The Sexual Conditions of Myzostoma glabrum (F. S. Leuckart).

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With Plate 10.

Myzostoma glabrum, a common parasite of *Comatula* in the Bay of Naples, presents the peculiarity of hermaphroditism associated with the existence of »complemental« or dwarf males. In my original account (1) of these latter it was concluded [1], that they were to be looked upon as remnants of a former primitive diœcious state, and that hermaphroditism in this, as in many other cases, was a secondary condition, induced, perhaps, by the parasitic mode of life.

Nansen, in a valuable work (6) on the genus, regarded the matter in a very different light; in his opinion the so-called dwarf-males had sprung from or were merely young protandrous hermaphrodites.

The results of investigations, undertaken to test the validity of Nansen's contentions, are given below. They were primarily not meant for publication [2], but only for the satisfaction of personal curiosity. As, however, Nansen's views have found acceptance in such standard works as Lang's Vergleichende Anatomie and Korschelt and Heider's Entwicklungsgeschichte, the matter cannot well be left unchallenged, seeing that I can find no evidence to support Nansen's suppositions, but much that strengthens my standpoint.

It may be well to recall a few of the facts as to the occurrence of *M. glabrum*.

[1] No. 1 of the appended list of memoirs.

[2] The first portion of this paper was originally written in 1890. Since then the material has twice undergone revision.

The common species of *Myzostoma* in the Mediterranean is *M. cirriferum*, which wanders freely about the disc and arms of its host. Every *Comatula* in the Bay of Naples is more or less infested with this parasite.

M. glabrum, on the other hand, is much rarer, not being found oftener, according to L. von Graff's observations (with which my own agreed), than on every third *Comatula*.

M. glabrum is a sessile parasite, and is found seated at the edge of the oral cavity of its host. The dwarf males may, or may not, be present on any particular hermaphrodite specimen; indeed, if several large hermaphrodite forms be found on one host, males will probably be absent[1]. The males, when present, are firmly fixed at the anterior median part of the dorsal region of the hermaphrodite. A true male has never been met with in any other position or on the disc.

In addition to the large hermaphrodites and their associated males, very small *M. glabrum* may also be found on the disc; in some cases these may be even smaller than the dwarf males. The true males rarely exceed about 1.01 mm in diameter, but young hermaphrodites measuring only about 0.75 mm may be found.

Diligent search of fresh specimens of *Comatula* would probably reveal still smaller disc-individuals, but in my material, collected at Naples in 1884, only a single one smaller than the above could be detected.

The points at issue may be stated as follows: — If Nansen were right in his contention, that the males were probably not fixed forms but merely young hermaphrodites, or hermaphrodites with rudimentary female organs, then one ought to find in some male or other rudiments (Spuren) or foundations (Anlagen) of the female organs; and, the larger the males examined, the greater the chance ought to be of meeting with traces of eggs or female organs[2]. Further, if the males were merely protandrous hermaphrodites, whose position on the larger forms was, therefore, purely accidental, as von Graff originally supposed, then very minute specimens of

[1] It appears to be quite possible that *M. glabrum* may exhibit a sort of sexual dimorphism, of such a kind that certain of the hermaphrodites may always be associated with other hermaphrodites only, while others may be connected with the males.

[2] The essential female organs are here meant. The question of ducts will be afterwards discussed.

M. glabrum found on the disc (i. e. those smaller than the average of the males), must also resemble the males in the enormous development of the testes, and in the apparent absence of ovaries. If ova were found in the small specimens on the disc, they ought also to be present in individual males of the same size, or in larger males.

But, if under these circumstances no traces of eggs were found, even in the largest males, there would, I think, be no escape from the inference formerly drawn as to their true nature.

To probe the matter, the largest males[1] that could be found were taken for comparison with the smallest hermaphrodites (from the disc).

Sections of a uniform thickness of $^1/_{133}$ mm were cut of all the forms examined, and their number counted by the clicks of the micrometer-screw. As the animals were killed, preserved, and prepared in all details in exactly the same way, and all embedded for the same length of time, the results appear to be quite trustworthy.

The forms more particularly examined included nine males (dorsicolous forms) and thirteen disc-forms or, according to my assumption, hermaphrodites.

In passing, it may be remarked, that repeated examination of all the sections of males made in 1884 revealed no traces of female organs.

Table 1. Males.

no.	number of sections	size	state of sexual organs	
1.	66	0.5 mm	ripe male elements, no eggs	(fig. 12).
2.	70	0.52 - - - - - -		(fig. 11).
3.	78	0.6 - - - - - -		
4.	79	0.66 - - - - - -		
5.	90	0.68 - - - - - -		
6.	97	0.73 - - - - - -		
7.	128	0.96 - - - - - -		(fig. 13).
8.	134	1 - - - - - -		
9.	151	1.13 - - - - - -		(fig. 15).

[1] Known as »males« by their position on hermaphrodite forms, as previously defined.

Table 2. Small forms from disc.

no.	number of sections	size	state of sexual organs
1.	93	0.7 mm	regular ovarial epithelium (figs. 7 and 8, fig. 10).
2.	94	0.7 -	very small eggs and regular ovarial epithelium.
3.	97	0.73 -	ovarial epithelium and small eggs (figs. 2 and 3).
4.	97	0.73 -	small eggs (fig. 1).
5.	100	0.75 -	well marked eggs (figs. 6 and 9).
6.	112	0.84 -	numerous very small eggs.
7.	138	1.03 -	large eggs.
8.	138	1.03 -	numerous large eggs.
9.	140	1.05 -	many large eggs and some in uterus.
10.	152	1.14 -	smaller eggs than preceding.
11.	160	1.2 -	small eggs, fairly numerous.
12.	168	1.26 -	many large eggs (figs. 4 and 5).

So far as the males are concerned, the result may be summarised thus: — always full of ripe spermatozoa and sperm mother-cells, and all traces of female cells absent. In all the forms of table 2, as in the males, numerous well-developed spermatozoa were present. This point will be referred to later on.

It may be assumed that we are justified in comparing the males nos. 4—7 (tab. 1) with the hermaphrodites nos. 1—9 (tab. 2). The extremes in both cases are of about equal dimensions, and each series contains a gradation of forms from those of about 0.576 mm in diameter to those of double that size.

It will be seen that undoubted eggs were found in all the hermaphrodites or disc-forms between these limits, the youngest and smallest individuals showing them in a very early phase of development. None the less, the ovarian nature of these cells was beyond question.

This being the case, one would, from NANSEN's standpoint, also expect to find some traces of ovaries in the males nos. 4—7. Not a single cell, which might have been identified as an egg-cell, could be detected in any of them, and the positions occupied by ovarian cells in the forms of the second table were here taken up by mother-

cells of spermatozoa (spermatogonia) or by developing spermatozoa themselves.

The appearances seen in the sections of the forms of tab. 2 revealed another fact, viz., that the hermaphrodites are also protandrous[1], a fact, which is true of many, if not of all, hermaphrodites.

Among the forms of tab. 2 not a single individual, which would *a priori*, from its position on the disc, have been regarded as probably hermaphrodite, turned out to be a male. In all, in addition to male organs, developing eggs could be detected.

It thus appears that on the most essential points both of NANSEN's contentions are negatived by the facts. The dwarf males are neither young protandrous hermaphrodites, nor do they contain the slightest trace of true female elements. Moreover, the places usually occupied by such female cells (i. e., as will presently be shown, along the dorsal or hæmal wall of the body-cavity) were filled by sperm-mother-cells, or by developing spermatozoa (figs. 7, 8, and 13).

NANSEN cites fig. 15 pl. 2 of his memoir in evidence of the presence of rudiments of ovaries in some complemental males, and says (6, p. 79): — »in branches of the uterus are situated some organs, similar to those in the hermaphrodites, and which are probably traces of ovaries« (comp. fig. 14).

Since then, in a paper to be cited subsequently, WHEELER (8) has shown that these deeply-staining organs of the hermaphrodites represent ovaries. He considers that these organs of NANSEN are the sole ovaries, a conclusion which is disputed on grounds of observation by PROUHO (7) and myself. Whilst there appears to be no doubt as to the ovarian nature of NANSEN's organs in the hermaphrodites, I must contest the correctness of NANSEN's view, which is, as will be seen anon, also supported by WHEELER, that they represent ovaries in the dwarf-males. In no true dorsicolous form have I been able to find any evidence in support of their ovarian character, and in all my numerous preparations of such individuals they have the appearance of testes.

NANSEN also adduces the presence of »oviducts« in the dwarf males as a further argument in favour of his view. This fact has,

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[1] For *Myzostoma* this was first established by VON GRAFF (Challenger Rep. Vol. 10 pag. 43). NANSEN on pag. 59 and elsewhere in his memoir has also expressed agreement with this view.

however, no bearings on the question, for it is only a hypothesis that they represent rudimentary oviducts in the male. It is even less of a presumption in favour of hermaphroditism, than the persistence of a trace of a Müllerian duct in the males of some Vertebrates. These ducts are ciliated, as stated by NANSEN (6 pag. 58, also pag. 59) and they open into the body-cavity.

They have since been described by myself as representing nephridia, a conclusion which has been confirmed by WHEELER, who has given a description of them in several species of *Myzostoma*. One can hardly conceive any other possibility than that they are the nephridia. Often they contain ova in the hermaphrodites, and as often spermatozoa or sperm-mother-cells. In the males they are well developed and ciliated. The part of the body, into which they open, is, as will be seen, a true cœlomic cavity. In the males their function can only be an excretory one.

The body-cavity and the development of the sexual organs.

Previous to the appearance of WHEELER's recent memoir a body-cavity had not been described in any of the 80—90 known species of *Myzostoma*. NANSEN and myself had, however, considered the space in which the sexual products ripen as probably the remains of a cœlom.

If exceedingly young individuals be taken for investigation — specimens which can just be seen with the naked eye — sections reveal the presence of a true body-cavity. The same fact can also be made out in many of the hermaphrodite forms of tab. 2.

The youngest individual examined measured, including the extended proboscis, about 0,2 mm. In section the ectoderm is a simple layer of cells, which has, even in earlier stages, secreted a fairly thick cuticle. Below lies the (at this stage) massive foundation of the ventral nerve-cord, and, to the right and left of this, the sacs of the setæ. In the centre is seen the wide alimentary tube, covered with a peritoneum. A continuation of this peritoneum lines the inner dorsal aspect of the body-wall. Above and lateral to the alimentary canal a space is seen, wich represents the body-cavity. As WHEELER has already noted, in individuals of this size the alimentary cæca are not yet formed.

Some of the forms comprised in the two tables show the presence of a body-cavity much more distinctly — at least on the hæmal

aspect of the body[1]. On the neural side the development of spermatozoa has progressed to such an extent — even in the youngest hermaphrodite — that all trace of the original peritoneal epithelium, as such, is lost. It has been almost, if not entirely, converted either into spermatozoa, or into cells of some of the intermediate stages of such formation.

The enormous development of the setal sacs, with their attached muscles and glands, etc., has also helped to destroy the simple character of the body-cavity on the neural aspect of the alimentary canal. But, on the other hand, it is possible in many sections to make out a regular epithelial lining of the body-cavity above or hæmal to the alimentary diverticula. In such sections as those figured in figs. 1, 2, and 4 the regular skin-epithelium is followed by the usual connective tissue and muscular sub-dermal layers, and these are bounded internally by the regular peritoneal epithelium already mentioned. This can be traced in favourable sections along the curve of the body, as far as the lateral margins of the under surface (figs. 5, 13).

Here and there a rather large egg-cell, projecting from the epithelium but forming one of its elements, may be noticed. In a series of sections of individuals of different sizes, such as those of tab. 2, it is not difficult to trace these undoubted egg-cells through all stages, from the youngest ones, hardly differing from the cells adjacent to them in the epithelium (figs. 2 and 7), to others, which, breaking loose from the latter, are thus set free to undergo their further development in the body-cavity itself (fig. 5) — a common occurrence among the Polychæta.

The appearances seen under the microscope support the conclusion, that in *Myzostoma* nearly the whole epithelial lining of the body-cavity is concerned in the production of sexual elements. In other words, this epithelium is a generative organ (Keimdrüse.)

In the smallest males examined the development of the sexual organs had proceeded at a much greater pace than in the hermaphrodites or disc-forms. Traces of the body-cavity were here difficult to detect, owing to the fact, that among the males much smaller individuals, than among the hermaphrodites, shewed the conversion of the cœlomic epithelium at various points of the hæmal aspect into sperm-mother-cells, or into still further stages of developing spermatozoa (figs. 11 and 12).

[1] Compare figs. 1—4, 6, and 7.

In both males and hermaphrodites, dorsicolous and disc-forms, the neural cœlomic epithelium is composed of the forerunners of male cells, and in the males the hæmal peritoneum is made up of similar cells. In the hermaphrodites, on the other hand, the latter portion of the cœlomic wall is almost entirely concerned in the production of egg-cells. A few cells may, however, give rise to spermatic elements (fig. 5).

On pag. 79 of his memoir NANSEN has summarised his objections to the view of the secondary or derived nature of the hermaphroditism of *M. glabrum*.

He writes: — »the diœcious species are the most parasitic forms, and if BEARD's view, that the Myzostomidæ have become hermaphrodites, because there is a tendency in parasitic life to produce hermaphroditism, is correct, it may, also, with some reason be concluded that the Myzostomida Cysticola, or most parasitic species, should especially be androgynous, but that is not the case; for most of these species are diœcious, whilst the most migratory ones, and consequently least parasitic forms, are especially hermaphrodites: and the little migratory species are, on the other hand, provided with dwarf males, which, according to BEARD's view, are more primitive than the hermaphrodites, and are remnants of a diœcious state. The most parasitic forms, and the little migratory species with dwarf males cannot be assumed to be the starting point of the migratory free-living species. The rudiments of testes visible in *M. cysticolum* are, to my mind, more probably remnants of an androgynous state than a budding development of male organs. If such rudiments, without male generative apertures, occur uniformly in all females, I cannot conceive how they can be a budding development, as they can have no opportunity of sexual function. Their regular occurrence cannot be accounted for solely by assuming a tendency in the ovaries to develop spermatozoa. The males of the diœcious species are smaller in relation to their females than the dwarf males are in relation to their hermaphrodites. If these males are about to become extinct, the contrary might be expected to be the case. The structure of the dwarf-males indicates, in one way or other, a relationship to the hermaphrodites. If the dwarf-males are more primitive than the hermaphrodites, I cannot account for the presence of oviducts. As above mentioned, I conclude that these oviducts must really be, either

remnants of hermaphroditism or the first development of female organs (in a young stage): the dwarf males are, consequently, only young hermaphrodites. I think it is indeed most probable that some hermaphrodites, at all events in their youth, perform exclusively a male function. Finally, if it is the case, as BEARD supposes, that the dwarf-males are primordial and the diœcious state the primary one, then the hermaphrodites must have been developed from males, and not from females as BEARD supposes«.

It may be well to take *seriatim* the statements made in the above summary. Our author creates artificial distinctions in the parasitism of the different species of *Myzostoma*. According to his conceptions the cystic forms are the most parasitic, those, like *M. cirriferum*, which wander freely about on the host, are least parasitic, while the fixed, but non-encysted, forms, like *M. glabrum*, occupy an intermediate position between the extremes of the parasitism. To my mind there is little or no difference in the degree of parasitism in all these cases. To whatever species of the genus it belongs, the individual *Myzostoma* probably spends its whole post-larval life on one individual host. It may be assumed that the parasitism was introduced for the good of the species, for its preservation. A fixed form, and especially an encysted one like *M. cysticolum*, it not so liable to destruction, as is a form, which can roam freely about within a circumscribed area. Individuals of *M. cirriferum* must always be in great danger of being either washed away or devoured by the host. The great abundance of *M. cirriferum* may be taken to be a provision against these dangers, but it is no doubt also due to the small size of the animal and its freedom of motion, for these two conditions admit of a much greater infection of one individual host, than do the corresponding conditions of life in *M. glabrum*. The objection that the least migratory forms cannot be assumed to have been the starting point of the migratory free-moving species is beside the point. It would only be relevant, if it were held, that the fixed and encysted forms resembled the ancestors of the free hermaphrodite species. We do not know what these ancestors were like, and all that is maintained is, that they must have been diœcious — that all original Myzostomidæ were once free non-parasitic forms is, of course, not open to question.

Regarding the rudiments of testes in *M. cysticolum*, as described by VON GRAFF, an assumption that they are a »budding development« is quite as justifiable as one to the contrary. Too much weight should

not be attached to either view, for so little is known of this species, that it is just possible that *M. cysticolum* may be a functional hermaphrodite with males.

True, von Graff could detect no male openings or male ducts in the supposed female of this species, but, judging by the figure on Pl. 13 of his monograph(4), it seems likely that he did not feel at liberty to make exhaustive use of the scanty material for an examination of this point. A recent study of his figures has not convinced me, that in this case male ducts were really absent, and it is, perhaps, not impossible that they were present as small nephridia. The question is, however, still an open one. Nansen maintains that the regular occurrence of these rudimentary testes in *M. cysticolum* cannot be accounted for solely by assuming a tendency in the ovaries to develop spermatozoa. But other cases are known, e. g. *Bufo*, *Cymothoe*, in which such a tendency is apparent, and in the hermaphrodite *M. glabrum* ovarian and testicular products may arise from neighbouring cells at first quite alike. It is urged that, if the males of the hermaphrodites were about to become extinct, the ratio of their size to that of the hermaphrodite, on which they sit, ought to be smaller than the corresponding ratio between the male and female of the diœcious species. The size of the males in the former has possibly little to do with this point. Their persistence or extinction depends primarily on their capacity to fulfil their functions. In this argument we again meet the assumption that the encysted forms are more parasitic than the fixed forms[1], along with the supposition that the absolute size of the male must play the same part in both cases.

The minute males of the encysted forms suffice, and, therefore, they are preserved.

That in many parallel cases the dwarf-males find it difficult or impossible to fulfil their appointed duties is proved by their condition in such groups as the Rotifera, where they are verging on extinction. The interesting observations of Weismann & Ischikawa[2] on the male

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[1] The parasitism is exactly the same in both, for the cyst is not formed by the parasite, and the question whether or not a cyst be formed probably depends on the position where the parasite affixes itself. A cyst or several around the mouth of the host would afford protection against the parasite at the cost of self-starvation.

[2] A. Weismann & C. Ischikawa, Weitere Untersuchungen zum Zahlengesetz der Richtungskörper. in: Z. Jahrb. Abth. Morph. 3. Bd. 1888 pag. 579.

of *Artemia* form a case in point, for here the male was utterly unable to copulate with the female.

Regarding the nature of the »oviducts« in the male NANSEN's argument might have validity, if an oviduct were always something *sui generis* and not usually a derivative of some other structure. Elsewhere reasons have been given for a belief that the »male oviducts« are in reality functional nephridia. This discovery, published in the Z. Anzeiger 1894, has been independently arrived at by W. M. WHEELER.

Agreement may be expressed with NANSEN in the opinion that some hermaphrodites in their youth perform exclusively male sexual functions. Indeed, this is a corollary to the view here taken of the origin of hermaphroditism, for only the germinal cells of a young individual are likely to possess the property of becoming converted into sexual products of the opposite sex.

NANSEN'S final contention that, if the dwarf-males were primordial and the diœcious state the original one, the hermaphrodites must have arisen from males and not from females, is negatived by the co-existence of true males. If males were absent, or if there were males, females, and hermaphrodites within the limits of the species *M. glabrum*, the argument might be sustained. As matters are, it is only another way of expressing inability to account for the presence of »oviducts« in the male. As we have seen, this is not at all a difficulty.

It is undoubtedly true, as NANSEN insists, that the questions involved in the origin and meaning of hermaphroditism are not yet solved.

The problem of the relationship, which may subsist between hermaphroditism and parthenogenesis, is one still awaiting solution. Early in 1884 I was able to fertilise[1] the eggs of a hermaphrodite *M. glabrum* with spermatozoa from the testes of the same individual. The larvæ produced developed quite normally for five days, when the usual fate of larvæ obtained in the ordinary way, i. e. by cross-fertilisation, overtook them.

From these experiments and from other considerations there is, as BOVERI and others have insisted, a strong temptation to regard

[1] These experiments were carried out with all necessary precautions, such as the use of clean dishes, filtered sea-water, etc. They have more recently been independently carried out by WHEELER with similar results.

parthenogenesis as a disguised hermaphroditism, in which each egg produces the equivalent of a spermatozoon for itself (in the second polar body) and in which self-impregnation occurs.

Boveri, Hertwig and others have in recent years thrown a flood of new light over this matter in their investigations into the egg- and sperm-formation in the Nematoda.

In this connection the Myzostomidæ form an interesting group for investigation; for in them, as in some other hermaphrodites, of two apparently similar cells, lying side by side, one may become an egg-cell, while the other may give rise to spermatozoa.

Boveri and Hertwig have shown that there is no essential morphological difference between the egg-mother-cell and the sperm-mother-cell, and thus, indirectly, they have helped to consolidate the view that hermaphroditism may arise as a secondary condition, in what were primarily diœcious forms. And theoretical difficulties in the way of the conclusion, that the hermaphroditism of *Myzostoma* may be a secondary state, are thus largely relieved. If the hermaphroditism were primitive in this case, two things would be difficult of explanation. The first of these would be the actual existence of true males, and the second their small size as compared with the hermaphrodites.

It is impossible to conceive that any natural cause should lead to the evolution of dwarf-males from hermaphrodites. An evolution of this sort would be meaningless in such cases as the Cirripedia, *Artemia*, or the Rotatoria, where it would ultimately end in a form unfitted for the struggle for existence, or even incapable of preforming sexual functions.

It is significant to note the comparative frequency of the association of dwarf-males and hermaphrodites, and of the occurrence of degeneration in such males. And, while it is rare — even impossible in the animal kingdom — to find males, hermaphrodites and females within the limits of a single species, the co-existence of true males, usually dwarfed, with hermaphrodites is not at all infrequent. With the doubtful exception of the Trematoda[1] parthenogenesis and hermaphroditism would appear never to obtain together within the limits of a single species. The one would apparently exclude the other;

[1] The recent work of W. R. Coe (Z. Jahrb. Abth. Morph. 9. Bd. p. 561) does not tend to verify the existence of parthenogenesis here.

although, from the standpoint of recent research, there is, in a morphological sense, little difference between them.

Granted that the number four be the typical one for the products of both sperm- and egg-mother-cells, three of these products get lost in any hermaphrodite fertilisation (in the form of the second polar body and the products of division of the first polar body), while only two are cast away in a parthenogenetic egg-cell. In addition, products of two mother-cells are required for the production of one fertilised egg of an hermaphrodite, whereas in parthenogenesis the same two cells would give rise to two (self-) fertilised eggs. There is, thus, in parthenogenesis a greater economy, but the advantages of cross-fertilisation are excluded. There must, undoubtedly, be some law, determining which of the two states, the parthenogenetic or the hermaphrodite, shall be the one adopted, if a departure from the diœcious condition become desirable.

Parthenogenesis endangers the continued existence of the male, its continuity, to a much greater extent than does hermaphroditism.

Years ago Weismann demonstrated that in certain cases of parthenogenesis the appearance of males tends to become cyclical, and that the interval between any two appearances tends to lengthen, till ultimately, as in *Artemia*, the cycle becomes practically infinite.

The cycle would appear to be introduced in parthenogenesis at an early period (Weismann), while in hermaphroditism it probably only occurs long after the state has become firmly established. If the view be accepted, that cross-fertilisation is the great factor in producing variations within a species, then in any given case continued existence is the less endangered by the introduction of parthenogenesis in the proportion that the species has become stable, or is in a condition of stable equilibrium. If unstable, hermaphroditism is the more favourable arrangement of the two, for it diminishes the variability in no degree, unless it be a self-impregnating hermaphroditism, a condition rarely or never actually met with. The case of *Myzostoma* typically shews, that great variability may co-exist with hermaphroditism, for within the limits of the genus the number of species with closely allied characters and yet differing from one another in some respects is very great[1].

In Wheeler's memoir (8) on the sexual phases of *Myzostoma*, to which reference has already been made, besides the description

[1] There is also in *M. glabrum* a great variation in the coloration.

of four new species, the sexual conditions are considered for several species, and it is concluded that the hermaphroditism of the genus is protandrous in nature. WHEELER on pag. 277 speaks of this result as affording »a simpler — and I trust also — a more satisfactory explanation of the sexual peculiarities of *Myzostoma*, than has been given by preceding authors«.

For one species (*M. pulvinar*) the validity of this interpretation is disputed, as will be seen anon, by PROUHO (7), and my researches lead me to deny it for another (*M. glabrum*). The explanation offered by WHEELER is, as a matter of fact, identical with that previously adopted by NANSEN, who was restrained from carrying it to the extremes, which have seemed possible to the former writer, by the hard facts of the anatomy of the complemental males (or, as PROUHO aptly terms them, the dorsicolous forms), and by his recognition of the diœcious characters of some of the cysticolous species.

As WHEELER has been able to prove that in certain cases (for it has not, as will be apparent later, been shown to be invariably so) NANSEN's »problematical organs« are ovarian in character, he has obtained a groundwork of fact, which might be of considerable importance, if it really possessed all the bearings he ascribes to it. NANSEN's organs were viewed by their discoverer as primordial ovaries, and, with the modification of this phrase to primordial or original sexual organs, I should now like to express agreement with him.

Before proceding to an examination of the bearings of the results of my own studies of *M. glabrum* on WHEELER's conclusions, two other points, among those treated of by him, may be referred to. These are the systematic position of the genus and the supposed sensory nature of the structures identified by NANSEN as glands.

Although since 1884 VON GRAFF may never have openly declared his position towards the view of the Chætopod relationships of the genus — as established in my dissertation and as now adopted by WHEELER — he has recognised in correspondence with myself that his own former opinion would require modification, and by implication he has adopted their Chætopod affinities in his monograph on the genus *Spinther*, as WHEELER himself notes. It is necessary to call attention to this, for on pag. 269 the latter author writes: — »two of the principal authorities on the Myzostomidæ, VON GRAFF and NANSEN, have never accepted this view« (of their Chætopod affinities).

It may also be remarked that, had von Graff, whom we rightly look upon as the chief authority on the group, felt bound to offer any objections, he would probably have done so in his Challenger Supplement (1887).

From Wheeler's introductory statements to his chapter on the relations of the Myzostomidæ to the Chætopod Annelids the reader might at first draw the inference, that the author was about to assign the genus to a different position in the animal scale, whereas in the sequel my former conclusions are only confirmed and made stronger by him. Throughout his work his dissent from the results of previous observers is insisted upon with such emphasis, and often in such strong and unusual language, that the more numerous occasions, where he finds himself in a position to confirm this or that previous discovery are apt to be lost sight of. But the points of agreement are far more numerous than those of difference.

Among other things an important advance would be, should it turn out to be correct, Wheeler's attempt to identify the segmental sacs with lateral sense organs of the Capitellidæ. Unfortunately, something more is wanting than the discovery of the passage of a nerve to each of these structures.

Glands are very often supplied by nerves, and, as it is probably unnecessary to insist, the essence of a sense-organ is not founded on the presence of a nerve alone, but also on the existence of a group of sensory cells within the structure in question. None such have revealed themselves to Wheeler or to any other previous observer, and here, once more, it appears to me, that Nansen's view had the facts on its side.

Every worker, or almost every worker, undergoes the experience of seeing some or other of his results set aside by succeeding investigators. As Weismann once remarked, these latter should never forget, that they stand, as it were, on their predecessors' shoulders.

A dissertation is not infallible — even to its author — ten years after it was written; and, when the facts of a thesis come to be revised by an experienced worker, with all the newer methods and the experiences of his predecessors at his disposal, and with an extensive knowledge of how to set about the work, they as often as not undergo considerable modification.

And now, in connection with the facts recorded in preceding pages, to inquire into Wheeler's conclusions as to the hermaphroditism of *Myzostoma*, or, to be more accurate, as to that of *M. glabrum*.

For, as a matter of fact, I feel no direct concern with any of those species of the genus, regarding which I am unable to criticise WHEELER's results from my own work, from that of others, or because of assumptions of his, whose justification can be challenged. Thus, I have nothing to say concerning *M. cirriferum* beyond accepted matters of fact. I feel under no obligation to investigate this form, for, as PROUHO shrewdly observes, there exists no reason *a priori* for supposing that what obtains for one species of the genus will hold for all. WHEELER, it may be observed, appears to overlook one difference in the life-history of *M. cirriferum* and that of *M. glabrum*, that in the former what he believes to be the young forms are never dorsicolous like certain small ones in the latter[1].

WHEELER's arguments regarding the subsequent hermaphrodite nature of the originally male dorsicolous forms in *M. glabrum* depend primarily on two premisses.

These are 1) the passage or migration of the dorsicolous forms, at a certain phase, from the back of the hermaphrodite to the disc; 2) the ovarian nature of NANSEN's organs.

One seeks in vain for direct proof of the first in his memoir. It is merely inferred, and from the following. WHEELER describes in all ten specimens of *M. glabrum*, ranging in size from 0.175 mm to 4 mm.

Of these six are dorsicolous, i. e., what I have termed males, while four are from the disc. The transformation takes place, according to him, when the animal is about 1 mm long. From the largest of the dorsicolous forms he figures in fig. 56 what is apparently an egg, lying on one of the »ovaries«. From my own examination of dorsicolous specimens it can only be stated that search has been long and laboriously made for any such appearance. One swallow does not make a summer, and the picture of one egg, even if there be no mistake as to the dorsicolous nature of the form, from which it was taken, does not make an hermaphrodite.

WHEELER's conclusion of the transformation of the dorsicolous form into the hermaphrodite is then a pure inference, and it is now necessary to examine the grounds, upon which he has been led to make it. In the first place, and above all else, comes the evidence

[1] It is true, that SEMPER described one such case, but as this has not been confirmed by anyone else, and not by WHEELER, it is very probable that by a slip of the pen SEMPER wrote *cirriferum* for *glabrum*.

afforded by the presence of »ovaries« in the dorsicolous forms. Of the existence of these structures there cannot be the slightest doubt — as to their interpretation, that is another matter.

If it can be shown that these structures, NANSEN's organs, are invariably ovarian in nature in the dorsicolous forms, as well as in the hermaphrodites, it, of course, follows that the dorsicolous forms of *M. glabrum* are not complemental males.

I have closely examined these structures in my own dorsicolous specimens, and can find no particle of evidence to show that they are ovaries. From the minute structure of the component cells it appears to me to be far more likely that they represent the original testes, for the cells bear a close resemblance to, amounting to identity with, the groups of sperm-mother-cells, »scattered« about in various places. But WHEELER brings forward what, though far too vaguely stated for its importance, appears to be positive evidence of the ovarian nature of NANSEN's organs in dorsicolous forms. In fig. 56 he figures a large egg, lying on the outer side of one of these structures, and on pag. 241 he remarks: — »specimens in this stage (6a, 1 mm long) are found, like those of the five preceding stages, attached to the backs of older individuals..... In some of the specimens a few of the oocytes have begun their growth while still in the ovary (compare pl. 12, fig. 56*d*)«.

In this passage and in the description of the plate it is not distinctly stated, that this figure is taken from a true dorsicolous specimen of *M. glabrum*. The reader is left to infer that this was really the case, and the author leaves a loop-hole to doubt, where the observation, which of all others would decide the matter, is concerned. A precise statement as to the place, from which the specimen was taken, as to the number of such apparently hermaphrodite dorsicolous forms in the author's possession, and as to the number of obvious eggs in each of these, might have settled the point for good. I would submit that WHEELER may have been mistaken in referring this figure to a true dorsicolous specimen of *M. glabrum*. It may be suspected that it was taken from the side wall of a hermaphrodite, and, as I recognised in 1884, such specimens are never true males, but always contain eggs, as well as spermatozoa. From the size of the egg, taken in conjunction with what I have said in preceding pages as to the development of eggs in small disc-forms of 0.75 mm and under, it is probable that this specimen contained a considerable number of eggs, and it, and any

fellows like it, must, in my humble opinion, be looked upon as disc-forms, which may have chanced to take up a position on the side-wall of an hermaphrodite. After all my labour in searching for eggs in true dorsicolous forms[1], labour, which has invariably resulted in negative finds regarding the presence of eggs, I feel entitled to ask, that a positive find, because decisive if clear, should be given in such a way, that there can be no doubt as to the sort of specimen, to which it relates.

From his description and figures it is abundantly evident that WHEELER has never seen the smallest true eggs in the disc-forms, as described by PROUHO and myself, and as figured here in pl. 10 figs. 1, 2, etc.

He even denies their existence and origin in such places as shown beyond doubt in these figures. Moreover, and this is important, he attaches no particular value to the position taken up by a small form on the back of a large hermaphrodite, although it is for the true males a very characteristic one, and is never adopted by a young hermaphrodite.

There is, and this has escaped WHEELER, a marked difference in appearance in section and even in the contour of the body[2] between young disc-forms and true dorsicolous specimens of the same size, and this is such that, once it has been recognised, it is made out with ease in specimens of *M. glabrum*, whose seat in life was unknown. As elsewhere pointed out, the cells of the dorsal peritoneum of the males are converted into spermatozoa, whereas in the hermaphrodites the cells of the same region yield mainly eggs (compare figs. 5 and 13).

WHEELER makes no reference to having met with dorsicolous forms of more than 1 mm in length. The table on pag. 295 contains one, which, even when embedded, measured 1.13 mm, and among my old sections there are several[3], which were certainly 1 mm and upwards in length, and none of these contain any ova at all. Every section has been repeatedly examined, and the result has always

[1] Dorsicolous as defined on the 4th page of my note in the Z. Anzeiger 17. Jahrg. 1894 pag. 400.

[2] Flattened in young hermaphrodites and more convex in the dorsal region in the males.

[3] The sizes of these were not noted, or the notes no longer exist, but at that time (1883—84) the largest dorsicolous specimens to be found were picked out, in order to test as far as possible their sexual nature.

been negative. Cells, like those of fig. 6, are frequently met with, but it is not difficult to determine that such cells are male in character — sperm-mother-cells of the first generation.

It has been shown in preceding pages, that the first eggs to arise appear as modified cells of the peritoneum (figs. 1, 2, etc.), and that their ovarian characters can invariably be made out in stages (of young disc-forms) far smaller than that of 1 mm, on which in his description WHEELER lays stress (pag. 241). In the general part (pag. 265) he is less inclined to emphasise the point, and leaves the exact period, at which the supposed transformation occurs, an open question.

We are told that the dorsicolous forms migrate to the disc at a stage, when they are somewhere about 1 mm[1], and that either before they do this or just afterwards they become hermaphrodite. In a case of this kind, where fresh material is not available, the only course open to another observer, anxious to test the point, is to take a series of dorsicolous forms, and compare them with a series of small forms from the disc[2].

WHEELER looks upon this procedure as an »error of method and one in common sense« and, none the less, the one lacking in the latter quality is in reality the same as his own!

As to the method, all the forms studied had been killed in exactly the same way; they were all embedded etc. at the same time, and were, in fact, from beginning to end, treated exactly alike. As there is, so far as I can see, no evidence of shrinkage in the specimens, and as they were all killed in the same way, it is not too great an assumption that any shrinkage was fairly even throughout the lot. If one had shrunk, then, probably, the others had been diminished in a corresponding ratio. But allowing some shrinkage[3] — and undoubtedly one must — WHEELER must apply it to all, and

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[1] It is nowhere stated whether the measurements are of living, preserved, or embedded specimens.

[2] This is really the method adopted by WHEELER, and his results differ from mine, because probably his examples were not numerous enough, and thus he failed to obtain disc-specimens smaller, and dorsicolous forms larger than 1 mm.

[3] Experiments recently made in another connection on the shrinkage of Elasmobranch embryos in various fluids and various strengths of alcohol have shown that by the time the specimens are in 90% alcohol the percentage of shrinkage is practically a constant quantity for embryos under 37 mm.

not merely to those in the one table. If the hermaphrodite forms of table 1 had shrunk, then the male forms must also receive their allowance. And thus no. 7 of table 2 would far exceed the size[1], at which, according to WHEELER, the transformation takes place. WHEELER (pag. 265) asks what the overlapping shown in the two tables on pag. 295, 296 has to do with the question at issue. Obviously, it reveals, that forms on the disc smaller than the true dorsicolous ones are already completely hermaphrodite, while the latter are purely male. It also establishes that, even if WHEELER be right regarding the transformation, the period varies very considerably, and in such a way that, while an individual of 0.7 mm may be already completely hermaphrodite, another of 1.13 mm may be male. But if one deny his right to make an assumption of change of position from back to disc at a certain stage, it proves more than this. On pagg. 239—242 we are given a series of forms, starting with functional males of 0.5 mm in length and ending with hermaphrodites of 1 mm[2]. The series commences with dorsicolous forms and ends with disc-individuals, and it is presumably intended, among other things, to convince the reader of the justice of his assumption that the dorsicolous forms leave the backs of the individual they are seated upon, and, taking to the disc, become hermaphrodite[3]. The tables show that the course of events is not that indicated by WHEELER. Variation may be allowed, but not the great amount demanded by the author, who asks, what he did not himself find, variation in the size, at which the specimens migrate to the disc. He is himself precise in his statements of size (living, preserved, or embedded?) and asks no variation, until he comes to deal with my unwelcome results. Thus his argument about absurdity etc. on pag. 265 is really directed against himself.

WHEELER would appear never to have seen smaller disc-forms than those of 1 mm or, at any rate, never to have studied such; yet these are at least as common as the dorsicolous forms. Had he examined such forms as nos. 1—5 of table 2 he would have seen that disc-forms of 0.75 mm are hermaphrodite, and that the earliest

[1] VON GRAFF states that he has seen dorsicolous forms of 1.5 mm.

[2] WHEELER's series begins below this size and ends above it, but the other forms have no bearings on the argument.

[3] If the dorsicolous forms are invariably young hermaphrodites it is not easy to perceive why they always act in this way, and why some of them do not retain their dorsicolous position after becoming hermaphrodites.

developed eggs arise from cells of the dorsal peritoneum and not from Nansen's organs. As apparently he has never examined forms from the disc under 1 mm the marked difference in outward shape and in section between dorsicolous and disc-forms of 1 mm and under has escaped him.

The transformation is assigned to a definite stage, that of 1 mm, and it is only afterwards that, with the facts of my two small tables before him, he is forced to make a new assumption, that of considerable latitude in the attainment of »sexual maturity«. But what does he understand by sexual maturity? On pag. 265, where the matter is discussed, there is no definition of it given; but, from the drift of the argument, it is obvious, that in this case Wheeler does not consider the individual to be sexually mature, until it has developed ovaries, as well as testes.

There would seem, however, to be no escape from the conclusion, that an individual *M. glabrum* is sexually mature, when it contains ripe spermatozoa, and this is almost certainly the case in all specimens over 0.5 mm in length.

I am not aware, that I have ever argued the question, as to the period, when »sexual maturity« occurs in *M. glabrum* — all I have dealt with has been the trifling problem of the sizes of specimens in which eggs as well as ripe spermatozoa were first to be found.

Wheeler's results give him this size as about 1 mm, and the only case figured by him may be challenged, among other grounds, on that, that the egg depicted is far too big to have just come into existence. My table 2 thus casts considerable doubt on the correctness of his conclusion. Does the author ask us to believe, that an egg of that size has just escaped from Nansen's ovary? Its actual diameter is rather more than 0.028 mm, whereas the largest eggs from an incipient hermaphrodite from the disc (such as those shown in fig. 1) measure only 0.006 mm in diameter!

Nothing is further from my mind, than any idea of maintaining the male nature of the dorsicolous forms, if there be any evidence directly contradicting this. The whole matter appears to me so trifling, that, having far more congenial and important work in hand, I should not feel called upon to discuss it, were it not, that observations of mine, of whose correctness new search has again and again convinced me, had been declared baseless on grounds of the most fallacious character.

Nor is entry into the field of controversy rendered more inviting

by the echoes of language, recalling rather the political platform than the scientific arena.

Before examining the remainder of WHEELER's ten paragraphs directed against my views, it may be urged, that WHEELER has, as yet, produced no evidence, clear and above suspicion, showing a) that NANSEN's organs in the dorsicolous forms of *M. glabrum* are ovaries, and not, as I maintain, testes, and b) that the dorsicolous forms become hermaphrodite and migrate to the disc.

On pag. 238 WHEELER writes: — »BEARD's observations on these young, which it pleases him to call ‚complemental males', will be considered in the sequel«; and on pag. 260: — »in BEARD's paper the cysticolous *Myzostoma inflator* and *M. murrayi* are confidently put down as ‚perfectly unisexual', an expression, which should be compared with v. GRAFF's rather guarded remarks on these species in the paper, to which BEARD evidently refers«.

The personal flavour of the former passage may be, perhaps, excused by its mildness as compared with other expressions employed in the work, which I must decline quoting.

During my stay in Naples in 1883—84 the sexual characters of the dorsicolous forms were tested by every means in my power. As no particle of evidence to the contrary could be found, it was finally concluded, that they were true complemental males (in DARWIN's sense) which remained male all their lives. Then VON GRAFF's notice of the two diœcious cysticolous forms arrived, and confirmed me in my conclusion. Even now repeated study of VON GRAFF's paper(3) does not enable me to find VON GRAFF's »rather guarded remarks« referred to, but not quoted by, WHEELER. But one does meet with — and this was also there in 1884 — a diagnostic table (pag. 126) of 22 species of *Myzostoma*, in which *M. cysticolum*, *M. inflator*, and *M. murrayi* are grouped together as »getrennt geschlechtliche Myzostomen, ohne Saugnäpfe, paarweise in Cysten ihrer Wirthe lebend«.

And on pag. 10 of his Challenger Report v. GRAFF writes: — »the suggestion made by VON WILLEMOES-SUHM, that some Myzostomida were in all probability diœcious, has been amply verified by my investigations« etc. And again, on pag. 11, in the section on the sexual organisation of the Myzostomida cysticola he remarks: — »I am able to state, that ..... each individual is either male or female, and that in addition the two sexes are unlike in appearance, the female being usually 50—100 times as large as the male«. These

passages may, I think, be taken as completely justifying an acceptation of the »perfectly unisexual«[1] or diœcious nature of *M. inflator* and *M. murrayi*, in other words, of the presence of purely diœcious species within the genus, and of a conclusion as to the existence of what it »pleases« me to call »complemental« or dwarf males.

When I established the existence of complemental males[2] in *M. glabrum* — as the facts forced me, not as it »pleased« me to do — this action was taken on two grounds. From my investigations it invariably resulted that these were true males, and they were always found to occupy a typical position upon and near the anterior end of the hermaphrodite. Anything found elsewhere was never a true dorsicole, and the two characters must be taken together in any attempt to overturn the conclusion.

I hold, until the contrary has been proved, that the specimen of fig. 56 was, in all probability, not a true dorsicole, but a young disc-form, which, in early life, had chanced to attach itself to the side wall of a larger hermaphrodite.

As to paragraph 1 (pag. 263) I have never felt myself under the least obligation to investigate *M. cirriferum*, for I have never made or desired to make any new statements about it. If dorsicolous forms had occurred in this species, it would not have been »quietly ignored«. There is no reason for supposing that the sexual conditions must of necessity be the same in both species, for among closely allied species both the hermaphrodite and diœcious states may obtain (e. g. *Polygordius*). And does not Wheeler himself (pag. 234) state, that »*M. cirriferum* is virtually hermaphrodite from the beginning of its sexual development«?

In paragraph 2 (pag. 264) it is with justice urged, that it has never been shown, that the dorsicolous forms do not grow beyond the stages found by me. But as little has it been proved that they do

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[1] This phrase is, perhaps, not a very happy one, but it has the advantage of having been used by Darwin in his Monograph on the Cirripedia. There, as is well known, Darwin discovered what he termed »complemental males«, regarding the original sexual condition of the group as diœcious. More recently Hoek has endeavoured (Challenger Reports Vol. 10) to establish a protandrous hermaphroditism for the Cirripedia, to my mind with little success. But it never occurred to the Dutch author to use such expressions as that it »pleases« Darwin to call certain things complemental males. Fortunately, there are zoologists, who can differ from their predecessors without using offensive phrases.

[2] The dorsicolous forms of Prouho (7).

grow to a larger size and become hermaphrodites! In the absence of direct proof on either side, the problem must be solved in the only way open, i. e., by the results of an examination of a number of the largest specimens obtainable. This is what from the start I have conscientiously endeavoured to carry out.

But »all the characters, in which the so-called complemental males of *M. glabrum*[1] ..... differ from the hermaphrodites« are emphatically not »simply the characters of younger individuals« etc.

The dorsicolous forms, owing to the immense development of male organs, are much plumper externally than disc-forms of like size, and, moreover, they have the dorsal peritoneum converted into sperm-mother-cells in those parts, which in hermaphrodites give rise to eggs. (Vide figs. 11, 12, 13.)

Paragraph 4 was previously considered. As to paragraph 5, I can assure WHEELER, that it is not correct to say, that »BEARD has spent no time in looking for those hermaphrodites, which have fewer than 93 sections«. I possess one disc-form, which is as small as WHEELER's smallest dorsicolous specimen, i. e. rather under 0,2 mm; but as sexual organs are undeveloped, I have not used it. That the other stages are wanting in my series is explained by the circumstance, that I never searched for them in Naples, and, later on, had to be content with the material previously collected.

But I fail to see what new facts they could have revealed; for Nos. 1—4 of table 2 (disc-forms) whose sizes are from 0.7 to 0.73 mm show what must be the very earliest stages of female organs, or rather, of eggs (figs. 1, 2 and 3). That in earlier stages the disc-forms are functionally male is admitted, but it has no bearings on the question at issue. Certainly, as WHEELER states, the hermaphrodites of sizes smaller than 0.73 mm are in the protandric state, but not as dorsicolous forms on the larger specimens.

I confess it is difficult to understand the drift of the following. WHEELER remarks (pag. 266) with reference to my table (in 2) showing that the hermaphrodites are far more abundant than the males, »if this be the case — and again I do not doubt the fact — we should

[1] I have omitted here »and allied species«, not feeling directly concerned with these, but it may be noted that WHEELER himself seems to »quietly ignore« VON GRAFF's statement, that in the eysticolous forms »the two sexes are unlike in appearance, the female being usually 50—100 times as large as the male«.

expect to find at least as many hermaphrodites as males among the stages of 66—93 sections«.

Why this should be so, is a complete puzzle. The stages of 66—93 sections were dorsicolous forms from hermaphrodites, and the picking of these had nothing to do with the making up of the table, showing the relative occurrence of hermaphrodite and dorsicolous forms[1]. Perhaps, it is supposed, that all the small hermaphrodites found were used and sectioned, but this was not the case. Whilst all the largest males were taken, only samples of the disc-forms were made use of, but such as formed a continuous series. I believe I have still several very small hermaphrodites, i. e. under 1 mm, unsectioned. If anyone believe that he can prove these disc-forms to be pure males, in which eggs are absent, as they ought to be on WHEELER's view, he is quite welcome to them.

I think it has been shown by my former table of relative occurrences of the two forms — and all my experiences confirm this result — that the dorsicolous forms occur most frequently, when only one large disc-individual is present, that they are very rarely met with where several large disc-forms infest one individual, and that, at a very favourable estimate, there are not more than 10 dorsicolous forms to every 50 large disc-specimens, i. e. hermaphrodites.

If the dorsicolous forms were merely young hermaphrodites, one would expect, that they would be at least as numerous as these, for are not young forms of animals usually more numerous than grown-up individuals? This argument is not effected by WHEELER's assumption — for it is nothing but a supposition — that the hermaphrodites live a long time, or by that relating to the destruction of the earliest stages. When an individual becomes dorsicolous it is far beyond the earliest and critical stages, and is in a position of comparative security.

Paragraph 6 relates to the rare occurrence of forms on the side-wall of a hermaphrodite. I have already discussed this point (pag. 309), and would only add, that the relatively small area around the mouth available on one *Comatula* for fixation of the parasites renders such an act on the part of future hermaphrodites not unlikely.

I have no recollection of ever having observed this phenomenon, where only one large hermaphrodite occupied the disc, and it is, as the published table shows, in such cases, that the dorsicolous forms

[1] This table was really made 10 years earlier in Naples.

are most numerous. The occurrence was only observed twice or thrice in several hundred *Comatula*, and it is very curious, that, if the dorsicolous forms can move about at will, as Wheeler asserts (pag. 266 foot-note), these two or three specimens should have turned out to be hermaphrodite, while all the other true dorsicolous specimens were pure males.

It would be of interest to learn, upon what observations Wheeler bases his conclusion, that the dorsicolous forms can shift their position. Is it, again, an assumption rendered necessary under his hypothetical scheme of the life-history of the animal? If it be based on observation, its importance, surely, entitles it to a better position than in a small foot-note of some two lines!

It cannot be denied that these forms do alter their position, but all my experiences of them at Naples convinced me that, once seated, they remain in one position.

Experiments were made in 1884 to test this very point. Comatulæ, infested with large hermaphrodites bearing dorsicolous forms, were kept alive for six weeks and longer and were examined from time to time. Never once was the slightest evidence of change of position noticed.

But this fixity of position is rendered far more certain by another circumstance, which would appear to have escaped Wheeler's notice. The dorsicolous forms insert their hooked setæ deeply into the tissues of the hermaphrodite, and, whereas the latter can be removed from its host with but slight damage, or none, to these setae, the dorsicolous forms are so firmly affixed to the hermaphrodites, that the two can only be separated with loss of many at least of the setæ of the former.

On pag. 267 Wheeler comments on the difficulty, which the young may be supposed to experience in first fixing themselves to the arms or disc of a *Comatula*, and recognises in the dorsal integument of a hermaphrodite a place of attachment easier of attainment and favourable for respiratory and nutritive purposes.

It has to be proved that the back of a hermaphrodite is softer than the disc of a *Comatula*, and, if there be the difference and advantages claimed by Wheeler, it is enigmatical why the dorsicolous forms are so rare, why the occurrence of two such on one hermaphrodite was only encountered by me once, and, in short, why the backs of the hermaphrodites do not bristle with such »young« individuals.

Paragraph 7 (pag. 267). As to NANSEN's organs, it may be conceded, that no reasons would appear to exist for terming them rudimentary. They are probably the original sexual organs, which existed prior to the adoption of the parasitic mode of life. They still function, but not as the sole sexual organs. In the hermaphrodites they represent ovaries, in the males testes. With the adoption of the parasitic mode of life, greater demands were made on the reproductive powers, and the sexual organs were reinforced by the conversion[1] of other parts, almost the whole, of the peritoneum to reproductive purposes for the production of eggs and spermatozoa[2]. No-one denies that sperm-cells arise here and there from cells of the peritoneum (comp. fig. 13), and all investigators of *Myzostoma*, with the sole exception of WHEELER, agree, that eggs also have a like origin (comp. figs. 2, 6, 10, etc.).

This is abundantly demonstrated in the present writing, and PROUHO (7) has, in opposition to WHEELER's conclusions, stated results identical with mine.

Paragraph 8 (pag. 268). With reference to the statement, quoted from my paper by WHEELER, to the effect, that »many of the extreme cysticolous forms have been shown to be diœcious«, while I hold this to be correct — for nothing has been proved regarding their sexual characters beyond that they are diœcious — it may be granted, that some of them may turn out to be more or less hermaphrodite. But, at the same time, the right must be denied to WHEELER, to make the assumption in the present state of our knowledge, that they, or any of those hitherto regarded as diœcious, are protandric hermaphrodites[3]. Argument from analogy, which

[1] Or better, perhaps, by the extension of sexual cells into these.

[2] It must be noted that here, as shown by PELSENEER to have been the case in certain Mollusca, the females have been converted into hermaphrodites, and thus the persistence of the original ovary as an ovary is explicable.

[3] In a foot-note on pag. 259 WHEELER indicates how in accordance with the conditions created by his conception of the domestic economy of the Myzostomidæ in general the association of a larger and smaller individual — respectively »senior« and »junior« according to him — in a cyst comes about. He writes: — »I believe that, in the case of the cysticolous species, the gall must be formed by a single individual, and that later a young Myzostome, when it abandons its pelagic trochophore stage, must enter through the aperture of the gall, and settle down to a quiet life with the senior individual. The latter probably dies at the end of its female stage and, undergoing decomposition, may perhaps serve as food [!] for its still vigorous junior partner. This one in turn may there upon become the senior partner of another young Myzostome,

Wheeler in his paragraph 10 refuses to allow me, cannot here with safety be employed, for it breaks down entirely, when *M. pulvinar* is brought into the discussion. And this brings us to the remaining paragraphs (9 and 10), in which Wheeler (pag. 268—269), very briefly, refers to this species. In a foot-note on pag. 289 he says regarding it: — »*M. pulvinar* is certainly peculiar in exhibiting two well-marked periods of sexual maturity during its life-time«. Wheeler believes, that here also the small males become converted into — not hermaphrodites this time but — large females! And with at least one such »peculiar« exception in the genus we are asked to acknowledge in Wheeler's views of the protandric hermaphroditism of *Myzostoma* »a simpler — and I trust also a more satisfactory explanation of the sexual peculiarities of *Myzostoma*, than has been given by preceding authors«!

The description, given in pag. 254, and intended to prove, that the males of *M. pulvinar* become females, carries no conviction, for it is not shown, that the cells depicted in fig. 49 actually become eggs. But no remarks of mine are necessary; for, apparently since Wheeler's manuscript left his hands, Prouho (7) has directly challenged his conclusions, and writes. — »je possède des coupes d'une jeune femelle de *M. pulvinar* de la dimension d'un mâle pygmée, me montrant, qu'à ce stade, il y a déjà dimorphisme complet et aucune trace de testicule, je maintiens que le *M. pulvinar* est bien une espèce dioïque avec mâle pygmée qui reste mâle et pygmée toute sa vie.«

And now, in conclusion, what is the present actual state of the whole matter? On grounds, which appeared to me convincing, in 1884 I announced, as the facts compelled me to do, the existence of complemental or dwarf-males with hermaphrodites in *M. glabrum*.

Since then, though more time has been expended on the question

and so on.« And thus, it may be added, the fabled *Phoenix* of old finds its realisation in the Myzostomidæ or — in the vivid imagination of a zoologist! To make the course of events a matter of necessity it is only requisite that the oldest individual A should give place to the »junior partner« B as soon as a new comer C enters the gall. That nothing in the above hypothetical course of events has ever been made out is, perhaps, a trifling detail. It is interesting, that even the decomposing body of the »senior« individual is made use of as food for the late junior partner — something without exact parallel anywhere else in the animal kingdom!

than it perhaps deserved, I have met with nothing at all seriously militating against my original view.

There are only two possible alternatives as to the hermaphroditism of the genus *Myzostoma*, that the hermaphroditism is primary, or that it has been derived from a diœcious condition. If it be primary, the existence of small complemental males, among other things, cannot be accounted for in view of what is really known regarding them in *M. glabrum* and *M. pulvinar*. But, if it has been derived from a diœcious condition, these small males admit of easy explanation.

If it be primary, we meet with difficulties in the »peculiar« conditions presented by *M. pulvinar*. In fact, it then becomes difficult to understand why there should be any diœcious species at all in the group; for, although many zoologists have recognised in the parasitic mode of life a tendency to the production or evolution of hermaphroditism, no-one, with the possible exception of Wheeler, has yet seen in it any leaning towards the evolution of separate sexes.

Assuming the males of a diœcious group to become small and »complemental« with the initiation of hermaphroditism in the females, there are in the long run only two courses open to the former: when the hermaphroditism of the original females becomes perfect, they may disappear, as useless organisms, or they may themselves become hermaphrodite.

Practically it is the latter which happens; for, although we have not yet probed to the bottom what determines the sex of a young form, there can, I think, be little question, that the results of Amphimixis will come into play, and that, with the diminution in the number of eggs fertilised by the true males, more especially, with the increasing irregularity with which eggs of consecutive generations are fertilised by the true males, i. e., with the great preponderance of the spermatozoa of hermaphrodites over those of the males, there will be fewer and fewer males produced, and, finally, they will disappear.

In parthenogenesis, as Weismann has shown, the appearance of males tends to become cyclical, but enormous periods of time will be required before the cycle becomes infinite, and the males disappear. In hermaphroditism there is one thing, which tends to preserve the males, and this is the close association, such as occurs in *M. glabrum* to some extent, and, more particularly, in *M. pulvinar*, of male and hermaphrodite, or of male and female. In this way it is practically

certain, that, even if the male be associated with a hermaphrodite, some of the eggs of the latter will be fertilised by the former, and, thus, the further production of male forms rendered more certain.

In other circumstances, more especially where the forms are free, as in *M. cirriferum*, the chances of a male meeting with a hermaphrodite, upon which to settle, must be small. There can be no close association of male and hermaphrodite here. And, as a matter of fact, it would be difficult, or impossible, to fix upon a single freely moving species in the animal kingdom, in which there is such a close association of male and female, or of male and hermaphrodite throughout life.

The intimate association is out of question, and, thus, the fertilisation of eggs by the male becomes rare, and, finally, perhaps very soon, ceases. Then the males rapidly disappear.

And now, to come back to *Myzostoma*, »der lehrreichsten aller Wurmgattungen«, as the late Fritz Müller sagely remarked! Owing to the various kinds of parasitism presented by the numerous species of the genus, parasitism, which in some cases has tended to the preservation of the males, in others to their extinction, in yet others to their conversion into hermaphrodites, we can, so far as at present known, divide the species up into: —

1. Purely diœcious forms with small males. (von Graff, Prouho.)	*M. pulvinar* and some cysticolous species.
2. Hermaphrodite forms with true males, which remain male. (Beard.)	*M. glabrum.*
3. Hermaphrodite forms with males, which, retaining their positions on the hermaphrodite, afterwards become female. (Prouho.)	*M. alatum.*
4. Hermaphrodite forms, in which the males have lost their dorsicolous position, and have either become extinct or converted into protandric hermaphrodites.	*M. cirriferum* and others.

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Description of Plate 10.

Alphabetical references.

co coelom
cu cutis.
ec ectoderm.
g gut.
n.s nervous system.
N.o Nansen's organs.
o.c egg-cell.
p.e peritoneal epithelium.
sp spermatozoa.
sp.c sperm-mother-cells.

All the figures except fig. 16 are from specimens of *Myzostoma glabrum*.

Fig. 1. Section of young hermaphrodite (tab. 2 no. 4) showing a regular ovarian epithelium (*o.e*) lining the dorsal aspect of the peritoneum. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 2. A similar section (tab. 2 no. 3) showing the same regular ovarian epithelium (*o.e*), but with growth of the egg-cells. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 3. From the same specimen as fig. 2. Here one egg-cell is rather large. A group of sperm-cells (*sp.c*) in the cutis. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 4. Section of a young hermaphrodite (tab. 2 no. 11). Here, owing to growth, the ovarian epithelium of the cœlom is no longer very regular. Zeiss obj. D. oc. 2. = 225 diam.

Fig. 5. Another section from the same, showing rupture of the cœlomic epithelium due to growth of ovarian cells. Zeiss obj. D. oc. 2. = 225 diam.

Fig. 6. Section of cœlomic epithelium (*p.e*) of a young disc-form (tab. 2 no. 5), showing early stages of egg-differentiation. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 7. A similar section from a young disc-form (tab. 2 no. 1) showing regular cœlomic epithelium with eggs. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 8. From the same animal. Showing two eggs (*o.c*) in the cœlomic epithelium. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 9. A section of a bit of the cœlomic epithelium with egg-cells. From a young disc-form (tab. 2 no. 5). Zeiss obj. F. oc. 2. = 500 diam.

Fig. 10. Section of body-wall and cœlomic epithelium of a young disc-form (tab. 2 no. 1). Zeiss obj. F. oc. 2. = 500 diam.

Fig. 11. Section of a much smaller male (tab. 1 no. 2) showing further stages in the development of spermatozoa. Zeiss obj. F. oc. 2. = 500 diam.

Fig. 12. Section of a male (tab. 1 no. 1). The development of male elements from the dorsal cœlomic epithelium has proceeded apace. There is no trace of a regular epithelium, or of ovarian cells. Comparison of this figure with figs. 1—5 demonstrates very clearly the differences, referred to in the text, between the dorsal cœlomic epithelium of male and of hermaphrodite specimens. Zeiss obj. D. oc. 2. = 225 diam.

Fig. 13. Section of a male (tab. 1 no. 6). In this case the regular cœlomic epithelium is becoming converted into sperm-mother-cells (*sp.c*). Zeiss obj. F. oc. 2. = 500 diam.

Fig. 14. Nansen's organs from a young disc-form (tab. 2 no. 5). Leitz obj. 7 oc. 2.

Fig. 15. Stages in the development of spermatozoa from a section of the lateral portion of the body below the alimentary cœca. From a large male (tab. 1 no. 9). In this specimen the cells of Nansen's ovary agree in all respects with the sperm-mother-cells here depicted. Leitz obj. 7 oc. 2.

Fig. 16. Transverse section of a young specimen of *M. cirriferum*, to show the cœlom (*co*). Zeiss obj. D. oc. 2. = 225 diam.