The Rhizocephala in the collection of the British Museum. By Dr. H. BOSCHMA, Leiden. (Communicated by Dr. W. T. CALMAN, F.R.S., F.L.S.)

(With 53 Text-figures, including PLATE 7)

[Read 9 November 1933]

IN 1928 I had the opportunity to study the collection of Rhizocephala in the British Museum (Natural History). During the time I stayed in London I made notes on many specimens in the collection, and afterwards the greater part of it was sent to Leiden for further examination. The study of this material has been delayed for various reasons, and I wish to express my thanks to Dr. W. T. Calman for his permission to keep the material much longer than at first had been arranged. To Dr. Isabella Gordon, of the staff of the British Museum, I am highly indebted for her readiness to identify a number of unnamed hosts of the parasites and for sending me material of the group which was found recently in the collections.

The material on which the present paper is based has been collected in various parts of the world. Besides a number of new species the material contains some specimens which are of special interest, viz. the type-specimen of *Sacculina rotundata*, that of *Lernaeodiscus galatheae*, and the new genus *Ptychascus*.

In the arrangement of the genera the simpler forms have been dealt with first, whilst the aberrant genus *Thompsonia* is placed at the end. Perhaps this is not altogether right, but it is difficult to decide whether *Thompsonia* is a primitive form or a highly specialized one.

I could not avoid describing a considerable number of forms as new species : consequently in the present paper, besides notes on 18 previously described species, descriptions are given of 11 new ones. Especially in the genus *Sacculina* many new species had to be recognized : among the 15 species of this genus dealt with here 9 are new.

This results from the fact that the material of the British Museum has been collected from various parts of the world, and as it is only in European waters that the Rhizocephala have hitherto been studied more or less completely, it is evident that in every collection from other parts of the world many new species may be found.

It might be doubted if it is really necessary to regard all the new species in the present paper as distinct forms. It is now firmly established that in the genus *Sacculina* there are a number of different European species, recognizable by constant characters derived from their anatomy and the structure of the chitinous coverings of the mantle. In studying the material

LINN. JOURN .--- ZOOLOGY, VOL. XXXVIII

of the British Museum I have made use of corresponding characters, and as the differences between the species dealt with in the present paper are of the same order as those between the European species, it is evident that the new forms described here may be regarded as distinct species. In some cases the material is rather scanty, and it would have been a great advantage if more material had been available, so that the variability of the species could have been studied. The specimens of the present collection have been described more or less elaborately, but it is possible that not all the characters mentioned are of specific value.

Genus Peltogaster.

PELTOGASTER PAGURI Rathke.

- Peltogaster paguri: Rathke (1842), Norman and Scott (1906), Pérez (1927, 1928 b, 1931 c, d).
- For other literature on the species cf. Boschma (1928 a).

Material examined :

Starcross, Devon, Parker coll., 1884, 24 specimens, each on one host (collection Norman).

Off Sunderland, 1863, 2 specimens (collection Norman).

Firth of Forth, J. Anderson coll., 1 specimen (collection Norman).

Firth of Forth, J. Anderson, 1861, 1 specimen.

Farland Pt., Cumbrae, 20 fathoms, Aug. 24, 1888, 1 specimen (collection Norman). All these specimens are parasites of *Eupagurus bernhardus* (L.).

The specimens are of rather uniform shape, though differing in size. The posterior end of the body is turned to the right, as usual in the species. All the specimens are mature, as they possess a well-developed mantle opening. The smallest specimens are those from off Sunderland; the greater diameter of these is 4 and 5.5 mm. respectively. In the 24 specimens from Starcross the greater diameter varies between 13 and 7 mm.

Sections have been prepared from two specimens; they show the peculiarities characteristic of the species: the simple colleteric glands and the strongly coiled vasa deferentia.

The external cuticle is smooth : it does not possess the little spines by which *Peltogaster curvatus* is characterized.

PELTOGASTER CURVATUS Kossmann.

Peltogaster curvatus: Kossmann (1873), Fraisse (1877), Smith (1906), Guérin-
Ganivet (1911), Duboscq (1912), Boschma (1927 c).
Material examined :
Naples, 1887, 8 specimens (collection Norman).
Zoological Station, Naples, 2 specimens on one host (collection Norman).
Off Valentia, Ireland, 1870, 1 specimen.
All these specimens are parasites of Eupagurus excavatus (Herbst).

When seen from the dorsal or ventral surface many specimens have smooth sides, whilst in other specimens the sides show an indication of lappets, probably as a result of contraction of the mantle. All the specimens possess the small conical excressences of the mantle which have been described by Duboscq

(1912) as a character of the species. They are also distinctly visible in the specimen from off Valentia, which proves that *Peltogaster curvatus* undoubtedly occurs in the Atlantic.

Genus GALATHEASCUS.

The only difference between *Peltogaster* and *Galatheascus* lies in the different manner of attachment to the hosts. The long axis of *Peltogaster* lies in the same direction as that of its host, whilst in *Galatheascus* the main axis is perpendicular to that of the host. It remains questionable whether this character suffices to classify these parasites in two different genera. A similar question arises in regard to the genera *Lernaeodiscus* and *Parthenopea*, each of which is attached to the host in a different way.

The genus *Galatheascus* may be defined as follows: Body elongate oviform. Mesentery very broad, extending from the anterior to the posterior extremity. Stalk in the median part of the body or in the anterior half. Mantle opening in adult specimens in the dorsal part of the anterior region. Colleteric glands small, simple, in the neighbourhood of the stalk. Testes consisting of a very short straight part at each side of the median plane, and a strongly coiled portion which passes into the vasa deferentia; the whole of the male genital organs in the region of the stalk. On the abdomen of Anomura, the long axis of the parasite perpendicular to the long axis of the host. Larvae hatching in the nauplius stage.

The diagnosis of the genus as given above differs in some respects from that given in a previous paper (Boschma, 1929) as a consequence of the study of the new species described below.

The representatives of the genus *Galatheascus* (which are hitherto known from European waters only) can be easily distinguished from the European species of the genera *Peltogaster* and *Chlorogaster* by their peculiar shape : they are much thicker in proportion to their length than the species of *Peltogaster* and *Chlorogaster*.

GALATHEASCUS STRIATUS Boschma.

Galatheascus striatus : Boschma (1929).

Material examined *:

Looe-Eddystone Grounds, near Plymouth, June 11, 1913, 1 specimen on Galathea strigosa (L.) (from the collection of the Marine Biological Association).

Diagnosis of the species (amended from Boschma, 1929).—Mantle opening extremely narrow. Stalk in the anterior half of the body. External cuticle of the mantle smooth, with shallow grooves (about 0.2 mm. apart), extending over the surface in a longitudinal direction. Internal cuticle with retinacula consisting of one to three spindles each. These spindles have a length of 20 to 25μ .

* Recently the British Museum received another specimen of *Galatheascus striatus* from the Zoology Department of the University of Reading. This specimen, which was collected at Port Erin, Isle of Man, is attached to the abdomen of *Galathea strigosa* (L.). From the only known specimen of this species a series of sections has been made. A detailed description of the characters of this specimen is found in the paper cited above.

GALATHEASCUS MINUTUS, sp. n.

Material examined :

Off Valentia, Ireland, 1870, 1 specimen on Galathea intermedia Lillj. (collection Norman).

Oban, Scotland, 1877, 1 specimen on Galathea nexa Embleton (collection Norman).

Diagnosis of the species.—Mantle opening comparatively wide, at the dorsal part of the anterior region (in young specimens at the ventral part). Stalk in the median region of the body. External cuticle of the mantle smooth, without grooves.

Although the two specimens differ in size and shape they belong undoubtedly to the same species. The specimen on *Galathea nexa* is more or less elongated; its anterior part is much thicker than the posterior part (fig. 1, b). This specimen has a length of 5 mm., a height of 3 mm., and a breadth of 2 mm. In the specimen on *Galathea intermedia* the dimensions are: length 2.5, height 2, and breadth 1.5 mm. approximately. The latter specimen has an



Fig. 1.—Galatheascus minutus. a, the specimen on Galathea intermedia; b, the specimen on Galathea nexa. The left side of the animals is represented; the stalk is seen below. $\times 6$.

oval shape (fig. 1, a). In the larger specimen the mantle opening lies at the anterior end of the parasite, slightly turned towards the abdomen of the host; it is surrounded by a more or less elevated ridge, so that it projects somewhat above the surface of the mantle. In the smaller specimen the mantle opening is a narrow pore which has not yet shifted towards the anterior end.

The state of preservation of the specimens is not particularly good, owing to the fact that they have been preserved for approximately sixty years. The larger specimen is somewhat better preserved than the smaller : in the larger specimen the visceral mass sufficiently shows the details of the colleteric glands and the male genital organs, whilst in the smaller specimen the latter organs have more or less loosened from the other parts of the visceral mass. In both specimens the muscles of the mantle have for the greater part vanished. Notwithstanding the insufficient preservation of the material the sections show distinctly enough that the anatomy of the species is in every respect similar to that of *Galatheascus* striatus. Testes and colleteric glands are found in the neighbourhood of the

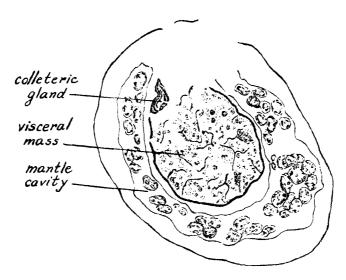


Fig. 2.—Galatheascus minutus, specimen on Galathea nexa. Transverse section. \times 36.

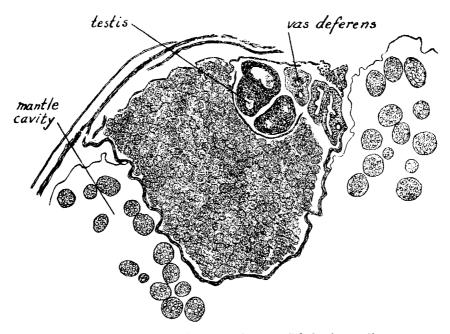


Fig. 3.—Galatheascus minutus, specimen on Galathea intermedia. Transverse section (the greater part of the mantle omitted). \times 50.

stalk. The colleteric glands (fig. 2) are found at each side of the visceral mass; they consist of small sacs with an undivided lumen. The testes (fig. 3) consist of a short straight part and a strongly coiled portion, to which the similarly coiled vas deferents is attached. The closed end of the testes is directed towards the posterior extremity of the body.

In comparison with the narrow mantle opening of the only known specimen of *Galatheascus striatus* this opening in the larger specimen of *Galatheascus* minutus is rather wide.

In both specimens of *Galatheascus minutus* the external cuticle of the mantle is quite smooth; it does not show the longitudinal grooves which are found in the other species of the genus. This cuticle is very thin (thickness approximately 4μ in the larger specimen; in the smaller specimen it is still thinner). On the thin internal cuticle of the mantle no retinacula have been found.

It is not absolutely certain that the specimens described here as Galatheascus minutus are specifically distinct from G. striatus. They differ from the latter species in the smoothness of their external cuticle. The grooves in G. striatus, however, may occur in old specimens only, and if this is so the character is not valid. Notwithstanding this it remains highly probable that the two forms are specifically distinct on account of the striking differences in size.

The smaller specimen of G. minutus is undoubtedly a young animal, but it is not immature, as the mantle cavity contains larvae. These larvae are insufficiently preserved, so that it cannot be demonstrated whether they show any differences from those of G. striatus.

Genus Chlorogaster.

In 1912 Duboseq emphasized the fact that Peltogaster paguri and P. curvatus differ widely from the species until then known as Peltogaster sulcatus and similar forms (which were often regarded as distinct species, e. g., P. longissimus and P. microstoma). The two larger forms have a more or less curved body, which is thicker in the anterior region than in the posterior part; they are usually solitary—only exceptionally are two or three found together on one host. On the other hand P. sulcatus and allied forms have an elongate body, whilst as a rule they occur in great numbers on one host. On account of these differences Duboseq founded the genus Chlorogaster with the type-species C. sulcatus. Guérin-Ganivet (1912) used the same name for this parasite. In two of my previous papers (Boschma, 1927 c, 1928 a) I kept the name Peltogaster sulcatus for this parasite, as the anatomy of the animals (at least as far as concerns the parts of the animal which project outside the host) does not show any striking difference from that of P. paguri and P. curvatus.

In a number of papers Pérez (1928, 1931 a, b, c) has shown that there are other differences between the two groups of parasites than those described by Duboseq (1912). Pérez found that the root system of *Chlorogaster sulcatus* consists of long branches with short ramifications. Each of the long branches

bears a single external sac. Furthermore, he could demonstrate that in each external sac a development of nauplius larvae takes place only once, afterwards the sacs fall off from the abdomen of the host and after the moult of the host new external sacs appear. A corresponding change takes place in the root system : after the external sacs have fallen off, their particular branch of the root system degenerates and the new external sacs originate each from a new branch, budding from the central part of the parasite.

In my opinion these differences are striking enough to justify the view that the elongate slender social forms constitute a separate genus *Chlorogaster*.

CHLOROGASTER SULCATUS (Lilljeborg).

- Peltogaster sulcatus: Lilljeborg (1859), Norman and Scott (1906), Pérez (1927), Boschma (1927 c, 1928 a).
- Peltogaster longissimus : Kossmann (1873), Guérin-Ganivet (1911).
- Chlorogaster sulcatus : Duboscq (1912), Pérez (1928 a, b, 1931 a, b, c, d).
- Chlorogaster longissimus : Guérin-Ganivet (1912).
- For other literature on the species cf. Boschma (1928 a).

Material examined :

- Off Valentia, Ireland, 1870, 4 specimens, detached from the host(s).
- Locality unknown, 3 specimens on (?) Eupagurus bernhardus (L.).
- Zoological Station, Naples, 7 specimens on the abdomen of a Pagurid (collection Norman).
- 40 miles NNW. of Achill Head, Ireland, 220 fms., 3 specimens on *Eupagurus excavatus* (Herbst) (collection Norman).
- Starcross, Devon, Parker coll., 1884, 7 specimens on *Eupagurus cuanensis* (Thomps.) (3 on one host, 4 on another, collection Norman).
- Starcross, Devon, Parker coll., 1884, 35 specimens on 8 hosts of the species Eupagurus cuanensis (Thomps.) (1 host with 9, 3 with 6, 1 with 5, 3 with 1 parasite).

The seven specimens from Starcross (3 on one host, 4 on another) are very small (greater length on an average about 3 mm.). They have a distinct mantle opening, well-developed testes and colleteric glands, but the mantle cavity does not contain eggs. In their anatomy they do not show any differences from larger specimens of *Chlorogaster sulcatus*, so that they undoubtedly belong to this species. There is, however, one peculiarity, which usually is not found in this species, viz., that the external cuticle of the mantle bears excrescences of an irregular shape (fig. 4, a, b). For comparison, parts of the cuticle of specimens from Danish waters (cf. Boschma, 1928 a) have been drawn in the same figure. Usually the cuticle in this species is quite smooth (fig. 4, c-e), but there are some specimens in which the thickness of the cuticle is very variable and therefore highly uneven (fig. 4, f), and other specimens in which the cuticle possesses irregular excrescences (fig. 4, g, h). In one specimen from Starcross (fig. 4, b) the excrescences do not differ greatly from those of the Danish specimens shown in fig. 4, g, h; in the other they are much more strongly pronounced. As they have a more or less characteristic shape only in one of the two specimens from which sections have been made, this peculiarity is probably due to individual variation. A further peculiarity of the

external cuticle of these small specimens is its thickness in comparison to the size of the animals. In full-grown specimens of *Chlorogaster sulcatus* the thickness of the external cuticle usually does not exceed 9 μ , whilst the part of the cuticle drawn in fig. 4, *a*, has a thickness of about 15 μ .

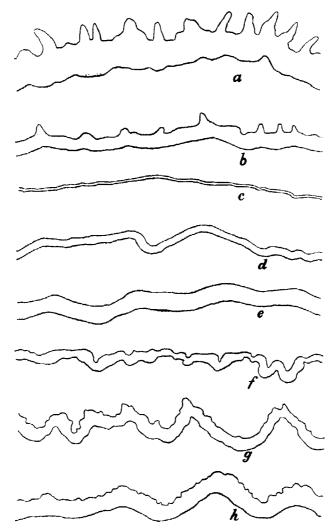


Fig. 4.—Chlorogaster sulcatus. Sections of the external cuticle of the mantle of different specimens. a and b, from two small specimens from Starcross; c, from a specimen on Anapagurus chiroacanthus from Danish waters; d-h, from specimens on Eupagurus cuanensis from Danish waters. $\times 530$.

The other specimens of the collection do not differ noticeably from previously recorded specimens.

Genus Peltogasterella.

The following is an amended diagnosis of the genus, based on the description by Krüger (1912), notes and drawings by Potts (1915), and the material in the British Museum.

Gregarious, body (external sacs) elongate, more or less cylindrical. Mantle opening at the anterior extremity, stalk at the posterior extremity. Mesentery broad (as in *Peltogaster*). Testes in the dorsal part of the visceral mass (next to the mesentery), opening backwards into the mantle cavity. Colleteric glands at the lateral surfaces of the visceral mass, consisting of simple flattened cavities. Nauplius larvae. On Paguridea.

PELTOGASTERELLA SOCIALIS Krüger.

Peltogasterella socialis: Krüger (1912), Potts (1915).
Material examined:
Puget Sound, Friday Harbor, F. A. Potts leg., a great number of specimens on one specimen of *Eupagurus alaskensis* Benedict.

Diagnosis of the species.—Body elongated, anterior part somewhat thicker than the posterior part. Male genital organs and colleteric glands in the posterior half of the body. Testes and vasa deferentia forming a more or less straight tube. External cuticle thin, smooth, without excressences.

The hermit crab with the parasites from the locality given above is probably one of the three specimens figured by Potts (1915, pl. ii, figs. 5–7). I have detached three specimens (external sacs) from their host, which have been cut into series of sections for the study of the anatomy. Two of these specimens have a length of 8.5 mm. and a thickness of 2.5 mm., the corresponding dimensions of the third specimen are 6 and 2 mm. respectively. The specimens are not altogether straight, they are somewhat bent, so that the dorsal surface is slightly concave. The stalk and mantle opening, which are found each at one extremity of the body, are shifted slightly towards the dorsal surface.

The visceral mass is broadly attached to the mantle, forming the mesentery. The musculature, except that of the sphincter of the mantle opening, is feebly developed. In the posterior half of the body, not far from the median region, at each side of the visceral mass the colleteric glands (fig. 5) are found. They are of comparatively large size in the specimens from which sections have been made: the glands consist of flattened sacs with an undivided lumen. Somewhat farther to the posterior region the testes are to be seen, one at each side of the median plane in the dorsal region of the body (fig. 6). Towards the posterior part of the body the testes gradually pass into the vasa deferentia, which, like the testes, have a more or less straight course.

The external cuticle of the mantle is very thin (about 4μ); it is quite smooth and does not show any excrescences. Retinacula have not been found on the thin internal cuticle.

Although it is not absolutely certain that the identification of the specimens is correct, I do not hesitate to unite them with Krüger's *Peltogasterella socialis*,

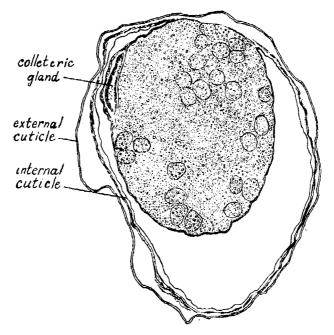


Fig. 5.—Peltogasterella socialis. Transverse section. $\times 36$.

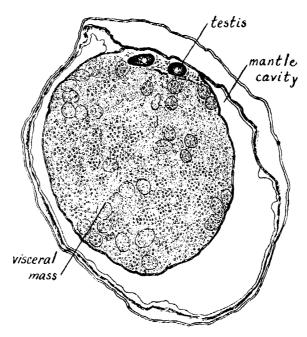


Fig. 6.—Peltogasterella socialis. Transverse section through a more dorsal region than that of fig. 5 (the greater part of the mantle omitted). \times 36.

as was done before by Potts (1915). They possess all the characteristics of the species, and the localities are not so far distinct that this makes it improbable that they belong to the same species : Friday Harbor as well as the Siberian and Japanese localities given by Krüger are parts of the northern region of the Pacific.

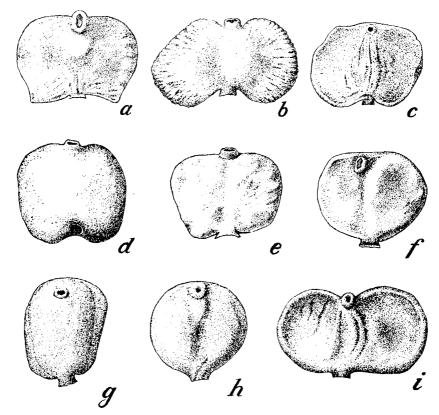


Fig. 7.—a, Sacculina duracina; b, Sacculina confragosa; c, Sacculina pertenuis; d, Sacculina bucculenta; e, Sacculina exarcuata; f, Sacculina hirta; g, Sacculina elongata; h, Sacculina teres; i, Sacculina plana. In all specimens the surface which was turned towards the thorax of the host is represented. The mantle opening is seen in the upper, the stalk in the lower part of the figures. $a, \times 2.8$; $b, c, d, and h, \times 3.2$; $e, f, and i, \times 2.4$; $g, \times 7.2$.

Genus SACCULINA.

SACCULINA DURACINA, sp. n.

Material examined :

Port Molle, Queensland, 14 faths., May 1881, Coppinger coll., 2 specimens on Lambrus longimanus L., presented by the Lords of the Admiralty.

Diagnosis of the species.—Male genital organs in the visceral mass. Testes more or less globular, the one behind the other, enormously enlarged. Colleteric

glands large, with a great number of tubes. External cuticle of the mantle thick (approximately 130 μ), its surface covered with spines, which are arranged in groups on common basal parts. Length of these excrescences approximately 30 μ .

The two specimens do not differ noticeably in shape and size, both of them are slightly oval with pointed edges at each side of the stalk. The breadth of one specimen is 11 mm., its height 9 mm., and its thickness 2.5 mm. In the other

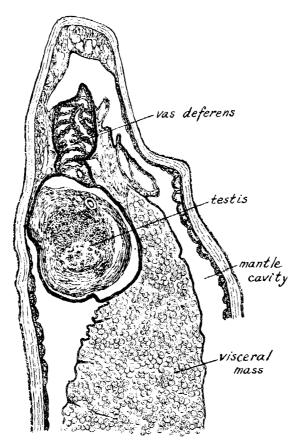


Fig. 8.—Sacculina duracina. Longitudinal section from a region ventral of the stalk. \times 26.

specimen the corresponding measurements are 11, 8, and 3 mm. respectively. The surface of the mantle is somewhat wrinkled, the abdominal surface shows a median concavity where the parasite touched the region of the gut of its host. In one specimen (fig. 7, a) the mantle opening lies at the extremity of a very short tube, in the other it does not project above the surface of the mantle.

One of the specimens has been cut into a series of sections. The study of this series (cf. figs. 8-10) does not reveal at once whether the male genital

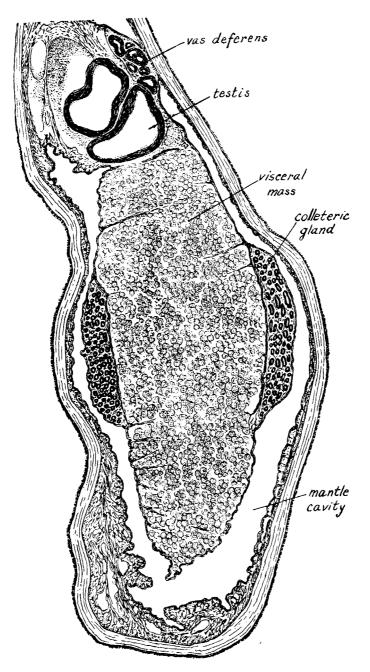


Fig. 9.—Sacculina duracina. Longitudinal section through the region of the stalk. $\times 26$.

organs are found in the visceral mass or in the muscular region in the neighbourhood of the stalk. In the sections represented in figs. 9 and 10 the mantle cavity extends posteriorly about half-way round the testes, in that of the other figure (fig. 8) at one side the mantle cavity reaches somewhat farther than the centre of the testis, at the other side it extends posteriorly much farther than the vas deferens. Undoubtedly the mantle cavity originally extended farther towards the posterior part of the body, but on account of the enormous development of the testes these organs have protruded outside the visceral

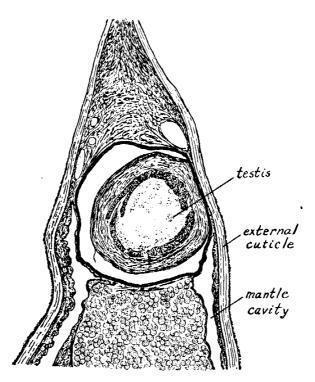


Fig. 10.—Sacculina duracina. Longitudinal section from a region dorsal of the stalk. $\times 26$.

mass and have more or less fused with the mantle, causing a partial obliteration of the posterior part of the mantle cavity. Consequently the testes appear situated more or less outside the visceral mass.

Fig. 8 represents a longitudinal section through the animal, showing the ventral part of one of the testes and the corresponding vas deferens. The wall of the latter possesses a quantity of ridges by which the lumen is reduced to a narrow, more or less tortuous canal. This region of the vas deferens passes into a short tube with a rather thick wall, the lumen of the latter being covered with a distinct layer of chitin. This part of the vas deferens is in direct

contact with the testis; the layer of chitin even projects for some distance into the testis. In fig. 8 the chitinous layer is found in the upper part of the testis; above the testis the short thick-walled part of the vas deferens is visible, and above this part the extremity of the vas deferens with its numerous ridges. The testis itself is a wide sac, which has pushed aside the ovary in the visceral mass, and at the other side almost touches the external cuticle of the mantle.

Towards the median region of the body this testis diminishes in size (in the region between those of figs. 8 and 9 the size of the testis is still larger than in the first figure), and then the second testis appears (fig. 9). In this figure also a part of the vas deferents of this second testis is to be seen. Towards

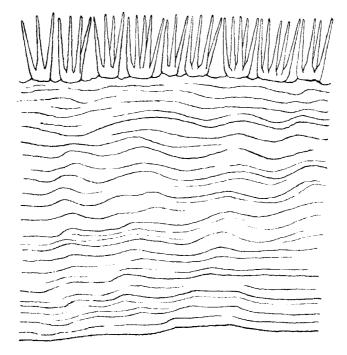


Fig. 11.—Sacculina duracina. Section of the external cuticle. \times 530.

the dorsal region of the animal the second testis gradually increases in size; its greater diameter is reached in the region of fig. 10. Here it almost touches the external cuticle of the mantle; the mantle cavity has been completely pushed aside in the region of this testis.

The colleteric glands (fig. 9), which occupy approximately the central region of the lateral surfaces of the visceral mass, are very large. They consist of a dense mass of narrow branched tubes.

With the exception of the sphincter of the mantle opening the musculature of the mantle is not very strongly developed. In the visceral mass only a few small muscles are seen protruding between the eggs of the ovary, originating from the thin muscular layer which covers the visceral mass.

The external cuticle of the mantle is much thicker than in most species of the genus, its thickness on an average amounts to 130μ in the specimen from which sections have been made. In both specimens the surface of this cuticle is covered with groups of spines arranged on common basal parts. In each group there are comparatively few spines generally from three to five (fig. 11). The spines have a smooth surface; they do not bear lateral hairs. From the basal part up to the extremities of the spines the excrescences have a length of about 30 μ .

Retinacula have not been found.

It is difficult to define the character of *Sacculina duracina*, as this species is more or less an intermediate form between *S. pilosa* and *S. rotundata*. The testes are not embedded completely in the visceral mass, and, on the other hand, they are not found in the posterior part of the body outside the visceral mass. When studying the sections one gets the impression that the testes were originally contained in the visceral mass and that gradually, by developing enormously in size, they protruded from this region till they touched the mantle, causing the posterior part of the mantle cavity to disappear.

As the new species Sacculina duracina represents in some respects an intermediate form between S. pilosa and S. rotundata (though being specifically distinct) the differences of S. duracina with these other species have to be mentioned here. From typical specimens of *rotundata* the new species differs in its peculiar excrescences. When one compares these excrescences with those of the specimens of S. rotundata described in the present paper it is evident at first sight that the excrescences of these specimens, besides being much larger, consist of much more numerous spines. Concerning the variability of the species S. rotundata we have to keep in mind that it still remains a question whether the specimens put together under this name in a previous paper (Boschma, 1931 c) really are representatives of the same species. This question, however, cannot be solved with the material available at present : the variability of a species can be studied only with an extensive material, preferably of parasites of the same host from a more or less restricted locality. Anatomically Sacculina duracina can be distinguished at once from S. rotundata by the different position of the testes.

The specimens belonging to Sacculina duracina cannot be identified with S. pilosa, they at least do not belong to the same species as the 'Siboga' specimens (cf. Van Kampen and Boschma 1925, Boschma 1931 c). Besides the differences in the situation and shape of the male genital organs, the colleteric glands are highly different : in S. pilosa they are rather small and contain comparatively few tubes, whilst in S. duracina they are of large size and contain numerous tubes. Moreover, in the specimens of S. pilosa from the 'Siboga' Expedition the external cuticle of the mantle is comparatively thin (about 20 μ), whilst S. duracina shows exactly the reverse.

In Sacculina vankampeni, S. pilosella, and S. compressa (cf. Boschma, 1931 c) the male genital organs are found in the posterior part of the body, just as in S. rotundata. This distinguishes these species from S. duracina. Moreover. the three species differ from the latter in the shape of their excrescences.

SACCULINA CARCINI Thompson.

Sacculina carcini: Thompson (1836), Boschma (1927 b, c, 1928 b), Pérez and Basse (1928), Popov (1929).

Sacculina similis : Giard and Bonnier (1887).

Sacculina benedeni : Popov (1929).

? Sacculina pauli : Popov (1929).

Portunascus corrugatus : Stebbing (1893).

Grapsisaccus benedeni : Stebbing (1893).

For other literature on the species cf. Boschma (1927 b). Material examined :

Starcross, Devon, Parker coll., 14 specimens on Carcinides maenas (L.) (collection Norman).

Starcross, Devon, 6 specimens on Carcinides maenas (L.) (collection Norman).

Polperro, Cornwall, 3 specimens on Carcinides maenas (L.) (collection Norman).

Wangeroog (S. of Heligoland), R. J. McKay don., Feb. 10, 1855, 1 ex. on Carcinides maenas (L.).

Oban, Scotland, 3 specimens on Carcinides maenas (L.) (collection Norman).

- Starcross, Devon, 1883, 5 specimens on Carcinides maenas (L.) (collection Norman).
- St. Leonards (near Hastings), 1888, 1 specimen on Portunus holsatus Fabr.

Lowestoft, B. B. Woodward don., 3 specimens on Portunus holsatus Fabr.

Falmouth Harbour, July 1884, 1 specimen on Portunus arcuatus Leach (collection Norman).

Hastings, Oct. 26, 1906, E. T. Connold don., 1 specimen on Pisa armata (Latr.).

The material of this species is interesting in so far as it contains a specimen on Portunus arcuatus Leach, a form which previously has been mentioned as a distinct species (Sacculina similis) by Giard and Bonnier (1887). Sections of this specimen proved that it does not differ in any respect from the specimens living on Carcinides maenas: the testes are united for a considerable part of their extent and occupy the same place as those of typical specimens; also the colleteric glands correspond in place, size, and structure with those of the parasites of Carcinides maenas.

Besides this specimen those on Portunus pusillus are interesting. These parasites were first mentioned by Delage (1884), and afterwards Guérin-Ganivet (1911) stated that the anatomical peculiarities of these animals correspond closely with those of the parasites of Carcinides maenas; accordingly he regarded them as representatives of the species Sacculina carcini. From one of the specimens on Portunus pusillus of the present material sections have been made which show also that the anatomical particulars are the same as those of typical specimens.

The specimens on Carcinides maenas and on Portunus holsatus do not differ noticeably from those previously known to occur on these crabs. The size and shape of these animals is rather variable; some have an oval shape, in 35

LINN, JOURN, -ZOOLOGY, VOL. XXXVIII

others the anterior margin possesses well-developed protrusions at the dorsal and ventral angle.

Stebbing (1893) mentions the names Portunascus corrugatus Giard and Grapsisaccus benedeni Kossmann as hosts of certain Cryptoniscidae. Evidently the parasites of Portunus corrugatus and of Pachygrapsus marmoratus are meant by these names. According to Smith (1906) the name Sacculina corrugatus was given by Giard to the parasite of Portunus corrugatus; I have, however, not been able to find this name in any of Giard's papers which I have seen. Kossmann (1872) gave the name Sacculina benedeni to the parasite of Pachygrapsus marmoratus. This form corresponds in every respect with the specimens of Sacculina carcini living on Carcinides maenas, and in all probability the parasite of Portunus corrugatus also does not differ from typical specimens of Sacculina carcini. Concerning the generic names Portunascus and Grapsisaccus I have not found any remark in publications by Stebbing and by Giard. It seems justified to regard them as synonyms of Sacculina carcini only.

The specimen on *Pisa armata* from the present collection is more or less globular; its dimensions are: breadth 18, height 16, and thickness about 8 mm. The region of the narrow mantle opening, which is turned towards the abdomen of the host, does not project noticeably above the surface.

In the English summary of his paper in the Russian language Popov (1929) enumerates three species of Sacculina, viz., S. carcini, S. benedeni, and the new species S. pauli. According to Popov in the Bay of Sevastopol S. carcini occurs rarely on Carcinides maenas, more often on Pachygrapsus marmoratus. A still more common parasite of the latter erab is S. benedeni. Popov does not mention the differences between these two "species" of Sacculina, and as I have not found any anatomical or structural differences between the two forms (cf. Boschma, 1927 b) I am convinced that they are not specifically distinct. The same probably holds good for the specimens described by Popov as Sacculina pauli (living on Brachynotus lucasi). Sacculina pauli differs from S. carcini in its mantle opening, which is extremely wide and surrounded by a high rugged cylinder. In my material of the parasites on Brachynotus lucasi (from the neighbourhood of Barcelona, cf. Boschma, 1927 b) this feature is not so pronounced. The anatomy and the structure of the cuticle of the specimens I have examined do not differ in any respect from those of specimens from Carcinides maenas. As Popov does not give any particulars of the anatomy of his specimens it remains to be proved whether they constitute a distinct species or not. For the present I am inclined to doubt this.

SACCULINA SINENSIS, sp. n.

Material examined :

Hongkong, Barney coll., 8 specimens on three specimens of *Leptodius exaratus* (M.-E.) (1 host with 5, 1 with 2, 1 with 1 parasite).

Diagnosis of the species,-Male genital organs in the visceral mass. Testes

more or less globular, completely separated. External cuticle covered with smooth slender hairs, which are loosely distributed on the surface and vary in length between 10 and 30 μ .

Four of the five specimens which are attached to the abdomen of the same host have approximately the same size, the fifth specimen is much smaller than the others (Pl. 7, fig. 12). The approximate dimensions of the four larger specimens are : breadth 4.5 to 5 mm., height 4 mm., and thickness 2 to 2.5 mm. These specimens have a more or less roundish-oval shape; the mantle opening lies at the extremity of a small flattened tube. In some of these animals the mantle is irregularly folded and wrinkled, probably as a result of preservation. The fifth specimen is more or less globular and its dimensions do not exceed 2 mm. in any direction. In the figure this small specimen is visible between two of the larger ones, at the left side of the abdomen of the host.

The two parasites which are attached to the abdomen of another host are of about equal size and shape. One of these has a breadth of 8.5 mm., a height of 6.5 mm., and a thickness of 4.5 mm., in the other specimen these dimensions are 8, 6.5, and 4 mm. respectively. In these specimens the anterior part is broader than the posterior region, consequently they are somewhat triangular in shape. The mantle is more or less wrinkled like that of the other specimens. One of the two parasites is attached to the extremity of the abdomen; its chief axis is parallel to that of its host. The surface of this parasite which was lying against the thorax of the host is more or less flat, the other surface shows a short concavity caused by the pressure of the abdomen of the crab against the parasite. The other specimen on the same host is attached to the median region of the abdomen and is directed towards the right side of its host. Both specimens are as little covered by the abdomen of the crab as those represented in Pl. 7, fig. 12.

The last specimen of the collection is intermediate in size between the other animals. It has a more or less circular shape; the dimensions are : breadth 6, height 5.5, and thickness 2.5 mm. The region of the mantle opening does not project above the surface of the mantle. The specimen is attached symmetrically to the abdomen of its host, so that a median groove is present at the posterior part of the surface which touches the abdomen of the crab.

Sections have been made from one of the larger specimens and from one of the four parasites which have a height of about 4 mm.

The male genital organs lie in the posterior part of the visceral mass (fig. 13). The testes are more or less globular ; they pass rather abruptly into the vasa deferentia. The latter at first consist of narrow canals, but towards the ventral part of the animal they obtain a wider lumen of irregular shape, as a result of ridges on the inner walls. The male genital organs consequently consist of a thicker dorsal and ventral part (the testes and the terminal part of the vasa deferentia), connected by a narrow tube. In the smaller specimen the testes of both sides do not differ noticeably in size ; in the larger specimen one of the testes is much larger than the other. The colleteric glands (fig. 14) lie approximately in the central part of the lateral surfaces of the visceral mass, somewhat nearer to the anterior than to the posterior region. They contain a fairly large number of comparatively narrow tubes.

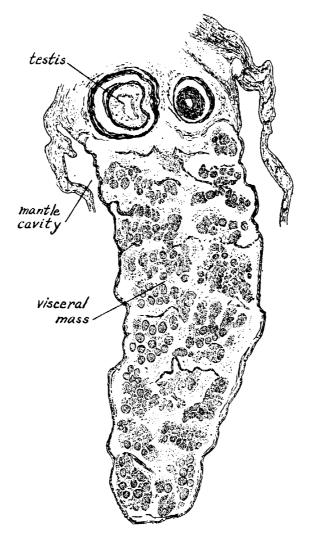


Fig. 13.—Sacculina sinensis. Longitudinal section through the visceral mass, showing the testes. \times 36.

In the visceral mass besides the developing eggs of the ovary a few muscular elements are to be seen. With the exception of the well-developed sphincter of the mantle opening the mantle is not strongly muscular.

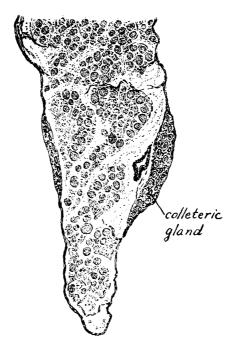


Fig. 14.—Sacculina sinensis. Anterior part of a longitudinal section through the visceral mass, showing the colleteric glands. \times 36.

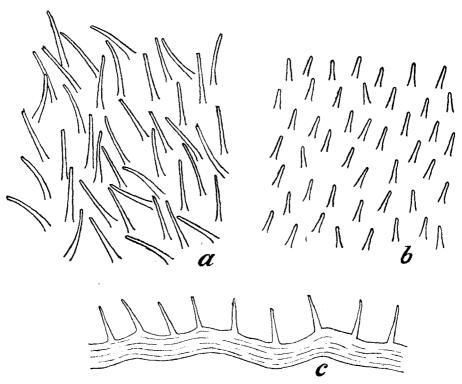


Fig. 15.—Sacculina sinensis. a, excrescences as they are distributed on the external cuticle from one of the larger specimens; b, the same from one of the four smaller specimens; c, section through the external cuticle of the same specimen. × 530.

In the larger specimen from which sections have been made the thickness of the external cuticle of the mantle varies from 15 to 40 μ , in the smaller specimen this thickness on an average amounts to 12 μ . In all specimens the external cuticle is covered with slender hairs, which differ in length in the various individuals and also in different parts of the mantle of each specimen. These hairs may attain a length of 30 μ (fig. 15 *a*), in other cases they are much shorter, even hairs of a length of about 10 μ occur (fig. 15 *b*). The hairs do not differ in structure from the main layers of the cuticle; they are comparatively loosely distributed on the surface of the cuticle. As a rule, the surface of the hairs is quite smooth, but sometimes small lateral hairs may be seen near the extremities.

Retinacula could not be detected in the parts of the internal cuticle examined for this purpose.

There are a number of species of the genus Sacculina, viz. S. carcini, S. weberi, S. nodosa, S. muricata, and S. microthrix, the four last-named described by the author in previous papers (Boschma, 1931 a, c, d), which correspond with Sacculina sinensis in having the external cuticle of the mantle covered with hairs or spines and by the position of the male genital organs, which are embedded in the visceral mass. These species may be distinguished from each other as shown in the following key :—

Testes partially united.

Excrescences of the cuticle with a small number of stiff lateral hairs, especially on the basal parts	weberi.
Excrescences of the cuticle without lateral hairs or covered with soft	
lateral hairs, which are more or less evenly distributed over the	
whole of their length.	
Excrescences short (to 18 μ)	carcini.
Excrescences longer (20–35 μ)	nodosa.
Testes completely separated.	
Testes more or less globular.	
Excrescences 3–8 μ long, densely arranged on the cuticle	microthrix.
Excrescences rather loosely distributed on the cuticle, 10–30 μ long	sinensis.
Testes more or less cylindrical	muricata.

SACCULINA CONFRAGOSA, sp. n.

Material examined :

Misaki, Japan, Alan V. Insole, Dec. 23, 1921, 2 specimens on *Pachygrapsus crassipes* Randall.

Diagnosis of the species.—Male genital organs in the visceral mass. Testes partially united. Dorsal extremity of the testes curved ventrally. Colleteric glands with a fairly large number of tubes, near the anterior part of the visceral mass. External cuticle smooth, with distinct small irregular areas with a diameter of 8–18 μ . Retinacula composed of a basal part and a small number (3 to 4) of spindles, which have a length of 10 μ approximately.

The two specimens differ in size, but not noticeably in shape. One of them

has a breadth of 19.5, a height of 13, and a thickness of 5 mm.; the corresponding dimensions of the other specimen (fig. 7, b) are 12, 7, and 3 mm. respectively. In both specimens the thoracal surface is more or less flat;

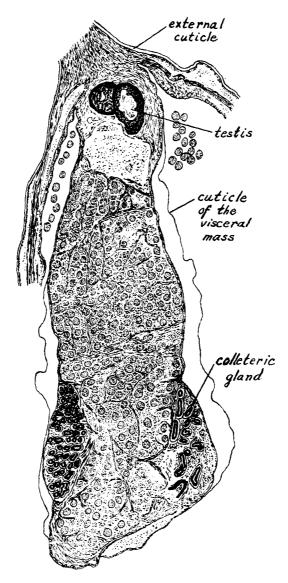


Fig. 16.—Sacculina confragosa. Longitudinal section through the visceral mass of the larger specimen. $\times 18$.

the abdominal surface has a median depression, which in the larger specimen is restricted to the region of the stalk, whilst in the smaller specimen it extends from the stalk to the neighbourhood of the mantle opening. In the median region of the body the height is smaller than that of the parts projecting at each side of the median plane of the host (i.e. the dorsal and ventral part of the parasites). The mantle opening is found at the extremity of a small tube. The surface of the mantle is more or less rough, uneven, and dimpled, especially in the ventral and dorsal regions.

The shape of the male genital organs is so peculiar that, after studying the sections of one of the animals, I thought that these organs were abnormal. Afterwards a series of sections was made from the second specimen, which show that in this animal corresponding features occur, so that the aberrant shape of the testes is in all probability a specific character. The shape of these organs may therefore be described here in some detail.

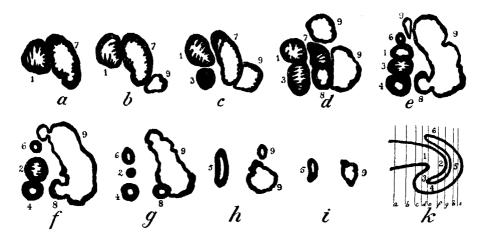


Fig. 17.—Sacculina confragosa. Transverso sections through the testes of the larger specimen in different regions of the body. The wall of the testes is drawn in black. a represents a section of the region of fig. 16, the following sections are nearer to the dorsal region, fig. i represents the extreme dorsal part of the testes. Fig. k indicates diagrammatically the plane of each of the sections. $\times 18$.

The male genital organs are found in the posterior part of the visceral mass. The testes are for the greater part of their length more or less cylindrical, passing gradually into the vasa deferentia. The latter parts of the genital organs are of fairly large size; their lumen, however, is rather narrow, as there are numerous ridges on the inner wall. In their ventral part the two testes are closely united, but the cavities remain completely separated (figs. 16 and 17, a, b). Gradually the testes again diverge towards the lateral regions of the visceral mass; in their dorsal part the two testes do not touch each other.

In the two specimens the dorsal extremities of the testes are different. In the smaller specimen the dorsal extremities of both testes are recurved

in a ventral direction, so that in longitudinal sections through the extreme dorsal part of the testes two separate cavities at each side of the visceral mass are to be seen (more or less as in fig. 17, d, with the exception of the two wide cavities at the right side of the figure, indicated by 9).

In the larger specimen the shape of the testes is much more complicated (cf. fig. 17). The dorsal extremity of the left testis (which is drawn in fig. 17 at the left side of the figures) has approximately the shape represented diagrammatically in fig. 17, k (the different parts of the testis are, however, more closely joined than drawn in this diagram). The numbers in this figure correspond with those of the other figures, the lines of fig. k represent the sections drawn in the other figures. At its extremity the left testis first is bent in anterior direction, projecting somewhat towards the ventral region; then it is recurved and at its extremity again bent towards the dorsal region. Consequently in some of the sections the lumen of the left testis can be seen as many as four times (fig. 17, e). For further particulars on the shape of this testis I refer to fig. 17. The numbers I to 6 in figs. a-i correspond with the numbers in the diagram k.

The testis of the right side also is somewhat curved, but the curve does not extend towards the ventral region; it is directed more or less towards the anterior region. In the sections of the dorsal part of this testis the cavity consequently has an oblong shape (this part is indicated by 7 in the figures). After this curve in anterior direction the right testis continues its course towards the dorsal region (indicated by 8 in the figures). This testis shows another peculiarity : connected with the extreme dorsal part there is a wide extension of the lumen, projecting as a voluminous pouch in a lateral direction (indicated by 9 in the figures). In figs. e and f the connection of this part with the main canal of the testis is visible.

All the sections of fig. 17 are from the dorsal half of the body, the section represented in fig. 16 lies somewhat nearer to the ventral surface than that of fig. 17, a.

The colleteric glands (fig. 16) are found at a short distance from the anterior part of the visceral mass. In the figure the median plane of the right colleteric gland and a part of the genital atrium of this side is visible; from the left colleteric gland a more marginal section is to be seen. The glands are fairly large and contain a great number of branched tubes.

The mantle is provided with a well-developed transverse musculature and the mantle cavity is surrounded by a strong sphincter.

With the exception of the irregular small furrows and dimples which are visible to the naked eye and cause the more or less roughened appearance of the specimens there are no excrescences of the external cuticle of the mantle. When strongly enlarged it appears to be quite smooth. On its surface the cuticle shows neat little areas with irregular contour, as they occur also in many other species of Sacculinidae with a smooth cuticle (fig. 18, a). The diameter of these areas varies between 8 and 18 μ .

In the larger specimen the average thickness of the external cuticle is about 25μ , in the smaller specimen it is much thinner (12μ) .

The internal cuticle of the mantle is covered with retinacula, which are more or less evenly distributed on the chitinous layer. They consist of a basal part, which is comparatively long, and a small number (usually 3 or 4) of spindles which possess small barbs (fig. 18, b, c). In the larger specimen the spindles have a length of about 13μ ; those of the smaller specimen are somewhat shorter (9 μ approximately).

Among the species of the genus *Sacculina* which have male genital organs embedded in the visceral mass there are, besides *Sacculina confragosa*, a number of other species which have a smooth cuticle or excrescences of a very insignificant character. It is rather difficult to find specific characteristics for these

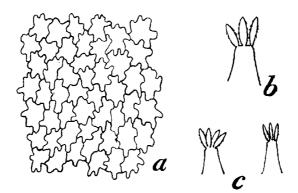


Fig. 18.—Sacculina confragosa. a, surface of the external cuticle of the larger specimen; b, retinaculum of the same specimen; c, retinacula of the smaller specimen. $\times 530$.

species, as many of them are very similar in their internal structure. The following is a synopsis of these species :---

Dorsal extremities of the testes curved in ventral direction, this part some- times with a lateral pouch Dorsal extremities of the testes more or less straight, not curved in ventral direction.	confragosa.
Dorsal parts of the two testes united into a single tube with a com- paratively wide lumen	pertenuis.
Ventral parts of the two testes lying close together, the two testes being separated by a thin septum only, or cavities of the ventral parts of the testes communicating.	
External cuticle with small ridges (height of these ridges $1-2 \mu$) External cuticle smooth or somewhat rough, without ridges.	caelata.
Ventral parts of the testes widely communicating, dorsal parts of the testes distinctly separated	scabra.
of the testes separated by a thin septum only Each of the testes with a comparatively thick wall, so that also in their	glabra.
ventral part they are completely separated	bucculenta.

One of the species in this key, S. glabra, has been described by Van Kampen and Boschma (1925), two in previous papers by the author (S. caelata Boschma 1931 a, S. scabra Boschma 1931 c), the other three are new species described in the present paper.

Among the six species in the key given above Sacculina confragosa alone shows the exceptional feature of the curved testes, and the character is perhaps of sufficient importance to warrant its separation as the type of a new genus. It cannot be placed in the genus Drepanorchis, on account of its complete mesentery, nor in Loxothylacus, for the visceral mass is directly attached to the muscular region which forms the base of the stalk. Moreover, the bent shape of the dorsal part of the testes seems to be somewhat variable : in one specimen both testes are curved in a ventral direction, in the other one is very slightly curved, the other has a double curve. For the present I keep the species in the genus Sacculina, though it differs from typical species of the genus in a very important character.

SACCULINA PERTENUIS, sp. n.

Material examined : Gulf of Suez, R. McAndrew, 1 specimen on *Pinnotheres* sp.

Diagnosis of the species.—Male genital organs in the visceral mass. Testes almost completely united, forming a single cylindrical tube with two vasa deferentia. Colleteric glands more or less hemispherical, with a fairly large quantity of tubes. External cuticle smooth, without distinct areas.

The specimen (fig. 7, c) is much flattened, especially in the dorsal and ventral parts. Its dimensions are: breadth 9, height 6.5, and thickness 2 mm. Apart from some grooves and irregular wrinkles, the surface of the mantle is quite smooth. At the abdominal surface there is a concavity in the neighbourhood of the stalk, caused by the pressure of the region of the gut of the crab against the parasite. The region of the narrow mantle opening does not project noticeably above its surroundings.

A series of longitudinal sections has been made from the only available specimen. The most peculiar feature of the anatomy is that of the united testes. These organs are found in the posterior part of the visceral mass (fig. 19). For the greater part of their extent they form a single tube, which in the extreme dorsal part gradually diminishes in size (fig. 20, e-h). The two vasa deferentia are separated (fig. 20, a). Soon after the vasa deferentia have passed into the testes the latter organs unite and their cavities communicate with each other. At first they are more or less, though imperfectly, separated (fig. 20, c), but towards the dorsal part the cavity does not show any more visible traces of the fusion of the two organs.

The colleteric glands (fig. 19) are of moderate size, they contain a fairly large number of branched tubes. These glands are found in the anterior half of the lateral surfaces of the visceral mass.

With the exception of the sphincter, which surrounds the mantle cavity, the mantle is not strongly muscular.

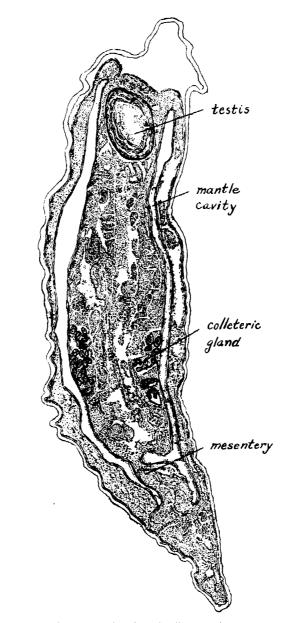


Fig. 19.—Sacculina pertenuis. Longitudinal section (the external cuticle of the mantle is much thinner than drawn in this figure). $\times 26$.

The surface of the external cuticle of the mantle, which has a thickness of approximately 10μ , does not show any special feature by which the species might be characterized. The cuticle is quite smooth, and does not show small areas such as are found in many other species of the family which have a smooth cuticle.

Retinacula could not be found on the parts of the internal cuticle of the mantle examined for this purpose.

The new species Sacculina pertenuis can be easily distinguished from S. scabra by the different shape of its testes. In S. scabra the testes are united in their ventral part only, the dorsal parts projecting separately in the visceral mass. The same holds true for the other species in the key on p. 498; in none of them are the testes as completely united as in S. pertenuis. For the other characters by which the species may be distinguished from related forms I refer to this key.

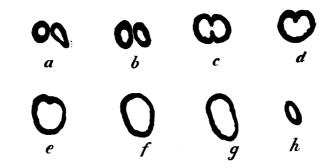


Fig. 20.—Sacculina pertenuis. Transverse sections through the male genital organs in different regions of the body. a, ventral region, showing the vasa deferentia; h, extreme dorsal part of the two united testes. The wall of the genital organs is drawn in black. $\times 16$.

SACCULINA BUCCULENTA, sp. n.

Material examined :

Martaban (Lower Burmah), E. W. Oates, 1888, 1 specimen on *Micippe mascaronica* Kossm.

Diagnosis of the species.—Male genital organs in the visceral mass. Testes completely separated. Colleteric glands in the anterior half of the visceral mass, with a fairly large number of tubes. External cuticle of the mantle not very thin (thickness from 15 to 30 μ), smooth, with distinct areas (diameter of these areas 8–18 μ). Retinacula with a basal part and 4–5 spindles, which have a length of about 7.5 μ .

The specimen (fig. 7, d) is somewhat inflated; it has a more or less circular shape. Its dimensions are : breadth 9, height 8, and thickness 5 mm. The mantle does not possess any grooves or wrinkles, only at the abdominal surface

there is a pronounced concavity at the region where the parasite touched the ridge marking the position of the gut of the crab. The mantle opening lies at the extremity of a short compressed tube in the median plane of the parasite.

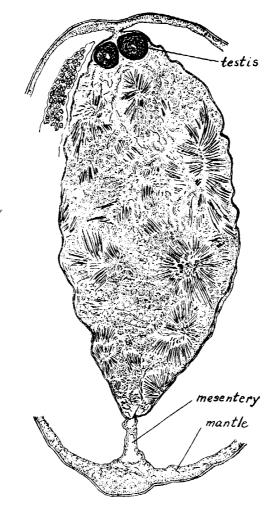


Fig. 21.—Sacculina bucculenta. Longitudinal section (the greater part of the mantle omitted). $\times 18$.

A series of longitudinal sections has been prepared from the specimen. The testes are more or less cylindrical tubes which gradually pass into the vasa deferentia. The dorsal region of the male genital organ is the more voluminous part; from here they taper gradually towards the male genital openings. The two testes remain completely separated for the whole of their course, and are of about equal size and length (fig. 21).

The colleteric glands (fig. 22) are found in the anterior half of the visceral mass. Relative to the size of the whole visceral mass the colleteric glands are comparatively small. They contain a fairly large number of branched tubes.

The specimen possesses a well-developed sphincter of the mantle opening; the other parts of the mantle are not strongly muscular. The visceral mass is surrounded by a thin muscular layer. A strange peculiarity of this specimen is the large quantity of muscles in the visceral mass. There are many groups of muscles, the components each radiating from a common centre and terminating freely in the visceral mass (figs. 21, 22). A considerable portion of the visceral mass is occupied by these queer muscles; there are merely

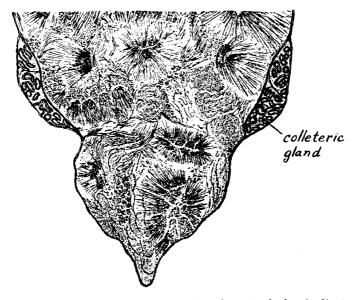


Fig. 22.—Sacculina bucculenta. Anterior part of a longitudinal section through the visceral mass. $\times 26$.

a few regions left where developing eggs can be seen. Probably this excessive development of the musculature in the visceral mass is not a normal character of the species. It may have arisen as a result of a kind of degeneration of the ovary of this specimen. Only a comparatively short time before the specimen was preserved, however, a great quantity of eggs had been extruded from the ovary, for the mantle cavity contains numerous embryos in the egg-membranes. The function of the ovary therefore was not diminished by the excessive development of the musculature.

The external cuticle of the mantle has a thickness of 15 to 30μ ; its surface is quite smooth. When strongly enlarged the surface is seen to be divided into small areas with an irregular contour, which have a diameter of 8-18 μ (fig. 23, a).

The internal cuticle of the mantle bears retinacula which are evenly distributed on its surface. They consist of a basal part and 4 to 5 spindles on which no barbs could be detected (fig. 23, b). The spindles have a length of approximately 7.5 μ .

In a previous part of this paper (p. 498) I have given a key to the species of *Sacculina* which have the male genital organs embedded in the visceral mass and have a smooth cuticle or a cuticle with very insignificant excressences. For the differentiation of *S. bucculenta* from the other species which possess these characters I refer to this key.

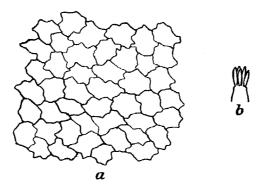


Fig. 23.—Sacculina bucculenta. Surface of the external cuticle of the mantle and retinaculum. \times 530.

SACCULINA ROTUNDATA Miers.

Sacculina rotundata: Miers (1880), Boschma (1931 c).
p.p. Sacculina pilosa: Van Kampen and Boschma (1925), Boschma (1928 b).
Sacculina aculeata: Boschma (1928 b).
Material examined:
Malaysia, Bleeker collection, 1 specimen from the abdomen of Eriphia laevimana Latr.

Goram Islands, W. Stalker coll., 1 specimen on Eriphia ? scabricula Dana.

In a previous paper (Boschma, 1931 b) I described the chief particulars of seven specimens from six different localities, which I referred to the species *Sacculina rotundata*. The specimens were different in some respects, but it was impossible to decide whether some of them should be regarded as distinct species or not. The material is too scanty to study the variability of those which without any doubt belong to *S. rotundata*.

It is almost certain that both specimens in the British Museum belong to $Sacculina \ rotundata$. The specimen on *Eriphia laevimana* is undoubtedly the type of the species, while that on *E.* ? scabricula corresponds closely with

'typical' specimens. The chief peculiarities of each specimen are described below :---

(1) The specimen on Eriphia laevimana.

A fragment only is present in the collection of the British Museum, viz. about half of the mantle; the visceral mass is completely lost. The specimen is labelled: 'Saculina rotundata from abdomen of Eriphia laevimana \mathcal{F} , Malaysia, Dr. Bleeker's coll., 80.15.' This is sufficient evidence that the specimen is the type of Sacculina rotundata described by Miers (1880). It is a fortunate fact that at least a part of this specimen has been preserved, for the excrescences of the external cuticle have been described by Miers in a rather general manner. He writes (Miers, 1880, pp. 470-471):—' The integument is armed with numerous minute spicules, which are most abundant and conspicuous near the distal opening, but quite imperceptible except under the

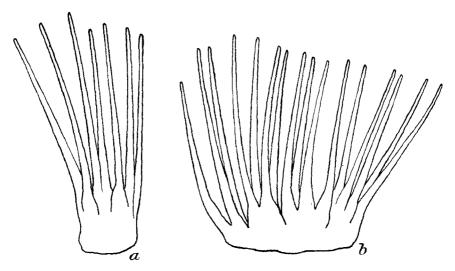


Fig. 24.—Sacculina rotundata. Excrescences of the external cuticle of the type-specimen. $\times 530$.

microscope. They seem to be rooted in the cellular tissue, beneath the outer cuticle, and furthermore differ from the spinules of *S. corculum*, and more nearly resemble the infra-cuticular spicules of *S. crucifera*, Kossmann, in being very slender, not broader at base; their apices are somewhat blunt. Such, at least, is the form of spicules taken from the vicinity of the distal opening of the sac (pl. xv, fig. 19)'. In these statements no mention has been made of the arrangement of the excrescences in groups on common basal parts, and also Miers's figure does not show distinctly that such an arrangement exists.

The part of the mantle which has been preserved is very brittle, but the excrescences are distinctly visible. They consist of a rather large number of long blunt spines, which are arranged on a common basal part (fig. 24). LINN. JOURN.-ZOOLOGY, VOL. XXXVIII 36 In the portions of the cuticle examined in this respect the length of the excrescences (from the base up to the extremities of the spines) varies from 90 to 120 μ .

Retinacula could not be found.

The anatomy of the specimen is completely unknown. Miers does not give any details, and, as stated before, the visceral mass is now lost. Notwithstanding this, it is almost certain that *Sacculina rotundata* has the characters

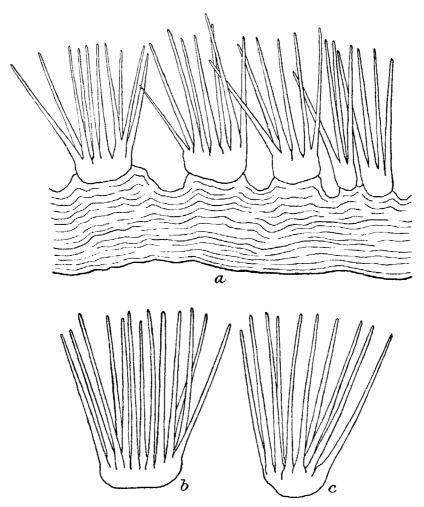


Fig. 25.—Sacculina rotundata. Section through the external cuticle, and excrescences from another part of the cuticle of the specimen on Eriphia? scabricula. $\times 530$.

given in a previous paper (Boschma, 1931 c). In three specimens identified as S. rotundata (one from the 'Siboga' Expedition and two from the Leiden Museum), all of which were parasites of Eriphia laevimana, the excressences of the cuticle are shaped almost exactly like those of the type-specimen, which

also was a parasite of *Eriphia laevimana*. When two or more specimens of *Sacculina* are parasites of the same host this fact does not yet indicate that they belong to the same species, but in this case the fact affords strong evidence of their identity. The excrescences of the cuticle correspond so closely in the four parasites from the same host that we may safely conclude that the anatomical characters of the type must have been like those of the other specimens, in which it could be studied.

(2) The specimen on Eriphia ? scabricula.

The parasite has a more or less oval shape, its dimensions are : breadth 6, height 4, and thickness 2.5 mm. The surface of the mantle shows some grooves, but there is not a concavity in the abdominal surface, owing to the fact that the parasite was attached near the extremity of the abdomen of the host, so that it was not covered by this part. The mantle opening lies on the thoracal surface, not far from the anterior margin; its surroundings do not project above the rest of the mantle.

As in the other specimens of *Sacculina rotundata* the male genital organs are found in the vicinity of the stalk, embedded in the muscular tissue between the stalk and the mesentery. One of the testes is somewhat larger than the other. The comparatively flat colleteric glands occupy the central parts of the lateral surfaces of the visceral mass. These glands contain a fairly large number of branched tubes.

The external cuticle of the mantle has a thickness of about 40 μ , it bears excressences of the typical shape. The length of these excressences (from their basal part to the extremities of the spines) may amount to 90 μ ; in some parts of the mantle, however, they are much shorter. Usually the excressences are composed of a large number of spines, but in some parts of the mantle they are somewhat smaller and possess a few spines only (fig. 25). The spines have a blunt extremity and do not bear lateral hairs.

There are no retinacula on the parts of the internal cuticle examined for this purpose.

SACCULINA EXARCUATA Kossmann.

Sacculina exarcuata : Kossmann (1874), Boschma (1927 a).
 Material examined :
 Shanghai, Jamrach, 1 specimen on Lambrus validus de Haan.

Diagnosis of the species.—Male genital organs in the posterior part of the body, outside the visceral mass. Testes more or less cylindrical, completely separated, gradually passing into the vasa deferentia. Colleteric glands almost hemispherical, in the central region of the lateral surfaces of the visceral mass. External cuticle covered with hairs or papillae which differ somewhat in length and shape in different specimens : usually they have a length of 18 μ approximately, in some specimens they are very short (12 μ) or very long (to 35 μ). Retinacula usually with a single spindle, sometimes with two or three. The length of the spindles varies between 13 and 23 μ ; they do not bear barbs.

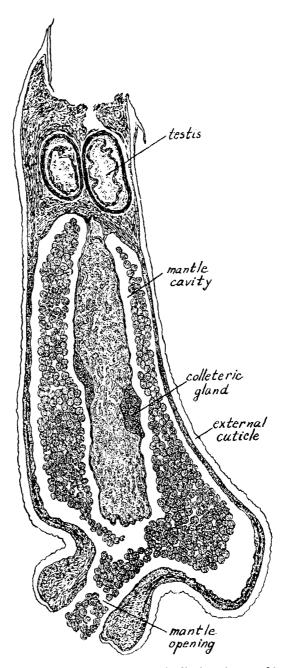


Fig. 26.—Sacculina exarcuata. Longitudinal section. $\times 18$.

The diagnosis given above is partially based on the specimen in the British Museum, partly on specimens to be described in a later paper from the collection of the Museum of Comparative Zoology at Harvard College, Cambridge, Mass.

The specimen in the British Museum (fig. 7, e) has a breadth of 12, a height of 9, and a thickness of 4 mm. It has a more or less oval shape and a comparatively smooth surface. The surface which was turned towards the abdomen of the host shows a concavity caused by pressure of the median ridge of the abdomen of the crab. The mantle opening lies at the extremity of a short conical tube at the anterior margin.

From this specimen a series of longitudinal sections has been made, which shows that the male genital organs are found outside the visceral mass. These organs (fig. 26) occupy the central part of the muscular region between the stalk and the visceral mass. The testes are short, but more or less cylindrical, the vasa deferentia are narrow straight canals. At the place of connection of these canals with the testes there is a slight curve in a lateral direction. Both testes are of approximately equal size ; their lumen is rather wide, but not enlarged excessively.

The colleteric glands (fig. 26) are situated at a short distance from the central parts of the lateral surfaces of the visceral mass, somewhat nearer to the anterior than to the posterior part. They are of moderate size and consist of numerous branched tubes. In the specimen from the British Museum these glands do not contain any chitinous matter. Probably a very short time before the parasite had been preserved the eggs had been extruded from the ovary into the mantle cavity, so that the formation of a new chitinous layer in the tubes of the colleteric glands had not yet taken place. The structure of these glands is, therefore, not so distinct as in many other specimens of Sacculinidae.

The visceral mass is more or less shrivelled as a result of the extrusion of the eggs. In the greater part of the mantle there are a few muscular elements only, except in the region surrounding the mantle opening where a strong sphincter is found. In the posterior part of the body, including the parts of the mantle in the vicinity of the stalk, a well-developed musculature is also present.

The thickness of the external cuticle of the mantle varies from 40 to 120μ . Its surface is rather dirty, but in several spots the excressences of the cuticle are visible in sufficient detail. The cuticle is covered with hairs which gradually diminish in thickness towards their extremity and vary in length between 22 and 28μ . These excressences bear numerous minute lateral hairs (fig. 27, a, b).

Great numbers of retinacula are found more or less regularly distributed on the internal cuticle of the mantle (fig. 27, c, d). They do not possess a pronounced basal part, but usually consist of one spindle, sometimes of two or three. The spindles have a length of approximately 17 μ , and they are not barbed. It is not altogether certain that the specimen dealt with here belongs to *Sacculina exarcuata*, but comparison with those in the Museum of Comparative Zoology at Harvard College makes it highly probable, especially as the specimen shows the characters of the species as given by Kossmann (1872).

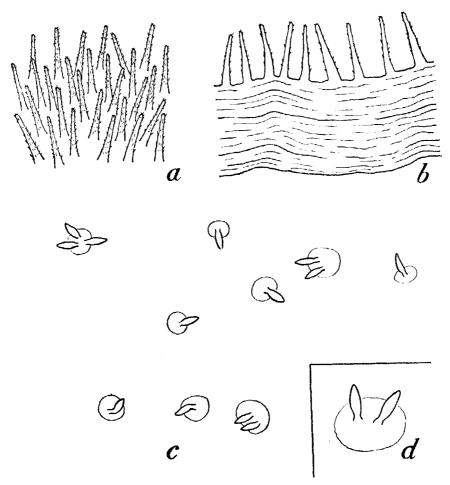


Fig. 27.—Sacculina exarcuata. a, excressences as they are distributed on the external cuticle; b, section through the external cuticle; c, retinacula as they are distributed on the internal cuticle; d, a single retinaculum. a, b, and d, $\times 530$; c, $\times 290$.

In a group of species of the genus *Sacculina* the following common characters occur: Male genital organs in the posterior part of the body, testes more or less cylindrical, gradually passing into the vasa deferentia, testes of both sides completely separated, external cuticle covered with hairs or spines which have the same structure as the main part of the cuticle. Besides *Sacculina*

exarcuata this group includes S. atlantica, S. hispida, S. comosa,	and S. micr-
acantha, described in previous papers (Boschma 1927 b, 1928 b, 1	1931 c). The
differential characters of these species are summarized in the follo	wing key :—
External cuticle covered with short spines (length 2–3 μ)	micracantha.
External cuticle covered with longer hairs or spines or with comparatively	
long papillae.	
Mantle opening surrounded by a circular area with a very thin external	
$\operatorname{cuticle}$	atlantica.
External cuticle in the neighbourhood of the mantle opening gradually	
diminishing in thickness.	
Excrescences long (50–70 μ).	
Excrescences with a thick basal part, covered with small lateral	
hairs	hispida.
Excrescences thin, smooth	comosa.
Excrescences comparatively short (up to $35 \ \mu \log$)	exarcuata.

SACCULINA HIRTA, sp. n.

Material examined :

Japan, 1 specimen on Cryptopodia fornicata (Fabr.), purchased from Jamrach.

Diagnosis of the species.—Male genital organs in the posterior part of the body, outside the visceral mass. Testes more or less globular, suddenly passing into the vasa deferentia. Testes completely separated, the one much larger than the other. Colleteric glands more or less hemispherical, with a comparatively large number of tubes. External cuticle covered with hairs (length 15–24 μ), bearing small lateral hairs. Retinacula with a single spindle or with 2–4 spindles (in the latter case not united on a common basal part); length of the spindles about 20 μ .

The strongly flattened specimen (fig. 7, f) has a more or less oval shape. Its dimensions are: breadth 12, height 8.5, and thickness 2.5 mm. The surface of the mantle does not show wrinkles or grooves; there is a ridge on the thoracal surface, running from the stalk to the mantle opening, and a corresponding concavity is found on the abdominal surface. Undoubtedly these irregularities are the result of the narrow space between the thorax and the abdomen of the crab. The mantle opening lies at the anterior part of the thoracal surface, at the extremity of a small tube.

In the longitudinal sections which have been made a striking feature is the flattened appearance of the visceral mass. The male genital organs are found outside the visceral mass, in the muscular region to which the stalk is attached (fig. 28).

The two vasa deferentia are short narrow canals, which are connected with the ventral part of the wide testes. The left testis projects much farther towards the dorsal surface than the right testis, the latter, moreover, being much smaller than the former. Fig. 29, c, shows the connection of the right testis with its vas deferens; the left vas deferens passes into its testis in a plane between that of fig. 29, d & c. The left testis is enormously enlarged (fig. 29, f, g). The cavities of the two testes remain completely separated.

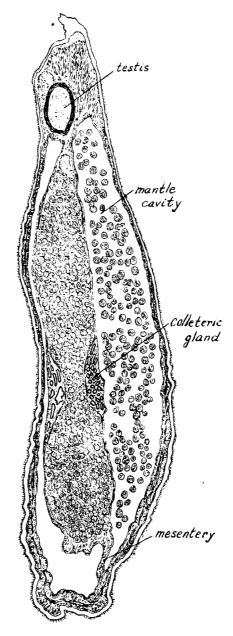


Fig. 28.—Sacculina hirta. Longitudinal section. $\times 18$.

In the central region of the lateral surfaces of the visceral mass the colleteric glands are found; they lie somewhat nearer to the anterior than to the posterior part. Although these glands are of very small size (at least in comparison to those of *Sacculina eriphiae*), they contain a fairly large number of branched tubes (fig. 28).

The external cuticle of the mantle, which on an average has a thickness of 20 μ , bears numerous hairs with blunt extremities (fig. 30, *a*, *b*). They are covered with minute lateral hairs. The excressences have a length of 15-24 μ and the thickness of their basal part may amount to 5 μ .

The internal cuticle of the mantle is covered with a great number of retinacula, which are more or less evenly distributed on this chitinous layer, but not arranged in lines (fig. 30, c, d). Each retinaculum consists of a single

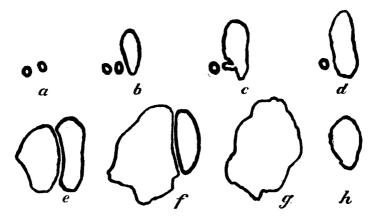


Fig. 29.—Sacculina hirta. Transverse sections through the male genital organs in different regions of the body. a, the ventral part of these organs, showing the vasa deferentia; h, the dorsal extremity of the larger of the two testes. $\times 18$.

spindle, which has a length of about 20μ and which bears distinct barbs. The spindles are directly united with the cuticle. Usually the spindles are not united into groups; only occasionally two or more are found closely together.

In many of its characters Sacculina hirta corresponds closely with S. eriphiae (Smith, 1906) and S. inflata (Leuckart, 1859): in these three species at least one of the testes is enormously enlarged, forming a wide thin-walled pouch; the testes (at least, the larger one) pass abruptly into the vasa deferentia. In these three species the excressences of the external cuticle have the shape of hairs or long papillae which do not differ in structure from the main layers of the cuticle. They can be distinguished from each other by the excressences of the internal cuticle, the retinacula. S. inflata does not possess retinacula; in S. eriphiae the spindles of the retinacula have an enormous size, whilst in S. hirta these spindles have the usual length (about 20 μ , fig. 30, c, d).

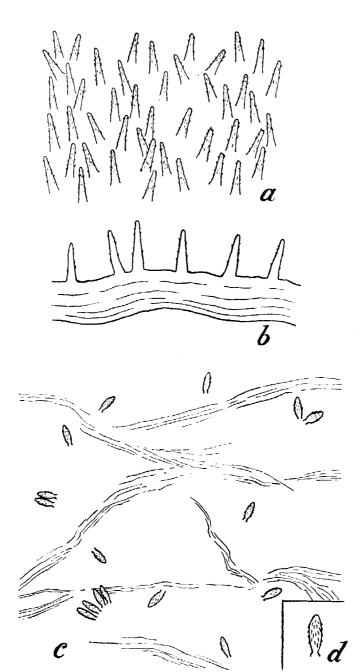


Fig. 30.—Sacculina hirta. a, excrescences of the external cuticle as they are distributed on the surface; b, section through the external cuticle; c, retinacula on the internal cuticle; d, a single retinaculum. a, b, and d, \times 530; c, \times 290.

SACCULINA INFLATA Leuckart.

Sacculina inflata : Leuckart (1859), Boschma (1927 b, 1931 b).
Sacculina triangularis : Anderson (1862), Boschma (1927 b).
For other literature on the species cf. Boschma (1927 b).
Material examined :
Firth of Forth, J. Anderson, 1861, 1 specimen.
Firth of Forth, J. Anderson, 1862, 3 specimens (collection Norman).
Starcross, Devon, Parker coll., 2 specimens (collection Norman).
Starcross, Devon, 4 specimens (collection Norman).
All these specimens are parasites of Cancer pagurus L.

In my paper on the European Rhizocephala (Boschma, 1927 b) I regarded the parasite of *Cancer pagurus*, *Sacculina triangularis*, as a species distinct from *S. inflata*, the parasite of *Hyas*. After this paper had appeared Professor Ashworth sent me a number of the parasites on *Cancer pagurus* from the Firth of Forth. The study of the anatomy of these parasites revealed that they belong to the same species as those parasitic on *Hyas*. For reason of priority the species must be named *Sacculina inflata* (cf. Boschma, 1931 b).

The shape of the specimens in the collection of the British Museum does not differ noticeably from that of previously recorded specimens (Anderson 1862, Boschma 1931 b). Many specimens are more or less pear-shaped, the anterior being much broader than the posterior part; other specimens are more or less oval. The dimensions of the largest specimen in the collection are: breadth 12 mm., height 9 mm., and thickness $4\cdot5$ mm. In many specimens the surroundings of the mantle opening do not project above the surface of the mantle, and in these the mantle opening is usually small. In other specimens this opening is found at the extremity of a short tube, the opening itself being comparatively wide. The surface of the mantle is often more or less uneven on account of ridges and grooves; but these, in part at least, may be the result of contraction after preservation.

Sections have been made from a single specimen. The size, shape, and structure of the colleteric glands and the testes do not differ in any important detail from those of specimens examined previously. One of the two testes is much larger than the other, which also is in conformity with previous statements.

The excrescences of the external cuticle have the typical shape. Retinacula have not been found ; undoubtedly they never occur in this species.

SACCULINA ELONGATA, sp. n.

Material examined :

^cChallenger ['] Expedition, Stat. 191, 800 faths., 23 Sept., 1874, 2 specimens on *Ethusina* gracilipes var. robusta Miers.

Diagnosis of the species.—Male genital organs in the posterior part of the body, outside the visceral mass. Testes more or less globular, completely separated, vasa deferentia narrow. Colleteric glands flattened, with a comparatively DR. H. BOSCHMA

small number of tubes. External cuticle with small hairs, consisting of a broad basal part and a slender pointed sharp extremity; they may possess a few small lateral hairs. Length of the excrescences varying between 12 and 24 μ .

The two specimens were attached each to one side of the median plane of the abdomen of the same host. They are very similar in shape and size (fig. 7, g);

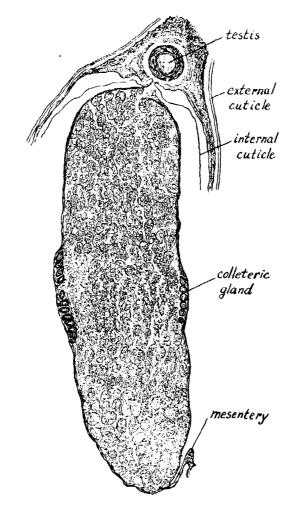


Fig. 31.—Sacculina elongata. Longitudinal section (the greater part of the mantle omitted). $\times 36$.

their dimensions are: breadth 3 mm., height almost 4, and thickness 2 mm. approximately. The elongated shape may be caused by mutual pressure of the parasites against each other, but this is not certain, as each of the two animals is fairly symmetrical. The mantle opening lies at the surface which

was turned against the thorax of the host, not far from the anterior margin. It does not project noticeably above the surface of the mantle. The mantle itself is so thin that the visceral mass is dimly visible from the outside.

From one of the specimens a series of longitudinal sections has been made. The male genital organs are found in the muscular region between the stalk and the visceral mass (fig. 31). The testes are approximately globular; one of them lies nearer to the ventral region than the other, so that in none of the sections are both the testes to be seen. The figure represents a section in which the testis which lies nearer the dorsal surface is visible. The vasa deferentia are short, narrow, comparatively straight canals, which penetrate as a chitinous tube through the wall of each testis.

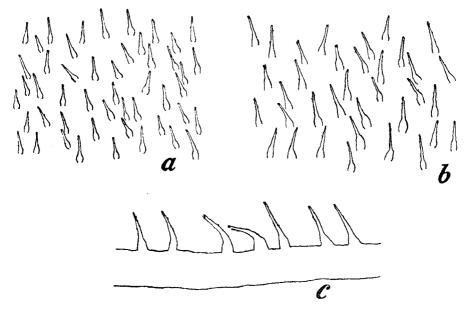


Fig. 32.—Sacculina elongata. a, excressences on the external cuticle of one of the specimens; b, excressences of the other specimen; c, section of the cuticle of the same specimen. × 530.

The colleteric glands lie in the central region of the lateral surfaces of the visceral mass. In these glands, which are strongly flattened, there is a small number of tubes, neatly arranged against the surface of the visceral mass (fig. 31).

The mantle is not highly muscular, except in the posterior part (the region of the stalk), and in the anterior region, where a strong sphincter surrounds the mantle opening.

The external cuticle of the mantle has a thickness of about 16μ (in the specimen from which sections have been made). Its surface bears soft hairs

which vary somewhat in different parts of the mantle (fig. 32). The length of these excrescences varies between 12 and 24 μ ; they consist of a more or less swollen basal part and a slender upper part on which sometimes minute lateral hairs may be seen.

Retinacula have not been found on the parts of the internal cuticle of the mantle examined for this purpose.

Five species of the genus Sacculina, viz. S. gonoplaxae Guérin-Ganivet (1911), S. hirsuta Boschma (1925), S. spinosa Van Kampen and Boschma (1925), S. echinulata Van Kampen and Boschma (1925), and S. leopoldi Boschma (1931 d), agree with S. elongata in the following characteristics: Male genital organs in the posterior part of the body; testes more or less globular, suddenly passing into the vasa deferentia; testes completely separated, not enlarged into a thin-walled wide sac; external cuticle covered with comparatively long hairs or spines, which have the same structure as the main layers of the cuticle. These species can be distinguished thus:—

Colleteric glands not projecting noticeably above the surfaces of the visceral mass.

Excressences of the external cuticle smooth or covered with very few lateral hairs.

Excrescences with broadened bases and pointed extremities	elongata.
Excrescences with rounded blunt extremities	leopoldi.
Excrescences with numerous lateral hairs or spines.	
Excrescences covered with little stiff pointed spines	spinosa.
Excrescences covered with small soft lateral hairs.	
Lumen of the vasa deferentia not strongly tortuous	gonoplaxae.
Lumen of the vasa deferentia strongly tortuous	echinulata.
Colleteric glands distinctly projecting above the surfaces of the visceral	
	Lingerton

mass hirsuta.

The specimen of Ethusina gracilipes with its two Sacculina elongata was collected in comparatively deep water (1440 m.) in the East Indies. Another species, Sacculina abyssicola Guérin-Ganivet (1911), a parasite of Ethusina abyssicola S. I. Smith, has been taken in still deeper water (3655 and 3975 m.) off the Atlantic coast of Africa. The internal organization of S. abyssicola is very similar to that of S. elongata. The male genital organs especially correspond closely in the two species : they are found in the region between the visceral mass and the stalk, the testes being more or less globular and abruptly passing into the vasa deferentia. In S. abyssicola the colleteric glands are, perhaps, more strongly broadened in a lateral direction than those of S. elongata, but this character may be of minor importance. The same holds true for the differences in external appearance of the two species, for the two species of S. abyssicola represented on figs. 10 and 11 of the plate in Guérin-Ganivet's paper have a different shape.

The structure of the external cuticle of S. abyssicola is unknown, and consequently I do not feel justified in identifying the specimens obtained by the 'Challenger' Expedition with this species. Moreover, it is improbable that they are specifically identical, because the localities are widely separated;

Sacculina abyssicola is known from the Atlantic near the north-west part of Africa, whilst Sacculina elongata lives in the East Indies.

Among the material collected by the 'Siboga' Expedition there is a parasite on *Ethusina gracilipes* var. *robusta* from a depth of 1300 m. in Makassar Strait, which we have described as *Sacculina sulcata* (cf. Van Kampen and Boschma 1925, Boschma 1931 c). The internal anatomy of this species closely resembles that of *S. elongata*: testes and colleteric glands correspond in place, size, and structure. The external cuticle of *S. sulcata*, however, is devoid of excrescences, and, as the 'Challenger' specimens possess distinct hairs of a typical form, they must be specifically distinct from the 'Siboga' specimen, although they live on the same species of host.

SACCULINA GONOPLAXAE Guérin-Ganivet.

- Sacculina gonoplaxae : Guérin-Ganivet (1911), Boschma (1927 b, c).
- For other literature on the species cf. Boschma (1927 b).

Material examined :

- ⁽Porcupine,' 1870, Station 36 (Lat. N. 35° 35', Long. W. 6° 26), 128 fathoms, 1 specimen on *Gonoplax angulata* (Penn.) (collection Norman).
- Naples, 3 specimens on one specimen of *Gonoplax angulata* (Penn.) (collection Norman).

The specimen from the 'Porcupine' Expedition has an oval shape; its dimensions are: breadth 6, height 4, and thickness $2\cdot 5$ mm. The surface of the mantle is smooth; there is only a concavity in the neighbourhood of the stalk, where the abdominal surface of the parasite touched the host. The shape of the three parasites from Naples is different from that of the other specimens; these three are more or less pear-shaped, probably on account of lack of room. The largest specimen of the three has the following dimensions: breadth $5\cdot 5$, height 4, and thickness $2\cdot 5$ mm. In this specimen the mantle opening is situated at the top of a short tube, in the two smaller specimens it does not project above its surroundings.

Longitudinal sections have been made from the specimen from the 'Porcupine' expedition and from one of the specimens from Naples. The anatomical peculiarities of these two specimens do not show any important differences, and, moreover, they correspond with those of the specimen from Naples which I examined some time ago (Boschma, 1927 c).

The male genital organs are embedded in the muscular region to which the stalk is attached. The testes are approximately globular, differing slightly in size in both specimens. The vasa deferentia are short tubes which are very slightly coiled and pass abruptly into the testes.

The colleteric glands of the 'Porcupine' specimen do not project above the surfaces of the visceral mass; in that from Naples they form a slight elevation of the visceral mass. In both specimens these glands are found a little nearer to the anterior than to the posterior region of the visceral mass. They contain a comparatively small number of branched tubes. In the 'Porcupine' specimen the musculature of the mantle is more strongly developed than in that from Naples. In the latter the visceral mass is rather flat, in the former it is much thicker owing to the more or less distended ovary.

The external cuticle does not differ in important details from that found in the previously known specimen. In both specimens from which sections have been made the thickness of this cuticle on an average amounts to 9 or 10 μ . The cuticle is covered with excrescences which are rather sparsely distributed on its surface; in the preparations examined they vary in length from 12 to 15 μ and bear numerous minute lateral hairs.

On the thin internal cuticle of the mantle no retinacula could be found. In all probability these excressences do not occur in the species.

Guérin-Ganivet (1911) described the parasite of Gonoplax angulata as a new species, Sacculina gonoplaxae. He did not find the testes in his specimen, but remarks that the colleteric glands are found exactly in the central part of the lateral surfaces of the visceral mass. In 1927 I had occasion to describe a specimen of this parasite from Naples. In this specimen the colleteric glands are found somewhat nearer the anterior than the posterior part of the visceral mass. The specimen, however, showed sufficient peculiarities to regard it as a representative of a distinct species, the diagnosis of which I formulated somewhat as follows :-- 'Testes outside the visceral mass, in the stalk. Colleteric glands with few, rather narrow tubes. External cuticle with hairs, which are not densely distributed, and which have a length of 15-18 μ ; they are covered with small lateral hairs. Retinacula unknown' (Boschma, 1927 c). Since then I have studied a great number of other species of Sacculina. The diagnosis of Sacculina gonoplaxae now can be given in the following manner: Male genital organs outside the visceral mass. Testes more or less globular, suddenly passing into the vasa deferentia. One of the testes somewhat larger than the other, but neither of the two enlarged into a thin-walled wide sac. Testes completely separated from each other. Colleteric glands in the central part of the lateral surfaces of the visceral mass, or (as usually in the species) somewhat nearer to the anterior region, comparatively small, with a few tubes only. These glands do not project noticeably above the surfaces of the visceral mass. External cuticle with hair-like excrescences, which have a length of $12-18 \mu$, and are covered with minute lateral hairs. The structure of the excrescences does not differ from that of the main layers of the cuticle. Retinacula unknown (probably not occurring in the species).

SACCULINA TERES, sp. n.

Material examined :

'Challenger' Expedition, Kei Islands, 1888, 2 specimens on one specimen of Notopoides latus (Henderson).

Diagnosis of the species.—Male genital organs in the posterior part of the body, outside the visceral mass. Testes completely separated, more or less globular,

the one larger than the other. Colleteric glands flat, with a comparatively small number of tubes. External cuticle covered with papillae, which at their extremities possess a number of small spines. The diameter of these papillae is $6-12 \mu$, their height may attain 20μ .

The two parasites were attached to the abdomen of their host, one at each side of the median plane. They are very similar in shape and size. One of the specimens is more or less circular (fig. 7, h); its dimensions are: breadth 8, height 7.5, and thickness 4 mm. In the other the corresponding dimensions are: 7, 7, and 5 mm. respectively. The latter specimen is somewhat more slender in the region near the stalk, and accordingly it is more or less pear-shaped. The surface of the mantle does not show any pronounced grooves or wrinkles. The mantle opening, which lies at the anterior end of the thoracal surface, does not project noticeably above its surroundings.

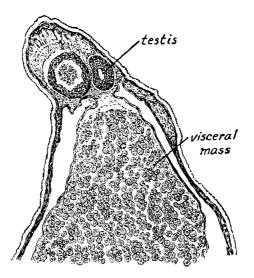


Fig. 33.—Sacculina teres. Posterior part of a longitudinal section. $\times 18$.

One of the specimens has been cut into a series of longitudinal sections. The male genital organs are found in the posterior part of the body, outside the visceral mass. The testes (fig. 33) are completely separated, more or less globular. One of the testes is slightly larger than the other. The vasa deferentia are short, somewhat curved, narrow tubes, which pass suddenly into the testes.

The colleteric glands (fig. 34) lie somewhat nearer to the anterior part of the visceral mass than to the posterior region. These glands are flat organs, which do not project above the surfaces of the visceral mass. They contain a small number of branched tubes.

LINN. JOURN. -ZOOLOGY, VOL. XXXVIII

The visceral mass and the mantle, with the exception of the sphincter of the mantle opening, are not strongly muscular.

The external cuticle of the mantle has a thickness of about 40μ in the specimen from which sections have been made. It is covered with typical excressences, which vary somewhat in size and distribution in the two specimens and also in different parts of the mantle of the same specimen. These excrescences are small papillae which have the same structure as the main layers

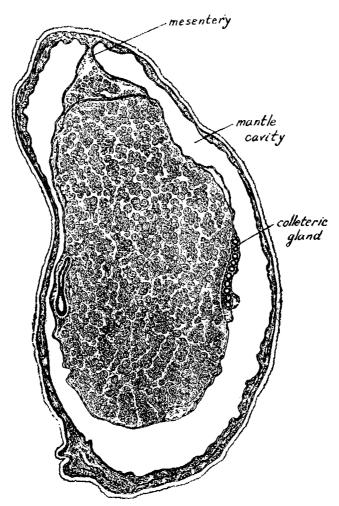


Fig. 34.—Sacculina teres. Longitudinal section. $\times 18$.

of the cuticle (fig. 35). The papillae may attain a length of 20 μ ; their diameter varies between 6 and 12 μ . At the centre of each papilla there is a small pit which opens at the top. The upper part of the papillae bears a fairly large number of minute pointed spines.

Retinacula have not been found in the preparations made for this purpose.

The species Sacculina hystrix, S. calappae, and S. verrucosa, described by Van Kampen and Boschma (1925), have many characters in common with Sacculina teres. In agreement with these species S. teres has the following peculiarities: Male genital organs in the posterior part of the body outside the visceral mass, testes completely separated; external cuticle covered with

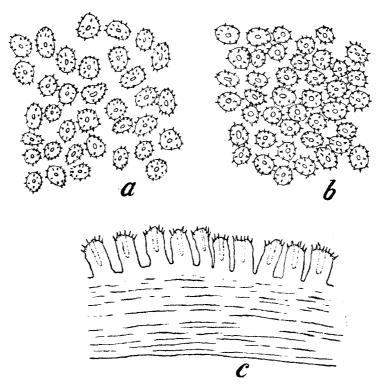


Fig. 35.—Sacculina teres. a, surface view of the excressences on the external cuticle of one specimen; b, the same in the other specimen; c, section of the cuticle of the same specimen. $\times 530$.

papillae or wart-like excressences, which possess small hairs or spines, the excressences not differing in structure from that of the main layers. S. teres differs from S. hystrix in having two well-developed testes. The shape of the testes (more or less globular) is different from that in S. calappae and S. verrucosa, both of which have testes of a more or less elongate form (cf. Boschma, 1931 c).

SACCULINA PLANA, sp. n.

Material examined :

Takao, South Formosa, 12 specimens on 8 specimens of *Grapsus strigosus* (Herbst) (4 crabs with 2 parasites each).

Diagnosis of the species.-Male genital organs in the posterior part of the body, outside the visceral mass. One testis only, with two vasa deferentia, the

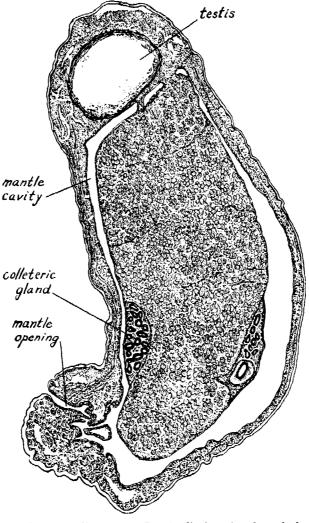


Fig. 36.—Sacculina plana. Longitudinal section through the mantle opening. $\times 26$.

testis more or less globular. Colleteric glands more or less hemispherical, with a fairly large number of tubes. External cuticle almost smooth, without

distinct areas. Retinacula with a single spindle, which has a length of approximately 18μ .

Although the shape of the parasites is somewhat variable they agree in being remarkably flat and broad (fig. 7 *i*). The measurements of one specimen are : breadth 16, height 8.5, and thickness 3 mm.; in another specimen the corresponding measurements are 12.5, 7.5, and 2 mm. respectively. Most specimens are smaller than those referred to above, and some of them are even broader in comparison to their height, so that the height may be less than one-third of the breadth. Generally the smaller specimens have a more or less oval shape; in one of them, e.g., the dimensions are : breadth 4, height 3, and thickness 1.5 mm. In the smaller specimens the surface of the mantle is usually quite smooth ; in the larger specimens there are a few grooves or wrinkles

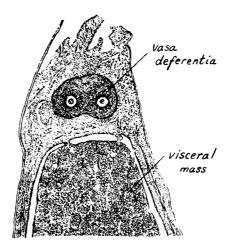


Fig. 37.—Sacculina plana. Posterior part of a longitudinal section of the same specimen as that of fig. 36, farther towards the ventral region. $\times 26$.

Generally there is a groove on the abdominal surface caused by the pressure of the ridge marking the position of the gut of the host. The mantle opening lies at the extremity of a very short tube (in some specimens this tube is not developed) at the anterior end of the thoracal surface.

Longitudinal sections have been made of three specimens, all of which show the same particulars, so that the characters of these specimens may be regarded as specific.

The male genital organs are found in the muscular mass to which the stalk is attached, outside the visceral mass. The two testes have completely fused into a common pouch (figs. 36 & 38), the two vasa deferentia are separate. In one of the specimens the dorsal region of the two vasa deferentia is surrounded by a common muscular layer (fig. 37). Different sections of the male genital organs of the specimen from which a section has been represented in fig. 38 are given in fig. 39. In this figure a shows the ventral part of the male genital organs, the two vasa deferentia. In b one of the vasa deferentia is passing into the testis; the left side of this figure shows a superficial section of the testis, the opening is the lumen of the vas deferents. In section c the testis already has a wide lumen, in d and e the vas deferents of the other side is seen passing

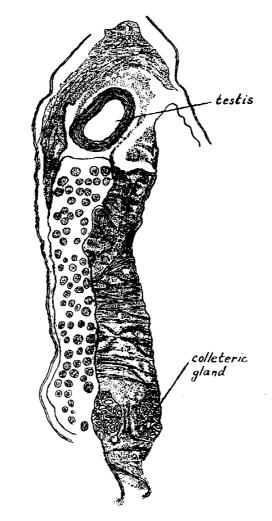


Fig. 38.—Sacculina plana. Longitudinal section of another specimen (the greater part of the mantle omitted). $\times 18$.

into the testis. Figures f and g represent sections of the dorsal part of the testis.

In the specimen from which the sections represented in figs. 38 and 39 have been made the testis has a rather thick wall, in another specimen (fig. 36) it forms a wide sack with a comparatively thin wall. In the third specimen

from which sections have been made (of which no figures are given here) the testis has a thick wall and a narrow lumen.

The colleteric glands (figs. 36 & 38) are found in the posterior part of the visceral mass. They are of medium size and do not contain a very large number of branched tubes.

In one of the sectioned specimens the visceral mass is very thin, as the eggs for the greater part have recently left the ovary, the mantle cavity containing many eggs. In the other specimen the visceral mass contains large quantities of eggs, whilst the mantle cavity is empty. The musculature of the mantle is not so very strongly developed (with the exception of the sphincter of the mantle opening and the musculature in the posterior part of the body). In the visceral mass some transverse muscles are visible, especially in the specimen in which the visceral mass contains only a few eggs (fig. 38).

When strongly enlarged the external cuticle of the mantle usually shows some grooves and other irregularities, but there are no excressences. The surface is not divided into small areas with irregular contour, as in many other species with a smooth cuticle. Sometimes the cuticle has a dotted appearance, caused by numerous microscopic pits (fig. 40, a).

On the internal cuticle of the mantle numerous retinacula are found, which are more or less evenly distributed (fig. 40, b, c). They consist of a single spindle, on which no barbs could be detected. The spindles on an average have a length of 18 μ .

Besides Sacculina plana there are a number of other species of the genus which have the following characters in common: Male genital organs in the posterior part of the body, outside the visceral mass; external cuticle without distinct excressences. The differences between these species are shown in the following key:—

Height of the body (distance between mantle opening and stalk) much	
longer than the breadth (distance between dorsal and ventral surface).	
External cuticle rough, with small grooves and fissures	anceps.
Height of the body smaller than the breadth.	
Testes more or less globular.	
Only one of the testes well developed or testes completely united.	
One of the testes rudimentary, but separated from the other. Surface	
of the cuticle with small areas of 12–16 μ in diameter	pustulata.
One testis present, with two vasa deferentia. Cuticle almost	
smooth, without definite structure at the surface. Retinacula	
with a single spindle	plana.
Both testes well developed.	
External cuticle consisting of prismatic columns with a central	
hyaline part	sulcata.
Structure of the external cuticle more or less homogeneous, its surface	
somewhat rough	rugosa.
Testes more or less cylindrical.	
External cuticle with small areas approximately 10μ in diameter,	
or rough (or covered with small globular excrescences). Colleteric	
glands with a large number of tubes	flexuosa.
External cuticle rough or covered with irregular excrescences of $6 \ \mu$	
length. Colleteric glands with a small number of tubes	bicuspidata.

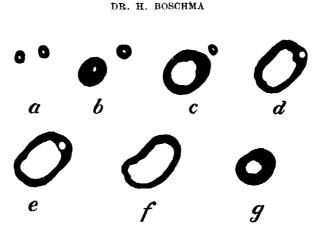


Fig. 39.—Sacculina plana. Transverse sections through the male genital organs in different regions of the body of the specimen of fig. 38. a, the vasa deferentia; g, the dorsal extremity of the testes. $\times 18$.

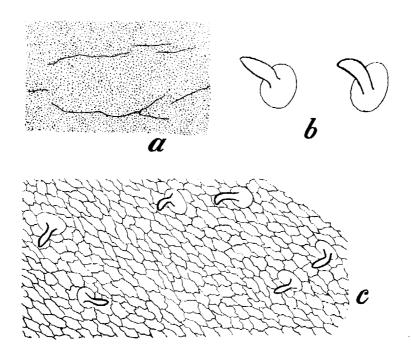


Fig. 40.—Sacculina plana. a, surface of the external cuticle; b, two retinacula; c, a number of retinacula on the internal cuticle of the mantle. a and $b, \times 530$; c, $\times 290$.

Sacculina flexuosa, described by Kossmann (1872), is one of the species dealt with in the present paper; S. sulcata and S. rugosa have been described by Van Kampen and Boschma (1925). Sacculina pustulata has been described by the author in a previous paper (Boschma, 1925), S. anceps and S. bicuspidata in another (Boschma, 1931 a).

SACCULINA FLEXUOSA Kossmann.

Sacculina flexuosa: Kossmann (1872), Van Kampen and Boschma (1925), Boschma (1928 b, 1931 a, c).

Material examined :

Amboina, Edw. Gerrard Jr., 1 specimen on Grapsus maculatus (Catesby).

The only specimen in the collection has a breadth of 19 mm., a height of 10 mm., and a thickness of 8.5 mm., this thickness being caused by the enormous quantities of eggs contained in the mantle cavity. Both surfaces of the mantle possess a few irregular grooves, the largest of which is found at the median region of the surface which was turned towards the abdomen of the crab. The peripheral parts of the mantle, especially the posterior parts of the dorsal and ventral region, show a great number of small warts, giving a more or less rough appearance to those parts of the mantle. The mantle opening has the shape of a narrow slit; it lies at the extremity of a short thick-walled tube, which is flattened in lateral direction. The distance between the mantle opening and the place of insertion of the stalk is somewhat shorter than the largest height.

Longitudinal sections have been made from the visceral mass and the region of the mantle adjoining the stalk. The most curious particular of this specimen is that, as in Kossman's type-specimen, the visceral mass is strongly curved in a lateral direction (fig. 41), so that two folds are present, one at the anterior part and another in the posterior region. The name *flexuosa* is derived from this character, which, however, does not occur in all the specimens. It seems, on the contrary, to occur very rarely in the species.

The male genital organs are present in the muscular posterior region of the body, from which the stalk takes its origin. The testes, which are rather large and comparatively long, are completely separated. In their ventral part they gradually pass into the vasa deferentia, which are large, but with a narrow lumen. This is caused by numerous ridges and lamellae protruding inwardly from the wall of the vas deferens (fig. 41). The dorsal extremity of the testes is slightly curved, so that in sections of the extreme dorsal part the lumen of the testes is twice visible.

The colleteric glands are large and contain numerous branched tubes. In the figure sections of the ventral part of the colleteric glands are represented; towards the median plane these glands are much more voluminous. The colleteric glands lie in the anterior half of the visceral mass.

The mesentery of the specimen is longer than is usual in Sacculina; it is complete in the dorsal half of the body, and, moreover, it is found for a short

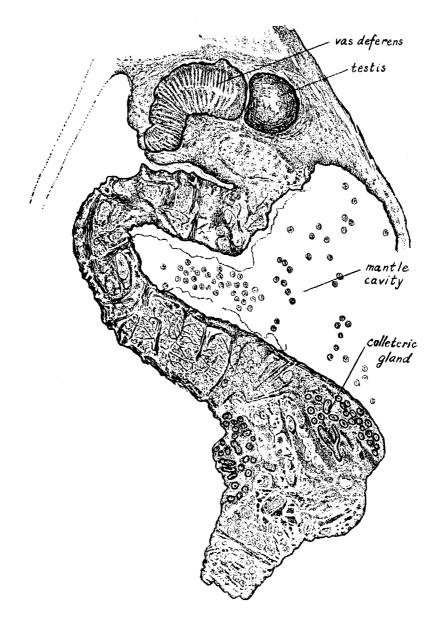


Fig. 41.—Sacculina flexuosa. Longitudinal section (the greater part of the mantle omitted). $\times 18$.

distance in the ventral half, uniting the visceral mass with the mantle. Kossmann (1872) remarks that the same feature occurred in the type-specimen of the species.

In the visceral mass some muscles are to be seen, especially in transverse direction. The mantle is strongly muscular. The mantle cavity was filled with an enormous quantity of eggs, which caused the swollen appearance of the animal.

With the exception of the small tubercles referred to above the mantle is smooth. In some parts the surface is somewhat, wrinkled, and in these parts minute stripes are visible. Excressences do not occur. The external cuticle of the mantle has a thickness of about 50 μ in the posterior part of the body, in the anterior region it is thicker.

On the thin internal cuticle of the mantle there are numerous retinacula, which are more or less regularly distributed (fig. 42). Each retinaculum

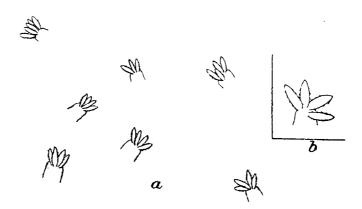


Fig. 42.—Sacculina flexuosa. Retinacula as they are distributed on the surface of the internal cuticle, ×290. At the right one retinaculum, ×530.

consists of a basal part and three to five spindles. The latter have a length of approximately 13μ and they bear distinct barbs.

In Kossmann's description (1872) of Sacculina flexuosa the following points are especially mentioned: the mesentery is longer than is usual in Sacculina, as it is found also in the ventral half of the body; the visceral mass is folded in a lateral direction; the external cuticle of the mantle has a thickness of $50-70 \mu$ and is slightly wrinkled. All these characters are found also in the specimen in the British Museum. There is, however, one particular mentioned by Kossmann, which does not hold good for the specimen dealt with here, viz. the shape of the male genital organs. According to Kossmann the testes are retort-shaped, whilst the vasa deferentia have the shape of a horseshoe, the opening of which is turned towards the stalk. From Kossmann's figure one would get the impression that the vasa deferentia run in a dorsal

DR. H. BOSCHMA

direction, the closed extremities of the testes being turned towards the ventral surface. In all probability Kossmann has made an error here. Perhaps the thick part of the male genital organs in his figure represents the vas deferens, which in this species has approximately the same thickness as the greater part of the testes. The curved part of the male genital organs then represents the closed extremity of the testis, which is also slightly curved in the British Museum specimen.

Kossmann's specimen was a parasite of Grapsus strigosus (Herbst) (= Grapsus grapsus), and the specimen obtained by the 'Siboga' expedition (Van Kampen and Boschma, 1925) was a parasite of the same host. The host of the specimen in the British Museum is given as Grapsus maculatus, a name which is synonymous with G. grapsus. Besides these two hosts the following crabs are known to be infested by Sacculina flexuosa: Varuna litterata, Macrophthalmus erato, Plagusia depressa, and the variety immaculata of the latter (cf. Boschma, 1928 b, 1931).

Genus PTYCHASCUS, nov.

Diagnosis of the genus.—Body laterally compressed, as in Sacculina. Mesentery thin, complete (extending from the stalk to the mantle opening). Inner surface of the mantle with a great number of septa which extend into the mantle cavity. Testes straight, in the posterior part of the body (as in Sacculina). Male genital openings in the ventral half of the mantle cavity. Colleteric glands with a number of branched tubes, approximately in the central part of the lateral surfaces of the visceral mass. Larva hatching in cypris stage.

The genus differs from *Sacculina* by the possession of the septa on the inner surface of the mantle, but corresponds closely with it in all other respects. In the only known species the mantle opening is found at the extremity of a long tube; it is not certain that this character will occur in other species of the genus (if such are discovered), so that for the present I prefer to regard it as a peculiarity of the species.

PTYCHASCUS GLABER, Sp. n.

Material examined :

Marajo Island, Amazon River, 1923, 2 specimens on Sesarma (Holometopus) benedicti Rathbun, 4 specimens on Aratus pisonii (Milne-Edwards) (2 on one host).

Diagnosis of the species.—Male genital organs in the posterior part of the body, outside the visceral mass. Testes more or less cylindrical, completely separated. Mantle opening at the extremity of a long tube, which is bent towards the dorsal surface. External cuticle of the mantle smooth, with distinct areas (diameter from 10 to 20 μ) of an irregular shape.

The specimens have a more or less oval shape, in some of them the median part of the dorsal and ventral region is somewhat pointed (fig. 43, a), in others the posterior part of the dorsal and ventral regions is more or less angular (fig. 43, b). The dimensions of one specimen on *Sesarma benedicti* are: breadth 7,

height 3.5, and thickness 2 mm., the other specimen is a little smaller. The largest specimen on *Aratus pisonii* has the following dimensions: breadth 12, height 7, and thickness 3.5 mm.; in the smallest specimen (one of the two on the same host, *cf.* Pl. 7, fig. 44) the dimensions are: breadth 7, height 4, and thickness 2 mm. The lateral surfaces of the animals are comparatively flat. The mantle is smooth with the exception of a few irregular grooves and wrinkles and a median groove at the surface which was turned towards the abdomen of the crab. This groove does not occur in the two specimens which lived together on the same crab, so that in the other specimens this groove is caused by the pressure of the ridge marking the position of the gut of the host.

Usually the mantle is comparatively thick, but in one specimen it is much thinner and more or less transparent, so that the place of insertion of the septa is dimly visible (fig. 43, a). The stalk may be surrounded by an area of the

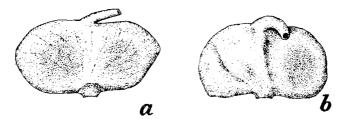


Fig. 43.—Ptychascus glaber, the specimens from which sections have been made. *a*, specimen on Sesarma benedicti; *b*, specimen on Aratus pisonii. The figure shows the surface which was turned towards the thorax of the hosts; the stalk is found at the lower part, the mantle opening at the upper part of the figures. *a*, $\times 5 \cdot 25$; *b*, $\times 3 \cdot 75$.

mantle with a thicker layer of chitin (fig. 43, a), but in most specimens this area is not pronounced.

In the anterior region the mantle is protruded into a long narrow tube, at the extremity of which the mantle opening is found. Curiously enough, this tube in all the specimens is directed towards the dorsal surface of the animal. The tube may reach a length of 2 mm. (in the largest specimen) and it is straight or somewhat curved (fig. 43 & Pl. 7, fig. 44).

From one of the specimens on *Sesarma benedicti* and from one of the specimens on *Aratus pisonii* series of longitudinal sections have been made. As the particulars of the two specimens correspond in every important detail, the description given here applies to both of them, unless special differences are mentioned.

With the exception of the septa on the inner surface of the mantle the anatomy of the specimens corresponds closely with that of *Sacculina*: the mesentery runs from the stalk to the tube at the extremity of which the mantle opening is found, and the testes are straight organs lying before the stalk.

The male genital organs are found in the posterior part of the body, outside the visceral mass (fig. 45). The testes are of fairly large size; towards the ventral part of the body they gradually pass into the vasa deferentia, which in the specimen on *Sesarma* form narrow tubes; in that on *Aratus* the wall of these canals is thicker. The testes remain completely separated for the whole of their extent.

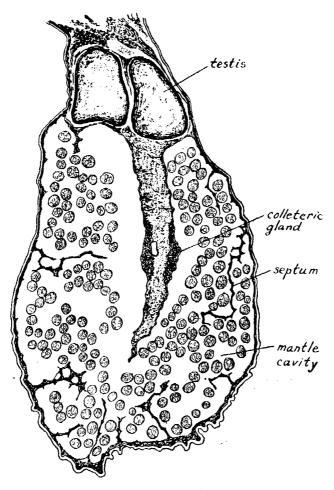


Fig. 45.—Ptychascus glaber. Longitudinal section of a specimen from Sesarma benedicti. $\times 36$.

The colleteric glands are found in the neighbourhood of the central part of the lateral surfaces of the visceral mass, somewhat nearer to the anterior region than to the posterior part (fig. 45). They contain a fairly large number of narrow branched tubes; in the specimen on *Aratus* more than in that on *Sesarma*.

The mantle is not strongly muscular except in the region where the tube of the mantle opening is connected with the mantle. This tube itself contains a well-developed muscular layer; its lumen is very narrow. In the visceral mass there are a few transverse muscles, and the posterior part of the body to which the stalk is attached contains some strong muscles.

The septa do not occur in large numbers. Between each pair of septa numerous eggs are found in both specimens. In the specimen on *Aratus* from which sections have been made the mantle cavity is so crowdedly packed with eggs that the septa are not easily visible, in that on *Sesarma* the septa are more distinctly visible, as there are fewer eggs present in the mantle cavity. The septa form thin lamellae which protrude with their free extremities between the eggs in the mantle cavity, dividing the mantle cavity into a small number of chambers which are most distinctly visible in sections through the extreme dorsal or ventral part of the animal (fig. 46). Probably the septa of *Ptychascus*

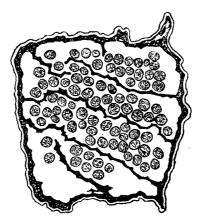


Fig. 46.—*Ptychascus glaber*, same specimen as that of fig. 45. Longitudinal section through the pointed dorsal part, showing the septa. $\times 36$.

have the same function as those of *Septosaccus* (cf. Duboscq, 1912), viz. forming separate brood-pouches in the mantle cavity for the developing eggs. It is not certain whether they also have a respiratory function or not.

The structure of the external cuticle of the mantle is similar in all the specimens examined. In the specimens from which sections have been made the external cuticle has a thickness of approximately 12μ (in the specimen on *Sesarma*) and 20μ (in the specimen on *Aratus*). Some parts of the external cuticle are more or less wrinkled, but for the greater part this cuticle is altogether smooth. When strongly enlarged the surface is seen to be divided into small irregular areas, which have a diameter varying betweeen 10 and 15μ (fig. 47). The cuticle does not possess excrescences.

On the internal cuticle of the mantle no retinacula could be found in the preparations made for this purpose. In one of the specimens on *Aratus pisonii* the mantle cavity contains fully developed cypris larvae (fig. 48). The length of these larvae varies between 175 and 235 μ ; they possess a pigmented eye, well-developed antennae, and six pairs of swimming-legs with long bristles, and there are also a few bristles at the extremity of the abdomen.

Besides *Ptychascus glaber* two species of Rhizocephala are known from fresh water, viz. *Sesarmaxenos monticola* Annandale from the Andaman Islands and *S. gedehensis* Feuerborn from West Java. In the description of *S. monticola* by Annandale (1911) two mantle openings are mentioned; probably only one of these is characteristic of the species, the other may have been formed by accident. According to Annandale the visceral mass is apparently attached to the mantle by a mesentery that surrounds the ring of attachment, but he does not mention how far it extends towards the mantle opening. The description is rather imperfect, and probably the only available specimen

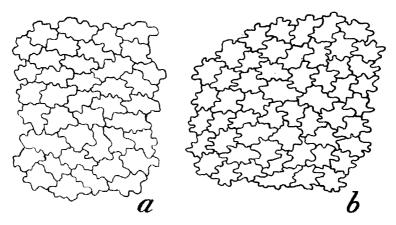


Fig. 47.—Ptychascus glaber. a, surface of the external cuticle of a specimen on Sesarma benedicti; b, surface of the cuticle of a specimen on Aratus pisonii. × 530.

was not in a very good state of preservation. It is interesting that the specimen contained cypris larvae in the mantle cavity.

The characters of Sesarmaxenos gedehensis have been described in detail by Feuerborn (1932). S. gedehensis has a mantle opening which is directed towards the left side of the host (as S. monticola); the mesentery is not only, as in Sacculina, a kind of ligament connecting the visceral mass with the mantle, but it is excessively developed and forms large folds which extend into the mantle cavity, forming brood-pouches for the developing eggs. The larvae hatch from the egg-membrane in the cypris stage.

In *Ptychascus* the structure of some parts is different from that of *Sesarmaxenos*, but a similar effect is accomplished. Externally the lateral surfaces of the animal are more or less bilaterally symmetrical: the base of the tube of the mantle opening is found approximately at the centre of the anterior

region. The tube itself, however, is directed towards the left side of the host, so that in most cases it projects from under the abdomen of the crab. Probably in fresh water Rhizocephala it is of great value to have the mantle opening not covered by the abdomen of the crab, so that the necessary constant supply of water in the mantle cavity is not prevented by this part of the host. Brood pouches are formed here by the septa on the internal surface of the mantle, and the mesentery does not differ in shape and size from that in *Sacculina*.

In *Ptychascus*, as in *Sesarmaxenos*, the young leaves the egg-membrane in the cypris stage. This affords further protection to the brood, and is probably a result of the freshwater habitat.

In Rhizocephala we consequently see a similar phenomenon to that occurring in many other groups of animals, so far as the protection of the brood is concerned. In the majority of genera the young leave the egg-membrane in the

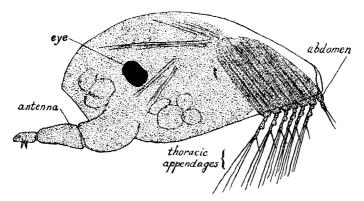


Fig. 48.—Ptychascus glaber. Cypris larva. $\times 290$.

nauplius stage. In some, however, as in *Clistosaccus*, *Sylon*, *Sesarmaxenos*, and *Ptychascus*, the young hatch in the cypris stage. The two former genera are typical arctic animals, the two latter occur in fresh water only.

Genus DREPANORCHIS.

DREPANORCHIS NEGLECTA (Fraisse).

Sacculina neglecta: Fraisse (1877).
Sacculina phalangi: Norman and Scott (1906).
Drepanorchis neglecta: Boschma (1927 b, c, 1928 a).
For other literature on the species cf. Boschma (1927 b).
Material examined:
Naples, G. W. Smith, 7 specimens on 6 specimens of Inachus mauritanicus Lucas.
Naples, 1887, 1 specimen on Inachus mauritanicus Lucas (collection Norman).
Dalmatia, from Heckel collection, 1 specimen on Macropodia rostrata (L.).
Plymouth, 1903, 2 specimens on 1 specimen of Macropodia longirostris (Fabr.).

The shape of the parasites does not differ from that of other specimens belonging to this species; generally they have a more or less rounded form, LINN, JOURN.—ZOOLOGY, VOL. XXXVIII 38 the height not greatly exceeding the breadth. The specimens differ in size; the largest in the collection (on *Inachus mauritanicus*) has a breadth of 13 mm.

It is interesting that two of the specimens are parasites of *Macropodia longirostris*, as the anatomy of specimens from this crab has not previously been studied. From one of these specimens a series of sections has been made. As was to be expected, the anatomy does not differ in any respect from that of the parasites of *Macropodia rostrata* and of the genus *Inachus*: the testes extend in a wide curve through the whole of the visceral mass and the colleteric glands are found in the anterior region of the visceral mass.

Besides the literature on the species given in a previous paper (Boschma, 1927 c) the occurrence of this parasite on *Macropodia rostrata* has been mentioned by Norman and Scott (1906), who named the parasite *Sacculina phalangi* Hoek: "On the abdomen of *Stenorhynchus longirostris* at Plymouth, 1903 (A. M. N.). The type-specimen of Hoek was parasitic on *Stenorhynchus rostratus*" (*l. c.*, p. 226). In all probability the specimens from Plymouth in the collection of the British Museum are those collected by Norman.

Genus LOXOTHYLACUS.

LOXOTHYLACUS ARISTATUS Boschma.

p.p. Sacculina pilosa: Van Kampen and Boschma (1925).
Loxothylacus aristatus: Boschma (1931 c).
Material examined:
Macclesfield Bank, H.M.S. 'Egeria', 42-46 fms., I specimen on Lambrus contrarius (Herbst).

The parasite has a more or less oval shape (fig. 49, a); its dimensions are : breadth 18.5, height 14, and thickness 7.5 mm. The mantle opening lies at the extremity of a rather pronounced tube, situated in the centre of the anterior margin. The surface of the mantle is almost smooth to the naked eye, only the marginal parts are somewhat pitted and grooved, and the surface of the parasite which was turned towards the abdomen of the crab shows a deep median groove, caused by pressure of the median ridge of the abdomen. When compared with the type-specimen the difference in shape of the two parasites is rather striking ; but as in the Sacculinidae the shape of the parasites of the same species on different hosts often presents great differences, this feature is of little importance. The same holds true for the differences in size : the specimen in the British Museum is more than twice as large as that obtained by the 'Siboga' Expedition.

The internal structure of the parasite was studied by means of a series of longitudinal sections. The male genital organs are embedded in the posterior part of the visceral mass. The testes are distinctly curved, but the curved part of each testis does not extend noticeably in a ventral direction and is chiefly directed anteriorly (fig. 50). The closed parts of the testes form rather wide pouches, with a thin wall which gradually becomes thicker towards the

posterior part of these organs (the region in the vicinity of the mesentery). The thick-walled part of the two testes runs along the mesentery and gradually passes into the vas deferens. The vasa deferentia communicate with the mantle cavity in the ventral half of the animal. The male genital organs remain separated for the whole of their extent.

The colleteric glands are found at each side of the visceral mass, not far from the central part, but somewhat nearer to the anterior than to the posterior extremity (fig. 50). These glands contain a large number of narrow branched tubes.

The musculature of the visceral mass, of the region of the stalk, and of the mantle is well developed. The mantle cavity contains a large quantity of eggs.

The external cuticle of the mantle is comparatively thick (on an average 80 μ); its surface is covered with excrescences which differ in structure from that of the main layers. Whilst the main layers of the cuticle are easily stained, the excrescences keep their transparent appearance also in stained sections.

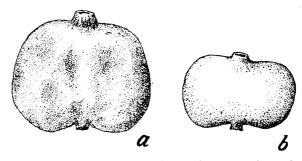


Fig. 49.—a, Loxothylacus aristatus; b, Loxothylacus spinulosus. The surface of the animals which was turned towards the thorax of their hosts is represented; the mantle opening is found in the upper part, the stalk in the lower part of the figure. $a, \times 2$; $b, \times 7.2$.

Each of these excressences consists of a small number of rigid spines, which are united proximally in a common base (fig. 51). In the greater part of the mantle these excressences have a length of 45μ ; in some regions they are slightly larger and in others smaller.

On the thin internal cuticle of the mantle no retinacula could be found.

The specimen dealt with here differs in some respects from the type-specimen of *Loxothylacus aristatus* (cf. Boschma, 1931 c). In the latter the testes are not enlarged into a voluminous pouch with a thin wall; but this difference between the two specimens may be due to the fact that the two are of different sizes and therefore the one may be much younger than the other. Moreover, the excressences of the external cuticle do not correspond in every detail in the two specimens. In the type-specimen the excressences are larger than those of the specimen dealt with here, and they are composed of a larger number of spines. These differences, however, are of minor importance, for in many

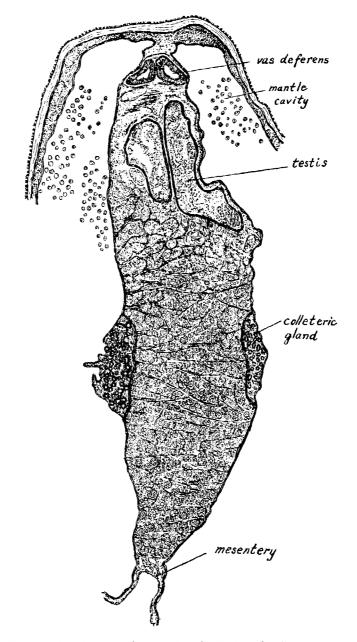


Fig. 50.—Loxothylacus aristatus. Longitudinal section (the greater part of the mantle omitted). $\times 15,$

species of Sacculinidae with excrescences of this kind the number of spines which are united on a common basal part varies in the different parts of the mantle. In the vicinity of the stalk the excrescences usually are less fully developed than on other parts of the mantle.

Loxothylacus desmothrix and L. setaceus (cf. Boschma, 1931 c) have excressences of approximately the same type as those of L. aristatus. In L. setaceus one of the testes is rudimentary, whilst in L. aristatus both testes have approximately the same size. L. desmothrix differs from the two other species by the peculiar structure of its excressences: the spines of each excressence are united into a number of thick branches, the latter are fused with the common basal part.

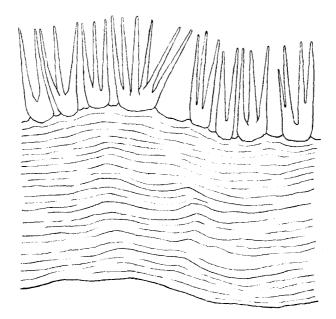


Fig. 51.—Loxothylacus aristatus. Section of the external cuticle. \times 530.

LOXOTHYLACUS SPINULOSUS Boschma.

Loxothylacus spinulosus : Boschma, 1928 b.
 Material examined :
 Hongkong, Barney coll., 2 specimens on two young specimens of Pilumnus seminudus.

The following is an amended diagnosis of the species, based on the specimens in the British Museum and on that in the Leiden Museum (cf. Boschma, 1928 b): Male genital organs rather strongly curved, in the posterior half of the visceral mass. One of the testes larger than the other. Collectric glands with a fairly large number of tubes. Surface of the external cuticle of the mantle divided into small areas with an irregular shape (diameter of these areas varying between 6 and 18 μ). The surface of the cuticle covered with small blunt excrescences, which have a length of 4-6 μ . Retinacula with one or two barbed spindles of approximately 13 μ length.

The two specimens from Hongkong have approximately the same size; the dimensions of one of them are: breadth 4, height 2.5, and thickness 1.5 mm.; in the other specimen the corresponding dimensions are: 4, 2.25, and 1 mm. respectively. One of the specimens has the dorsal and ventral region neatly rounded (fig. 49, b); in the other specimen these parts are protruded into small points, so that the animal has an angular shape. In both specimens the surface of the mantle is smooth and there is a short concavity near the stalk on the surface which was turned towards the abdomen of their hosts. The mantle opening lies at the extremity of a very short tube in the central part of the anterior region.

From the specimen represented in fig. 49, b, a series of longitudinal sections has been made. The visceral mass is attached to the mantle at some distance from the stalk, the mesentery is complete, and the testes are curved, so that the specimen undoubtedly belongs to the genus *Loxothylacus*.

One of the testes (that of the right side) is much larger than the other. Its closed part forms a comparatively wide sac, whilst the corresponding part of the other testis is not noticeably enlarged (fig. 52). The curve of the testis is rather narrow, so that in longitudinal sections the testes are seen lying just before the vasa deferentia. The latter are narrow canals, which run along the mesentery, and the male genital openings are found in the ventral half of the body.

In comparison to the size of the body the colleteric glands are of good size (fig. 52). They contain a number of branched tubes. The glands lie approximately in the centre of the lateral surfaces of the visceral mass, somewhat nearer to the anterior than to the posterior region.

The animal is not strongly muscular. With the exception of the region of the stalk and the sphincter of the mantle opening there is a thin muscular layer beneath the external cuticle. The visceral mass contains hardly any muscles. In comparison to the size of the whole animal the visceral mass is extremely small. The mantle cavity is wide and more or less inflated, but contains only a few eggs.

In the specimen from which sections have been made the external cuticle of the mantle has a thickness of $15-25 \mu$. In both specimens the surface of this cuticle shows, at least in many parts, neat little areas which have an irregular shape (fig. 53, a). In the centre of each area the cuticle may bear a small, more or less blunt excrescence (fig. 53, c). When the surface of the cuticle is examined these excrescences often are little distinct; in sections, however, they are clearly visible. The excrescences of the cuticle may reach a height of 6μ .

On the internal cuticle of the mantle retinacula occur which consist of a basal

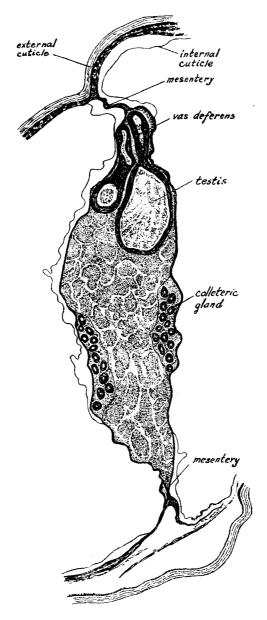


Fig. 52.—Loxothylacus spinulosus. Longitudinal section (the greater part of the mantle omitted). \times 72.

part and one or two spindles (fig. 53, b). The latter have a length of approximately 13μ ; their barbs are distinctly visible.

It is not altogether certain that the specimens from Hongkong belong to the same species as the specimen from the Pacific Ocean (cf. Boschma, 1928 b). There are some differences, but they are not striking enough to justify specific separation. In the first place, there is a difference in the shape of the testes. In the specimen in the Leiden Museum one of the testes is larger than the other, just as in the specimen in the British Museum, but in the former the curve of the testes is much wider than that in the latter specimen. The colleteric glands of the Leiden specimen are larger than those of that in the British Museum and contain a larger number of branched tubes. These differences, however, may be due to the fact that the visceral mass of the British Museum specimen is much smaller than that of the other.

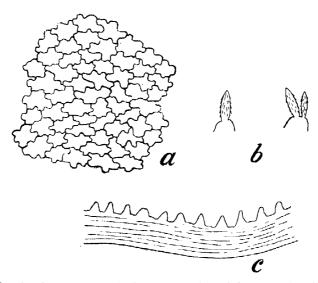


Fig. 53.—Loxothylacus spinulosus. a, surface of the external cuticle; b, retinacula; c, section of the external cuticle. × 530.

The excressences of the external cuticle also show some differences, but these again are of minor importance. They are shorter and slenderer in the specimen in the Leiden Museum.

Loxothylacus spinulosus can easily be distinguished from all other species of the genus, as all these other species have excressences of larger size.

Genus PARTHENOPEA.

After having studied the anatomy of *Parthenopea subterranea* (cf. Boschma, 1927 c) I came to the same conclusion as Kossmann (1873), viz. that it does not differ in any important detail from the genus *Lernaeodiscus*. The most

striking difference between the two genera, in my opinion, was the pronounced bilateral symmetry of *Parthenopea* in contradistinction to the asymmetrical species of *Lernaeodiscus*. Since then I have demonstrated that *Lernaeodiscus porcellanae* Müll. has a neatly bilaterally symmetrical structure (cf. Boschma, 1931 a; also the description and figures of the species by Müller, 1862, already give evidence of this symmetry), so that the differences between *Parthenopea* and *Lernaeodiscus* are still less significant. There remains, however, the fact that the orientation of the parasites in regard to their hosts is different in the two genera : in *Parthenopea* the dorsal surface of the parasite is directed towards the left side of the host, whilst in *Lernaeodiscus* it is directed towards the abdomen of the host.

PARTHENOPEA SUBTERRANEA Kossmann.

Parthenopea subterranea : Kossmann (1873), Boschma (1927 c), Popov (1929). Material examined :

Naples, G. W. Smith, 1 specimen on Callianassa stebbingi Borrad.

Naples, 1887, 1 specimen on Callianassa stebbingi Borrad. (collection Norman).

Zoological Station, Naples, 3 specimens on *Callianassa stebbingi* Borrad. (collection Norman).

The specimens in the collection of the British Museum do not differ in any important detail from other specimens of the species.

Until recently *Parthenopea subterranea* was known only from Naples; Popov (1929) records the species from the Bay of Sebastopol (Black Sea).

Genus LERNAEODISCUS.

LERNAEODISCUS MUNIDAE (Smith).

Triangulus munidae: Smith (1906). Lernaeodiscus munidae: Boschma (1928 a, b). For other literature on the species cf. Boschma (1928 a).

The specimen does not differ in any important detail from those dealt with in the papers cited above. Its mantle is smooth and does not possess marginal lappets.

LERNAEODISCUS GALATHEAE (Norman & Scott).

Sacculina galatheae : Norman & Scott (1906). Lernaeodiscus galatheae : Pérez (1908), Boschma (1927 c, 1928 a). For other literature on the species cf. Boschma (1928 a). Material examined :

Plymouth, 1889, I specimen on Galathea intermedia Lillj. (collection Norman, labelled : Sacculina galatheae Norman, type).

Firth of Forth, Henderson, 1885, 1 specimen on Galathea nexa Embleton (collection Norman, labelled : Sacculina galatheae, sp. n.).

Naples, G. W. Smith, 1 specimen on Galathea nexa Embleton.

Norman and Scott (1906) published the following notes on this species: Sacculina galatheae, sp. n. We give this name to a little form found on the abdomen of Galathea intermedia, taken off Plymouth in 1889. There is little or no character in the species of this genus; but it can hardly be supposed that the very small form found upon G. intermedia can be the same as that which is common on Carcinus maenas' (l. c., p. 226). The copy of the cited book in the British Museum (Natural History) has been there since April 1906, and, as the mongraph on the Rhizocephala by Smith (1906) had not appeared before August of that year, it is evident that the species should be named Lernaeodiscus galatheae (Norman & Scott).

The type-specimen has a breadth of nearly 5 mm.; the specimens on *Galathea nexa* have a breadth of nearly 6 and 4 mm. respectively. In the type-specimen and in the smallest specimen there are no marginal lappets on the mantle; in the largest specimen these lappets are slightly developed. The mantle opening is turned more or less towards the right side of the host.

According to Smith (1906) Lernaeodiscus galatheae occurs at Naples as a parasite of Galathea intermedia and G. dispersa (=G. nexa). In a previous paper (Boschma, 1928 a) I described the anatomy of specimens on Galathea intermedia. The anatomy of the parasite on Galathea nexa being hitherto unknown, sections have been made of the specimen from the Firth of Forth. The anatomy of this specimen does not differ in any respect from that of the parasites of G. intermedia; collectric glands and testes have the same shape and structure, so that this parasite undoubtedly belongs to the same species.

Genus Sylon.

SYLON HIPPOLYTES M. Sars.

Sylon hippolytes : Sars (1870), Boschma (1928 a, 1931 a).

- For other literature on the species cf. Boschma (1928 a). Material examined :
- Greenland, 'Valorous' Expedition, 3 specimens on Spirontocaris ? polaris (Sab.) (2 on one host, collection Norman).
- Tromsö, Schneider coll., 1889, 3 specimens on Spirontocaris ? pusiola (Kröyer) (collection Norman).
- Shetland, 1865, 4 specimens on *Pandalina brevirostris* (Rathke) (collection Norman). Norway, 1878, 1 specimen on *Pandalina brevirostris* (Rathke) (collection Norman).
- Greenland, 'Valorous' Expedition, 1875, 2 specimens on Spirontocaris spinus (Sowerby).

In a previous paper (Boschma, 1928 *a*) the results are given of a detailed study of the anatomy of the specimens of the genus *Sylon* living on different hosts. I concluded that there are no characters for establishing different species among the known specimens, and in consequence I consider them all to be representatives of *Sylon hippolytes*.

All the specimens in the collection have been preserved for more than forty years, so I could not expect to find any more details in their anatomy than those laid down in my previous paper. Two specimens of *Sylon* on *Pandalina brevirostris* have been cut into sections to ascertain whether their anatomy is in accordance with that of specimens from other hosts. The

structure of specimens on Spirontocaris polaris, S. pusiola, and S. spinus has been studied before (Boschma, 1928 a), so that no more sections have been made of the specimens on these prawns. In the sections of the specimens on *Pandalina brevirostris* I have not found any differences from those on other hosts and I am thus convinced that they do not belong to a distinct species. One of the parasites of *Pandalina brevirostris* is an old specimen, strongly shrivelled (length 8 mm., breadth and thickness 2 to 2.5 mm.); the other sectioned specimen from the same host is a very young parasite which had recently penetrated through the cuticle of its host.

Genus THOMPSONIA.

The following diagnosis of the genus is quoted from Potts (1915, pp. 28, 29): 'A colonial Rhizocephalan infecting various Decapod Crustacea. Root system diffuse, widely distributed in body of host, sending branches into thoracic and abdominal appendages, which give off numerous sacs containing reproductive cells and becoming external at a moult of the host. These *external* sacs consist of a mantle and visceral mass without an intervening mantle cavity \cdot mantle thin and devoid of muscle fibres. Visceral mass contains ovary only without generative ducts, testis, or nerve ganglion. Development probably parthenogenetic. Nauplius stage omitted from life-history, larvae liberated at Cypris stage, after disintegration of the visceral mass, through apical cloacal aperture which appears in the mantle at a late stage. Moulting of host not prevented.'

The different species and the unnamed specimens of the genus mentioned in literature are given in the following list :—

Name.	Host.	Locality.	Author.
Thompsonia globosa	Melia tessellata.	Philippine Islands.	Kossmann, 1872.
Thompsonia sinensis	?	China ?	Keppen, 1877.
Thylacoplethus haddoni .	Betaeus malleodigitus.	Fiji Islands.	Bate, 1888.
	Alpheus avarus.	Torres Strait.	Coutière, 1902 b.
Thylacoplethus edwardsi.	-	Thursday Island.	Coutière, 1902 b.
Thylacoplethus heurteli		Fernando Veloso.	Coutière, 1902 b.
Thompsonia japonica Thompsonia dofleini	Pilumnus sp.	Japan.	Häfele, 1911 a. Häfele, 1911 a.
Thompsonia chuni	Parapagurus.	D. Tiefsee Exp.	Häfele, 1911 <i>a</i> .
Thompsonia japonica		Japan.	Krüger, 1912.
Thompsonia japonica	Pagurus striatus.	Japan.	Krüger, 1912.
Thompsonia affinis		Japan.	Krüger, 1912.
Thompsonia sp Thompsonia sp	Synalpheus brucei.	Torres Strait. South Africa.	Potts, 1915.
Thompsonia sp	Thalamita prymna.	Torres Strait.	Potts, 1915.
Thompsonia sp	Alpheus maileoaiguus.	Sulu Archipelago.	Van Kampen & Boschma, 1925.

It is improbable that all the specific names in this list are valid, but it is not possible to give distinct specific characters of all the different forms which have been described in detail. The chief peculiarities of these forms are given below.

Thompsonia globosa has a spheroidal shape, it possesses a long stalk (Kossmann, 1872). Two specimens only are known, which were attached to the legs of the crab *Melia tessellata*. They contained larvae. Length of the parasites (including the stalk) 1.8 mm., thickness 0.75 mm.

Concerning *Thompsonia sinensis*, described by Keppen (1877) in a paper in the Russian language, I cannot give any particulars, as I have not seen the paper. The title of this paper is found in Taschenberg's 'Bibliotheca Zoologica', vol. ii, p. 1227.

The specimens on *Alpheus (Betaeus) malleodigitus* mentioned by Bate (1888) were attached to the pleopods of the host. The parasites have an elongated shape and possess a short stalk with a proximal constriction. They occurred in fairly large numbers on their host. The size of the animals is not given. Bate writes : 'within each small sac was an embryo' (p. 566), but fig. 5 par. of pl. ci shows four of these embryos escaping from a fissure in the mantle.

Coutière (1902 a-e) describes three species of the genus *Thylacoplethus*, which was shown by Potts (1915) to be a synonym of *Thompsonia*. They are described as small ovoid sacs attached to the ventral surface of the abdominal segments of the hosts. One species (*Thylacoplethus haddoni*) has a length of 1.5 mm, and a thickness of 0.5 mm.; in another species (*T. heurteli*) these dimensions are 4.5 and 1 mm. respectively, whilst the third species (*T. edwardsi*) is intermediate in size between the two others. It is highly improbable that each of these forms represents a distinct species. Coutière does not give any specific characters, but perhaps he was convinced that each species of host had its own parasite (Giard's theory of the specificity of the parasites).

Three species of the genus *Thompsonia* have been described by Häfele (1911 a), viz. T. japonica, T. dofleini, and T. chuni. Of one of these, T. japonica, extensive material was available, and the author was thus able to describe all the peculiarities of this species in detail (Häfele, 1911 b). Thompsonia japonica has a comparatively long stalk, the body is more or less elongate; the dimensions are : length of the body 2 mm., thickness 0.8 mm., length of the stalk 1.2 mm. The parasites occur in great numbers on crabs of the genus Pilumnus, especially on the thoracic legs and on the abdomen. Thompsonia dofleini was found by Häfele in abundance (about 1500 specimens) on a specimen of Neptunus pelagicus. According to Häfele the shape of these parasites does not differ from that of T. japonica, but the figure of the species shows an animal of much more slender form. T. dofleini is somewhat smaller than T. japonicu. A strange characteristic of this species is the presence of a genital pore, provided with a chitinous cover: a feature not known in other representatives of the The third species described by Häfele, Thompsonia chuni, is a parasite genus. of Parapagurus. It is much larger than T. japonica (Häfele does not give the

exact dimensions) and has a more or less spheroidal shape. The stalk is very short.

Krüger (1912) mentions Pagurus striatus as a new host for Thompsonia japonica. He writes that perhaps T. japonica is a synonym of Kossmann's T. globosa, as the shape of the parasites is very similar. In the same paper Krüger describes the new species T. affinis, a parasite of Diptychus sp., which differs from T. japonica by its spheroidal shape. In comparison with T. japonica the external sacs of T. affinis attain one-half to three-fourths of the size of the former. A further difference between the two forms is found in the cypris larvae: those of T. japonica possess pigmented eyes (cf. Häfele, 1911 b), whilst the larvae of T. affinis have eyes which are completely devoid of pigment. This character proves that the two forms are specifically distinct.

Potts (1915) describes the life-history of specimens of *Thompsonia* on *Synalpheus brucei*. These parasites are pear-shaped and about 1 mm. long. In the same paper mention is made of parasites of the genus on *Actaea rüppellii* (pear-shaped to round, 1 mm. long) and on *Thalamita prymna* (elongate, 3 mm. long). According to Potts, it is probable that the three forms are specifically distinct, but as specific characters are lacking he does not give specific names to these forms. The three forms of *Thompsonia* dealt with by Potts were attached to the appendages of their hosts.

The specimen of *Thompsonia* described by Van Kampen and Boschma (1925) is interesting in that it is a parasite of *Alpheus malleodigitus*, the species which was found by Bate (1888) infected with a fairly large number of other parasites of the same genus. The two forms are widely different. The 'Siboga' specimen (Van Kampen & Boschma, 1925) is solitary ; it is attached to the ventral surface of an abdominal segment of the host ; it is more or less globular and the stalk is not sharply limited from the rest of the body. On the other hand, the 'Challenger' specimen (Bate, 1888) is gregareous, attached to the appendages of the host, it is more or less elongate and has a short stalk surrounded by a groove at its place of attachment to the body. In all probability the two forms constitute different species of the genus. The 'Siboga' specimen has a length of 1.5 mm. (length of body including the stalk 2 mm.) and a thickness of 1.5 mm.

Thompsonia sp., on Actaea rüppellii, Scottsburgh, Natal, 1902, Natal Government Museum.

Thompsonia sp., on Synalpheus brucei, Murray Is., Torres Strait, F. A. Potts.

The characters of these specimens have been described by Potts (1915), and figures of the hosts with the attached parasites are found in the same paper (l. c., pl. i, figs. l, 2, & 4). Some of the parasites are rather larger than the dimensions given by Potts : those on *Synalpheus* may attain a length of nearly 1.5 mm., those on Actaea a length of 2 mm. (not including the stalk). From each lot a few of the external sacs have been cut into series of sections, which, however, do not show many details of structure. The external sacs of the parasites of Synalpheus are filled with a great number of embryos in the egg-membrane, whilst those of the parasites of Actaea contain younger stages of development. In some specimens from Actaea a central hollow piece of tissue projects from the stalk into the mantle cavity (or the degenerated visceral mass?) between the eggs.

In both these forms the external sacs are in a too far advanced state of development to show the particulars described by Häfele (1911 b) in the youngest stages of his *Thompsonia japonica*.

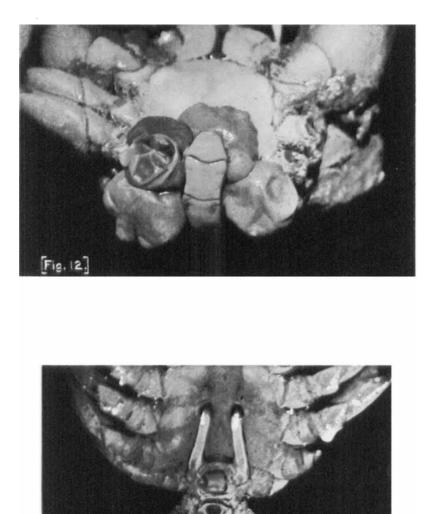
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Fig. 12. <u>SACCULINA SINENSIS</u>. Five specimens on the abdomen of <u>LEPTODIUS EXARATUS</u>.×4.5 Fig. 44. Two specimens of <u>PTYCHASCUS GLABER</u> on the abdomen of <u>ARATUS PISONII</u>.×3.75

Fig. 44