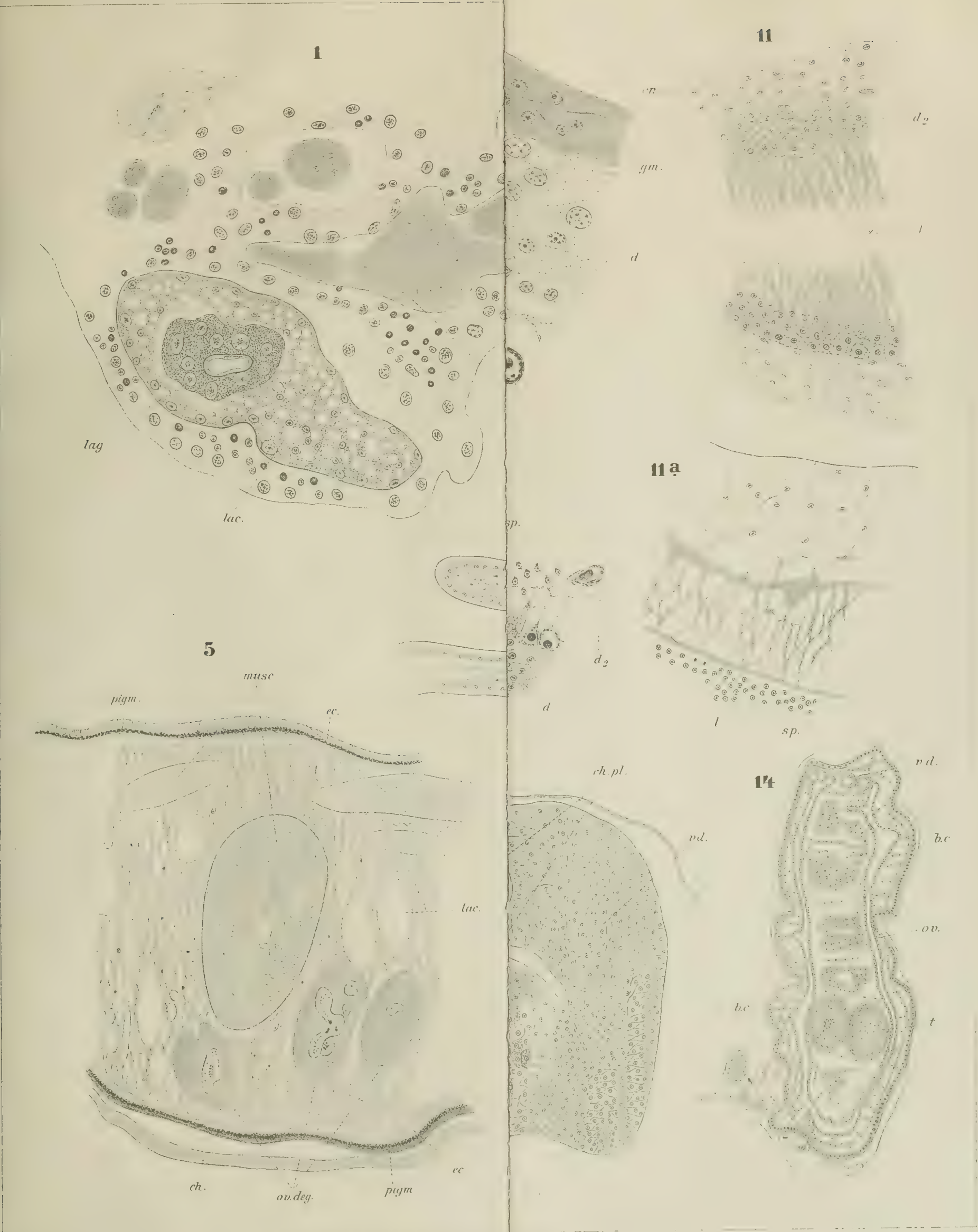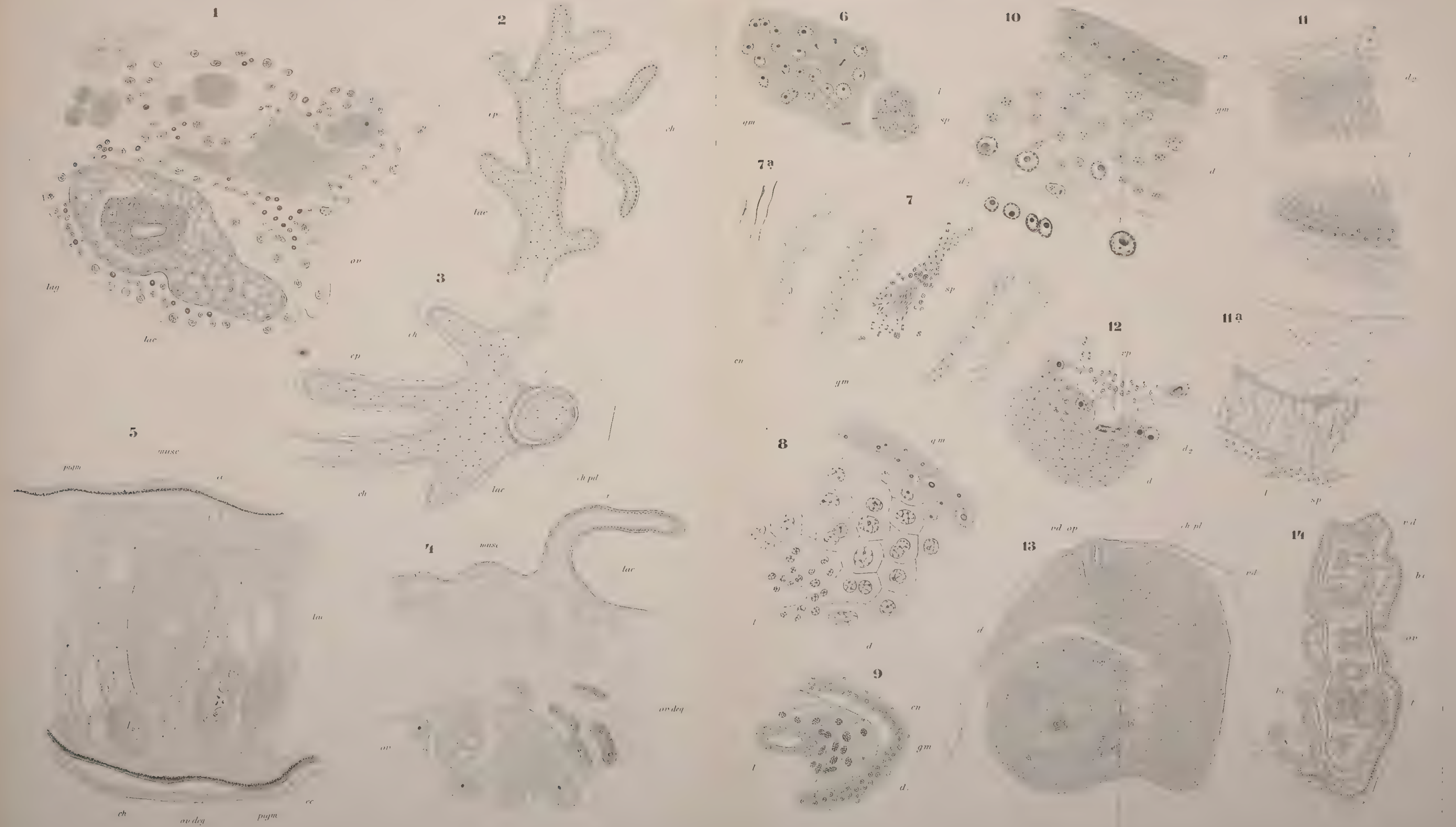
Plate 3.

Maturation and Fertilization of Ovum of *Peltogaster curvatus*.

ep ovarian epithelium. *p.b1* first polar body. *p.b2* second polar body. *sg* segmentation spindle. *sp1* first maturation spindle. *sp2* second maturation spindle. ♂ spermatozoon or male pronucleus. ♀ female pronucleus.

Fig. 1. Section through a piece of ovary of *Peltogaster curvatus*, certain of the eggs having already begun the maturation process. × 650.

Fig. 2. Longitudinal section through the first maturation spindle, showing tetrads. × 1300.

Fig. 3 and 3a. Longitudinal sections through the first maturation spindle (metaphase). × 1300.

Fig. 4 and 4a. Longitudinal section through the first maturation spindle (metaphase, spindle having rotated). × 1300.

Fig. 5 and 5a. Transverse section through equatorial plate of first maturation spindle (metaphase). × 1300.

Fig. 6. Formation of second spindle immediately after telophase of first. Whole preparation. × 650.

Fig. 7. Equatorial plate of second spindle (*sp2*) with 14 chromosomes. Transverse optical section of whole preparation. × 1300.

Fig. 7a. Egg at same stage as Fig. 7, but left in sea water to separate chromosomes. × 1300.

Fig. 8 and 8a. Transverse section through second maturation spindle (metaphase). × 1300.

Fig. 9. Second maturation spindle (*sp2*), travelled away from 1st polar body (*pb1*) (metaphase). Whole preparation. × 650.

Fig. 9a. Second maturation division (late telophase); first polar body (*pb1*) placed on egg envelope and degenerating. Optical section. × 650.

Fig. 10. Fertilization, spermatozoon (♂) having just entered and lying alongside female pronucleus. Section. × 1300.

Fig. 11. Passage of pronuclei (♂ and ♀) to centre of egg. 1st polar body still attached to egg envelope, 2nd polar body lying within it. Optical section. × 650.

Fig. 12. Passage of pronuclei to periphery of egg. Section. × 650.

Fig. 13. Growth and further passage of nuclei. Optical section. × 325.

Fig. 14. Two pronuclei arrived at periphery near 2nd polar body. Whole preparation. × 325.

Fig. 15. Same as 14. Section. × 650.

Fig. 16. A case where lobation of nuclei shown in 15 has led to division into three nuclei. Section. × 650.

Fig. 17. Formation of aster for first segmentation division, and of spireme in nuclei. Section. × 1300.

Fig. 18. First segmentation division (anaphase). Section. × 1300.

Fig. 19. First segmentation division (metaphase). Whole preparation. × 325.

Fig. 20 and 20a. First segmentation division (metaphase). Section. × 1300.

Fig. 21 and 21a. First segmentation division (telophase). Section. × 1300.

Fig. 22. First segmentation division (late telophase). Section. × 1300.

1.

sp.1.

ep.

18.

p.b.2.

p.b.2.

20.

s.g.

2. sp.1.

4. sp.1.

20a.

3.   **3a.**

4a.

21.

sp.1.

sp.1.

6. p.b.1. sp.2.

p.b.2.

5.

21a.

22.

5a.

pb2
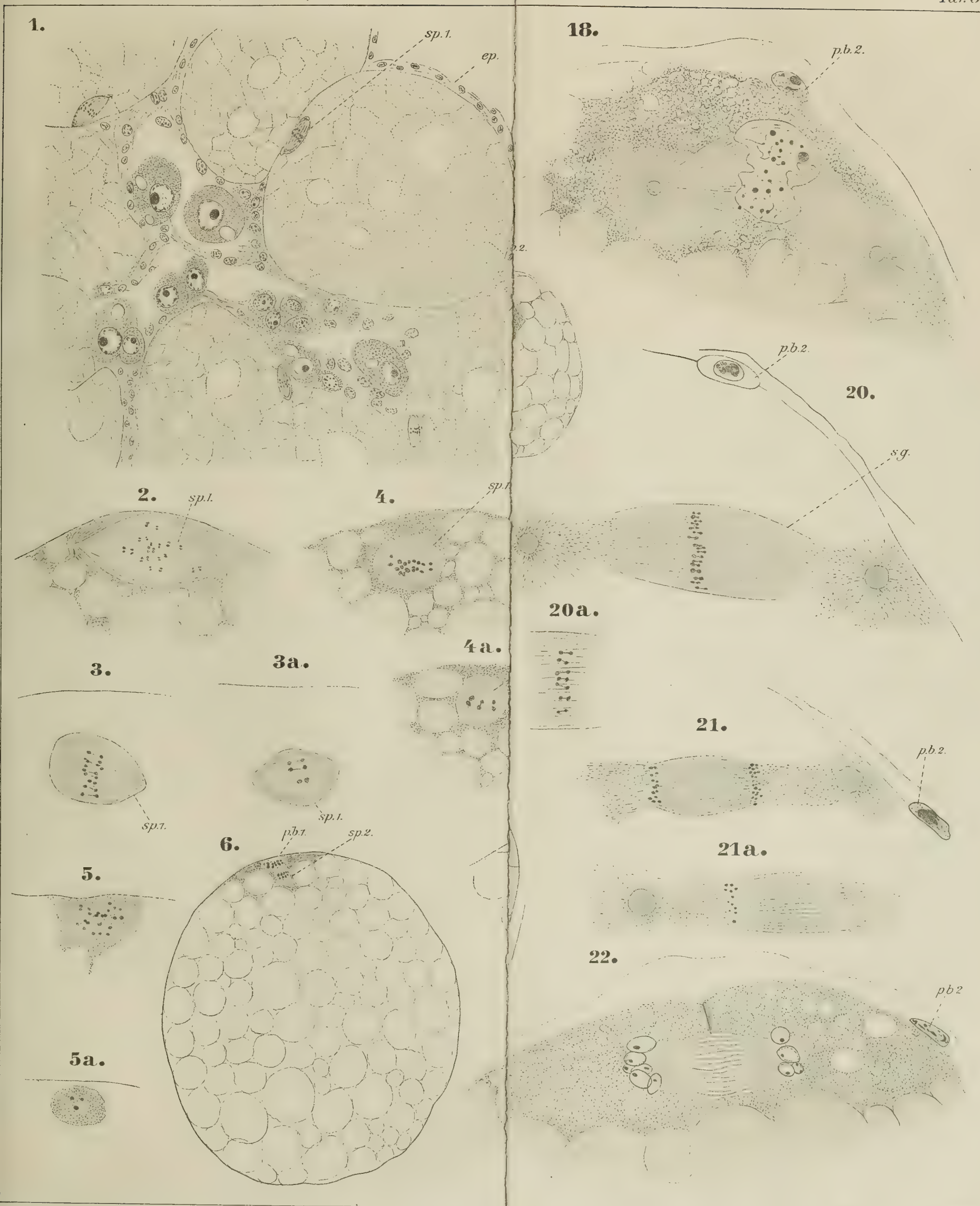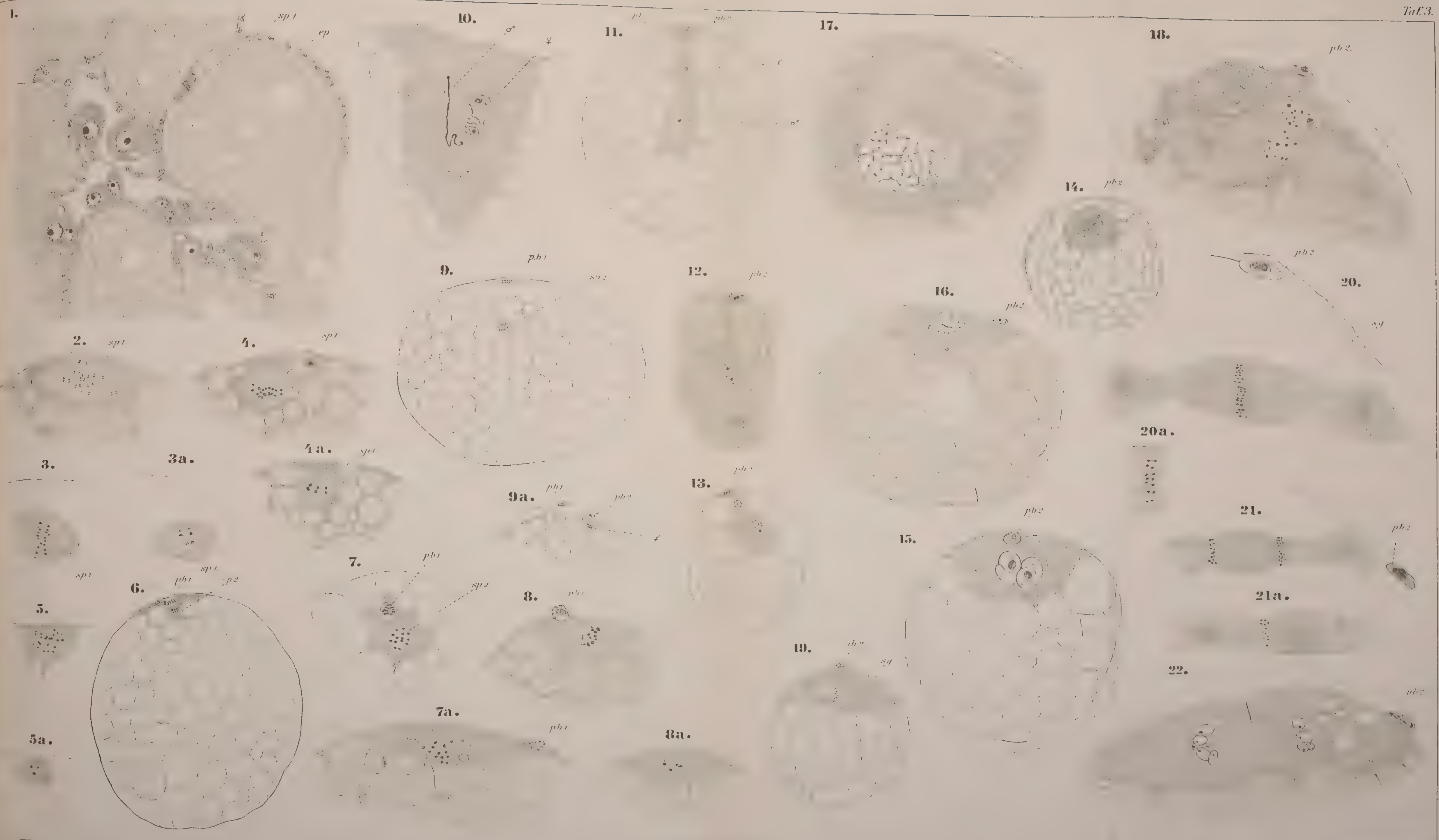
Plate 4.

Embryonic Development and Larval Stages.

Figs. 1—16 and 18 refer to *Peltogaster curvatus*, Figs. 17, 19 and 20 to *Sacculina neglecta*.

Ab abdomen.   *Ant* Antenna of Cypris.   *1, 2, 3* 1st, 2nd and 3rd segments of Nauplius.   *1stA* 1st antenna.   *2ndA* 2nd antenna.   *ch* chitinous investment of Kentrogon.   *E* Endoderm cells.   *Em* Embryonic cells.   *Ect* Ectoderm.   *Fh* frontal horns.   *G* glands of Cypris.   *h* chitinous tendons of Cypris.   *md* mandible.   *musc* muscles.   *t* tentacles.   *th.app* thoracic appendages.   *Th* thoracic rudiment.   *sk* skeletal support. *ves* vesicle representing antennal gland.   *VP* ventral plate.

Fig. 1. Two cell stage.   Whole preparation side view. $\times$ 140.

Fig. 2. Two cell stage.   Horizontal section through upper pole.   650.

Fig. 3. Four cell stage.   Whole preparation viewed from lower pole. $\times$ 140.

Fig. 4. Four cell stage.   Horizontal section through upper pole. $\times$ 650.

Fig. 5. Formation of blastoderm.   Longitudinal section. $\times$ 650.

Fig. 6. Formation of blastoderm, later stage.   Whole preparation. $\times$ 650.

Fig. 7. Gastrulation.   Optical section. $\times$ 650.

Fig. 8. Gastrulation.   Optical section, later stage. $\times$ 650.

Fig. 9. End of Gastrulation, breaking up of archenteron.   Optical section. $\times$ 650.

Fig. 10. Segmentation of lateral germ bands.   Whole preparation.   Dorsal view. $\times$ 650.

Fig. 11. Segmentation of lateral germ bands.   Horizontal section. $\times$ 650.

Fig. 12. Formation of Nauplius.   Lateral view, whole preparation. $\times$ 650.

Fig. 13. Formation of Nauplius.   Ventral view, whole preparation. $\times$ 650.

Fig. 14. Horizontal section through 13. $\times$ 650.

Fig. 15. Transverse section through 13, cutting ventral plate and first two appendages. $\times$ 650.

Fig. 16. Transverse section through 13, anterior to 15. $\times$ 650.

Fig. 17. Free swimming Nauplius of *Sacculina neglecta*.   Ventral view. $\times$ 175.

Fig. 18. Free swimming Nauplius of *Peltogaster curvatus*.   Ventral view. $\times$ 175.

Fig. 19. Free swimming Cypris of *Sacculina neglecta*.   Lateral view. $\times$ 350.

Fig. 20. Horizontal section through fixed Cypris of *Sacculina neglecta*. $\times$ 325.

Plate 5.

Endoparasitic development of *Sacculina neglecta*.

The plane which bisects the mesentery longitudinally is spoken of as the longitudinal plane; the plane transverse to this as transverse. — The parts of sections tinted red belong to the host.

app abdominal appendages of crab. *bas* basilar membrane of Sacculina. *bc* brood pouch or mantle cavity. *b.sac* body of Sacculina. *c.g* colleteric gland. *ch* chitin. *ch.ext* external chitin of thorax of crab. *cor* blood corpusculus of crab. *c.t* central tumour. *ct.cav* cavity of central tumour. *div.inf* inferior diverticulum of gut of crab. *div.sup* superior diverticulum of gut of crab. *ep1* internal epithelium of brood pouch. *ep2* external epithelium of brood pouch. *ep3* internal epithelium of perisomatic cavity. *ep4* external epithelium of perisomatic cavity. *ext.ep* external ectoderm of crab. *gn* nervous ganglion. *gut* gut of crab. *l* epithelium of root. *liv* liver diverticulum of crab. *mes* mesentery. *m* muscle cells. *m.c* mesenchymatous cells. *musc* muscular layer. *mus.l* longitudinal musculature. *mus.t* transverse muscles of mantle. *musc.c* circular muscles of mantle. *n* "nucleus" or body rudiment of Sacculina. *op* opening of perisomatic cavity. *ov* ovary. *p.c* perisomatic cavity. *r* roots of Sacculina. *sp* spider cells. *t* testes. *v.d* vas deferens. *x* definitive position on crab's gut of adult Sacculina body.

Fig. 1. Upper part of gut of *Inachus scorpio*, near stomach, with a Sacculina interna migrans (*sac*) attached to liver diverticulum. $\times$ 23.

Fig. 2. Mid-gut of *Inachus scorpio*. Sacculina a little lower than in Fig. 1. $\times$ 23.

Fig. 3. Section, slightly oblique, through Sacculina of Fig. 2. $\times$ 140.

Fig. 4. Same as Fig. 3, a small portion greatly enlarged. $\times$ 650.

Fig. 5. Mid-gut of *I. scorpio*, with Sacculina growing down towards definitive position (*x*); nucleus (*n*) already differentiated. $\times$ 23.

Fig. 6. Section through tumour and nucleus of Sacculina of Fig. 5. $\times$ 650.

Fig. 7. Section through tumour and nucleus of a Sacculina interna. Later stage than Fig. 6. $\times$ 325.

Fig. 8. Mid-gut of *I. scorpio* with Sacculina attaining to definitive position *x*. $\times$ 23.

Fig. 9. Section through tumour and nucleus of Sacculina of Fig. 8. $\times$ 325.

Fig. 10. Longitudinal section through gut and ventral wall of thorax of *I. scorpio* with a Sacculina interna in definitive position, showing that the parasite is completely internal at this stage. $\times$ 70.

Fig. 10a. Mid-gut of *I. scorpio* with Sacculina interna in definitive position, ready to come out. Only some of the roots are drawn. $\times$ 23.

Fig. 11. Longitudinal section through mesenterial plane of Sacculina interna to show formation of perisomatic cavity (*p.c*) by means of invagination. $\times$ 325.

Fig. 12. Horizontal section through central tumour and developing body of Sacculina to show further development of perisomatic cavity. $\times$ 140.

Fig. 13. Same as 12, but deeper section: and more enlarged to show histology of development. $\times$ 325.

Fig. 14. Transverse section through a later stage, showing perisomatic cavity (*p.c*) fully developed. $\times$ 140.

Fig. 15. Transverse section through middle of body of Sacculina interna, late stage, to show development of testis. Tumour and perisomatic cavity and mantle omitted. $\times$ 650.

Fig. 16. Same as 15, but still later stage; Sacculina ready to be evaginated. Showing development of colleteric glands (*c.g*). $\times$ 45.

Fig. 17. Transverse section of portion of body of Sacculina of about same age as Fig. 14, to show formation of nervous ganglion (*g.n*) from outer wall of brood cavity (*b.c*). $\times$ 325.

Fig. 18. Section through the root of a Sacculina interna. $\times$ 650.

Pl. 5.

Plate 6.

Endoparasitic development of *Peltogaster*. Complemental Males of *Sacculina*.

The parts of sections tinted red belong to the host.

Ant Antenna of Cypris. *Ap* thoracic appendage. *b.c* brood pouch or mantle cavity. *ch* chitin. *ch.ext* external chitin of host. *cl* cloaca or mantle opening. *ct* central tumour. *Ec* Ectoderm of Cypris. *Ect* Ectoderm of host. *Em* embryonic cells of Cypris. *ep1* internal epithelium of brood pouch. *ep2* external epithelium of brood pouch. *ep3* external epithelium of mantle. *liv* liver of host. *mes* mesentery. *n* nucleus from which visceral mass is formed. *musc* muscle. *ov* ovary. *r* roots. *sp* spider cells. *t* testis. *vis.mass* visceral mass.

Fig. 1. Outline drawing of stolon-like tumour of Peltogaster internus, with roots beginning to grow out. $\times$ 23.

Fig. 2. Section through a young Peltogaster internus of about same age as Fig. 1. $\times$ 140.

Fig. 3. High power drawing of anterior region of tumour marked *n* in Fig. 1. $\times$ 650.

Fig. 3a. High power drawing of a root of Peltogaster internus figured in Fig. 1.

Fig. 4. Longitudinal section through central tumour and body of a Peltogaster internus, in the act of being protruded from the body of its host. $\times$ 140.

Fig. 5. High power drawing of Fig. 4, to show differentiation of organs. $\times$ 325.

Fig. 6. Transverse section through a young Peltogaster externus. $\times$ 40.

Fig. 7. Figure from side of *Eupagurus prideauxii* carrying on its abdomen 22 specimens of *Peltogaster socialis*. $\times$ 2.

Fig. 8. Lateral view of a single specimen of *Peltogaster socialis*. $\times$ 5.

Fig. 9. Section through the central tumours of two *Peltogaster socialis* internus lying within the abdomen of the host. $\times$ 70.

Fig. 10. Section through central tumour of a *Sacculina neglecta* interna, in which are seen two visceral masses with their mantle cavities. $\times$ 325.

Fig. 11. Fourteen Cypris larvae fixed round the cloaca or mantle opening of a young Sacculina externa. $\times$ 70.

Fig. 12. Section through the mantle opening (*cl*) of a young Sacculina externa to which are attached Cypris larvae. Two of these are shown in the figure; one of them contains embryonic cells (*Em*) which pass through the antenna; the other is already empty. $\times$ 325.

Fig. 13. Longitudinal horizontal section through a Cypris larva found on a young Sacculina externa but not yet attained to the mantle opening. $\times$ 650.

Fig. 14. Transverse section through Fig. 13. $\times$ 325.

Fig. 15. Longitudinal sagittal section through a Cypris larva fixed near mantle opening of a young Sacculina externa; the Embryonic cells pass through the antenna. $\times$ 1300.
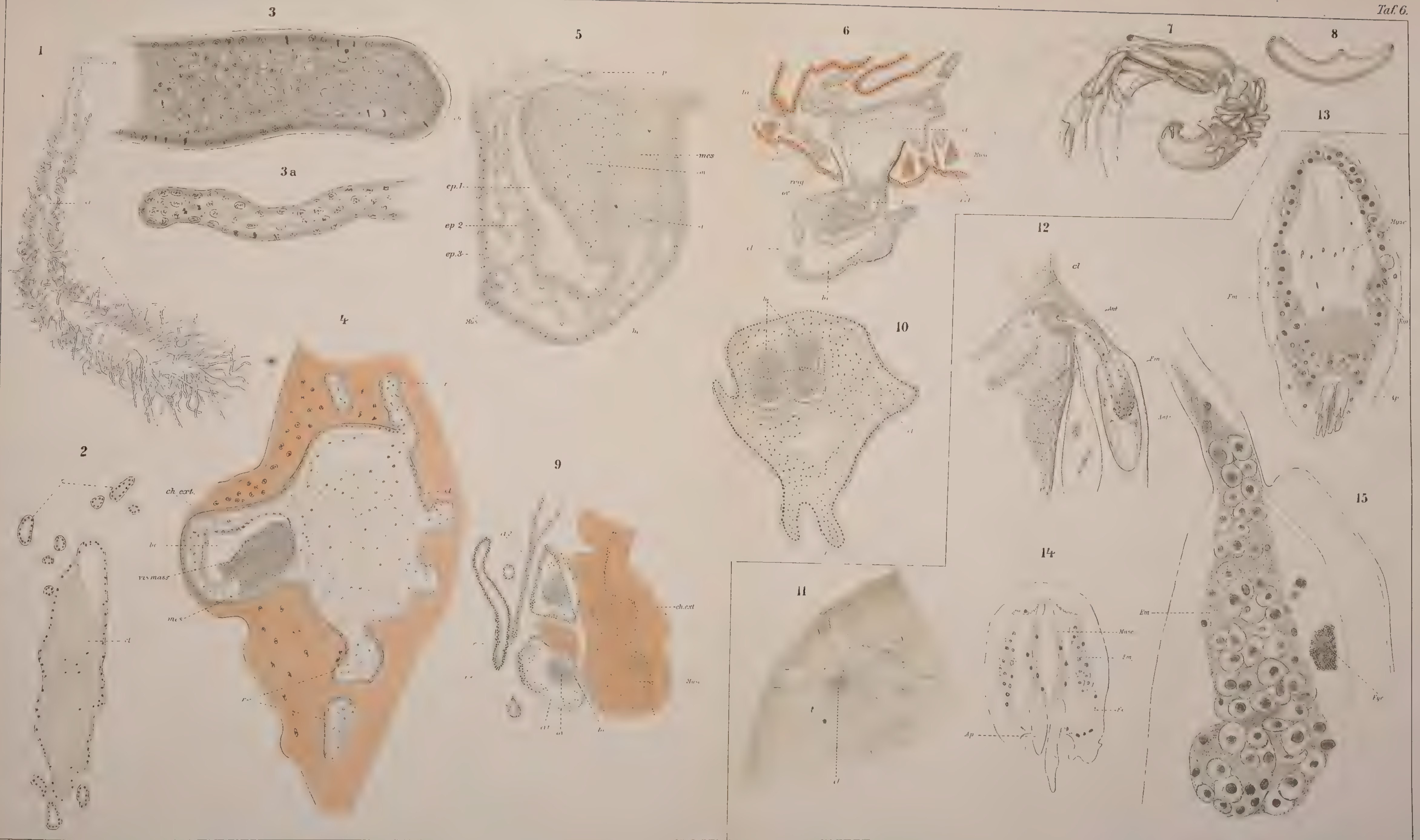
Plate 7.

The effect of the parasites on their host. Parasites of the parasites.

(Figs. 1—21 refer to *Inachus scorpio.*)

ov ovary. *p* copulatory style. *S* scar of Sacculina. *t* testis.

Fig. 1. Adolescent female, dorsal view. Nat. size.
Fig. 2. Abdomen of Fig. 1, ventral view. $\times$ 2.
Fig. 3. Adult female, dorsal view. Nat. size.
Fig. 4. Abdomen of 3, ventral view. $\times$ 2.
Fig. 5. Abdomen of adult infected female, ventral view. $\times$ 2.
Fig. 6. High male, dorsal view. Nat. size.
Fig. 7. Middle male, ditto.
Fig. 8. Low male, ditto.
Fig. 9. Infected male, dorsal view. Nat. size.
Fig. 10. Same as Fig. 9, but more modified. Nat. size.
Fig. 11 and 12. Abdomina of infected males, ventral view. $\times$ 2.
Fig. 13. Abdomen of normal uninfected male, ventral view. $\times$ 2.
Fig. 14. Infected male of *I. scorpio*, modified into perfect hermaphrodite form. Dorsal view. Nat. size.
Fig. 15. Abdomen of Fig. 14, ventral view. $\times$ 2.
Fig. 16. Infected male, modified into perfect hermaphrodite. Dorsal view. Nat. size.
Fig. 17. Abdomen of Fig. 16, ventral view. $\times$ 2.
Fig. 18. Hermaphrodite crab, found in nature, not bearing any signs of Sacculina. Dorsal view. Nat. size.
Fig. 19. Abdomen of Fig. 18, ventral view. $\times$ 2.
Fig. 20. Section through hermaphrodite gonads of recovered crab of type figured in Figs. 14—17. $\times$ 45.
Fig. 20a. Enlarged drawing of a piece of hermaphrodite gonad, showing ova and sperm lying together in same tube. $\times$ 325.
Fig. 21. Male, experimentally recovered from Sacculina in Aquarium, which formed hermaphrodite gonad. Nat. size. Ventral view.

art dorsal artery. *b.c* brood pouch. *c.g* colleteric gland. *cl* mantle opening. *h* external chitin. *co* nerve cord. *end* endoderm. *ect* ectoderm. *E* eye. *gn* ganglion. *h* heart. *m* mantle. *mes* mesentery. *n* phagocytic cells. *ov* ovary. *op* opening of spermatheca. *o.t* ovotestis. *pr* proboscis. *ri* ring of attachment. *sp.th* spermatheca. *t* testis. *visc.mass* visceral mass.

Fig. 22. Cryptoniscus larva of *Danalia curvata*, male stage. Dorsal view. $\times$ 40.
Fig. 23. Same as Fig. 22, ventral view. $\times$ 40.
Fig. 24. Transverse section through hinder part of thorax of Cryptoniscus larva to show testis. $\times$ 175.
Fig. 24a. Spermatozoa from testis of larva. $\times$ 1300.
Fig. 25. Transverse section through hinder part of thorax of Cryptoniscus larva, some time after fixation. The phagocytic cells (*n*) absorb remains of testis. $\times$ 175.
Fig. 26. Transverse section through anterior part of thorax of Cryptoniscus figured Fig. 25, to show ovary (*ov*). $\times$ 175.
Fig. 27. Whole view from side of *Danalia curvata* shortly after fixation and loss of larval appendages. $\times$ 80.
Fig. 27a. Optical section from dorsal view of *Danalia curvata* at same stage as Fig. 27, to show great development of phagocytic cells (*n*). $\times$ 175.
Fig. 28. Transverse section through middle of thorax at about same stage as Fig. 27. $\times$ 175.
Fig. 29. Transverse section through thorax of *Danalia curvata*, when nearly adult. $\times$ 40.
Fig. 29a. Spermatozoa from spermatheca of Fig. 8. $\times$ 1300.
Fig. 30. *Inachus scorpio*, ♀, bearing on abdomen two specimens of *Sacculina neglecta* and one specimen of *Danalia curvata*, on which are two Cryptoniscus larvae fertilizing it. $\times$ 2.
Fig. 31. *Galathea dispersa* with *Lernaeodiscus galatheae* on abdomen. Ventral view. $\times$ 4.
Fig. 32. *Galathea dispersa* with *Danalia ypsilon* on abdomen. Ventral view. $\times$ 4.
Fig. 33. *Lernaeodiscus galatheae*, viewed by transparency in situ on its host. $\times$ 12.
Fig. 34. *Lernaeodiscus galatheae*, lateral (right) view, mantle cut away to show visceral mass, position of organs and mesentery. $\times$ 12.
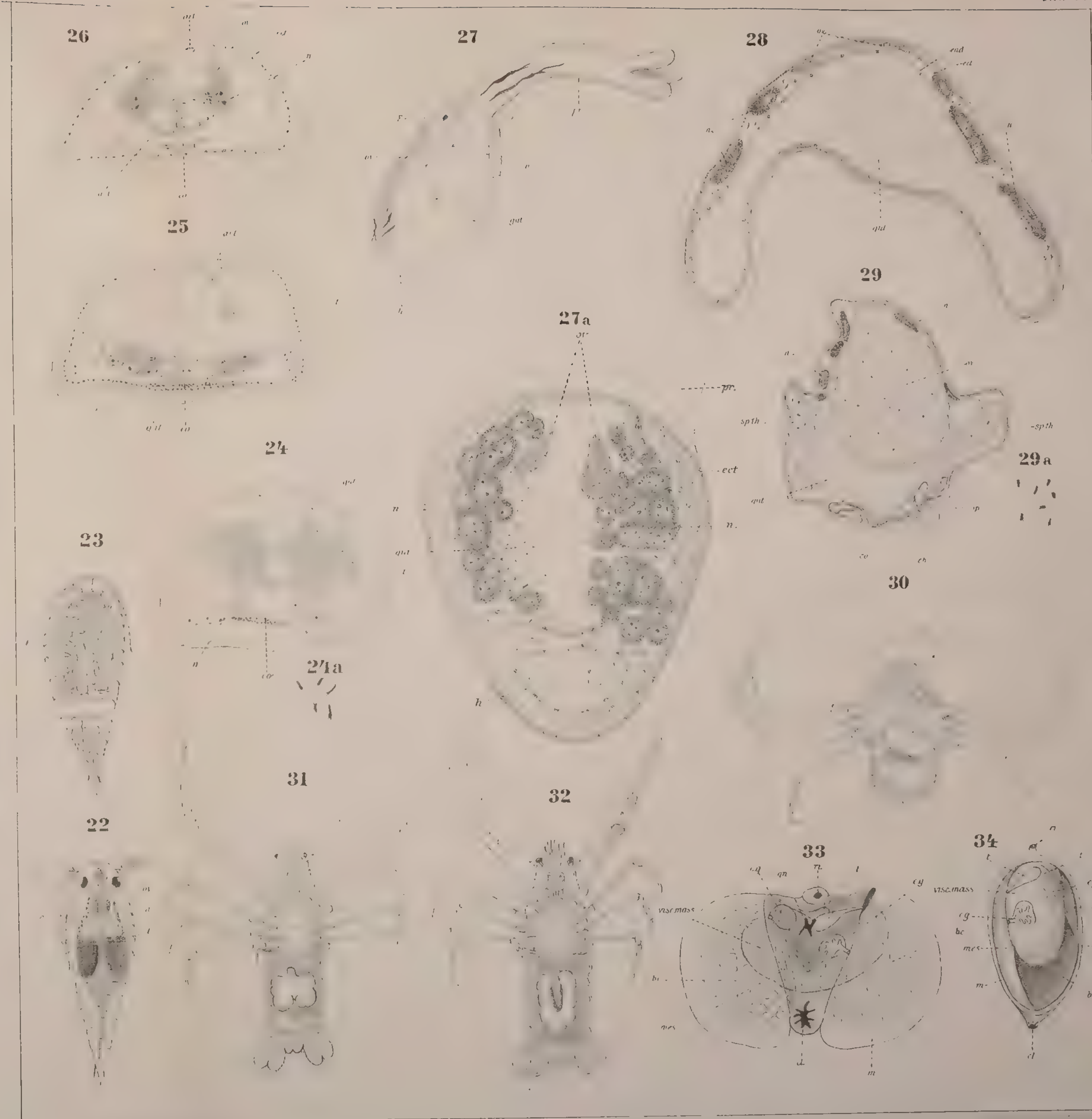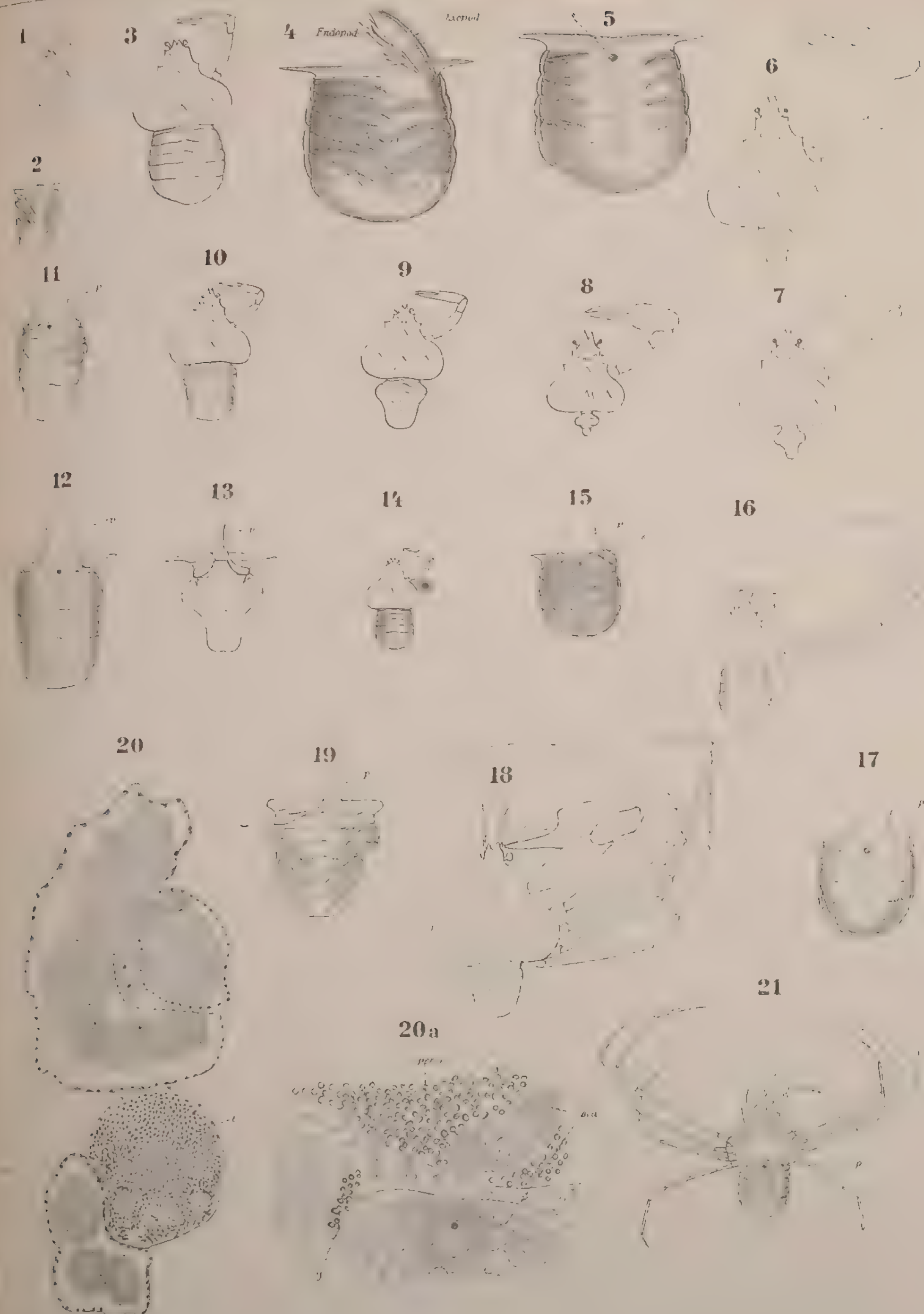
Plate 8.

Sylon, Clistosaccus, Duplorbis and Scalpellum.

ch chitin. *Cls* mantle openings. *coll* colleteric gland. *ect* ectoderm. *Em* embryos. *gn* ganglion. *lac* lacunar tissue. *mes* mesentery. *mes.can* mesenteric canal. *m* mantle. *m.c* mantle cavity. *ov* ovary. *Ring* ring of attachment. *sp1* primary spermatocytes. *sp2* secondary spermatocytes. *sp3* spermatids and spermatozoa. *spd* spermatids. *spm* spermatozoa. *spg* spermatogonia. *st* stalk. *t* testis. *visc* visceral mass. *visc.ect* external epithelium of visceral mass. ♂ supposed complemental male.

Fig. 1. *Hippolyte fabricii* with *Sylon*. Nat. size.

Fig. 2. *Sylon*, viewed from dorsal or mesenterial surface. ✕ 4.

Fig. 3. *Sylon*, transverse section through anterior region of body. ✕ 25.

Fig. 4. *Sylon*, transverse section through body, in region of mantle openings (*cl*) and nervous ganglion (*gn*). ✕ 40.

Fig. 5. *Clistosaccus*, ideal longitudinal section.

Fig. 6. *Clistosaccus*, transverse section through extreme anterior region of body to show colleteric gland (*coll*). ✕ 12.

Fig. 7. *Clistosaccus*, transverse section through middle of body. ✕ 12.

Fig. 8. *Clistosaccus*, section through testis showing stages in spermatogenesis. ✕ 700.

Fig. 9. *Calathura brachiata* in ventral view, with three specimens of *Duplorbis calathurae* in marsupium. ✕ 4.

Fig. 10. *Duplorbis*, whole specimen viewed from mesenterial surface.

Fig. 11. *Duplorbis*, whole specimen viewed from ventral or antimesenterial surface.

Fig. 12. *Duplorbis*, section taken longitudinally to morphological long axis, transversely to actual long axis of body, in the mesenterial middle line, showing mesenterial canal (*mes.can*), stalk (*st*) of attachment, visceral mass (*visc*) and mantle cavity (*mc*) etc. ✕ 40.

Fig. 13. *Duplorbis*, section longitudinal to morphological long axis, showing colleteric gland (*coll*) of one side, visceral mass and ovary. ✕ 175.

Fig. 14. *Duplorbis*, section similar to foregoing, but at an extremity of body, to show mantle cavity full of embryos and the supposed complemental male (♂). ✕ 40.

Fig. 15. *Duplorbis*, longitudinal section through mesenteric canal, showing histology. ✕ 650.

Fig. 16. *Duplorbis*, transverse section through stalk and mesentery, showing mesenteric canal. ✕ 80.

Fig. 17. *Duplorbis*, transverse section through stalk, where the latter enters body of host, showing opening of mesenteric canal into host. ✕ 80.

Fig. 18. *Duplorbis*, transverse section through supposed complemental male in mantle cavity. ✕ 650.

Fig. 19. *Duplorbis*, stages in spermatogenesis taken from supposed complemental male. ✕ 1300.

Fig. 20. *Scalpellum vulgare*, transverse section through the body of a complemental male, showing mantle (*m*), testis etc., for comparison with Fig. 18. ✕ 160.

Fig. 21. *Scalpellum vulgare*, stages in spermatogenesis taken from complemental male. ✕ 1300.