

- II. *Some Observations upon the Structure of two new Species of Hectocotyle, parasitic upon Tremoctopus violaceus, D. Ch., and Argonauta Argo, Linn.; with an Exposition of the Hypothesis that these Hectocotylæ are the Males of the Cephalopoda upon which they are found.* By A. KÖLLIKER, Professor of Physiology and Comparative Anatomy in the University of Zurich. Communicated by ROBERT BROWN, Esq., V.P.L.S. &c. &c.

Read April 15th and May 6th, 1845.

WHILST visiting Messina and Naples during the summer of 1842, I found two worms resembling the *Hectocotyle Octopodis*, described by Cuvier as found upon the *Octopus granulosus*, Lam.; the one upon the *Tremoctopus violaceus*, Delle Chiaje (*Octopus velifer*, Fér.), the other upon the *Argonauta Argo*, L. At first sight I took them for epizootic worms, to which, from their white colour and numerous suckers, they bore a great resemblance; but when I examined them more accurately, I met with so many peculiarities, a few of which I will here mention, namely the existence of a heart, arteries and veins, branchiæ, and coloured contractile pigment-cells, that at length I was compelled to abandon that idea. Proceeding with my examinations, I soon found that the animals were all males; and remembering that that sex of the *Argonauta* and *Tremoctopus* was not as yet known, I supposed that I had discovered the males of those *Cephalopoda*. I must confess that at first I did not place much reliance upon this conjecture, for the great dissimilarity between the supposed sexes surprised me so much that I scarcely dared to believe it to be well-founded. However, as I proceeded further with my researches, I found more and more to strengthen my supposition, so that finally I was led to regard it as very probable. But before proceeding to submit the arguments on which I formed my opinion, I propose to give a slight sketch of my anatomical researches with respect to the above-mentioned animals.

*Description of the Hectocotyle of Tremoctopus violaceus.*1. *External Form.*

This animal very much resembles the *Hectocotyle Octopodis*, which Cuvier has described in the 'Annales des Sciences Naturelles' for the year 1829*, the anterior part of the body being long, worm-like, and provided with two rows of suckers on its ventral surface, the posterior short and of an oval shape; but independently of its being much smaller, it differs also at first sight from *H. Octopodis* in the back being fringed with a great number of little branchial appendages, and the posterior extremity having a long process.

The *anterior part* of the body varies in length from $1\frac{1}{3}$ – $1\frac{2}{3}$ of an inch, is thickest in the middle, and diminishes towards both extremities. Without the branchiæ and suckers it would be nearly cylindrical, but in the natural state the cephalic portion is almost quadrangular, while that immediately behind is flat, and has sharp margins. Its colour is almost entirely pure white; it exhibits however at the branchiæ some azure tints, and here and there some yellowish hues; there are also some remarkable spots on the back, of which I shall speak presently. The *upper surface* of this anterior part bears in its cephalic portion the branchial appendages and the spots just mentioned; the upper surface of the posterior portion, on the contrary, is perfectly smooth; the spots are arranged in two slightly-irregular rows between the branchiæ along the middle of the back; they are circular, about $\frac{1}{20}$ th of a line in diameter, of a brown or violet colour, and about 50 in number. The branchial appendages are placed on a low, mantle-like margin, which takes its origin from the side of the animal between the suckers and the coloured spots; the appendages have a conical form, are 1 line long and $\frac{1}{8}$ th of a line broad: during life those next to the middle of the back stand vertically erect, the others successively assume a more inclined direction, and the outermost lie nearly transversely. The appendages are disposed in irregular longitudinal lines; their number is considerable, amounting to about 250 on each side.

The *ventral surface* of the anterior part is quite smooth in the middle, and slightly convex from side to side; on each of its margins are situated 40 or 41

* 1re Série, t. xviii. p. 147.

suckers, which are disposed alternately, and bear the strongest resemblance to those of the *Tremoctopus* itself.

The *posterior part* of the body is a large oval sac, of 5 lines in length, to which the penis is appended. The sac is quite as large as the largest part of the body, and incloses a great many convolutions of a small canal and one large duct. The penis is situated on the abdominal surface, and takes its origin from the foremost part of the oval sac: it is conical and partly free, partly confined in a delicate membranous sheath, which is attached to the ventral aspect between the last six suckers; its form and length vary according as it is contracted or extended; in the first case it is 4 lines long, $\frac{1}{2}$ a line thick, and curved; in the latter, 7 lines long, $\frac{1}{4}$ of a line thick, and nearly straight.

2. *Structure.*

a. *Skin.*

The skin of the animal consists of two layers; the exterior is the epidermis, formed by delicate, polygonal cells, of a diameter of 0·018–0·036^{'''}, which contain round nuclei; the interior, the corium composed of cellular tissue, the outer fibres of which are disposed longitudinally, and the inner transversely. The coloured spots, already mentioned, form a very remarkable object in the description of the skin; each of them is a cell, containing a nucleus and a great many coloured granules, and exhibits during life the same curious phænomenon which R. Wagner has discovered in the pigment-cells of *Cephalopoda*, viz. a regularly alternate expansion and contraction. As in the example just quoted, the colour of the cells varies according as the granules are assembled together in a mass or scattered about in the expanded cell. With regard to the power which effects these contractions, it is not yet proved whether it lies in the contractile membrane of the cells, as Wagner supposes, or in the contractile cellular tissue which surrounds them, an opinion which I have lately advocated.

I have yet to mention some peculiar minute pores which are found on the anterior part of the ventral surface. They are arranged in rows of four or five on each side between the mesial line and the suckers, thus forming a continuous series. Each opening is elliptical in figure, the longest diameter being 0·024–0·012 P. L., and conducts to a canal of the same size, which

penetrates through the muscular envelope of the body into the abdominal cavity. These organs are probably an apparatus for conveying water into the abdominal cavity, resembling that of the *Radiata* and *Mollusca*.

b. Muscular System.

This system is highly developed; the suckers and the penis are both furnished with muscles, and there is also a peculiar muscular envelope of the body. The latter has a very curious organization: it consists of three layers, the external of which is 0·048 P. L., and the innermost 0·024 P. L. in thickness; both are formed by circular fibres, the former being continuous with the corium, and the latter containing a tubular cavity, through which the intestine passes. The middle layer is formed of longitudinal fibres, which are arranged in such a manner as to form numerous septa or partitions, radiating from the centre to the circumference, *i. e.* from the central to the external layer, thus presenting very much the appearance of a carriage-wheel. There are, moreover, other very short transverse fibres uniting these septa. Consequently the entire envelope of the body consists of four distinct species of fibres, very singularly disposed.

The muscles of the acetabula are the following. Each one is attached to the muscular envelope by two large retractors; and it has besides a small layer of circular fibres surrounding it externally, and a thick stratum of longitudinal ones internally.

The penis has a slight layer of transverse as well as longitudinal fibres.

The muscles seen with the microscope are, like those of the human intestine, composed of large flat fibres with nuclei, and neither showing transverse lines, nor being united in bundles.

c. Intestine.

As far as I could trace the intestine by dissection and with the microscope, it appeared to be very simple. The mouth is placed at the anterior extremity just above the foremost sucker, and is small and elliptic, without any lips or teeth. The intestine itself is a cylindrical tube, which nearly fills the cavity of the body, and runs straight through its whole anterior worm-like part till it reaches the oval sac. Whether it finishes here or not I cannot tell, because, notwithstanding repeated examinations, I was not able to find an anal orifice.

It may, however, be conjectured that the intestine, if it does not end in a cæcum, passes into the part which I have called penis, and ends at its extremity. With regard to minute structure, the intestine is composed of an exterior muscular layer and a thick epithelium.

d. Vascular System.

Though I have not been able to investigate the whole vascular system clearly, yet I have seen enough to convince me that it is more complex than could be expected from the simple external form of the animal.

The heart is situated in the middle of the back between the branchiæ, on the outside of the above-mentioned muscular envelope of the body, being covered only by the skin. It has an oval shape, being about $\frac{4}{10}$ ths of a line in length and $\frac{1}{10}$ th of a line in breadth, and seems to consist of an auricle and a ventricle. As I only discovered the heart after my return from Italy, in dissecting the individuals brought with me in spirit, I can say nothing about its contractions; nor am I able even to explain its connexion with the vessels. The only fact which I distinctly saw is, that two large vessels take their origin from the heart, the one from the part which I judge to be the auricle, the other from the ventricle.

With regard to the vessels of the branchiæ and the body my inquiries have been more successful. On each side of the back of the animal there are in the cephalic portion, just beneath the branchial appendages, two large vessels close together: the one situated most externally, which has a diameter of 0.096^{'''}, may be called the branchial artery; the other, of 0.048^{'''} diameter, the branchial vein.

The branchial arteries give to each branchial appendage a single branch, which, after having formed some ramifications, is connected by capillary anastomosis with the branchial veins. The branchial arteries take their origin from two venæ cavæ, which come from the posterior part of the body, and are formed by the junction of all the smaller veins of the body, among the most conspicuous of which are those of the generative organs and the skin.

The branchial veins are formed by a great number of small veins, which take their origin from the above-mentioned system of capillaries included in the branchial appendages. I could not trace these vessels to the heart; neither

was I able to discover vessels, which, from a connexion with the aorta, would appear to be the arteries of the body.

With regard to minute structure, the capillaries are formed by one single, delicate membrane provided with nuclei; the larger vessels have in addition to this membrane a layer of muscular fibres more or less thick.

e. Nervous System and Organs of Sensation.

The only fact which I can furnish with regard to the nervous system is, that there exists a small nerve running alongside the intestine, which is provided, as far as I have observed, with one ganglion containing nucleated cells. This nerve is included in a sheath of cellular tissue, and gives off branches to the intestine.

I was equally unfortunate in my endeavours to discover the organs of sensation, being, after the most careful observation, unable to find organs either of sight or hearing or tentacles.

f. Organs of Generation.

All the specimens which I saw were males. The testicle is formed by an extremely long, small and tortuous tube, which fills nearly the whole of the sac above mentioned, and can easily be perceived in the living animal through the pellucid membrane of the sac. The vas deferens is provided with a strong muscular layer, and has its posterior part included in the oval sac; whilst the anterior part, which is narrower, runs through the middle of the penis, and opens at its extremity by a small orifice. The semen, when taken from the living animal, presents the appearance of a silk thread. It consists of innumerable spermatozoa, which have the same size and form as those in *Octopus vulgaris*, and which originate from small cells filling the end of the testicle.

Description of the Hectocotyle of Argonauta Argo.

Delle Chiaje in his memoirs has given a very unsatisfactory figure and description of this animal, which he has named *Trichocephalus acetabularis*. Many years later Costa found specimens of the same animal, and described it also imperfectly, though better than Delle Chiaje, in the 16th volume of the

new series of the 'Annales des Sciences Naturelles,' page 185, under the title of *Prétendu parasite de l'Argonaute*. According to his opinion the animal is only a part of the *Argonaut*, perhaps a spermatophore, of a singular shape. According to my own opinion, which will be explained hereafter, the body discovered by Delle Chiaje and Costa is indeed a distinct animal, and, as I hope to be able to prove, most probably the male of the *Argonaut*. As this animal is very like the *Hectocotyle* of the *Tremoctopus* in its exterior shape and structure, I propose to give only a brief account of those points in which they chiefly differ.

The *Hectocotyle* of the *Argonaut* is worm-like, 7 lines long and $\frac{1}{2}$ a line in breadth, thicker in its posterior than in its anterior part, and provided at the latter with a filiform appendage 6 lines in length. The ventral surface of the body is furnished with two rows of suckers alternately disposed, forty-five on each side; the dorsal surface is smooth, without branchiæ, but provided in its posterior part with a great many round or elliptic spots of a red or violet colour. The appendage is thickest at its origin, and gradually decreases till it becomes very small. In two of the three animals which I obtained, the end of this appendage was quite free; in the third one I found it fixed to the posterior part of the body, that is to say, the end of the process pierced through an opening in the back, just at the part where the coloured spots commenced, and was connected with the male organs in a manner which I shall hereafter describe. Attached to the superior surface of the appendage, close to its junction with the head of the animal, are two delicate triangular membranes, one on either side; they are connected to the appendage by one side, the other being free.

The structure of the animal is very similar to that of the *Hectocotyle* of the *Tremoctopus*. The skin, the contractile coloured spots or pigment-cells, the muscular envelope of the body, the structure of the suckers, are nearly alike in both, size alone excepted. I found however only one large vessel on each side, and instead of branchiæ a great multitude of capillary vessels in the filiform appendage and in the skin of the dorsal surface. I could not detect a heart, nor was I able to find either nerves or organs of sensation. The intestine, which commences with a small orifice just beneath the basis of the appendage, could be traced through the whole body, but no anal opening was to be found.

On the contrary, the male organs were readily traced, and appeared highly developed. The testicle presented the same structure as that of the *Hectocotyle* of *Tremoctopus*, and was inclosed in a large elliptic sac in the dorsal surface, just where the pigment-cells were placed: it gave origin to a small vas deferens, which could not be traced to any great length in two of my specimens. In the before-mentioned animal, however, in which the end of the appendage pierced through an opening in the back, the vas deferens was connected with the appendage, and ran closely attached to its superior surface until it reached the basis; hence it took its course backwards, and entered there a peculiar long tube situated under the sac containing the testicle. This tube, which is composed of two membranes, the internal being thick and muscular, the external thinner and of a mother-of-pearl lustre, may be regarded as the penis. In its interior the vas deferens makes a great many convolutions till it reaches the hindermost part of the body, where it opens together with the penis by a small orifice. The semen and the spermatozoa resemble those of the *Hectocotyle* of the *Tremoctopus*.

Having thus shortly stated the result of my observations on these two species of *Hectocotyle*, I proceed to the most important part of this essay, that is to say, to a statement of the reasons which induce me to regard these *Hectocotylæ* as the males of the Cephalopods on which they live.

But first I must prove that the *Hectocotylæ* described are really animals, inasmuch as Costa considers one of them as a detached portion of the *Argonauta*, or as a part of the seminal apparatus. According to my observations, there can be no doubt of the object in question being a distinct animal, as I had it for hours living in my room, and observed its energetic and evidently voluntary motions. Neither can the *Hectocotyle* be a part of the seminal apparatus, for it is not to be supposed that in that case it would be provided with vessels, nerves, muscles, pigment-cells, &c.; nor a detached portion of the Cephalopod on which it is found, no injury being observable on the latter, and the *Hectocotyle* always living perfectly free on its surface.

As it is therefore placed beyond all doubt that the two *Hectocotylæ* are animals, the question is reduced to whether they stand in a nearer relation to their Cephalopods,—whether, in fact, they are the males of these Cephalopods,

or whether they are to be regarded as animals quite different, and belonging perhaps to the class of *Epizoa*. According to my conviction the first is the correct view, which I hope best to prove by showing how I myself arrived at this conclusion.

After I had concluded the anatomical examination of the two *Hectocotylæ*, I for the first time entertained doubts of their relation to Epizootic worms, as for example *Tristoma* and *Myzostoma*, which they so perfectly resemble in their outward appearance, when I considered that not one of these worms, although not unfrequently provided with a highly developed vascular system, possesses two kinds of vessels, that is to say, arteries and veins, a heart and branchiæ. Yet this alone, as may easily be believed, would not have been sufficient to induce an opposite conclusion, if other facts had not attracted my attention and compelled me to examine more carefully. In the first place, I was compelled to recognize the remarkable similarity of the *Hectocotylæ* furnished with numerous suckers and violet pigment-spots with the arms of the Cephalopods on which they live; a similarity which extends so far that the suckers of *Hect. Argonautæ*, with reference to the form and arrangement of the muscles, perfectly resemble those of the Argonaut, while those of the *Hect. Tremoctopodis* accurately represent those of the *Tremoctopus*; and the colour of the pigment-spots in each of the two animals belonging to each other perfectly coincided. Continuing to meditate on the subject, I called to mind several other points of agreement. First, the spermatozoa of *Hectocotyle*, which (like those of *Sepia*, *Octopus*, &c.) are furnished with a moderately long cylindrical body and a long filiform appendage; and secondly, the contractile pigment-cells, which occur in *Hectocotyle* exactly as in the Cephalopods, which is the more important, inasmuch as these remarkable cells have hitherto been found in no other animals. Lastly, I discovered the interesting fact, that the fibres which form the muscular mass of the arms of the Cephalopods are arranged in exactly the same complicated manner in three layers as those which form the muscular envelope of the body of the *Hectocotylæ*.

All these facts at length led to the conviction that there existed a remarkable agreement between the *Hectocotylæ* and their Cephalopods; and the more I considered the subject, the more I felt compelled to believe in a cer-

tain relation between them. It was then that the view first occurred to me that the *Hectocotylæ* might be the males of the Cephalopods on which they live, when I called to mind that the twelve specimens of *Hect. Tremoctopodis violacei* and the three of *Hect. Argonautæ* which I had obtained at Messina were all males, and that although a very large number of Argonauts had been examined with reference to their sexual organs, no one had yet been fortunate enough to discover male organs in them. I can prove that of 280 Argonauts, of which Poli examined 30, Delle Chiaje 50, Van Beneden 3, Owen 100, Broderip 60, and myself 50, there was *not a single male*. On this assumption it was easy to explain why no one had hitherto been able to detect the male of *Argonauta*, although it must be admitted that males are very abundant; for as Owen, Madame Power, myself and many others have observed, nearly all the female Argonauts carry about with them impregnated bags of eggs, containing embryos more or less developed. On the other hand, I could not attach too much importance to this view, as it appeared too hazardous to believe that the small vermiform *Hectocotylæ* with their (as far as could be ascertained) imperfect organization, could be the males of some of the larger *Cephalopoda*, which stand so high as regards their structure. I was compelled indeed to admit that something similar takes place with regard to some animals of the class *Crustacea*; in which, as Nordmann has shown, in the genera *Achtheres*, *Lernæopoda*, *Tracheliastes*, &c., the males are not only many times (frequently a thousand times) smaller than the female, but also live only upon the females attached in the neighbourhood of their sexual openings, and moreover (which is of the greatest importance) are quite different in their external form and in their structure. Nevertheless, in spite of this important analogy, I did not yet venture to attach full credit to my conjecture, more especially because other genera of Cephalopods, as for example *Sepia*, *Sepiola*, *Octopus*, *Eledone*, &c. possess males of the common form; and because I was not in a condition (as Nordmann had done with reference to the above-named parasitical *Crustacea*) to refer the deviating form of the *Hectocotylæ* to any even embryonary form of *Cephalopoda*.

So far had I arrived by my own investigations; that is to say, I had good grounds for the *conjecture* that the two *Hectocotylæ* were the males of certain Cephalopods, but I was not in a condition to place it beyond doubt, when

fortunately my attention was directed to a letter from Madame Power, which Professor Maravigna of Catania had communicated in the year 1835 to the Società Gioenia of that place, in which are contained facts which appear to solve all doubts, and to show on the fullest evidence that the view which I had arrived at through the observations above given is the true one. As I know Madame Power's letter only by a notice given of it by M. de Blainville in the 'Annales des Sciences Naturelles,' 2^{de} série, vol. vii. p. 173, I can only quote what is there given. De Blainville says :

“ Madame Power, ayant en sa possession un grand nombre de ces animaux [Poulpes de l'Argonaute] remplis d'œufs, elle s'est assurée que jamais le Mollusque, à aucune période de son existence dans l'œuf, n'est pourvu de coquille, et qu'il naît ou vient à la lumière entièrement nu ; mais qu'il se fabrique une coquille après sa sortie.”—“ Madame Power, conduite à répéter ses observations, arriva aux mêmes résultats que la première fois, et elle ajouta à son premier Mémoire non seulement un Supplément dans lequel elle consigna les faits qu'elle avait nouvellement observés, mais elle envoya en même temps à la Société Gioénienne ainsi qu'à son secrétaire, les œufs du poulpe de l'Argonaute et les petits poulpes récemment sortis de l'œuf, avec des individus qui avaient déjà plusieurs jours de naissance, et d'autres pourvus de coquilles de différens âges, tous élevés par elle et qu'elle avait vu croître et se développer sous ses yeux. M. Maravigna affirme avoir spécialement observé parmi les petits poulpes qui lui ont été envoyés, l'un d'eux sortant de l'œuf auquel il étoit encore attaché, et qui étoit entièrement depourvu de coquille. Ainsi ajoutait-il, les faits observés par Madame Power conduisent à conclure que non-seulement le poulpe de l'Argonaute est le véritable constructeur de sa coquille, et qu'il ne la construit pas dans l'œuf, mais après sa naissance ; mais encore que le petit poulpe, au sortir de l'œuf, ne ressemble pas entièrement à ce qu'il sera par la suite ; c'est alors une sorte de petit ver (*vermicello*) pourvu de deux rangées de ventouses dans la longueur, avec un appendice filiforme à une extrémité et un petit renflement vers l'autre, où il paraît que sont les organes de la digestion ; en sorte que, suivant M. Maravigna, on pourrait supposer que ce ne serait d'abord qu'un appendice brachial extrêmement petit, duquel se développeraient ensuite autant de parties qu'il est nécessaire pour le constituer tel qu'il doit devenir par la suite.”

So far De Blainville. According to my views it follows from these observations of Madame Power, which Maravigna, as he told me himself, has repeated, (presupposing that they are entitled to full confidence,) that undoubtedly a vermiform animal quite similar to the *Hect. Argonautæ*, which possesses two rows of suckers, is thicker at one end, and furnished at the other with a fili-form appendage, is contained in the eggs of the Argonaut. It would thus be proved that the *Hectocotyle* which has male organs only, is the male of the Argonaut. But however much I may wish to give full credit to the observations of Madame Power and Maravigna, I will not conceal some objections which occur to me on the subject. Madame Power and Maravigna state that they have seen the young vermiform Argonaut escape from the egg. It is easy to perceive that everything depends on the interpretation to be put on this expression. If it is not to be taken literally; if they merely mean to say that in the egg-bag of an Argonaut they have found little worms which resemble the arm of an Argonaut, nothing whatever is proved by it. But if we are to take the observation exactly as it is related and not otherwise, it is of the greatest importance. In this latter case the only remaining question would be, whether Madame Power and Maravigna in fact found an entire egg-bag attached to the shell of *Argonauta* full of *Hectocotyle*-like embryos, or whether they saw among eggs with the common embryos a few with vermiform animals. In the latter case the eggs might have been the eggs of *Hectocotyle*; in the former no doubt could remain that the *Hectocotylæ* are the males of the Argonaut. It is obvious that having made no observations of my own on this point, I can give no decided opinion. All that I can say is, that if Madame Power and Maravigna have actually seen an entire egg-bag of *Argonauta* full of *Hectocotyle*-like embryos, I for my part have not the smallest doubt that the *Hectocotyle Argonautæ* is the male Argonaut. At all events, as the fact would be in a high degree contrary to all analogy, and must actually be regarded as wonderful because single of its kind, new observations are necessary before it can be regarded as established.

I believe that I have now said all that can be adduced in favour of the conjecture that the *Hect. Argonautæ* is the male Argonaut. As regards the *Hectocotyle* of the *Tremoctopus*, I cannot adduce the same facts in its favour, as I have not seen it escape from the eggs of the *Tremoctopus*. Still I have not

the smallest doubt, that if it were established that the *Hect. Argonautæ* is the male of the Argonaut, a similar relation would be admitted for the *Hectocotyle* of the *Tremoctopus*. The same may be said with still greater certainty of Cuvier's *Hectocotyle Octopodis*, (which has not since been observed by any one,) more especially because this animal, size excepted, almost entirely agrees with the *Hectocotyle Argonautæ*.

In conclusion, I sum up in a few words all that may be said upon this subject.

1. The *Hectocotylæ* have arteries and veins, a heart and branchiæ, and are therefore very probably not Epizootic worms.

2. *Hect. Argonautæ* and *Hect. Tremoctopodis* bear a close resemblance to *Cephalopoda* in general, and in particular to the genera on which they live. for they have

a. The same spermatozoa.

b. Contractile pigment-cells.

c. Similarly formed and similarly organized suckers.

d. The same remarkable arrangement of the muscular fibres; the *Hectocotylæ* in the muscular envelope of the body, the Cephalopods in the arms.

3. Among 280 Argonauts examined not a single male was found.

4. Nevertheless, the males must be very abundant, inasmuch as nearly all the Argonauts possess impregnated ova.

5. The *Hectocotylæ* live in the neighbourhood of the female sexual organs of their Cephalopods, and are all males.

6. The eggs of the Argonaut contain, according to Madame Power and Maravigna, embryos perfectly resembling the *Hect. Argonautæ*.

If this last position is correct, the *Hectocotyle Argonautæ* is undoubtedly the male of the Argonaut.