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INVESTIGATIONS ON
THE ANATOMY AND SYSTEMATIC
POSITION OF THE PARASITIC
SNAIL *ENTOCOLAX* VOIGT

BY

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WITH 38 FIGURES IN THE TEXT

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PREFACE

The joint authorship of this paper does not mean that the two authors have worked together while performing the investigation. First HEDING made a study of the specimens of *Entocolax* found during his work on *Myriotrochus*. The result of this study is the first chapter in the present paper. Then, thinking a further microscopical investigation of the material by a malacologist to be needed, for clearing up the problem of the so-called "pseudopallial cavity" and the systematic position of the genus *Entocolax*, he passed the specimens over to MANDAHL-BARTH. The result of MANDAHL-BARTH's investigation is given in Chapter II of the present paper. Actually the two chapters of this paper thus should be regarded as two different papers made by two different authors, but on account of both dealing with the same subject, and both being based on the same material, it was found that a joining of the two papers into one would be a very practical feature, facilitating the use of the results of these investigations for other students of this peculiar parasite.

Chapter I.

Entocolax ludwigi Voigt.

- Entocolax ludwigi*. VOIGT. 1888. *Entocolax ludwigi*, ein neuer seltsamer Parasit aus einer Holothurie. Zeitschr. wiss. Zool. Bd. 47, pp. 658—689, pl. XLI—XLIII.
- — SCHIEMENZ. 1889. Parasitische Schnecken. Biol. Centralblatt. Bd. IX. No. 18, pp. 567—574; No. 19, pp. 585—594.
- — HEDING. 1934. *Entocolax trochodotae* n. sp. Vidensk. Medd. Dansk naturhist. Forening, Bd. 98, pp. 207—214.
- Non: *Entocolax ludwigi*. SCHWANWITSCH. 1917. Observations sur la femelle et le mâle rudimentaire d'*Entocolax ludwigi* Voigt. Journal Russe de Zoologie. Tome II, Liv. 1—2, pp. 1—247, pl. I—IV.

Locality: Nordre Strømfjord, 380 m. Dr. NORDMANN. Station 11 a.
July 8th 1911 6 specimens.
Tasiusak (at Angmagssalik) 10—0 m. 7th Thule Expedition St. 19.
August 9th 1933 5 specimens.
Dusenfjorden at the anchorage, 20—25 m. Treaarsexpeditionen til
Christian den X's Land. August 10th 1933. 1 specimen.

Host: *Myriotrochus rinkii* Steenstrup (typical specimens).

Position in the host: All these 12 specimens were found in the body cavity of *Myriotrochus rinkii* with their posterior end (the siphon) bored into the body wall of the host and with the anterior end either floating freely in the coelomic fluid or, in a few (2) cases, attached to the intestine of the host. Just as it is the case with *E. trochodotae*, the attachment of *E. ludwigi* to the intestine of the host seems to be more or less incidental and always rather light.

Why the larger specimens of *E. ludwigi* and *E. trochodotae* often are found with their mouth attached to the intestine of the host is not quite clear. It could be supposed that the parasite sucks its nourishment from the intestinal wall of the host or from some vessel there. That the attachment of the parasite to the intestine is not merely casual, due to adhesion during capture and fixation, is distinctly seen from the cases where a small protuberance from the intestinal wall has been sucked into the mouth of the parasite.

That *Entocolax* (that is the two species studied by me, and *E. schiemenzi*; not *E. schwanwitschi*, the latter being characterized by having

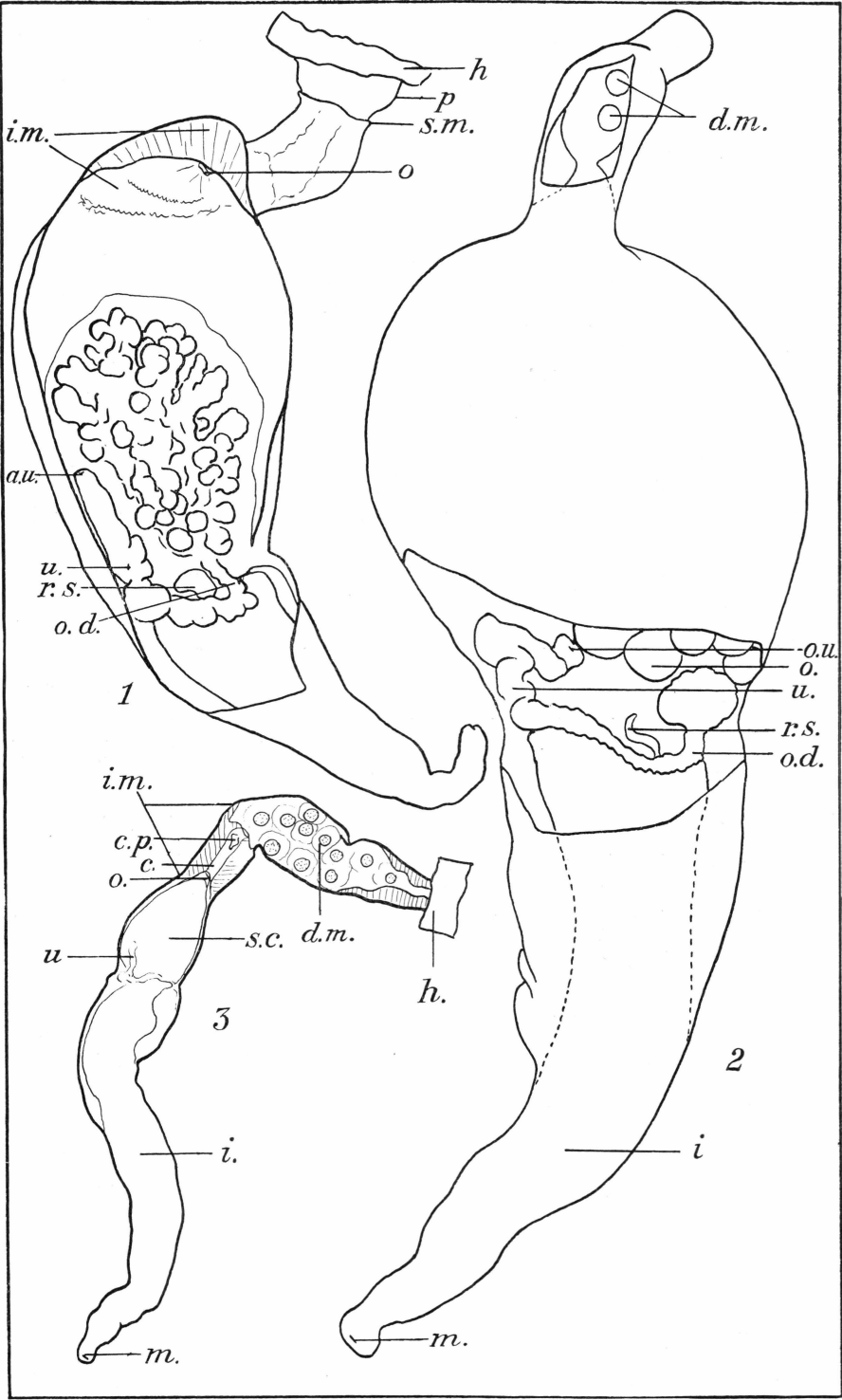


Fig. 1—3.

its siphon in the intestinal wall of the host) do not prefer the intestinal vessels of the host can be concluded from the fact that none of the specimens which I have observed attached to the intestine of the host have been attached to intestinal vessels. That the here named three species of *Entocolax* always should get their nourishment from the intestine of the host is certainly impossible, as the young and quite small specimens, on account of their small size, cannot reach the distance from the body wall of the host to the intestine. It may therefore be considered the most likely that *Entocolax* (and this can be supposed to hold good for all the species) takes its nourishment from the coelomic fluid of the host, and that the possible attachment to the intestine of the host, or other places in the body cavity of the host, takes place in order to fasten the, in the adult specimens, rather heavy anterior end with the sexual cone, so that the hazard of a severing of the, on account of the presence of the brood, very dilated and thin-walled brood-pouch is reduced.

While thus the attachment of the mouth seems rather incidental and most likely can be changed during the stay of the parasite in the host, the attachment of the siphon to the body wall seems to be very intimate, and, as far as can be seen, permanent throughout the entire lifetime of the parasite.

At it appears from textfigures 4 & 5 the siphon does not end, as stated by SCHWANWITSCH (Op. cit. Pl. I, fig. 1—3; 9) with a simple opening. At a superficial observation it looks as the *Entocolax* is fastened to the body wall of the host by a lip-like ring-shaped fold, out of which, in some (mainly older) specimens, protrudes a rather solid, pear-shaped organ which penetrates the ring-muscle-layer. From this organ a pore through the epidermis of the host forms a passage to the surrounding water.

This description of the attachment of the siphon in the body wall of the host is based on the large specimens with developed young in

Fig. 1—3. *Entocolax ludwigi* Voigt, three female specimens.

1. Young specimen from Tassiusak with eggs in the brood-pouch (not shown in the figure), cluster-shaped ovary, and a distinct, thickwalled part (*i. m.*) between the brood-pouch and the siphon.
 2. Older specimen from the Dusenfjord, with embryos in the brood-pouch and remains of the dwarf-males (*d. m.*) in the siphonal cavity.
 3. A quite young specimen from Nordre Strømfjord, Gonads and brood-pouch not yet developed. Siphon well developed, filled with dwarf-males (*d. m.*). Distinct, thickwalled part (*i. m.*) between brood-pouch and siphon.
- c.* canal between brood-pouch and siphonal cavity; *co.* cocoon; *c. p.* pear-shaped organ; *d. m.* dwarf-males; *h.* host; *i.* intestine; *i. m.* intermediate part between siphon and brood-pouch; *m.* mouth; *o.* opening from brood-pouch into the intermediate section; *o. d.* oviduct; *o. u.* opening from uterus into the brood-pouch; *p.* peritoneum of the host, surrounding the organ bored into the body-wall; *r. s.* receptaculum seminis; *s. c.* sexual cone; *s. m.* lip-shaped siphonal margin; *u.* uterus.

the cocoons. In the younger specimens the pear-shaped organ is not visible macroscopically, and whether it there is completely lacking or present in an undeveloped stage is impossible to decide. Likewise, it has not been possible to disclose an opening through the skin of the host in the younger specimens.

Practically all the specimens, both of *E. ludwigi* as well as of *E. trochodotae*, were found in the host with their siph placed close behind the dorsal tentacles, only one specimen was found with its siph fastened

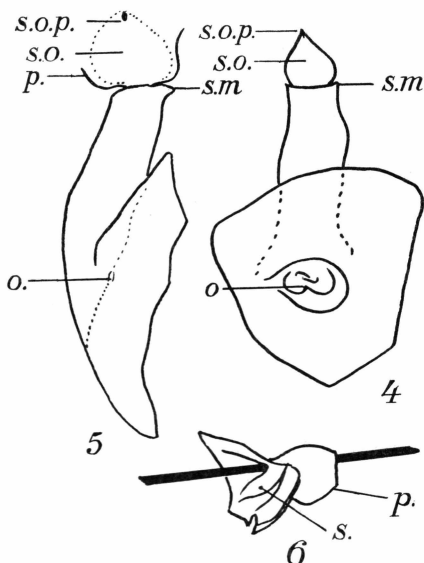


Fig. 4—6. *Entocolax ludwigi* Voigt. Siph of an adult female. 4 and 5 the same preparation seen from two sides; 6. the distal most part of the siph with a sounder through the pore in the skin of the host into the siphonal cavity.

s. siph; s. o. siphonal organ, bored into the body-wall of the host; s. o. p. orifice of siphonal organ, corresponding to pore in the skin of the host; explanation of other letters as in figs. 1—3.

about one third the length of the host behind its tentacles, but also in this case the parasite was attached in the dorsal interradius of the host.

This position seems not to be accidental, as both the host-species are burrowing animals, and, at least *Myriotrochus*, lie in the mud with only the dorsal tentacles and a small part of the dorsal interradius exposed in the mud-surface. If the parasite shall be able to remain in connection with the free water there is no other place for it to attach itself than in the dorsal interradius close behind the tentacles, exactly where it is always found.

In connection with the position of the *Entocolax* in the host arises the question how the host is infested and whether the way of infection is in relation to the position of the siph?

All we know with certainty in this regard is that the specimens studied by SCHWANWITSCH experimentally were shown to attack the host through the intestinal channel. Considering the different structure of the end of the siphon in the small and the large specimens of *E. ludwigi* it seems, at the first glance, as if this difference supports the opinion of SCHWANWITSCH. It could thus be supposed that the quite young *Entocolax* entered through the intestine of the host, and there upon moved from this and out to the body wall where that is exposed to the free water. Arrived there they attach themselves, and during the further development the pear-shaped organ is formed, and the connection to the water is obtained at a time where the brood is ripe to be shed.

That this, however, cannot be the case is shown from the following facts: Firstly, it is striking that even the smallest specimens (in *E. trochodotae* even a specimen of very near the same size as the shell bearing larvæ) are firmly attached in the ringmuscle-layer of the host in such a way that one cannot help thinking that they must have crept in from the outside. Secondly, the animals studied by SCHWANWITSCH, and which attack their host through its intestinal channel, are characterized in their remaining with the siphon attached on, or rather in the intestinal wall of the host. Thirdly, the young females of *E. ludwigi* become infested with the dwarf-males at a time where the pear-shaped organ-complex has not yet developed. This indicates that there is a passage from siphon to the surrounding water already at a rather early stage in the development. The possibility of the males infesting the young females at such young a stage that the latter have not yet even attached themselves to the body wall of the host is disproved by the small specimens, which are well attached but without any males; indeed, without a developed siphonal- or fertilization cavity. The only acceptable explanation of these conditions is, that the young *E. ludwigi* attack the *Myriotrochus* on the parts of its dorsal skin which are exposed to the water, and that they there bore their way into the body cavity without ever leaving hold of their entrance-hole.

The supposition that *E. ludwigi* should be able of attacking the host by either ways, viz. through the intestine, as it has been shown by SCHWANWITSCH, and through the skin and the body wall, such as I believe it to be the case in the specimens observed by me, is, of course, an explanation of these two contradictory observations. In that case it is, however, more than peculiar that all the specimens studied by SCHWANWITSCH behave in one way, and that all the specimens observed by VOIGT and me (as well *E. ludwigi* as *E. schiemenzi* and *E. trochodotae*) behave the other way. I have seen but one specimen of *Entocolax* placed with its siphon attached to the intestinal wall of the host; but this specimen was from the Kara Sea, and the host was not *Myriotrochus rinkii* but

M. eurycyclus; just the species which must be supposed to have been the host for SCHWANWITSCH' specimens of *Entocolax*. The most reasonable explanation seems thus to be that we are dealing with two different species of *Entocolax*, each one with its own host, and its own biology¹⁾.

Eidonomy: The preserved specimens of *Entocolax ludwigi* resemble small, yellowish white pear- or sausage-shaped bladders, more or less filled with a granular mass, and for non-specialists it is very easy to mistake them for the gonads of the host. The facts that the infested specimens of *Myriotrochus* usually are more or less parasitically kastrated, and that the parasite is sitting in the dorsal interradius, exactly where the gonads should be, make this mistake only the more likely.

Further investigation shows that there is a rather typical difference between the quite young specimens of *Entocolax* and the larger, ripe ones with brood.

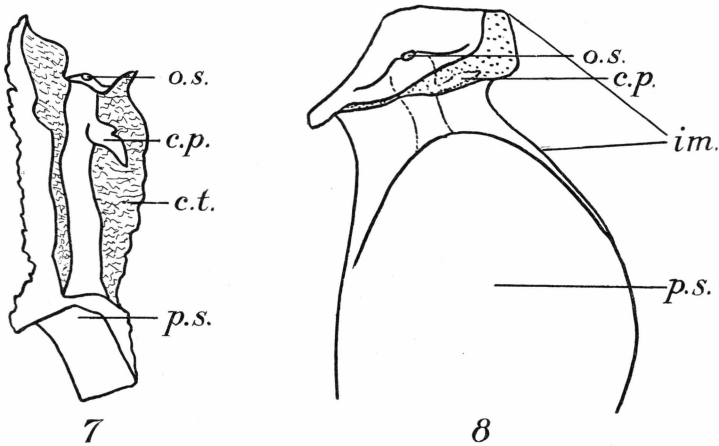
The relatively ripe specimens from Tasiusak and the Dusenfjord (textfig. 1—2) are some 30—35 mm of length. They consist of two sharply separated parts, the trunk and the sipho. The trunk is about 25 mm long and is elongately pear-shaped, while the sipho, which measures only some 5 mm, is cylindrical, as a rule with a bladder-shaped swelling on the middle. On account of the semitransparency of the body wall it is possible to see already from an outer observation that the trunk consists of three parts, the brood-pouch (the so-called pseudopallial cavity) with the cocoons, the sexual cone with uterus and oviduct, and, lowermost, the cone-shaped undifferentiated stomach and gut.

Against these ripe specimens the young specimens from G. G. U. station 11 (textfig. 3) show a quite different construction. They measure about 15 mm in length and are all evenly worm-shaped, there is thus no distinct difference between trunk and sipho. A more thorough investigation shows that these young specimens (cf. textfig. 3) in their posterior end, towards the body wall of the host, carry an about 5 mm long bladder filled with fully developed dwarf-males. Anterior to this bladder there is a rather firm piece with thick walls and a narrow passage. A pseudopallial cavity is not found, the sexual cone being found directly anterior to the thickwalled part.

Anatomy: If a fully ripe specimen with large youngs in the brood-pouch is opened it is found that the sipho is only an empty tube limited from the large brood-pouch by a small membrane, which is perforated in the middle by a quite small opening. In such large specimens the sexual cone is merely a compact, apparently undifferentiated, yellowish-

¹⁾ It may be remarked that an investigation of the outer appearance of *M. eurycyclus* seems to show this species to live with its entire body burrowed in the mud, wherefore, evidently, the easiest way for the *Entocolax* to attack this host must be through the mouth and the intestinal canal.

brown cone, which rests on the upper side of the intestine vaulting in between the cocoons. If, on the other hand, a specimen with somewhat younger larvae in the cocoons is opened (cf. textfig. 2), it is found, that the siphon in this case is not empty but contains some ball-shaped bodies, which on comparing with other specimens must be interpreted as the remains of the dwarf-males. A very thorough investigation of the brood-pouches in three specimens showed neither the dwarf-males or remains of such to be found in the brood-pouches, while remains of the males were found in the siphonal cavities. A still younger specimen (cf. text-



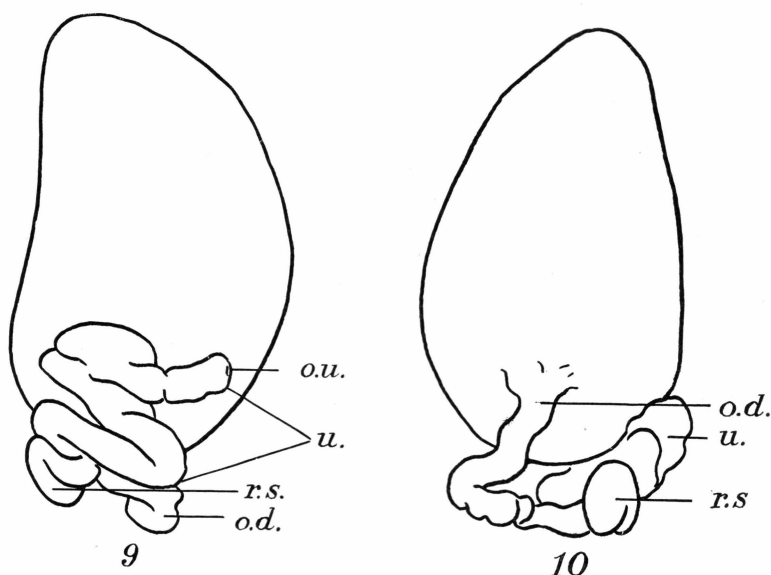
Figs. 7—8. *Entocolax ludwigi* Voigt. The thick-walled section between brood-pouch and siphon in a very young specimen, 7 (entire specimen shown in fig. 3), and in a somewhat older specimen; 8. showing the canal and the pear-shaped diverticle (*c. p.*). *c. p.* pear-shaped diverticle of the canal in the intermediate section; *c. t.* connective tissue; *o. s.* opening of the canal into the siphonal cavity; *p. s.* brood-pouch.

fig. 1) had no larvae but cleaved eggs in the cocoons. In this specimen the sexual cone is still merely a large thin-walled bladder containing a cluster-shaped ovary with oviduct, receptaculum seminis, and uterus. In this specimen it is furthermore seen that the part on the border between the brood-pouch and the siphonal cavity is a relatively thick-walled partition containing a narrow passage.

In one of the youngest specimens (textfig. 3) this thickwalled part is relatively very large, viz. almost half as long as the siphon and of about the same length as the, at this stage undeveloped, sexual cone. The brood-pouch lacks, as stated above. A closer study of the thickwalled part shows the wall to consist of a clear jelly-like tissue, inforced by an irregular mass of strands of connective tissue (cf. textfig. 7). Longitudinally through this tissue runs a narrow, but well limited channel, which in its one side is provided with a small vesicle (cf. textfig. 7). In another, somewhat larger specimen from the same host (cf. textfig. 8) the thick-

walled part is shorter, and the small vesicle has been partly reduced; finally, in the large specimens with fully developed brood-pouch and only a thin partition between the brood-pouch and the siphonal cavity, it appears that the thickwalled part has completely disappeared.

The gonad itself, the content of the sexual cone, consists in all specimens of a small egg-shaped body (textfigs. 9 and 10). The different parts of the ovary can, as in the specimen figured in fig. 1, be arranged



Figs. 9—10. *Entocolax ludwigi* Voigt. Sexual cone of adult female with oviduct (*o. d.*), receptaculum seminis (*r. s.*), and uterus (*u.*). *o. u.* opening from uterus into the brood-pouch.

in a loose cluster, or they may be pressed so close together that the individual branches cannot be distinguished. In either case the individual branches of the ovary are imbedded in a loose granular mass, apparently a very loose connective tissue.

The outlet from the ovary to the brood-pouch — the oviduct — consists of two parts, corresponding to the conditions in the species *trochodotae* and *schwanwitschi*. The proximal part is rather thin-walled. It begins as a collecting chanel between the different parts of the ovary and should here in its proximalmost part perhaps rather be conceived as a cavity in the lobed ovary. In its distal part, on the other hand, it is formed as a real oviduct. How far the ovary proper reaches, or, in other words, where the border between the ovarian cavity and the oviduct is situated cannot be stated without a cytological investigation, as a part of the lower ovarian branches perhaps rather should be inter-

preted as secondary glands. At least, there is so great a difference in appearance, i. e. colour and consistency, of the lower ovarian branches and the part which is sitting closer together filling the end of the sexual cone, that this difference in function seems rather reasonable.

The distal end of the ovarian duct, commonly named the *uterus*, is distinguished very clearly from the oviduct in having remarkably thick, glandular walls. Undoubtedly uterus is the organ which forms the

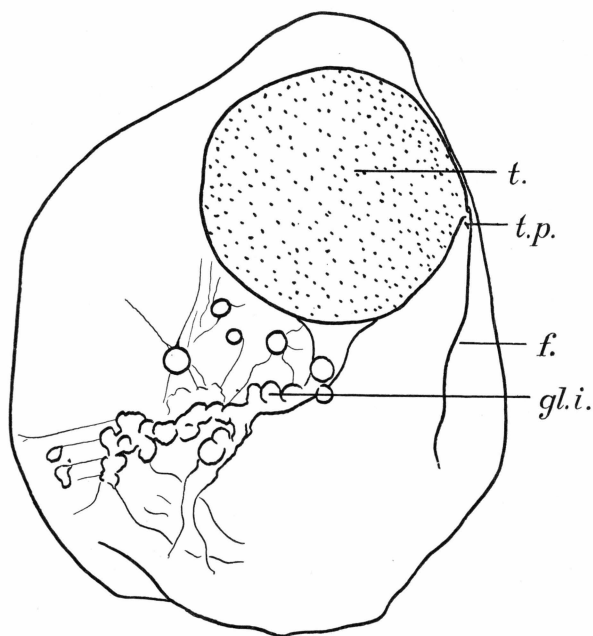


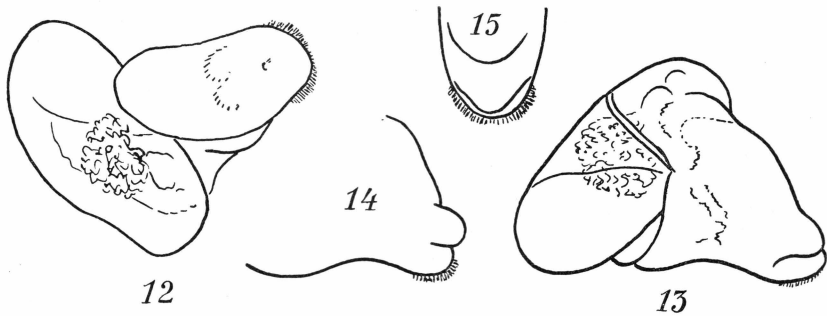
Fig. 11. *Entocolax ludwigi* Voigt. Dwarf-male. *t.* testicle; *t.p.* opening of testicle (spermoduct); *f.* fold in the body-wall; *gl.i.* rudiments of glands, intestine, etc.

clear, yellow, chitinous cocoons, which surround as well eggs as young during their stay in the brood-pouch. Between the two sections of the gonoduct, oviduct and uterus, is found a small, sometimes exceptionally well developed at other times rather indistinct vesicle, usually interpreted as a receptaculum seminis.

Dwarf-males: As mentioned above (p. 11) there is in the siphonal cavity of some of the young females found a relatively large number of (15—25) very reduced dwarf-males (cf. textfigs. 3 and 11). They consist of a very thin and clear, ball-shaped bladder, in which is seen one ball-shaped testicle and some rudiments of some larval intestinals. The testicle which is faintly whitish, is provided with a very short, almost rudimentary vas deferens. In this regard the males of *E. ludwigi* are distinguished from the males of the species from the Kara-Sea

described by SCHWANWITSCH, as the latter are said to have a rather long vas deferens. Of course, one cannot put very much stress on this difference, as it may be due to different methods of fixation, or to different stages of development (= stages of reduction) on account of age.

Youngs: The large, cracked specimens from Tasiusak contain a rather large number of youngs (cf. textfigs. 12—15), and a part of these are so well developed that they undoubtedly are ripe to be born. They are somewhat different from the figures of SCHWANWITSCH (Op. cit. Pl. II, figs. 27—28), but a real comparison is unfortunately impossible

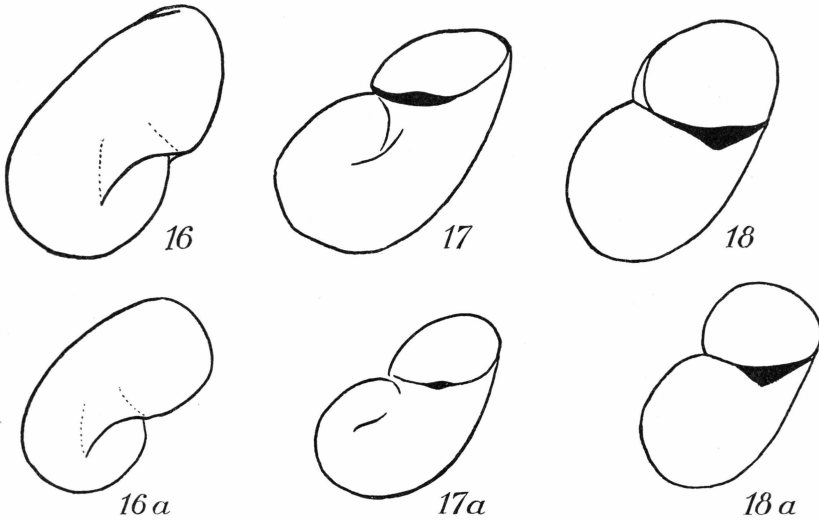


Figs. 12—15. *Entocolax ludwigi* Voigt. An embryo from a ripe cocoon, seen in different views.

on account of the unclearness of the said figures. A comparison of the shell-contours shows a small, but rather characteristic difference between the two forms, and an investigation of the youngs from a couple of *Entocolax* from the Kara-Sea shows the shells of these latter (the soft parts are very poorly preserved) to agree very well with the shell-contours given by SCHWANWITSCH. In order to show the difference I have here (cf. textfig. 16—18) drawn two shells, one from Greenland, and one from the Kara Sea, both seen from three different sides, and, to make the comparison as valuable as possible, I have, as far as I have been able, turned the shells in the same way having them lying side by side during the process of the drawing. From these figures it is seen that, besides a small difference in shape, there is a not unconsiderable difference in size.

Classificatory remarks: A comparison of the here described specimens of *Entocolax* from Greenland with the description given by SCHWANWITSCH of *Entocolax* from the Kara Sea, as well as a comparison of the greenland specimens with the few and rather poorly preserved specimens from the Kara Sea in the Copenhagen Museum, shows that we undoubtedly have two different species of *Entocolax* from the arctis.

One of these, the one from Greenland, corresponds so exactly to the description given by VOIGT of the type of *Entocolax ludwigi*, that there can be no doubt that we have here the *Entocolax ludwigi* Voigt. The other, described by SCHWANWITSCH, and by him referred to *E. ludwigi*, is a new species which very appropriately ought to be named after the man, who has described it in such a satisfactory way, and, especially through the discovery of the dwarf-males, contributed considerably to our understanding of the entire group of animals dealt with here.



Figs. 16—18. Shells of embryos of *Entocolax ludwigi* Voigt 16—18, and of *Entocolax schwanwitschi* Hdg. 16 a—18 a.

***Entocolax Schwanwitschi* n. sp.**

Entocolax ludwigi. SCHWANWITSCH. 1917. Observations sur la femelle et le mâle rudimentaire d'*Entocolax ludwigi* Voigt. Journ. Russe de Zoologie T. II, L. 1—2, pp. 1—247, pl. I—IV.

Diagnosis: Entoparasitic, strongly transformed, dioecious snails without shell. The females about two cm of length, with an undifferentiated gut in the one end and a simple ovary with rather complicated ducts in the other end. Other organs lacking, or at least not found with certainty. It is characteristic for the adult female that a part of the genitals has been developed into a brood-pouch, an erroneously named "pseudopallial-cavity".

Contrary to the conditions in *E. ludwigi* the genital opening in this species is fastened to the intestinal wall of the host, through which the young animal has bored its way into the body cavity of the host. Further the genital opening seems not to be provided with such a pear-shaped organ as is usually found in *E. ludwigi*.

The males are reduced to ball-shaped bladders containing faint rudiments of the larval intestinals together with a well developed, ball- to pear-shaped testicle with a long vas deferens. The males, according to SCHWANWITSCH, are found in the brood-pouch of the female, but they must be supposed normally to be found in the part of the genitals which in older interpretations is named the siphonal cavity.

The eggs, which are congregated in groups in chitinous cocoons, are developed in the brood-pouch of the mother into shell-bearing larvae with a distinct, though faintly developed, velum. The larvæ are deposited in the intestinal canal of the host, wherefrom they pass into the sea together with the faecal matter. They swim around until they find another host, which they infest through the mouth into the intestine and finally bore their way into the body cavity.

Size of the shell-bearing larvae about 400 μ .

Host: as far as known, only *Myriotrochus eurycyclus* Hdg.

Locality: Kara Sea.

Nearest related species: *Entocolax ludwigi* VOIGT.

Remarks: *E. schwanwitschi* is distinguished most distinctly from *E. ludwigi* in the way it is placed in the host; *ludwigi* always being fastened with its genital opening to the body wall of the host. Of morphological characters must especially be pointed out that the genital opening in *schwanwitschi*, according to SCHWANWITSCH, is simply lip-shaped or ring-shaped, while it in *E. ludwigi*, at least in large specimens, is developed into a peculiar sort of ovipositor bored into the body wall of the host. *E. schwanwitschi* seems to be a rather small form, not usually measuring more than c. 2 cm, while *E. ludwigi* measures around 3 to 3.5 cm. Corresponding to this the larvæ of *schwanwitschi* measure about 400 μ in length of shell, while the larvæ of *ludwigi* are as large as 600 μ .

Whether there may be a specific difference between the males of the two species cannot be said with certainty with our present knowledge, but it seems that the vas deferens is considerably longer in *shwanwitschi* than in *ludwigi*.

It must also be stated that, according to our knowledge for the time being, the two species are not found in the same host, but each one in its own species of the genus *Myriotrochus*.

Chapter II.

Of the material of *Entocolax* studied by HEDING two specimens, viz. those figured in fig. 2 and 3, were stained with parakarmin, embedded in paraffin, and cut into serial sections of a thickness of, as a rule, 10 μ . The series, however, were not continuous, the specimens being divided by HEDING into several parts on account of the anatomical investigation. From the one specimen (fig. 2) the ovary and the intestine was sectioned, it was intended to be cross-sections, but due to difficulties in the orientation the sections became slightly oblique. From the other specimen (fig. 3) the siphon was cut into longitudinal sections while the passage between siphon and the "pseudopallial" cavity (fig. 7) was cut into cross-sections, finally also the posterior part of the intestine was cut into sections. From this latter specimen the ovary and the surrounding parts, unfortunately, could not be made into serial sections, on account of its falling completely into pieces on putting it through Xylene before the embedding. All the sections were afterwards stained with C. C. HANSEN's Hematoxylin and embedded in Canadabalsam in the usual way.

Unfortunately the poor preservation of the material, which already makes an anatomical investigation under the binocular microscope very difficult, is so bad that it, as a rule, is very hard to see the histological details; it is thus especially hard to identify certain types of cells, as e. g. glandular cells, the nuclei for a very considerable part having flown out, whereby large parts of the cells in question become vigorously stained by the hematoxyline. Further it is, as a rule, very difficult to distinguish between muscle-cells and the cells of the connective tissue; on the other hand, it is quite easy to determinate the limits for the epitheliums, just as, curiously enough, the cilia can be recognized.

On account of the sections not allowing a more thorough cytological description, and such also partly having been given by VOIGT and especially by SCHWANWITSCH, we shall here content our selves with the consideration of some few special sections through different parts of the oviduct, which may furnish some important contributions to the

understanding of the building of *Entocolax*, and by which it further more is possible to explain in the main features the development of the species.

1. Microanatomical investigation.

Before beginning the discussion of the sections through the different parts of the oviduct it must be stated that the order in which

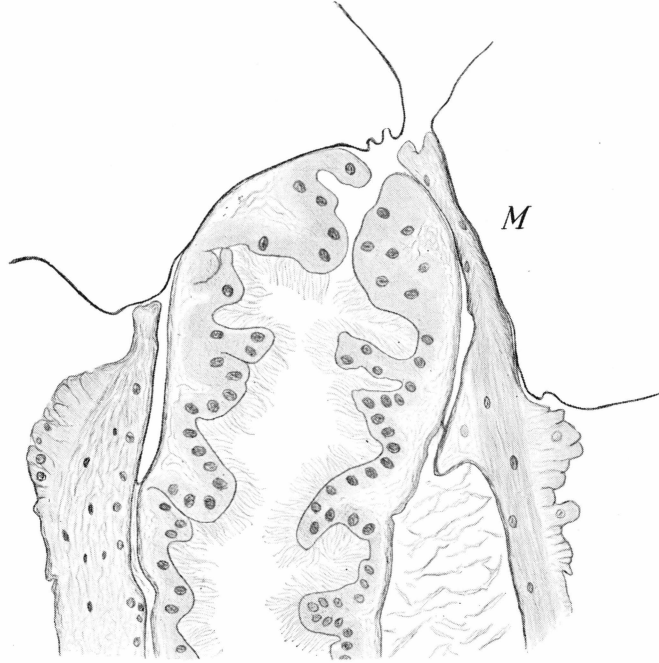


Fig. 19. *Entocolax ludwigi* Voigt. Longitudinal section through point of siphon. $\times 200$.
M. skin of *Myriotrochus* (cf. text).

these different parts are taken is distal-proximal, which means that we shall begin with the siphon and there from follow the oviduct upwards towards the ovary.

Figure 19 shows a longitudinal section through the point of the siphon, which, as it appears from the figure, consists of two well distinguished parts, an inner tube and an outer tube, the latter representing the epidermis and surrounding the former. These two tubes are at the point of the siphon not connected with each other, there being a distinct, though exceedingly narrow space between them; more proximally this space is larger and filled by a peculiar, very loose connective tissue. The inner tube has an even and smooth outer surface, while towards the lumen the wall is strongly folded. These folds protrude strongly nearly everywhere, whereby the lumen of the tube is reduced con-

siderably. With regard to the construction of the wall of the inner tube, there can on the sections be distinguished three layers: innermost a single-layer ciliated epithelium, consisting of rather high epithelial cells with large nuclei and numerous and long cilia; below the ciliated epithelium lies a somewhat unregular layer of connective tissue, which reaches up into the folds. On the sections this layer appears much lighter than the other two on account of its much smaller number of nuclei. Whether there now follows one or two muscle-layers cannot be distinguished with certainty. Finally there is outermost found a stronger coloured, very thin layer, the nature of which cannot be distinguished on the present material, there being apparently neither cell-limits nor nuclei, which, however, must be supposed to be due to the poor preservation. Right out at the opening of the siphon there are in *Entocolax ludwigi* no cilia, such as SCHWANWITSCH has figured it to be the case in *Entocolax schwanwitschi* (cf. SCHWANWITSCH 1917 T. 1. fig. 9).

The outer tube consists likewise of three layers which, however, do not stand out quite as sharply against each other as in the inner tube, but the layers can yet in several places be distinguished clearly.

Innermost, that is towards the outer surface of the inner tube, is found a generally indistinct epithelium without cilia, outside of this follows a layer which, most likely, in the main consists of connective tissue, but it is possible that this layer also contains some muscle-cells. The connective tissue is arranged in definite directions, almost longitudinally; but, as far as can be seen, the fibrilla towards the end of the tube run more obliquely, converging towards the edge. Outside the connective tissue is finally found a single layer of epithelial cells of different height and likewise without cilia. On account of the varying height of the epithelial cells the surface of the tube has a peculiar tufty appearance, a feature which, however, can be seen only in the microscope, the single tufts corresponding to the single epithelial cells. The outer tube is cut off obliquely in such a way that its free edge surrounds the point of the siphon as a slanting annular fold, which on the one side reaches to the mouth of the inner tube, while it on the other side stops at the muscle-layer of the skin of the holothurian. Further the annular fold, formed by the free parts, is narrowing and considerably more so towards the edge than proximally, where there is found connective tissue between the two tubes. The edge itself is somewhat thickened, as can be seen on fig. 19, from which figure it also appears that there is an open connection between the lumen of the siphon and the surrounding world, there being a hole through the skin of the *Myriotrochus*. This is not without importance, VOIGT not having observed any such hole through the body-wall of *Myriotrochus rinkii*, neither does SCHWANWITSCH state any hole to exist off the opening of the siphon

of *Entocolax* where it is attached to the intestinal wall of *Myriotrochus eurycyclus*.

How are now these two tubes to be interpreted? Through the inner tube the youngs are born, and this must therefore be interpreted as the most distal part of the female gonoduct, while the outer tube only forms the limit of the body towards the outside i. e. the epidermis; but — as we shall see later — the outer tube represents in reality the mantel, and the thickened, obliquely cut off edge is the mantle edge.

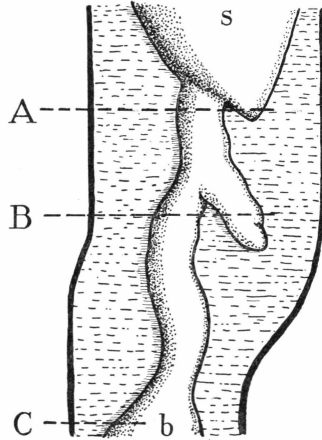


Fig. 20. *Entocolax ludwigi* Voigt. Drawn reconstruction of the canal between brood-pouch (b.) and siphon (s.). The lines A, B, and C indicate the position of the sections shown in figs. 21—23. $\times 50$.

While the cilia are very numerous in the siphon near the point, they become more and more sparse farther in, until they, in the space where the dwarf-males are staying, hardly are discernible. In this space the walls of both the inner and the outer tube, which here lie quite close with only a thin layer of connective tissue between them, are considerably thinner than at the point of the siphon. These thin walls as well as the sparse cilia are, most likely, the result of the pressure of the many growing dwarf-males, which forces the wall to give way so that the room is enlarged. More proximally, where the dilatation is less, the wall is again thicker and the cilia more distinct.

The next part of the female gonoduct we are to discuss is the interesting canal which HEDING discovered in the young specimen (fig. 3) between the chamber with the dwarf-males and the part of the gonoduct which later becomes the storage for the eggs (the "pseudopallial" cavity). Fig. 20 is a drawn reconstruction of this canal corresponding to Fig. 7. The stippled lines A, B, and C show the situation of the cross-sections which are figured in the following three figures (figs. 21—23). The first

of these (fig. 21) shows a section which has hit the canal immediately before its opening into the cavity with the dwarf-males, also the anteriormost part of this cavity has been hit, which means, as it also appears from fig. 20, that this canal opens obliquely into the chamber with the dwarf-males. This proves clearly that the siphonal cavity cannot be interpreted merely as a simple dilatation of the female outlet, in reality it is a special section into which the gonoduct proper opens. For the rest the canal, as far as it can be distinguished, is formed from the same three layers as the inner tube in the sipho and is further, like

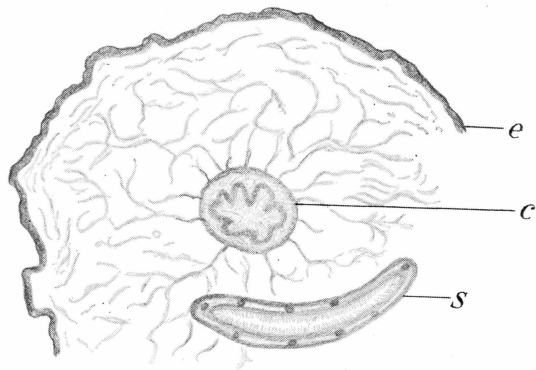


Fig. 21. *Entocolax ludwigi* Voigt. Transverse section corresponding to the line A in fig. 20. $\times 85$. e. epidermis; c. the canal proper; s. the proximal end of the siphonal cavity.

the latter, surrounded by a mantel of openmeshed connective tissue, which only is considerably thicker than in sipho; outside on this connective tissue is found the same dotted epidermis which surrounded the sipho.

Fig. 22 shows a section through the middle part of the canal. This section has also hit the diverticle which, as far as it can be seen, is build in exactly the same manner as the canal itself. Glandular cells do not seem to occur neither in the canal nor in the diverticle, but on account of the poor preservation of the material this cannot be decided with full certainty.

Finally fig. 23 shows a section through the wall of the canal just on the transition to the "brood-pouch". Here the interior wall which, by the way, still consists of a single layer ciliated epithelium, is not folded any more, and the two layers next following to the epithelium, the light and the dark, which were found both in the sipho and the canal, have apparently disappeared here, the loose, openmeshed connective tissue lying directly on the ciliated epithelium. From this transitory place one proceeds evenly into the "brood-pouch", the wall of which

is build in nearly the same way, only is the layer of connective tissue between the inner and the outer epithelium much thinner, and it appears that the inner epithelium is entirely devoid of cilia. At the basal part of the ovary the interjacent connective tissue again becomes thicker, the inner and the outer epithelium receding from each other, but while the outer continues throughout the rest of the animal, i. e. the anterior

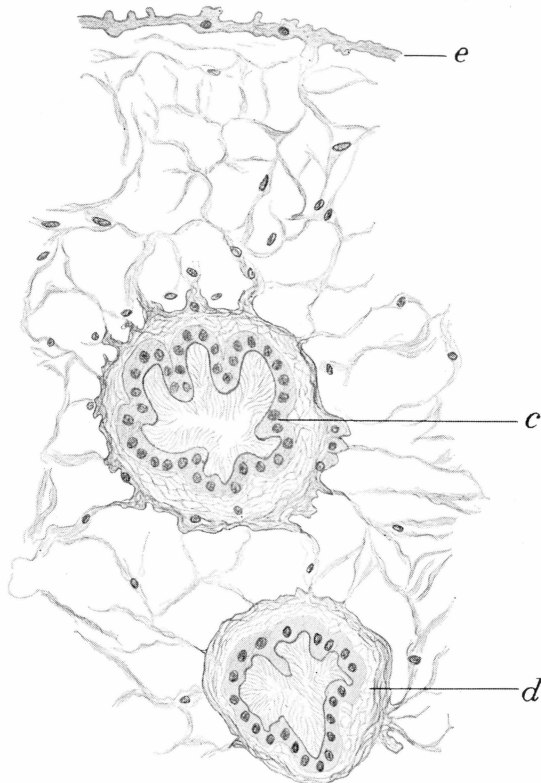


Fig. 22. *Entocolax ludwigi* Voigt. Transverse section corresponding to the line B in fig. 20. $\times 200$. *e.* epidermis; *c.* the canal; *d.* diverticle.

part containing the intestine, the inner turns over and encompasses the sexual cone outside the epithelium of the ovary. From fig. 24, which shows a section through the brood-pouch a little above the place where the inner epithelium turns over, it will be seen that the part of the epithelium which covers the ovary has somewhat higher cells than the part which limits the brood-pouch towards the outside.

This bending of the epithelium in the brood-pouch has been both observed and figured by VOIGT (Op. cit. 1888, plate XLII, figs. 24—25, which show it in cross section) he merely interpreted it wrongly, thinking, when he saw the same types of tissue occur twice in the wall in the

inverse order, that the wall was a duplicate, which in his opinion could only be the mantle, because he, in the beginning, had the animal wrongly

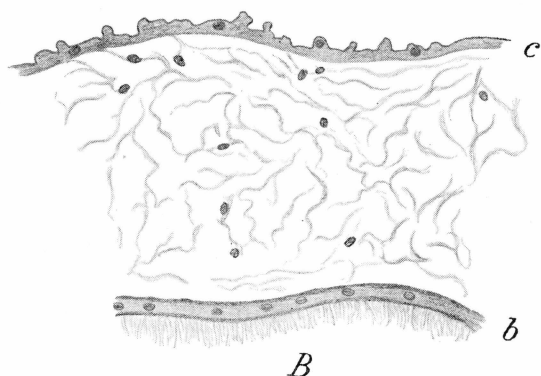


Fig. 23. *Entocolax ludwigi* Voigt. Transverse section corresponding to line C in fig. 20. $\times 200$. c. epidermis; B. brood-pouch; b. outer epithelium of brood-pouch.

orientated and interpreted the orifice of the sipho as the real oral opening. SCHIEMENZ' interpretation will be discussed later.

Basally in the brood-pouch opens the canal which hitherto has been interpreted as the female gonoduct proper. The inner walls of this

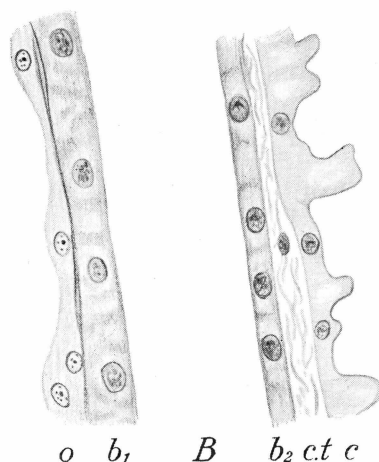


Fig. 24. *Entocolax ludwigi* Voigt. Longitudinal section through the proximal part of the brood-pouch. $\times 500$. e. epidermis; c. t. connective tissue; B. brood-pouch; b_1 and b_2 inner and outer epithelium of brood-pouch; o. epithelium of ovary.

canal consist of high, single layer, ciliated epithelium with numerous unicellular glands. Transverse section of this canal are figured by SCHWANWITSCH (Op. cit. 1917, Pl. II, figs. 25, 26). It has hitherto been interpreted as oviduct and uterus, of which the oviduct is the proximal,

more or less strongly twisted part, and uterus the distal more straight part. On the oviduct is, as mentioned by HEDING, found a more or less well developed swelling, which serve as a receptaculum seminis. In the quite young specimens of *Entocolax ludwigi* it has not been possible to make out this receptaculum seminis, wherefore it must be supposed

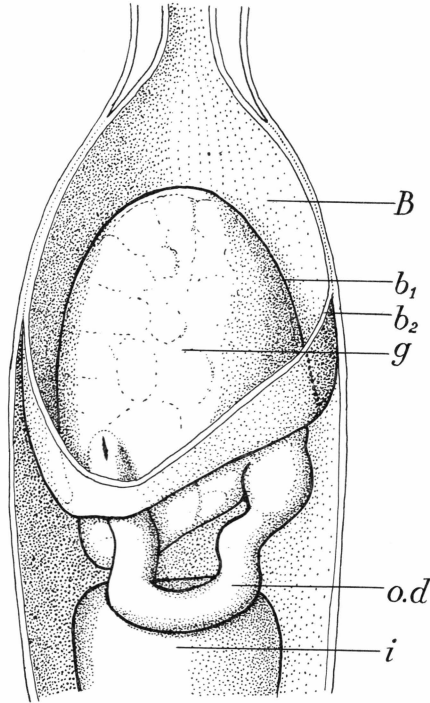


Fig. 25. *Entocolax ludwigi* Voigt. The opening of the oviduct into the brood-pouch, somewhat schematic. g. ovary; o. d. oviduct; B. brood-pouch; b_1 and b_2 inner and outer epithelium of brood-pouch; i. intestine.

that it is not formed until in the later stages, probably not until the dwarf-males have become ripe.

It is extremely difficult, even at an anatomical investigation of the animal under the binocular microscope, to see how this supposed uterus opens into the brood-pouch, the walls of the latter being so thin that, in spite of the most careful dissection, it is hardly possible to avoid the damaging of it, the more so because it is extremely difficult to see where it lies on the outside of the ovary and the uterus. After having stained a quite young, intact specimen with parakarmin it could, however, be done tolerably, especially when the serial sections were used for comparison. The result of this combined investigation is shown in fig. 25, where it will be seen that the "uterus" is partly covered by

that part of the wall of the brood-pouch which lies up around the ovary. Regarding the opening itself of the "uterus" the orifice could not be seen with absolute certainty, but it looked as if — which also the serial sections indicate — the "uterus" opens into the brood-pouch by a very narrow slit, which normally is closed altogether and only opened during the passage of the eggs. On comparing these results with the results of SCHWANWITSCH (cf. e. g. his fig. 21 on Pl. II) they will be found to agree beautifully, only it must be remembered that in the ripe specimens the ovary is much larger and the gonoduct much longer and more twisted.

2. The development of *Entocolax*.

When comprising the results arrived to in the preceeding section it is seen that in several points there is a considerable disagreement with the common interpretation, which is due to SCHIEMENZ (1890). According to the theory of SCHIEMENZ the brood-pouch of *Entocolax* (and of *Entoconcha*) should be a pseudopallial-formation, an enormous development of the pseudopallium, which in *Mucronalia* is found as an annular fold around the rostrum, and which in *Stilifer* and related forms develops considerably and finally surround the shell covering it completely, apart from a small opening above. When KOEHLER & VANEY in 1903 described *Gasterosiphon deimatis* (under the name of *Entosiphon*), which just appeared to be the missing link in the chain of development from *Mucronalia* and *Stilifer* to *Entocolax* and *Entoconcha*, SCHIEMENZ' interpretation was shared by nearly everybody, yet there is a few who remained in doubt, thus e. g. VANEY (1913) and THIELE (1929).

Already at a quite superficial consideration there is, however, something speaking for the supposed pseudopallium in *Entocolax* and the real pseudopallial-formations in *Mucronalia*, *Stilifer*, and others not being homologous, viz. their different position on the animals. The real pseudopallium has its beginning around the rostrum, thus very much anterior, in front of the head, while the supposed pseudopallium in *Entocolax* is fastened much higher up around the ovary. Of course, it could be supposed, that a considerable lowering of the ovary had taken place, or a just as considerable displacement of the pseudopallium, but in itself this would be rather unlikely, and as we shall see in the following, there is, indeed, not found any pseudopallium at all in *Entocolax*, so that just that animal which gave SCHIEMENZ the occasion for his theory can now no more be interpreted as belonging to that chain of development.

Histologically there is also an essential difference between the genuine pseudopallium in the *Stiliferidae* and the supposed in *Entocolax*.

There exists, as far as I know, only one histological investigation of a genuine pseudopallium, viz. the one by RosÉN (1910) of the Stiliferid *Megadenus*, the pseudopallium of which in size and development lies between *Mucronalia* and *Stilifer*. According to RosÉN the pseudopallium of *Megadenus* consists on both the in- and the outside of a cylindro-epithelium with cilia, but we have just in the previous section seen that there are no cilia on the outer or the inner epithelium of the brood-pouch of *Entocolax*, further are these epithelial cells not at all cylindrical, at most it may be said that there in the outer epithelium are found a few single, protruding cells which are almost cylindrical, but the main part are so low that they cannot even be termed cubical. Further RosÉN writes that the epithelium of the outer side of the pseudopallium consists of higher cells than does the epithelium of the proboscis. Anything corresponding is neither found in *Entocolax*, where the epidermis has the same dotted, irregular epithelium from the oral opening to the point of the siphon.

More clearly, however, than both the position and the histology of the pseudopallium, the hitherto unknown younger stages of *Entocolax*, which have not yet been dilated and transformed by the egg-masses, show that the brood-pouch and the siphonal cavity in *Entocolax* certainly cannot be a pseudopallial cavity. By such a formation can only be understood a cavity formed by the turning over and growth of a pseudopallium, but here we are dealing with a real gonoduct in which several, distinctly separated sections can be distinguished. As we have seen, the gonoduct is surrounded by a loose connective tissue and this again by the epidermis.

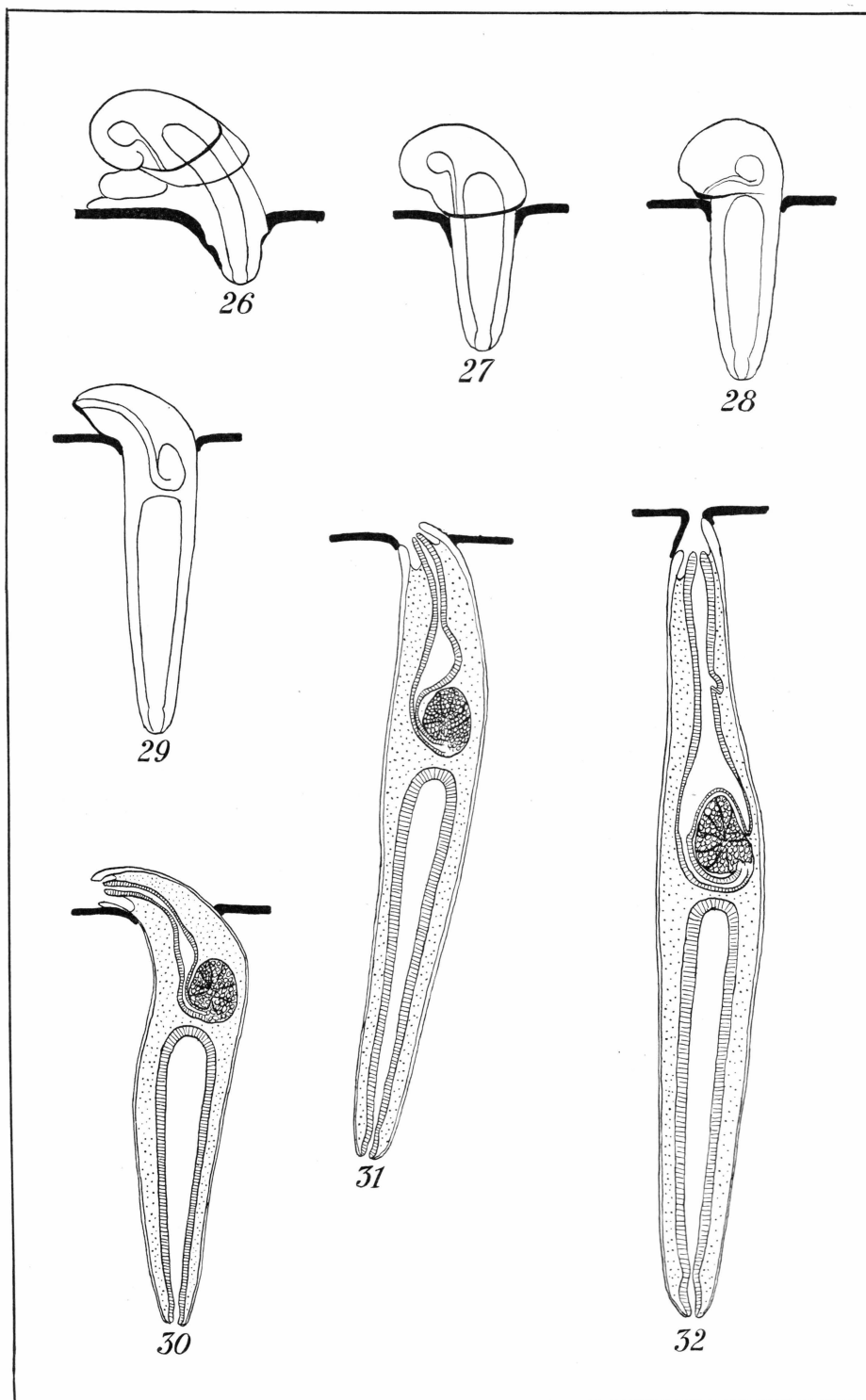
The gonoduct in the young, ripe, but not yet egg-laying *Entocolax* consists of the following sections: Nearest to the ovary is found a small ball-shaped swelling which represents the beginning of the oviduct. The oviduct proper is in the beginning a relatively straight and rather narrow tube, which in the later stages grows considerably, especially in the length, wherefore it becomes strongly winded, besides there is formed a protuberance which acts as receptaculum seminis. The distalmost part of the oviduct is somewhat thicker and remains, also in the later stages, straight; the section, which hitherto has been interpreted as uterus, seems to contain more glandular cells than the rest of the oviduct and is undoubtedly of importance at the formation of the cocoons (cf. SCHWANWITSCH 1917). After the oviduct follows a strongly distended, thin-walled section, the wall of which on the side towards the ovary has been turned in, most likely on account of the growth of the ovary; further an enormous dilatation of this section takes place when the eggs are to be developed, on account of its serving as a brood-pouch. The section after this strongly distended part is again a more narrow

tube, a "vagina"¹⁾, on which is found a short, sac-shaped diverticle, the function of which is unknown. The vagina opens obliquely into the siphonal cavity, which supposedly should be interpreted as an adjustment to the dwarf-males which, as known, reside here.

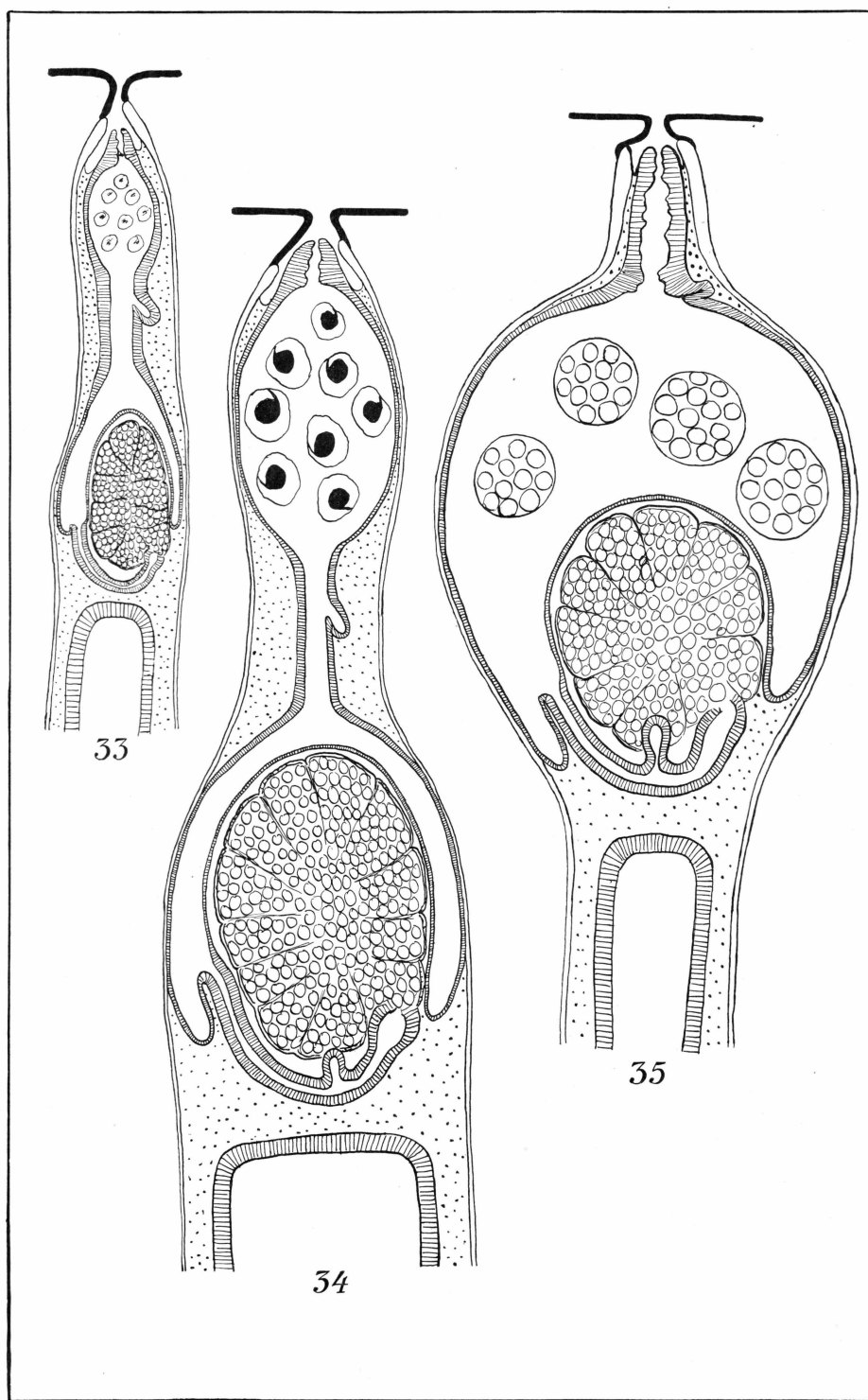
As shown by HEDING in the first chapter an apparently considerable reduction of the vagina takes place when the eggs come into the brood-pouch and this therefore is dilatated, later, when the brood-pouch has reached its maximal size this reduction becomes nearly complete. However, it is not a real reduction of the vagina which takes place, but the vagina enters into the formation of the brood-pouch, becoming by and by more and more dilatated as a result of the increasing dilatation of the brood-pouch, which thus means that the posterior part of the finished brood-pouch in reality is the dilatated vagina. The vagina being distended quite considerably it becomes, of course, shortened, by which the vaginal diverticle at first is pressed together (fig. 8) and finally disappears completely. As the closed, but not yet disappeared vaginal diverticle is situated in the brood-pouch near the transition to the siphonal cavity, and as it has been observed in only one specimen with cleaved eggs in the brood-pouch, it is near to assume that the closed orifice which VOIGT (1888, p. 661, figs. 11 and 34) observed on the inside of the posterior part of the brood-pouch and interpreted as a respiratory orifice in reality has been the closed vaginal diverticle, VOIGT's specimen was also having cleaved eggs. The supposed closed orifice, which VOIGT mentioned, caused SCHIEMENZ to advance the rather peculiar assertion, that it in reality was the mouth of the pseudopallial cavity through which the eggs were laid, while siphon was only a transformed gland of the foot. This theory has rightly been rejected by the later authors.

As shown above there can now hardly be any doubt that we are dealing with a real gonoduct in *Entocolax*, and no pseudopallial formation. In this case, however, the entire theory of the development as advanced by SCHIEMENZ must be abandoned, but how can we then suppose the development of *Entocolax* to take place? How does the larva, which completely resembles all other veliger larvæ, develop into the strongly transformed, to the parasitical life adapted, adult *Entocolax*? Here about we still know nothing with absolute certainty, the smallest specimens of *Entocolax* hitherto found already in general having the transformed shape of the adult, but it is very likely that the development takes place as shown schematically in figs. 26—35. It must be mentioned expressly

¹⁾ When I have preferred to name this section "vagina" and not "uterus", it is for the reason that the uterus in the prosobranchs is distinguished by a great richness of glands, while glandular cells appear to be completely lacking in this section.



Figs. 26—32. Scheme of the supposed development of *Entocolax ludwigi* Voigt.
Cf. text p. 30.



Figs. 33—35. Scheme of the supposed development of *Entocolax ludwigi* Voigt.
Cf. text p. 31.

that these figures are all purely schematic and only take regard to the coarsest main features.

The development of *Entocolax*, most likely, takes place in the following manner: the quite tiny larva, which has come out into the free from the brood-pouch of the mother-animal through its vagina and the siphonal cavity, search out, supposedly after swarming for a short time, a *Myriotrochus* on the skin of which it settles. The attachment is done on a certain place, viz. on the part of the *Myriotrochus* which reaches up above the sea-bottom, that is the anterior part of the dorsal side. Here the larva makes its way in (fig. 26). How this boring is done is unknown, there having not yet been found any organs in the larva which could be used for this purpose. When the anterior part of the larva has pierced the skin of the host, the shell and the operculum, which now merely are hindrances, are cast off, and the larva bores it way farther and farther in. This, most likely, is done in the way that the anterior part of the larva grows, while the viscera and the mantel remain on the surface of the holothuria (fig. 27). When it must be supposed that the mantel and the entire viscera remain outside the holothuria in the quite young stages of *Entocolax*, it is because the larvae, as shown by SCHWANWITSCH (Op. cit. 1917) are in possession of a respiratory organ in the shape of a respiratory epithelium in the mantle cavity. The conditions for an oxygen consumption may likely neither be so good as long as the snail only reaches into the epithelium of the holothuria, as when it reaches so far that it on all sides is surrounded by coelomic fluid.

While the anterior part of the young *Entocolax* still grows evenly, it must be supposed that a peculiar one-sided growth of the part of the animal still remaining on the outside of the holothuria now takes place. This is to be understood in this way: The posterior part of the viscerasac which, as commonly known, is not covered by the mantle grows as well in length as in width, while the part which is covered by the mantle, as well as the mantle itself, does not grow to a noteworthy extent; in this way the mantle will apparently be collected more and more on the one side, while the other side is dragged into the epidermis of the holothuria (figs. 28—29). At last the mantle edge will be situated as an almost ring-shaped fold, which finally, at the continued growth, will close together and become a real ring-shaped fold. This fold remains on the outside of the holothuria whereby the snail maintains the connection with the surrounding water, in the beginning from regard to the respiration, later primarily from regard to the brood.

The following figures (figs. 30—35) show the later stages in longitudinal sections, and here is shown the development of the generative organs. Already in the preceeding figures the ovary and the gonoduct

have been drawn although these organs, naturally, in the younger stages are present as rudiments only. It is done to show the turning of the generative organs which takes place, the rudimental ovary being dragged downwards, i. e. forwards in the animal, while it grows farther and farther down in the skin of the holothuria, the orifice of the gonoduct, on the other hand, remaining directly inside the mantle edge. Figs. 30 and 31 show stages with beginning dilatation of the middle part of the gonoduct, which later develops into the brood-pouch. In fig. 32 is shown the further development; here the turning in of the wall of the swelling has begun, caused either by the growth of the ovary or the growth of the gonoduct itself. Further in this figure is shown the beginning formation of the vaginal diverticle and the siphonal swelling. Regarding the latter it must be remarked, that it is in no way improbable that it is not formed in direct continuation and continuity with the rest of the gonoduct. This probable possibility has, however, for the sake of the perspicuity, been paid no regard, just as the reduction of the mantle and the nervous system has not been shown either, because we cannot have any well founded opinion as to when this reduction takes place.

The further development of the generative organs is shown in figs. 33—35, which schematically reproduce real, known stages, of which, however, the one figured in fig. 33 had no siphon. It must furthermore be remarked that the cavity of the brood-pouch in figs. 33 and 34 from regard to the clearness has been drawn relatively much too large, in reality the two blades lie quite close to each other. Besides the fig. 35 has not been magnified as much as the preceding figures. In fig. 33 males have entered the siphonal cavity where they are getting sexual ripe. Supposedly on account of the growth of the males the siphonal cavity is distended, for finally, when the males have reached their maximal size, to assume the shape of a large oblong bladder, the wall of which lies quite close to the epidermis, only parted from the latter by a thin layer of connective tissue. In these two stages vagina is a rather long tube with well developed diverticle, while the brood-pouch lies as a double walled hood over the ovary, which, in fig. 34, has reached its maximal size. On this figure is also shown the beginning of the swelling of the oviduct, which later develops into the receptaculum seminis.

Finally fig. 35 shows the fecundate, egg-producing female *Entocolax*. Here the dwarf males have vanished, and the cavity of the siphon has been strongly reduced; besides, the vagina forms now a part of the wall of the brood-pouch, which on account of the eggs has been enormously distended, at the same time the vaginal diverticle has been pressed together. Receptaculum seminis is enlarged and contains the sperma of

the dead males. The oviduct is in reality much longer and more coiled than shown in the schematic figure.

When the eggs in the brood-pouch develop into larvæ a couple of more changes take place, thus the brood-pouch becomes still more distended and the vaginal diverticle disappears finally completely.

As it will be seen this theory agrees much better with our present knowledge about *Entocolax* than does the theory advanced by SCHIEMENZ.

After the above had been written the material of *Entocolax trochodotæ* Heding in the Zoological Museum of Copenhagen was taken up

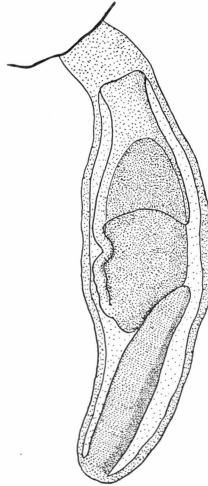


Fig. 36. *Entocolax trochodotæ* Hdg. Young female $\times 50$.

for a renewed examination. The results which HEDING (1934) published, appeared from a simple anatomical investigation with the aid of a binocular microscope. At this renewed investigation it was tried whether it should be possible to observe some more details in regard to the building of the animal by clearing them in glycerine; it being out of the question to make serial sections from them, on account of the material being so badly preserved that it beforehand was precluded that this method could give any results at all. The three youngest stages of *E. trochodotæ* was put in FAURÉ's Glycerine-Gum solution and observed under stronger magnification by the aid of a monocular microscope. It was found that they in no way appeared as figured by HEDING; but that they actually, in the most beautiful way, confirm the above advanced theory on the development of *Entocolax*. In fig. 36 is figured one of these cleared younger stages, corresponding to HEDING's fig. 6 and 9 (Op. cit. 1934). It will be seen that in HEDING's fig. 6 the animal is figured far more correctly than in fig. 9, which latter to some extent seems to be inspired by the theory of SCHIEMENZ. For the sake of the

completeness it must be remarked that HEDING acknowledged my interpretation when the preparations were shown to him.

3. Classificatory remarks.

When SCHIEMENZ' theory must be abandoned the reason for placing the *Entocolax* systematically after the Stiliferids naturally becomes null and void, as this was based on the supposed pseudopallium, which, as we have seen, not at all is present in *Entocolax*. The question therefore rises, where in the system is the proper place of *Entocolax*?

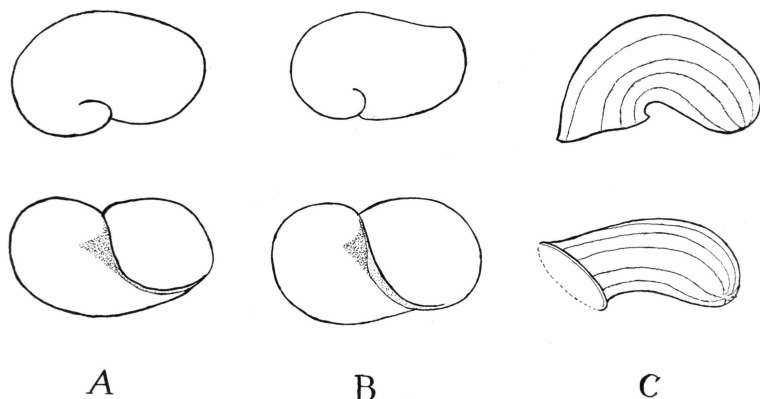


Fig. 37. Embryonic shells of A. *Entocolax* (from SCHWANWITSCH); B. *Entoconcha* (from MÜLLER); C. *Enteroxenos* (from BONNEVIE).

Before we begin the discussion of the placing of *Entocolax* in the system it will be reasonable to see also whether *Entoconcha* and *Enteroxenos*, that is the entire family *Entoconchidae*, should be moved, or — in other words — whether *Entoconchidae* is a natural family or not. For the judgement hereof is found a series of papers, partly on *Entoconcha* (JOHS. MÜLLER 1852, BAUR 1864) partly on *Enteroxenos* (BONNEVIE 1902, 1904, and 1906).

On basis of the anatomy of the adult animals alone nothing can be decided with certainty, as the differences which are found may be owing to a more or less thorough transformation due to a more or less adaptation to the parasitic life; but in connection with other characters the anatomical differences may at least be able to offer an indication. According to the anatomy *Entocolax* and *Entoconcha* seem to be more closely related to each other than to *Enteroxenos*, which is, by far, the most transformed of the three; the entire alimentary canal having disappeared in the latter, while the other two have a rather long and well developed alimentary canal, although an anus is lacking. Besides, according to BONNEVIE (1902, 1906), *Enteroxenos* is hermaphroditic

while as well *Entocolax* as *Entoconcha* have separate sexes, even though the male sex only appears in the shape of strongly reduced dwarf-males.

This difference in the anatomy of the adults, which in itself does not necessarily mean that they do not belong together, is, however, supported to a very considerable degree by a comparison between the embryos of the three genera, and is further confirmed by an observation of the spermatozoa.

We shall now first look at the embryonic shells (fig. 37) of the three genera, respectively *Entocolax* (A), *Entoconcha* (B), and *Enteroxenos* (C). As it appears from fig. 37 A and B the embryonic shells of *Entocolax* and *Entoconcha* are nearly identical. Both are quite smooth and structureless, and have a little more than one whorl conically wound, while the embryonic shell in *Enteroxenos* (fig. 37, B) has a quite different, almost cucumber-like appearance, the shell being furnished with longitudinal ribs, and not comprising more than $\frac{1}{2}$ to $\frac{3}{4}$ of a whorl, which is not wound in a screw but lies in one and the same plane. The shape of the orifice is also quite another than in the other two. We arrive thus to exactly the same result as when observing the adult animals, viz. that *Entocolax* and *Entoconcha* are closely related, while *Enteroxenos* is far more different.

If we look at the spermatozoa of the three genera we also arrive to the same result. Fig. 38 a and b shows the spermatozoa of *Entoconcha* drawn respectively after MÜLLER and after BAUR. They don't seem to be identical; for the first there is a rather considerable difference in the shape of the head in the three figured spermatozoa. The explanation of this is, supposedly, that the head in reality is broad and flat, almost as the middle of the three figured, and in the other two figures it is seen more or less from the edge. But thereupon also the point of the tail is differently figured by the two authors. It is possible that MÜLLER's figure is correct, but it is more likely that the long, thin point, drawn by BAUR, often turns up along the side of the tail, in which case a figure just as MÜLLER's will appear; or perhaps, as suggested by BAUR, it is unripe spermatozoa which MÜLLER has figured. Fig. 38 c and d are spermatozoa of *Entocolax* (after SCHWANWITSCH 1917, fig. d is drawn from spermatozoa in the receptaculum seminis) and here we again meet the same difference in the shape of the head as in *Entoconcha* and we may explain it in the same way. Finally fig. 38 e shows spermatozoa of *Enteroxenos* (copied from BONNEVIE 1904); these are of a quite different type the spermatozoa of the other two genera having as well a connection piece as a head piece.

Finally, in the ontogenetic development of *Enteroxenos*, there seem to be so great diversities with the development of *Entocolax*, that any

possibility of relation must be considered out of the question. The larva of *Enteroxenos* is reformed in the intestinal wall of the *Stichopus* as small, of two cell-layers consisting balls, which develop directly into the adult *Enteroxenos* simply in the way that the balls at first become oval and thereafter grow longer and longer, while the two

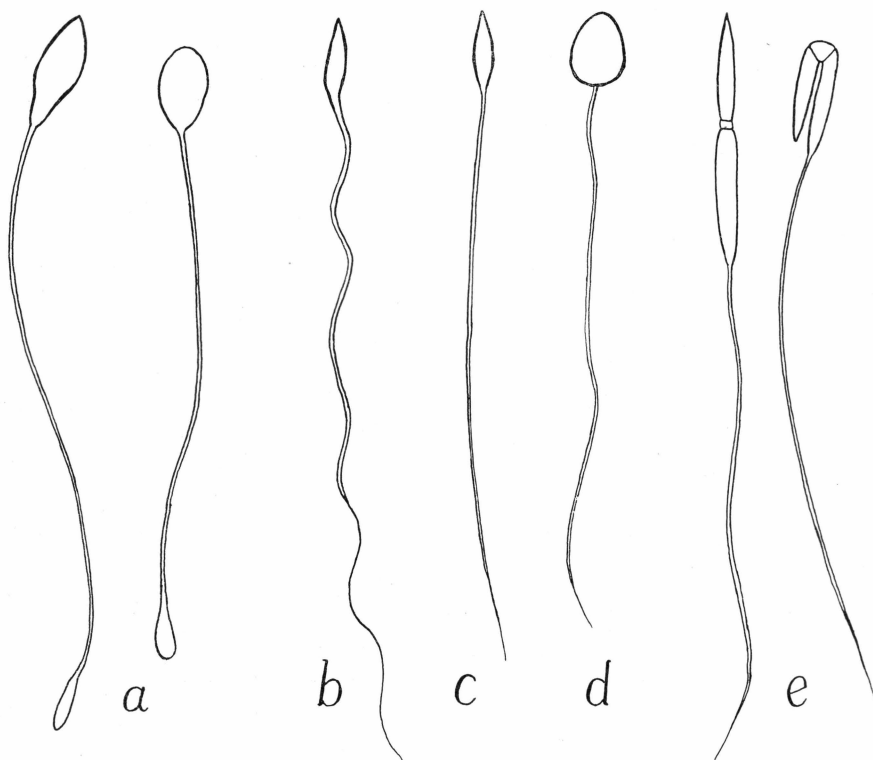


Fig. 38. Spermatozoa of a—b *Entoconcha* (a. from MÜLLER, b. from BAUR), c—d. *Entocolax* (from SCHWANWITSCH), e. *Enteroxenos* (from BONNEVIE).

cell-layers remain all the time, the outermost becoming the epidermis, and the innermost the lining of the central cavity. Between the two layers develop some mesenchymatic cells, which form the connective tissue. There is thus in the development of *Enteroxenos* at no time a stage which is in agreement with the theory of SCHIEMENZ, which BONNEVIE none the less approve, — although with some doubt — as holding good also for *Enteroxenos*, on account of this animal's, according to BONNEVIE, great likeness with *Entocolax* and *Entoconcha*. Later authors have completely overlooked BONNEVIE'S well founded doubt and without any reservation placed *Enteroxenos* directly after *Entoconcha* as the last link in SCHIEMENZ' chain of development.

According to what here has been explained it can therefore not, as thinks SCHWANWITSCH (1917), be sufficient just to divide the old family *Entoconchidae* into two subfamilies, because it is in no way certain that the two families *Entoconchidae* and *Enteroxenidae*, which latter must be established for *Enteroxenos* alone, at all can be placed near each other in the system; but more about this later.

It is connected with rather much difficulty to find the correct place in the system for these entoparasitic snails, because the organs usually used as systematic characters in the *Prosobranchiata* either lack completely or are present only in very strongly reduced form. We are actually confronted with the problem of on the basis of strongly transformed generative organs together with the spermatozoa and the embryos to place these snails in a system founded on characters in the nervous system, radula, shell, nephridia, etc. However, it is not quite as impossible as it may seem at the first glance.

There is at hand a large pictorial work by RETZIUS (1906) on the spermatozoa, among which also of the *Prosobranchiata*. Of the by RETZIUS figured prosobranch-spermatozoa the spermatozoön of *Melanella* (*Eulima*) is in shape almost identic with the spermatozoa of *Entocolax* and *Entoconcha*, in the details it differs apparently somewhat, yet no more than it may be owing to the different treatment. On the other hand, RETZIUS has not figured any spermatozoön which even reminds about the spermatozoa of *Enteroxenos*. This means thus that the spermatozoa indicate that the *Entoconchidae*, but not the *Enteroxenidae*, even though the pseudopallial theory must be abandoned, still should be placed among the aglossæ of the *Prosobranchiata*.

While the males of the *Entoconchidae* are so strongly transformed that their generative organs cannot be used for the clearing of the systematic position of the family, there is a possibility when the question is of the female, especially the young, from the eggs not yet transformed generative organs. It is true that a homologising with the female generative organ in the rest of the *Prosobranchiata*, and especially in the *Aglossa*, is connected with the possibility of considerable errors, partly because the generative organs of numerous forms yet having not been investigated, and partly — and herein lies the greatest source of error — because there reigns a not inconsiderable confusion in the homologising of the separate sections of the gonoduct in the different genera of the *Aglossa* (compare IWANOW, 1937, p. 168). It appears, however, that the female generative organ can be derived from the corresponding in the genus *Melanella*, of which some few species have been investigated, I. eg. by JONKER (1916) and ADAM (1934).

In *Melanella* the gonoduct consists of a gland-rich oviduct, the end-part of which carries cilia. In to this ciliated section opens a recepta-

culum seminis; at the side of this is found another diverticle which contains glandular cells and is interpreted as a provisorial shell-gland. This latter may also be present just as a simple terminal swelling of the gonoduct. In the very peculiar *Paedophoropus dicoelobius* Iwanow¹⁾ (IWANOW 1933 and 1937) are also found two diverticles, a proximal secondary gland, and a distal receptaculum seminis. If we now suppose that a generative organ of this type grows in the length, that the secondary gland, plus the surrounding part of the gonoduct, develops into a brood-pouch, whereby the glandular function must be supposed to recede, we arrive to a generative organ just as the one found in the young female *Entocolax*.

If this homologising is correct, the section of the gonoduct in *Entocolax*, which was named "vagina" will in reality correspond to the uterus in the rest of the aglossa *Prosobranchiata*; but in these — as. by the way, in the *Prosobranchiata* in general — uterus is rich in glands, while we have just seen that glandular cells appear to be lacking in this section in *Entocolax*. Even though this is the case, it does not necessarily have to be taken as a serious hindrance for the homologising, it being very likely that the glandular cells have disappeared from this section, where there no longer is use for any secretion, the section serving only as an outlet for the hatched larvæ. The functional meaning with the uterus, to form the cocoons, has been transferred to another section of the gonoduct, viz. the straight part of the oviduct, before the opening of this into the brood-pouch, and here glandular cells are found in considerable numbers. This section of the oviduct thus becomes analogous with the uterus in the other forms, but not, as hitherto supposed, homologous. The vaginal diverticle must, according to the here explained, be interpreted as a rudimentary receptaculum seminis, while the actually functioning receptaculum seminis in *Entocolax* must be interpreted as a new formation caused by the degeneration of the original receptaculum seminis, which has resulted from the enormous development of the brood-pouch.

Finally, as regards the embryos and their shells, these fit very well with several of the aglossa *Prosobranchiata*, among which again especially well with *Paedophoropus dicoelobius*, the spermatozoa of which, by the way, also correspond exactly to the spermatozoa in the *Entoconchidae*. Upon the whole there are reasons to perceive the *Paedophoropus* as the nearest relation of the *Entoconchidae*, which is to be understood in this way, that they can be derived from a common primitive form among the Melanellids, from which they have developed in so different directions that they cannot be referred to the same family.

¹⁾ *Paedophoropus* is considered by IWANOW (1937) — and undoubtedly correctly — to be a derivation from the Melanellids.

We know now in the aglossa *Prosobranchiata* three essentially different series of development of entoparasitic snails, which all can be derived from the Melanellids:

1. *Stiliferidae*, the least transformed, with pseudopallium, of which all degrees of development are known, until *Gasterosiphon*, where the pseudopallium is enormously developed and functions as a brood-pouch.
2. *Paedophoropodidae*, which is not much more transformed, but where it is the foot which is developed into a brood-pouch.
3. *Entoconchidae*, which is the most transformed. Here the brood-pouch is formed by a section of the gonoduct.

Whether *Enteroxenidae* represents a fourth series of development must remain in the uncertain, as, from our present standpoint, nothing can be said with certainty about the systematic position of this family, even not whether it at all belongs in the *Aglossa*.

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