

with the posterior limb vertical and finely serrated. Dorsal spines of moderate strength. Upper margin of the soft dorsal convex; dorsals continuous, but separated from each other by a deep notch. Caudal emarginate; anal with long anterior and short posterior rays. Upper and lateral parts dark olive-coloured, each scale with two, three, or more whitish dots. A black line along the hind margin of the præoperculum.

Of this species a gigantic example, 3 feet long, has been sent by Herr Kubary from Ponapé. The collector says that it exceeds sometimes one metre in length, and that the natives call it "Koil."

Sphærodon euanus.

D. $\frac{10}{10}$. A. $\frac{3}{10}$. L. lat. 51. L. transv. 5/17.

Eye very large, one third the length of the head, equal to the width of the interorbital space, and more than the height of the præorbital. Scales on the cheek in four series, forming together a narrow vertical band. Dorsal spines rather feeble, broader on one side than on the other, the longest being a little shorter than the eye. The third anal spine much longer than the second. The first ventral ray produced into a filament. Coloration uniform, without any spots on the vertical fins. Posterior half of the pectoral fin light-coloured; base of the pectoral without black.

One specimen, 13 inches long, from Eua, Friendly Islands.

XVII.—*Notes towards the History of the Genus Entoniscus.*
By A. GIARD*.

[Plate X.]

I. HISTORICAL.

ALMOST all the zoologists who have studied the parasitic Cirripedes belonging to the group Suctoria have been induced also to pay attention to certain Isopod Crustacea of the family Bopyridæ, the history of which is intimately bound up with that of those animals. This was my own case when, in 1873, I commenced my researches upon *Sacculina carcini*. In fact this parasite itself bears a parasite, *Cryptoniscus larvæformis*, upon which I have already published some preliminary re-

* Translated by W. S. Dallas, F.L.S., from the 'Journal de l'Anatomie et Physiologie,' 1878, pp. 675-700.

marks*. In order to elucidate some doubtful points in the degraded organization of the *Cryptonisci*, I was obliged to have recourse to the examination of other Bopyridæ of less anomalous structure. I have thus collected materials of considerable importance upon this family of Isopods. But most of these animals are of great rarity; and the difficulty of tracing their embryogeny is also very great—a single female containing a great number of ova, it is true, but all in the same stage of development. Hence I have not yet been able to bring the monograph which I have projected to a point of perfection sufficient for the commencement of publication. I will now, however, at least make known some results obtained in the case of a very sparingly distributed genus, the genus *Entoniscus*†. I hope by this means to hinder from useless researches those who might be tempted to attack the same subject, and to furnish some data which will be made use of hereafter for a more general treatise‡.

The genus *Entoniscus*, established by Fritz Müller in 1862, includes animals which had been met with by Cavolini as long ago as 1787. Cavolini had observed *Sacculinæ* upon several species of crabs; and he regarded these parasites as the broods (*ponte*) of a small species of *Cyclops* grafted by the mother upon the tail of the Brachyurans. After bringing forward his observations upon this subject he adds:—

“Besides the *Cyclops* which we have just described, there is in the sea another insect which fixes its brood upon the body of our crabs, but in a manner much more inconvenient for those animals. It is, in fact, in the very midst of their viscera that the eggs are attached. Hitherto the *Depressus*§

* Giard, “Sur l'éthologie de *Sacculina carcini*,” *Comptes Rendus de l'Acad. des Sciences*, 1874.

† A preliminary communication upon these animals has been printed in the *Comptes Rendus de l'Acad. des Sciences* (12th August, 1878). See *Ann. & Mag. Nat. Hist.* ser. 5, vol. ii. p. 346.

‡ I have already indicated briefly certain conclusions of this memoir. See *Arch. de Zool. expér.* tom. ii. 1873, p. 513, and tom. iii. 1874, *Notes et Revue*, pp. iii & iv.

§ It is impossible not to recognize *Grapsus varius* in the fine description given by Cavolini of his *Granchio depresso*:—

“Questo granchio è copiosissimo per gli scogli del nostro cratere, e sembra godere piuttosto di stare in secco, massimamente quando, pel calor della state, le acque presso i lidi si riscaldano, o si albanano: su di questi scogli di erbe vestiti è curiosa cosa vedere come in terra seduto, or con una, or con ambe le mani, colga quella verde conferva e alla bocca l'accosti. La forma del suo corpo è quadrilatera schiacciata, il colore di un verde cupo: le braccia son crasse e valide poco meno del paguro (*Eriphia spinifrons* of modern authors); la sua carne è mucilaggiosa, e molto poca. Ma ciò che lo rende singolare, è la velocità del corso: bisogna esser destro per dargli sopra la mano; altrimenti o fugge sullo

alone has appeared to me to be attacked. On the side of the stomach, at the point where the liver is situated, one sees a very voluminous mass, of a more or less yellowish or leaden colour, according to the degree of its maturity, occupying the place of the ovarian branch of the crab. This body pushes through the ribs of the carapace, and thus insinuates itself into the branchial cavity. It is not difficult to separate it from the crab, to which we find it to be attached by cellular tissue; the anterior part of this ovarian body, that which is placed in the viscera, becomes mature first, and consequently it is much more dilated, *a*, while the other, *b*, which is situated between the ribs, is still immature, and retains the impression of these solid parts. The ovarian sac is formed of a transparent tissue, and contains in this state the graduated series of the development of the ova which it encloses: the most mature are in *a*, and are visible to the naked eye only as a granular substance; in the figure, however, they have been drawn a little larger, in order to avoid confusion; the less advanced ones are in *b*. Seen by the microscope, the latter are of a rounded form, *c*; those which are a little less immature are figured at *m*; those which most nearly approach maturity are uniform and emarginate, as at *n*; lastly, the hatched embryos have the form represented in *r*, and run in all directions in the drop of water placed under the lens of the microscope. These insects have the body divided into a great number of rings, the first of which bears two eyes; the tail is bifurcate; and the last joint of the first four pairs of feet is claviform.

“This insect belongs to the race of the *Oniscus squilliformis*, very well described by Pallas; it presents a certain analogy with the species described under the name of *Oniscus locusta** by that illustrious naturalist, a species very frequent in the organic rubbish thrown up on the sand and bathed by the sea in its movements to and fro; it is our *sand-flea*. However, the species which is developed at the expense of the blood of the crab is much smaller than this sand-flea. It is true that I have been able to see this insect only at the

scoglio fin ch  in mare precipiti, o vero in una prossima buca si rimpiaatta : perci  dai nostri pescatori si chiama *Granchio spirito*.”

In the same memoir Cavolini describes and figures:—1, a Gregarina parasitic on the *Grapsus*, which he calls *T nia*; 2, the zo a of the *Grapsus* (pl. ii. figs. 7, 8, & 9). As early as 1768 Slabber, for his part, had discovered the metamorphoses of the Decapods; but it was only in 1823 that Vaughan Thompson generalized these observations, which had been completely forgotten.

* ‘*Spicilegium Zoologicum*,’ fasc. ix. pp. 50–55 (Berolini, 1767).

moment of its exclusion; but the size of the eggs which I have found attached to the feet of our sand-flea has taught me that the young of this latter must be of a size greatly superior to that of the insect which I have described and drawn issuing from the ovaries contained within the body of the crabs.

“Now in what way does the mother *Oniscus* introduce her brood into the body of the crabs, when this body is completely defended by a hard and crustaceous skin? Here I must argue by conjecture, but by necessary conjecture, until it may be possible to obtain ocular proof of the fact of this penetration. We have already described above the two cavities situated one upon each side of the body of the crab, and in which the branchiæ move. The water enters and issues from these by two apertures provided with valves, and situated at the sides of the mouth in front of the lateral commissure of the upper portion with the lower portion of the carapace. The anterior part of these cavities is formed of a delicate membrane which clothes the viscera of the crab. We can therefore understand with the greatest facility that the mother insect penetrates with the water into such a cavity, and, perforating its delicate wall, introduces her brood into the body of the crab; the mother insect enters then in the same manner as the ova of *Serpulæ* or of oysters, which I have frequently found hatched or fixed against the ribs which exist in the above-mentioned branchial cavity.

“We have, therefore, in the crabs two cases of grafting of animal parts; the brood of these two insects, which need for their development juices elaborated in an animal body, could not be brought to its term by the mother. Nature has taken upon herself to furnish it with a fat and devoted nurse, namely the body of our crabs. The mother makes a small aperture in the skin which covers the intestine; sometimes she fixes her brood to the outside, sometimes introduces it into the body of the crab, enclosed in a membrane performing the part of a placenta; and, as the eggs contained in this membrane are animated and tend to develop themselves, it is certain that the canals of this ovary are suckers absorbing the liquids of the vessels of the living crab. By inosculating with these latter and forming anastomoses with them, they constitute a *system continuous* between the *living body* of the crab, and another *body*, likewise *living*, which tends to complete its evolution. In point of fact, a foreign foetus has become the actual progeny of the crustacean, and has developed itself upon this animal in the same fashion as, among the Mammalia, the abdominal foetuses are developed nearly as they would be in the uterus, which is their normal and true

place of abode. If in a plant we make an incision and introduce into it a living branch of another plant, there is produced a graft by inosculation and union (*raccordement*) of the vessels; exactly the same thing takes place in our animals.

"I do not know whether, hitherto, any animals which graft themselves have been known. It seems to me that the opposite of what I have just indicated had rather been observed; it had been seen that the eggs of one animal deposited in the body of another animal produce tumours, which, by bursting, form regular wounds. This is the case with those flies which lay their eggs under the skin of cattle, in their nostrils, or their intestines, and which thus occasion a tumour, and afterwards a sort of blister, the matter from which nourishes their progeny*. Certainly the two parasites of the crabs just mentioned are rather grafted animals than animal galls. These latter are met with only in plants attacked by animals. The egg of an insect deposited upon a plant becomes soaked with the juices of the latter and grows at its expense; but it is not strictly correct to say that the canals of the egg anastomose with those of the plant and become continuous with these latter"†.

It is evident, from Cavolini's description and the figures which accompany it, that in this case, as in that of *Sacculina*, the supposed ovigerous sac is nothing but a crustacean degraded by parasitism; and the form of the young enables us to recognize immediately that we have to do here with an Isopod belonging to the group Bopyridæ. The few errors of detail which exist in the description of the larva or of the adult animal will be referred to hereafter. They cannot, however, in any way modify this first conclusion. As will be seen, these observations of Cavolini were very remarkable if we consider the period at which they were published.

Unfortunately, in this question of the Bopyridæ, as in that of the Suctoria, the bibliography is complicated in a regrettable manner; the very great difficulty of bringing together the original memoirs, often written in languages and published in repertories which are but little known, causes one to content one's self with quoting them from imperfect abstracts or unfaithful translations. Hence one has several times taken

* "Œstri larvæ latent intra pecorum corpus, ubi per totam hyemem nutriuntur: fonticuli vice gerunt &c."—LINNÉE.

See also the works of Vallisnieri and of Réaumur.

† See Cavolini, 'Memoria sulla generazione dei pesci e dei granchi' (Napoli, 1787), pp. 190-194, pl. ii. figs. 17, 18. We have thought it worth while to translate this curious passage *in extenso*, because now-a-days Cavolini's memoir is hardly to be procured.

the trouble to demolish errors which did not exist in the authors incriminated, and to rediscover truths which had long been known

Thus, quite recently, in his interesting memoir on the genus *Cryptoniscus*, P. Fraisse (2, p. 41)*, giving an analysis of the memoirs of Cavolini, makes the Italian naturalist say that it is very difficult to separate the *Entoniscus* (the supposed ovigerous sac) from the viscera of the crab. It is evident that if Fraisse had had the text of Cavolini before him he would not have translated "questo corpo non è difficile separare" by "er sagt (Cavolini) dass er sehr schwer zu trennen sei."

I am equally unable to understand why Fraisse (*l. c.* p. 41) reproaches Steenstrup with having falsified the sense of Cavolini's observations, saying that the Isopods observed by the latter were in the *Sacculina* and not in the body-cavity of the crabs. The following is, in fact, the very judicious appreciation, given by Steenstrup, of the facts observed by Cavolini:—

"Among the excellent observations," he says, "contained in the valuable memoir of Cavolini, we find figured a very curious mass of irregular form entirely filled with more or less developed ova. This mass was found in a crab; by one of its extremities it was fixed to the inner stomachal wall; by the other it was fixed between the two partitions which bound at the sides the segments forming the thoracic cavity of the crab. In fig. 18, *m, n*, Cavolini has represented ova taken in the mass in various stages of development; in fig. 18, *rr*, he has figured two young animals at the moment of their issuing from the egg. Cavolini compares these young animals to the *Oniscus squilliformis* described by Pallas, and designates them by that name. It is impossible not to recognize in the description and drawing of these embryos a form very nearly allied to the *Liriope* of Rathke, so near that one can hardly separate it therefrom; one is consequently led, in spite of one's self, to a comparison with the larvæ of *Bopyrus*. The form of the young therefore shows us that this mass filled with ova is, in all probability, nothing but a degraded crustacean parasite, and even an animal of the family Bopyridæ; only the animal is still more deformed, and, one might say, more monstrous than any other type of Bopyride, and even then *Peltogaster* and *Pachybdella*. It is more than an *Epi-zoon*; it is an *Entozoon*, a sort of intravisceral worm, since, like the singular Gasteropod (*Entoconcha mirabilis*) disco-

* These references throughout indicate the works of which a list is given at p. 157.

vered by Johannes Müller in *Synapta digitata*, it is also solidly attached to an internal organ."

It is clear from this passage that Steenstrup perfectly understood the general relations of the *Entoniscus* to the crab. Instead of referring to the Danish text, or to the German translation of Creplin, which is very correct, Fraisse has no doubt spoken of Steenstrup's work only from what Lilljeborg says of it. The latter (4, p. 291, 'Annales') has, in fact, confounded the *Entoniscus* observed by Cavolini with the *Liriope* (now *Cryptoniscus*) described by Rathke; and he has, moreover, very wrongly ascribed the same confusion to Steenstrup.

Even the learned carcinologist Spence Bate has not been able to keep himself clear of several errors in the citation which he makes of Cavolini's memoir*, in connexion with the genus *Cryptothiria*, Dana. He says:—"Cavolini first described and figured two different crustaceous animals (one of which he doubtingly referred to the *Oniscus squilliformis* of Pallas) which he had found parasitic within a sac attached to the tail of a crab belonging to the genus *Portunus* or *Carcinus*." There are, as will be seen, nearly as many inaccuracies as words in this short reference.

The first and only zoologist who, since Cavolini, met with parasites of the genus *Entoniscus* was Fritz Müller, who appears not to have known the observations of the Italian naturalist. It was in 1862 that Fritz Müller formed the genus *Entoniscus* for an Isopod crustacean which he had met with in the visceral cavity of a *Porcellana* of the coast of Brazil, and which he named *Entoniscus porcellanæ* †.

In 1871 the talented zoologist of Desterro made known a new species of the same genus (*Entoniscus cancerorum*), a parasite of several species of *Xantho*.

Besides these two species, Fritz Müller has also met with *Entonisci* under the following circumstances:—

1. In a small species of *Porcellana* which is found rarely among the Sertularians and Bryozoa upon the rocks (a single female of *Entoniscus* which could not be studied, so that it is impossible to assert that it belongs to the species parasitic on the common *Porcellana*).

2. In a *Porcellana* named by Fritz Müller *Porcellana (Polyonyx) Creplinii*. It is allied to *Porcellana biangulata*, Dana (*Polyonyx*, Stimps.), and usually occurs in pairs in the tubes of *Chaetopterus*. Only three times did Müller meet with

* 'British Sessile-eyed Crustacea,' vol. ii. pp. 262 & 264.

† According to F. Müller this species of *Porcellana*, of a blackish-green colour, is excessively common under stones at Desterro. (Five per cent. of these crustaceans harboured the parasite.)

isolated individuals—once a female, twice a male. Each of these three individuals harboured an *Entoniscus*, whilst none were ever found in the paired individuals. Fritz Müller concludes from this that the presence of the *Entoniscus*, like that of the Rhizocephala (Suctoria), superinduces sterility in the animal infested, whence the abandonment of the latter by its partner.

The *Entoniscus* of *Porcellana Creplinii* differs from that of the ordinary *Porcellana* by the colour of the ovaries and the form of the ovigerous lamellæ.

3. In an *Achæus* living under rocks among Bryozoa and Ascidia; a single couple of *Entonisci*; the male, which is very characteristic, allows it to be affirmed that this species is distinct from *E. porcellanæ* and *E. cancerorum*.

This, therefore, makes at least four, and perhaps five, distinct species of this singular genus, all inhabiting a small corner of the Brazilian coast.

It would be very odd if a group of parasites, living upon animals so widely distributed as the Decapods, were localized in so small a space. It may be asserted, without fear of deceiving ourselves, that, when they are more carefully sought for, the species of the genus *Entoniscus* will soon be met with, more or less, everywhere.

It was with this idea that, during a residence of several weeks that I made at the Pouliguen (Loire-Inférieure), I carefully examined many Decapods of that interesting locality; and I was especially urged to this investigation by the extreme abundance, in the locality, of *Grapsus varius*, which I knew had furnished Cavolini with the first species of the genus *Entoniscus* *.

II. BIOLOGY AND ANATOMY.

The *Grapsi* collected in the small bays formed by the very broken coast of the Pouliguen on the side of Penchateau are very frequently infested by an *Entoniscus* which may be easily recognized as identical with that described by Cavolini, and which, for that reason, I propose to name *Entoniscus Cavolinii*.

The parasite is met with in both the males and the females. According to the statistics of my researches, it is found most

* I believe that *Grapsus varius* cannot go further north than the mouth of the Vilaine: I do not know it beyond Piriac; and it certainly does not exist at Concarneau. We find, besides, at the Pouliguen a number of southern types; without mentioning the flora in which this southern character is very strongly marked, we may cite, among insects, *Argynnis pandora*, *Dejopeia pulchella*, &c. &c.

frequently in the former. Of five infested individuals, four belonged to the male and one to the female sex. But I have learned from my investigations of the *Rhizocephala* that such statistics, to be of any value, must be founded upon hundreds of individuals *collected in the same locality*. Now my *Grapsi* came from various parts of the coast; and I have examined, at the utmost, two hundred individuals. I believe we may estimate at one in thirty the number of crabs which bear the parasite*.

Sometimes one finds two *Entonisci* in the same crab; and in this case one of them has hampered the growth of the other, which is a favourable circumstance for the observation of intermediate stages, always rare among parasitic animals, in consequence of the rapidity of the retrogression.

Entoniscus Cavolinii, like the species studied by Fritz Müller, is enclosed in a fine membrane in continuity with that which lines the inner surface of the branchial cavity of the crab. It is placed between the liver, the stomach, and the heart of its host. Generally the head is concealed among the hepatic cæca, and in part hidden under the anterior ovigerous sac; the tail is recurved upon the ventral part, and passes under the heart of the crab. The parasite is sometimes on the left, sometimes on the right side of its host, most frequently on the left side (three times more frequently) as it seems to me.

The general form is rather difficult to describe; moreover it varies according to the age and position of the parasite. We have represented it (Pl. X. fig. 1), as accurately as possible, from a living individual twisted upon itself. The colour also varies according to the state of development of the ova with which the animal is almost entirely surrounded; it is straw-yellow when the ova are but little advanced; at maturity it acquires the lead-grey tint so well observed by Cavolini. This tint is due to the formation of a peculiar pigment in the embryo.

We have represented in Pl. X. fig. 2 the same individual untwisted in such a manner as to bring the head into its normal position. In this figure the walls of the incubatory cavity and the abdominal plates are supposed to be removed,

* It is remarkable that none of the *Grapsi* that I have examined bore a *Sacculina*. Fritz Müller remarked a frequent coexistence of *Entoniscus porcellanæ* and *Lernæodiscus porcellanæ*. My zealous collaborateur, J. Prié, whose attention I had called to this point, has also never met with *Sacculina Benedenii*. Moreover the Suctoria seem to prefer calm and slightly impure waters; they are much more frequently found upon the various Decapods of the Bay of Penbronn, at the Croisic, than on the same crabs collected on the open shore of Pouliguen.

so as to show the real form of the body, composed almost exclusively of the ovary and the digestive tube.

The incubatory chamber is composed of an anterior ventral cavity communicating laterally with two latero-anterior cavities. Besides these three cavities, which are in communication, and form, so to speak, a trilobate cavity, the whole dorsal part also presents a vast incubatory chamber, bilobed posteriorly, and falling laterally in two folds, which meet upon the ventral line when they are filled with ova.

These various parts are more clearly visible in the animal before it is completely transformed into the stage represented by Pl. X. figs. 3, 4 *. We then see distinctly the trilobed ventral cavity and the two chitinous crests of the ventral border of the dorsal chamber.

This curious arrangement of the incubatory chambers is very different from that indicated by Fritz Müller in the case of *E. porcellanæ* and *E. cancrorum*. The first of these two species presents thoracic plates which only differ from the ordinary plates of the Bopyridæ by their much greater development and fringed appearance. The second certainly presents an anterior ventral incubatory chamber; but this chamber appears much more reduced than in *E. Cavolinii*, and does not seem to communicate with the dorsal part of the parasite.

The terminal portion of *Entoniscus*, or that which corresponds to the abdomen of the other Isopoda, is most frequently recurved towards the ventral side of the parasite. At the dorsal part of the first segment of this abdomen we see the heart beating, which has never appeared to me to form a hernia as in *Entoniscus porcellanæ*.

The ventral portion of the abdomen bears five pairs of folded and undulated lamellar appendages, corresponding to the five pairs of ramified appendages of the abdomen in *Ione*. These appendages decrease in size from the origin of the abdomen to the extremity of the body; so that, apparently, the first pair forms two large lateral tufts, and the last four pairs a median posterior tuft, equivalent to each of the first two. The last pair of appendages, however, are not very visible, and are formed by a simple fold of skin on each side.

The body terminates in a triangular expansion presenting two dorsal folds. There does not appear to be an anus, which is explained, as we shall see, by the arrangement of the digestive tube.

* These figures relate to *E. Moniezii*, but, for the point now before us, they may equally apply to *E. Cavolinii*.

The lamellar appendages of the abdomen of our *Entoniscus* greatly resemble those which Fritz Müller has described and figured in *E. porcellanæ*. But in the latter the fringed laminae are situated beneath the thoracic segments, and the abdomen is occupied by sabre-shaped feet.

In *Entoniscus cancrorum* Müller found fringed abdominal folds; but these folds, much less developed than in *E. Cavolinii*, form, on each side of the abdomen, an undulated continuous border, which does not extend so far as to the terminal part of the body.

From this point of view also, *E. Cavolinii* therefore differs considerably from the species hitherto described.

The head, of which we speak last of all, because, of all the external parts of the animal, it is the least visible at the first glance, is concealed beneath the folds of the ovigerous sac, and presents the form of a double sphere (Pl. X. figs. 2, 5). The anterior part, in which the mouth is situated, is furnished with two lamellar folds; we find no trace of antennae; and, by its internal organization, this head should rather have the name of *cephalogaster*.

When we free the parasite from its ovigerous sacs and the ova or embryos which they contain, we obtain a body of a pretty constant form, composed in great part of the ovary and the digestive organs of the *Entoniscus*.

The ovarian body presents four lateral prolongations, two anterior and two posterior (Pl. X. fig. 2), which are directed from above downwards, towards the ventral part of the *Entoniscus*. We distinguish besides, also on the ventral part, two or three pairs of much smaller eminences, which, with the preceding, perhaps represent the traces of the thoracic feet which have disappeared. Vestiges of these organs are still, in fact, to be seen upon the less degraded animal in the stage represented by figs. 3, 4.

On the dorsal part we observe two long median protuberances slightly bent from behind forwards. The posterior is the longer one.

All these prolongations remind us of those observed in an animal allied to *Entoniscus*, namely *Cryptothiria balani* (*Hemioniscus*, Buchholz), of which I have been able to examine several individuals collected at Wimereux, in the interior of the *Balanus balanoides* which cover the Tour de Croy.

It is well known that, in certain species belonging to high groups, parasitism often recalls peculiarities of organization which are only to be met with in the larvæ of the other species of the same group. These phenomena of reversion to the

atavistic type by parasitic retrogression have frequently led astray the zoologists who busy themselves solely with taxonomy, and sometimes even embryogenists. Starting from this idea, one might be tempted to compare the singular dorsal processes of *Entoniscus* with the analogous protuberances which are observed in a great number of Crustacea in the zoëa-stage. It is a comparison which naturally occurs to the mind; and I thought it necessary to indicate it in my preliminary communication upon the genus *Entoniscus*. I have since reflected that more or less similar protuberances occur in a great number of parasitic Crustacea belonging to inferior types, notably among the Copepoda, where evidently they cannot have the same significance. Hence, while calling the attention of zoologists to the remarkable constancy of these appendages in *Entoniscus Cavolinii*, I do not venture to pronounce in so affirmative a manner upon their true morphological value.

If we pass to the internal anatomy of the *Entoniscus*, we shall see that it presents nothing particularly remarkable. Compared with the *Bopyrus*-type, our crustacean has only undergone a considerable reduction of its various systems of organs.

The tegumentary system, cuticle and dermis is very like that of the other Isopods. It is clothed internally with a muscular layer, which enables the animal to perform rather slow vermiform movements of contraction.

The nervous system appears to me to be reduced merely to the cervical and anterior ventral ganglia; but my researches in this direction are too incomplete to enable me to deny absolutely the existence of the ventral chain. The movement of the abdominal plates even leads me to suppose that this chain does exist.

The digestive tube commences with a mouth constructed for sucking, and placed at the lower part of two folds in the form of a sucking-cup; the mass in the form of a brain, called the *head* by Fritz Müller, is hollowed internally by a cavity, the walls of which are lined with folds and villousities like those in the stomach of the *Bopyri*. These villousities have already been indicated by Rathke, Cornalia, and Panceri. This is therefore a true gastric cavity; and this apparatus, as a whole, would be better called *cephalogaster*.

The digestive apparatus is then continued by a short straight tube, terminated cæcally, at the anterior part of which the so-called hepatic cæca open.

I have sought in vain for a terminal intestine comparable to that described by Buchholz in *Hemioniscus*; I have been

unable to find any thing like it. Here, therefore, we have a fresh confirmation of the general law, according to which the more internal a parasite is, the more degraded is its digestive tube. This progressive degradation, which goes on increasing from the genus *Bopyrus* to attain its maximum in the *Entoniscii*, passing through the genera *Hemioniscus* and *Cryptoniscus*, reminds us precisely of what is observed in the Diptera of the family *Æstridæ*, in which the degradation becomes progressively more marked from the cuticular types to the gastric types, passing through the cavicular forms.

The hepatic cæca (for which I retain this old name, but without wishing to prejudge their true physiological part) are certainly homologous with the organs of the same appearance which we meet with in all Isopoda*.

These cæca form two large lateral sacs which occupy all the thoracic portion and even a part of the abdomen of the *Entoniscus*; their internal cavity is very spacious, as may be seen from the section drawn in fig. 7. The wall is covered with slight glandular folds, enclosing a brown substance, the aspect of which reminds one of what we have agreed to call liver in invertebrate animals.

Kowalevsky was the first† to indicate that the racemose hepatic cæca described by Rathke‡ in *Bopyrus* ('Icones zootomicæ' of V. Carus, Taf. xi. fig. 1, *h*) do not open directly into the digestive tube, but that they all open into a common canal, which itself opens at a single point into the stomach, as in the other Isopods. This observation is perfectly correct; and I have been able to verify it in several species of *Bopyrus* and *Phryxus*. All the difference between the hepatic gland of the *Bopyri* and that of the *Entoniscii*, therefore, consists in that in the former this gland becomes ramified and acquires a higher degree of differentiation. It may be said to be a difference analogous to that which exists between the simple pulmonary sac of the Amphibia and the complicated lung of Mammalia and Birds.

The circulatory system consists, in the first place, of a median dorsal vessel, upon the course of which is placed the heart, the beatings of which are very visible through the transparent integument of the animal. There are besides, on

* These organs likewise exist in the *Cryptoniscii*, in which I have indicated them, mistaking, however, their true relations. There cannot be any connexion between the ovary and these enormous cæca which open into the digestive tube.

† Kowalevsky, 'Entwicklungsgeschichte der Rippenquallen,' Einleitung, p. vii, Mém. de l'Acad. de St. Pétersb. 1866.

‡ Rathke, 'De Bopyro et de Nereide.'

the ventral side, lateral vessels which send forth branches to the fringed plates of the abdomen.

These fringed laminae may be regarded as true branchiae. Moreover they occupy the position of the branchial laminae of the normal Isopods. Their excessive development in the *Entonisci* is easily explained in the following manner.

We have stated that the *Entoniscus* in the body of its host is completely surrounded by a fine membrane. This membrane does not belong to the parasite; it is the continuation of the membrane which clothes the viscera of the crab and separates them from the branchial cavity. This membrane is gradually drawn back by the growth of the *Entoniscus*, which is thus enclosed in a sort of pouch formed by invagination. From this it results that the *Entoniscus*, as Fritz Müller justly points out, is an external parasite, although it appears to be in relation with the most internal viscera of its host.

That the Bopyridae need well aerated water constantly renewed, appears clearly from the position which they take up in the various animals to which we find them attached. The typical *Bopyri* lodge themselves in the branchial cavity of the *Macrura* and *Anomura*, where they draw from their host a revived blood, and themselves find constant fresh supplies of water. Therefore their respiratory apparatus is, in general, but slightly developed. The *Phryxi* attach themselves to the abdomen of *Paguri* at the spot where the ova are collected in the females of those animals—that is to say, at the point where the movements of the infested animal also allow of a ready renewal of the water. Nevertheless, as this renewal is less perfect than in the preceding case, the abdominal laminae are already much better developed than in the *Bopyri* properly so called.

In the *Entonisci* the position of the animal, in a deep invagination of the inner wall of the branchial cavity of the crabs, renders respiration much more difficult. Hence the respiratory lamellae have attained a much more considerable development, and their undulated and crisped surface converts them into regular sponges constantly impregnated with liquid. Their movement of contraction, however, enables them to drive off this liquid, and to draw in fresh supplies when the necessity for so doing is felt.

In *E. porcellanæ*, in which the abdominal feet have retained an ancestral form, it is the appendages of the thorax that have been modified and converted into undulated lamellae.

It is clear, moreover, that these various peculiarities are serviceable not only to the adult Bopyridae, but also to their

embryos, which, like the ova of all the other Crustacea, need, for their development in the incubatory cavities, perfectly aerated water. It is only necessary to place a female of *Bopyrus*, separated from her host, in a glass filled with sea-water, even very pure and renewed several times a day, in order to see that the development of the ova, contained under the ventral lamellæ, is soon arrested.

We have given above the description of the ovary. It will be sufficient to add that near the aperture of the ventral ovigerous sac we find two colleteric glands, the secretory ducts of which open not far from the apertures of the ovary near the small ventral eminences (Pl. X. figs. 7 & 2). These glands no doubt secrete the shell of the egg. There are analogous glands in *Hemioniscus*.

Notwithstanding careful search, I have been unable to meet with the male of either of the two species of *Entoniscus* that I have observed. I have vainly sought for it upon the body of the female and upon the crab parasitized. The notion that these *Entonisci* may be hermaphrodites evidently presents no absurdity *à priori*. In fact we are acquainted with hermaphrodite types in certain zoological groups which are composed principally of forms with separate sexes. Speaking very generally, parasitism, or even fixation (which is only a first degree of parasitism), pretty frequently induces the development of the two sexes in the same individual (Cirripedes*, Ascidia, Acephala).

As long ago as 1866 Kowalevsky† observed the testes and the mobile spermatozoids of a fine *Peltogaster* parasitic on *Callianassa subterranea*, and since described by Kossmann under the name of *Parthenopea*. He states, in the memoir, that he has met with hermaphroditism in several other species of *Peltogaster* and *Sacculina*.

Kossmann, in a memoir upon the Suctoria, has also figured (in 1872) the spermatozoids of several species, but did not see the mobile form of those elements. Kossmann's memoir was first published in a journal which is not much diffused ('Ver-

* The hermaphroditism of the parasitic Cirripedes of the group Suctoria or Rhizocephala was long in doubt in consequence of the numerous errors which have been published on this question. It is not very long since Hesse described as the male of *Peltogaster* a Bopyride Isopod crustacean! Such fancies would not deserve to be noticed here if they had not acquired a certain importance, even in foreign countries, by the support they have met with from certain Parisian *savants*. It is not without astonishment that we find a man of the importance of Spence Bate still asking in 1878, "What do we know of the male of the Suctoria?" (Ann. & Mag. Nat. Hist., June 1878).

† Rippenquallen, see note, p. 149.

handl. der phys.-med. Gesellsch. in Würzburg,' Bd. iii. Heft 4, p. 296, pls. xvi.-xviii.). Without knowing of these previous investigations, I occupied myself with the same question in 1873; and I then gave, in the 'Comptes Rendus' of the Academy of Sciences, the description of the testis and perfectly mature spermatozooids in *Sacculina carcini* and in two species of *Peltogaster*.

But in the present cases this hypothesis of hermaphroditism loses much of its probability, if we consider that Fritz Müller has described the male of all the species of *Entoniscus* that he has met with. There is very little probability that, in the same genus, species so nearly allied should present a physiological and morphological dissimilarity of such importance; and I prefer to assume that my unskilfulness, or my limited opportunities, have prevented me from meeting with the males of *E. Cavolinii* and *E. Moniezii*. I need not say that I have searched fruitlessly for a testicular gland, and that I have observed nothing resembling the spermatozooids of the Bopyridæ.

The youngest females of *Entoniscus Cavolinii* that I have been able to observe were in the same stage of development as the young *Entoniscus Moniezii*, figured Pl. X. figs. 3 & 4. The general form was identical; one saw the same rudiments of thoracic limbs, the commencement of the formation of the ventral ovigerous sac, and the two lateral ventral folds of the future dorsal pouch. But there were as yet no traces of the ovarian prolongations.

As a difference of specific value between *E. Cavolinii* and *E. Moniezii* at this period of evolution, I will indicate only the much greater development of the first pair of abdominal laminae in *E. Moniezii*. In *Entoniscus Cavolinii* the first four pairs of laminae have then nearly the same development; and it is only afterwards that the first pair grows more than the others.

III. EMBRYOGENY.

The anatomical details which we have just given present a great number of gaps, which will be excused, I hope, by all zoologists who have paid attention to the study of parasites. The scarcity of materials and the obscurity of the subject are two terrible obstacles, over which it is very difficult to triumph.

What we have now to say as to the embryogeny of these animals is still more incomplete; and, unfortunately, long years will probably be necessary to arrive at satisfactory notions upon this subject. Notwithstanding the innumerable quantity of ova which the female *Entoniscus* contains, it may be

said that we find ourselves in a state of actual poverty, since all these ova are at the same degree of development, and it is impossible to make them continue their evolution outside of the maternal organism.

I can say scarcely any thing about the embryo before its escape from the egg. The segmentation appears to be holoblastic; the embryo is bent backward, like that of all the Bopyridæ. The first six pairs of thoracic feet appear at first all similar; the seventh segment is destitute of appendages.

The five pairs of abdominal feet, which, in my opinion, correspond to the natatory feet of the *Cypris* form of the Cirripedes, or to the cirri of the adult *Lepas*, appear first, and all together.

On each side of the embryo, at the stage represented by fig. 9, we see a line of refringent bodies. I have seen similar lines in the embryos of several genera of Bopyridæ. In *Entoniscus* we see later on at the same place (fig. 9) two lines of pigment-cells. The pigment of *Entoniscus* has never offered me the characteristic odour of that of the *Cryptonisci*, an odour which is correctly indicated by Dr. P. Fraisse.

The embryo at the moment of its escape from the egg (fig. 10) is about 0.3 millim. in length. It presents two pairs of antennæ: the inner ones, which are short, are terminated by two tufts of setæ; the outer ones, which are much longer, are formed of six joints, of which the third bears two setæ, much longer than the others. The front is nearly straight, as in the embryo of *Entoniscus porcellanæ*. Besides the lateral eyes, which are double and correspond to the definitive eyes of the ordinary Isopods, it possesses a median eye, presenting exactly the structure of the nauplian eye of the Copepods &c. We find in it, in fact, two crystallines (figs. 11, 12), two optic nerves, and a strong black pigment-spot, the anvil-like form of which perfectly recalls that of the eye of the nauplius of the Cirripedes or of the free Copepods.

Fritz Müller indicates in the middle of the front of the embryo of *E. porcellanæ* a transparent spot, which, no doubt, is only the rudiment of a similar nauplian eye.

Dr. Fraisse has also observed something analogous in a species of *Cryptoniscus* (*C. monophthalmus*, Fr.). The male of this species possesses a single median eye instead of the lateral eyes of the other types of the same genus*.

* The *Cypris*-larva of an undetermined Cirripede, taken at Wimereux in September in the muslin net, also presented three eyes—the median eye of the nauplius and the two ordinary lateral eyes of the pupa-stage. A median pigment-spot also exists, besides the lateral eyes, in a branchiopod crustacean, *Holopedium gibberum*, Zaddach.

The presence of a nauplius-eye very distinctly formed in the embryo of *E. Cavolinii* appears to me to be of some importance as a trace of the nauplius phase in the embryogeny of the Isopods. Hitherto we had no factual argument to appeal to in order to connect the Isopods with the original form common to all the Crustacea. The opinion of Fritz Müller, who regards the embryonic membrane of *Ligia* or *Oniscus* as representing the naupliian skin, seems to me destitute of foundation. In all the groups in which embryonic membranes exist, these membranes are superadded in certain forms as protective organs of the typical embryo without modifying its essential characters. They are in general exodermic folds performing the part of an amnios. This is what takes place, for example, in insects, where these membranes may be formed in various fashions, and have no real morphological significance from the point of view of comparative embryogeny. These membranes are most frequently determined by physiological reasons, and may disappear or be retained in very nearly allied types.

The presence of the eye, so characteristic of the nauplius, seems to me, on the contrary, a mark of great value for the phylogeny of the Arthrostraca.

Each of the feet of the first five thoracic pairs terminates in a prehensile hand (fig. 8), of which the penultimate joint is oval, and bears two denticles on the side which is turned towards the opposable claw.

The sixth pair of thoracic feet, so exceedingly characteristic for the distinction of the species of the genus *Entoniscus*, does not at all resemble the same part in the types hitherto described. It consists of five joints; that which corresponds to the hand of the other pairs is more elongated (fig. 6, *a*), and terminates, on its inner margin, in a small curved fixed tooth; its outer border is produced into a straight rod, as long as the joint which supports it, and furnished at its extremity with a tuft of rigid setæ.

Here, then, we find a remarkable confirmation of the law demonstrated by Darwin and Fritz Müller:—When, in a group of animals, an organ presents an exceptional development, this organ is at the same time subject to great variability in the various species of the group.

It is probable that this sixth pair of feet aid the embryo to make its way into the interior of the crab in which it is to undergo its retrograde metamorphosis. The variations which it presents in the different species of *Entoniscus* are consequently in relation to the peculiar conformation of the branchial cavity of the animal infested.

The five pairs of abdominal feet are all constructed in the same fashion: the basal joint bears one or two setæ; the terminal setigerous joint presents a straight margin (fig. 10, *a*) which bears two setæ; a third is inserted at the acute extremity.

The only internal organs visible in the embryo are the hepatic cæca and the heart, which latter is seen beating actively in the dorsal part of the first segment of the abdomen.

In the following Table I summarize the characters of the embryo of *E. Cavolinii*, compared with those of the species described by Fritz Müller:—

<i>E. PORCELLANÆ.</i>	<i>E. CANCROURUM.</i>	<i>E. CAVOLINI.</i>
Length at hatching 0·2 millim.	Length at hatching 0·3 millim.	Length at hatching 0·3 millim.
Frontal margin nearly straight.	Frontal margin arched.	Frontal margin nearly straight.
Unpaired transparent spot on the frontal margin.	No such spot.	A median nauplian eye on the frontal margin.
Inner margin of the hand of the first five pairs of feet smooth.	Inner margin of the hand furnished with denticles.	Inner margin of the hand furnished with two teeth.
Sixth pair of feet short, three-jointed; terminal joint elliptical, without a hook.	Sixth pair of feet of five joints, with a hand furnished with a hook.	Sixth pair of feet of five joints, with a hand furnished with a hook and a rod.
Last segment of the thorax wanting (?).	Last segment of thorax present.	Last segment of thorax present.
Fifth pair of abdominal feet still but little developed, destitute of setæ.	Fifth pair of abdominal feet present, like the preceding ones.	Fifth pair of abdominal feet like the preceding ones.
Basal joint of the abdominal feet furnished with a seta.	Basal joint of the abdominal feet with two setæ.	Basal joint of the abdominal feet with one seta (?).
Terminal joint of the abdominal feet lancet-shaped.	Setigerous joint straightly truncate.	Setigerous joint straightly truncate.

The larvæ of *Entoniscus* can live for several days in seawater. I have kept some alive that I had carried from the Pouliguen to Paris, and from Paris to Lille. In ten days they died without showing any modification. These embryos swim in the position described by Fritz Müller—that is to say, with the body recurved towards the ventral surface, and the sixth pair of thoracic feet projecting at the sides.

I incline to think, however, that with these animals, as with the other Bopyridæ, copulation takes place before the commencement of parasitic life. In most Isopods the male is

smaller than the female; and sometimes the difference of size in the two sexes is very great. Several species of *Idotea* are remarkable in this respect. It has frequently happened to me to capture these animals in the muslin net; and almost always one meets with them in couples; the male, one third or one fourth the size of the female, is placed between the feet of the latter on the abdominal surface, absolutely in the same position as the male of the Bopyridæ. This is the case also with various Cymothoadæ; and in some species of this group it is necessary, as in the Bopyridæ, that copulation should precede parasitism. This occurs notably in a curious Javan species described by Herklots*.

In the course of this memoir I have several times alluded to a second new species of *Entoniscus*, which I have also met with at the Pouliguen, and which I have named *E. Moniezii*, dedicating it to R. Moniez, preparator of zoology at the Faculty of Sciences of Lille, who accompanied me in my journeys on the shores of the Loire-Inférieure.

This species appears to be very rare, since I have seen only two individuals of it—an adult female and another at a less developed stage (figs. 3, 4), both found in the same example of *Portunus puber*. This crab had been collected at the island of Leven, opposite to the point of Peu-Château and the open coast of Pouliguen. In order to find it again I have in vain examined several hundreds of the *Portunus* fished on the coast.

I have already indicated above some differences between this species and that of Cavolini in the stage represented (figs. 3, 4).

The adult individual unfortunately contained only slightly developed embryos; and I was unable to compare these embryos with those of the species from the *Grapsus*. The differential characters were furnished to me by the colour of the ovary and of the ovigerous sacs—peculiarities of which Fritz Müller ought to have made use to distinguish the various *Entonisci* parasitic on *Porcellanæ*. In *E. Moniezii* the ovigerous sac is of a nankeen-yellow, instead of presenting the greyish-yellow colour of *E. Cavolinii* at the same grade of evolution of the eggs. The ovarian gland is yellow with a rosy tint; it is straw-yellow in the parasite of the *Grapsus*.

* J. A. Herklots, "Deux nouveaux genres de Crustacés vivant en parasites des poissons: *Epicthys* et *Icthyoxenos*," Archives Néerlandaises, tome v. 1870, p. 120 (*Icthyoxenos Jellinghausii*).

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EXPLANATION OF PLATE X.

- Fig. 1.* *Entoniscus Cavolinii*, adult, natural size. V, ventral surface. D, dorsal surface; *t*, head recurved towards the belly; *o*, posterior extremity, also recurved towards the belly; *a β γ*, ovigerous sac, through which the dorsal protuberances are distinguished; *λλ*, anterior lateral protuberances; *τ τ*, posterior lateral protuberances; K, ventral ovigerous sac.
- Fig. 2.* The same, freed from the ovigerous pouches to show the form of the body. The letters have the same signification as in fig. 1. *c*, heart; *p, q, r*, prominences (traces of thoracic limbs?).
- Fig. 3.* Young *Entoniscus Moniezii*, much enlarged, seen from the side. *o*, mouth; *l*, buccal ovigerous plates; *h*, hepatic cæcum; *1, 1'*, the first two fringed abdominal lamellæ; *2, 3, 4, 5*, last pairs of fringed lamellæ; *r*, rudiments of thoracic limbs.
- Fig. 4.* Embryo in the same stage, seen from the back.
- Fig. 5.* Head (*cephalogaster*) and mouth of *E. Cavolinii*, with its sucking-disks.
- Fig. 6.* Terminal joint of the sixth pair of thoracic feet of the embryo: *a*, of *E. Cavolinii*; *b*, of *E. cancrorum*; *c*, of *E. porcellanæ*. The last two from Fritz Müller.
- Fig. 7.* Section of *E. Cavolinii* towards the anterior third. *vd*, dorsal vessel; *h h*, hepatic cæca; *gl*, colleteric glands opening at the entrance of the ventral ovigerous sac.
- Fig. 8.* Terminal joint of the first five pairs of thoracic feet of the embryo of *E. Cavolinii*.
- Fig. 9.* Embryo of *E. Cavolinii* still in the egg. A, seventh thoracic segment still destitute of appendages; *pi*, line of pigment-cells.
- Fig. 10.* Embryo newly hatched. *c*, heart; *a*, terminal joint of an abdominal foot.
- Fig. 11.* Head of the embryo, showing the antennæ and the eyes. N, nauplian eye; *o, o, o', o'*, the ordinary eyes.
- Fig. 12.* The nauplian eye much magnified. *l*, crystalline (double lens); *n*, optic nerve; *pi*, pigment-spot.



Giard, Alfred. 1879. "XVII.—Notes towards the history of the genus *Entoniscus*." *The Annals and magazine of natural history; zoology, botany, and geology* 4, 137–157. <https://doi.org/10.1080/00222937908679805>.

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