

# The Sexual Phases of *Myzostoma*.

By

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With Plates 10—12.

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## Preface.

The parasitic genus *Myzostoma*, which FRITZ MÜLLER ('85) correctly styled »die in Bezug auf ihre Geschlechtsverhältnisse merkwürdigste und lehrreichste aller Wurm-gattungen«, has been but little studied of late. v. GRAFF, NANSEN and BEARD have given such a full and clear account of the anatomy and sexual phases of these highly modified Annelids, that few morphologists would feel inclined to enter a field which seems at first sight to promise so little that is new and interesting. Nor should I have made this attempt had not Prof. EISIG incidentally called my attention to a peculiar Myzostome, *M. pulvinar*, of which we had found several specimens while on a collecting expedition to the Gulf of Sorrento. A study of this and the commoner Mediterranean species (*M. cirriferum* and *M. glabrum*) led to the following paper, in which I shall attempt to give a simpler — and I trust, also — a more satisfactory explanation of the sexual peculiarities of *Myzostoma*, than has been given by preceding authors.

For the opportunity of studying at the Naples Zoological Station I am indebted to the Smithsonian Institution, and to Prof. DOHRN who most generously permitted me to enjoy the privileges of his laboratory after the expiration of the term for which I was appointed. I am also indebted to Professors PAUL MAYER and HUGO

EISIG for much kind assistance and to Signor LO BIANCO for the abundance of *Myzostoma* material with which he supplied me. I would, moreover, express my sincerest thanks to Prof. F. JEFFREY BELL and to Dr. GÜNTHER of the South Kensington Museum for permission to examine the Challenger Crinoidea and v. GRAFF's types of the Challenger *Myzostomidae*. The two gentlemen have also kindly allowed me to section and describe the new species of *Myzostoma* which I found while looking over the Crinoids.

In the fixing of the different species of *Myzostoma* for histological study, I have obtained the best results with corrosive sublimate and the corrosive-acetic and picro-acetic mixtures. The sections (5—7.5  $\mu$  in thickness) were fixed to the slide by means of the albumen and water method (see BUMPUS '94, pag. 721, and TOYAMA '94, pag. 126) and stained with HEIDENHAIN'S iron-alum haematoxylin followed by a saturated aqueous solution of Orange G. The diffuse plasmatic stain of the Orange G forms an excellent background for the black or blue of the haematoxylin. This method enabled me to obtain a very clear — I might say, lithographic — stain. The various carmines and cochineals failed to give satisfactory pictures of the small nuclei and vague cell-contours which render the *Myzostomidae* so unfavorable from a histological standpoint. Even with the best results in staining, it is necessary to work almost constantly with an immersion objective.

### Part I. Descriptive.

v. GRAFF in his taxonomic papers wisely refrained from subdividing the genus *Myzostoma*, although he appears to have recognized the lack of uniformity in the species. He was doubtless well aware of the necessity of utilizing internal as well as external anatomical characters in delimiting groups of species, but the state of preservation of the Challenger specimens and their value as types made a thorough examination impossible. It is, perhaps, as well that the genus was not subdivided into several genera, for it now appears from facts to be recorded in the present paper, that the adolescent stages of several, and probably of all species of *Myzostoma* are remarkably similar in their organization, although the adults may present differences to which a systematist might attach generic values. The final estimate of these characters must depend on a thorough morphological analysis of all the species of the group and

this may be left to future investigators; for the purposes which I have in view I propose to group the species according to their habits, thus:

I. Migratory species; i. e. species which move about freely on the Crinoids which they infest. Type: *M. cirriferum*, Leuck.

II. Stationary species; i. e. sluggish species which rarely if ever leave the spot where they have settled on the Crinoid. Type: *M. glabrum*, Leuck.

III. Cyst-producing species; i. e. species which produce galls or swellings on the discs or arms of their Crinoid hosts. Type: *M. cysticolum*, v. Graff.

IV. Entoparasitic species; i. e. species which inhabit the alimentary tract of their Crinoid hosts. Type: *M. pulvinar*, v. Graff.

All the species of these various groups may be arranged in a series of increasing parasitism, or, strictly speaking, commensalism, from the primitive and most typical forms of the first group to the very aberrant species of the fourth group. The departure in the adult from the juvenile condition increases in a corresponding manner: the young and adult of forms like *M. cirriferum* being very similar, while the young and adult of *M. pulvinar* are very dissimilar. The nine species which I shall consider in the present paper may be distributed among the four groups as follows:

- |                           |   |                                 |
|---------------------------|---|---------------------------------|
| I. Migratory species      | { | <i>M. cirriferum</i> , Leuck.   |
|                           |   | <i>M. circinatum</i> , n. sp.   |
| II. Stationary species    | { | <i>M. glabrum</i> , Leuck.      |
|                           |   | <i>M. alatum</i> , v. Graff.    |
| III. Cysticolous species  | { | <i>M. platypus</i> , v. Graff.  |
|                           |   | <i>M. belli</i> , n. sp.        |
|                           |   | <i>M. cryptopodium</i> , n. sp. |
|                           |   | <i>M. eremita</i> , n. sp.      |
| IV. Entoparasitic species | { | <i>M. pulvinar</i> , v. Graff.  |

#### 1. *Myzostoma cirriferum*, Leuckart.

The habits and general structure of this commonest of the Mediterranean species of *Myzostoma* have been so fully described by LOVÉN ('42), v. GRAFF ('77), NANSEN ('85) and others, that I may here restrict my account to the reproductive organs and the sexual phases. During February and March nearly all the specimens



of *Antedon rosacea*<sup>1</sup> at Naples are found to be infested with a variable number — sometimes several dozen — specimens of this species. At this season the specimens vary from 0.2—2.5 mm in length. v. GRAFF ('77) gives the size of this species as 4 mm, and I infer from this datum that all the specimens I have seen were young or little more than half grown. There may be but one brood during the year, but if this is the case, the period of oviposition must extend over several weeks or perhaps months.

The ovaries — the »problematical organs« of NANSEN — are easily seen in horizontal sections through the mid-region of the body of specimens 1.75—2.5 mm in length (Pl. 10 Fig. 1 *ov.a* and *ov.p*). They project as two deeply staining protuberances from either side of the intestine. The relations of these bodies to the body-cavity and gut-diverticula are more clearly apprehended in cross-sections (Fig. 4 *ov*). Under a low magnification the cells of the ovary appear to be arranged in rows so that the organ often resembles a tuft or tassel. As seen in the figure it lies just dorsal to the base of the intestinal ramification (*int.r*). The continuity of the lumen of the intestine (*int*) and that of the ramification could be readily seen in the preceding section which I have not figured. The cavity into which the ovary projects is one of the body-cavity ramifications which in their totality have been wrongly called the ovary by all preceding writers who have had occasion to mention these structures. The mere presence of ova in different stages of growth in an organ does not of necessity make it an ovary, and this, I maintain, is the only evidence which has been advanced in favor of such an interpretation. It is quite evident that this criterion would make an ovary of the body-cavity of any typical Annelid.

In Fig. 4 several ova in different stages of maturation are seen along the dorsal boundary of the coelomic cavity and there are also a few mature ova floating in the lumen of the ramifications. The testes (*ts*) are well-developed and consist of masses of cells in all stages of spermatogenesis imbedded in the parenchyma of the dorsal part of the body. Similar masses occur also in the ventral parenchyma and lateral to the parapodia in other sections. The vesiculæ seminales (*v.s*) are full of mature spermatozoa, still enclosed in plas-matic masses and awaiting liberation into the water through the so

<sup>1</sup> v. GRAFF ('87, pag.4) found specimens of *M. cirriferum* also on another Crinoid, *Antedon petasus*, Düb. and Kor.

called »penes«. These latter organs do not lie in the plane of the section figured.

The sections thus far described for the purpose of orienting the reader show only that specimens of *M. cirriferum* are hermaphrodite, i. e. contain both mature ova and spermatozoa side by side. These sections represent the condition which obtains during the greater part of the animal's life. For further details and clearer figures the reader may be referred to v. GRAFF'S beautiful monograph ('77), in which the hermaphrodite phase of *M. cirriferum* is correctly described.

The facts on which I wish to lay particular stress are only brought out by the study of an unbroken series of individuals of *M. cirriferum* of different ages, and I venture to maintain that had such a study of this one species been undertaken earlier, much of the confusion which has arisen respecting the sexual phases of *Myzostoma* would have been avoided. The account here given is based on a large number of specimens, but for the sake of brevity I have constructed what I consider to be a typical series from somewhat fluctuating measurements. Such variations are unavoidable because the animals suffer a varying amount of contraction during killing and preservation, and because the changes in the reproductive organs often make their appearance somewhat earlier in some individuals than in others.

Stage 1. 0.225 mm long. In *Myzostomes* of this stage the intestine is very simple in its structure, consisting of a straight median tube with three very short diverticula on either side. There is but a single pair of ovaries consisting of oogonia. The testes are present as larger masses of spermatogonia, ventral to the short intestinal ramifications. A few of the spermatogonia are dividing, but there are as yet no spermatozoa.

Stage 2. 0.25 mm long. The intestine has undergone little change. There is no body-cavity. The ovaries are more distinct and consist of a triangular mass of cells on either side wedged in between the base of the intestine and its incipient branches. It is possible to distinguish two kinds of cells intermingled in the ovary, the one with larger clearer nuclei sometimes in karyokinesis, the other with smaller more deeply staining nuclei. The former are the oogonia and youngest oocytes, the latter I shall designate as accessory cells. The dividing spermatogonia in the testes are more numerous than in stage 1, but still there are no mature spermatozoa.

Stage 3. 0.275 mm long. This stage shows a slight advance beyond the preceding. A small cavity — the first trace of the body-cavity, which probably exists *in potentia* before this stage — makes its appearance as a small space surrounding the ovary. It probably arises by a separation of the dorsal and ventral layers of the peritoneal epithelium. These two layers have probably become closely applied to each other through the rapid growth of the parenchyma in the dorsal and ventral extraperitoneal regions of the body.

The general appearance of the ovary is that of the preceding stage, but at its periphery a few of the cells tend to detach themselves from the greater mass and to fall into the incipient body-cavity. When closely studied, these loosened cells prove to be in reality small cell-clusters, each consisting of a larger and clearer oocyte and two accessory cells. The latter are closely applied and, as it were, moulded to the rounded surfaces of the oocyte. When two accessory cells are present they usually lie on opposite surfaces of the oocyte, but they may lie side by side on adjacent surfaces. When this latter arrangement obtains the series of 3 cells forms an angle, so that it is often possible to see but one accessory cell, the other being concealed by the oocyte. Perhaps in certain cases only one accessory cell is present. In this third stage there are no mature spermatozoa, though the testes are more voluminous than in preceding stages and contain many dividing spermatogonia and spermatocytes.

Stage 4. 0.3 mm long. The gut-diverticula have lengthened somewhat; the body-cavity has extended itself laterally from the ovary and over each intestinal ramification. Within this body-cavity it was possible to observe a few free oocytes with their accessory cells evidently moving away from the ovary.

Besides the dividing spermatogonia and spermatocytes many developing spermatids and a few quite mature spermatozoa were found in the parenchyma ventral to the intestine.

Stage 5. 0.35 mm long (Pl. 10 Figs. 16 and 17). In this stage the intestinal branches have lengthened and the superjacent diverticula of the body-cavity (*coe*) are coextensive with or even exceed the intestinal branches in length. The ovaries still consist of a single pair of flattened cell-masses. Figs. 16 and 17 represent two successive sections — the former passing through the body of the ovary, the latter grazing its posterior end. The oocytes with their accessory cells (*o.m*) are seen swimming in the body-cavity. A few have already apparently attached themselves to the peritoneal



epithelium (Fig. 16 *o.m*). In this figure one of the oogonia is seen dividing at *oog*, the spindle being seen from the pole. Ventral to the intestinal branches numerous spermatogonia are dividing (*spg.p*) and the section also shows a mass of spermatids with nuclei elongating to form the heads of the spermatozoa (*sp*). In the other sections of the same series there are many mature spermatozoa.

Stage 6. 0.33—0.55 mm long. The intestinal and coelomic diverticula increase still further in length and their lateral ends begin to form secondary ramifications. The ultimate tips of these branches end just above the insertions of the parapodial setae. The triplet-cells, i. e. the migrating oocytes with their accessory cells, still occur in the ramifications of the body-cavity. Some of these have attached themselves to the dorsal wall of the body-cavity and have begun to grow into ova; but the number of growing oocytes is limited as yet. The number of mature spermatozoa, however, has increased considerably and many have already found their way to the vasa deferentia.

Stage 7. 0.6 mm long (Fig. 3). By this time the »uterus« or that portion of the body-cavity which lies in the mid-dorsal line, has been formed by the fusion of the circumovarial body-cavity extending inwards from either side. Testicular follicles have made their appearance in the parenchyma over the body-cavity. The vesiculæ seminales are full of ripe spermatozoa, and the animal probably discharges them into the water from time to time. Many of the oocytes have attached themselves to the dorsal peritoneum of the body-cavity and its ramifications. Some of these oocytes have already attained about a fifth or fourth of their adult volume.

Stage 8. 1 mm long. In this stage the ramifications of the intestine and body-cavity have extended themselves still further into the flattened lateral edges of the body and have undergone further subdivision into minute branches. The number of ova attached to the dorsal walls of the body-cavity and its ramifications has greatly increased, but none of them have as yet reached maturity. The ovaries themselves show an indication of division on either side into two masses. This is readily seen in horizontal sections like Fig. 2 (*ov.a ov.p*). On one side of the figure the ovary is trilobed, but the middle and posterior lobes are together evidently the equivalent of the posterior ovarian lobe (*ov.p*) on the opposite side of the body.

Stage 9. 1.75—2.5 mm long. The ultimate ramifications of the intestine and superjacent body-cavity have extended them-

selves far beyond the parapodial insertions into the thin lateral rim of the body. There are two pairs of ovaries which are no longer flattened but of a tuft-like character. Many of the ova in the body-cavity have reached maturity, and in specimens 1.75 mm long the uterus (Fig. 5 *ut*) is often distended with eggs ready to be discharged through the uterine orifice (*o.ut*). The posterior ends of the nephridia (»ovioducts« of NANSEN) form an unpaired tube (*neph*) which opens into the anterior end of the cloaca in the midventral line. They do not carry off the ova (unless these be dead and imperfectly developed), as NANSEN supposed, but probably function as excretory organs. In this stage the testes are fully developed and all the available interstices in the parenchyma are stuffed with masses of spermatozoa and cells undergoing spermatogenesis.

Stage 10. 4 mm long. This stage I have not seen, but the measurement is given by v. GRAFF ('77, pag. 6) and is evidently that of mature individuals. For reasons which will be obvious from my description of other species, it is highly probable that some individuals of this stage will be found to have the testes much reduced or altogether wanting, and the greater number of the ova nearly or quite mature.

From a consideration of these ten stages it follows:

- 1). that *M. cirriferum* is virtually hermaphrodite from the beginning of its sexual development;
- 2) that in stages 4—8 it is functionally male;
- 3) that in stage 9 it is functionally hermaphrodite;
- 4) that in stage 10 it is probably functionally female.

It is evident that this interpretation of the stages briefly described above, with the exception of the first point, may be attained by a superficial examination of the different stages, and without tracing the ova to their true source in the ovary. But the origin and growth of the ovum is of so much importance when we come to examine other species or generalize on the sexual phases of the Myzostomidae, that it will be necessary to consider the history of the ovum in somewhat greater detail.

And first it must be noted that the emigration of the ova from the ovary is not confined to stages 4 and 5, but continues throughout the animal's life. Whether there are definite periods of emigration or whether there is a continual detachment and emigration of young oocytes from the ovary, it is impossible to say, for, although the first migration into the empty body-cavity may be readily observed,



the course of later adventitious oocytes would be very difficult or impossible to trace between the closely packed ova with which the body-cavity is soon filled.

The triplet-cells, though always recognizable as oocytes and accessory cells in the ovary, except in the very earliest stages, are most easily studied in the peripheral portion of the organ just before or during their detachment. The series of changes which the ovum of *M. cirriferum* undergoes from the triplet-stage to maturity is represented in Pl. 10 Figs. 6—15. All of these ova were drawn under the same power (ZEISS hom. im.  $\frac{1}{12}$  oc. 3). The ova in Fig. 6 *a—d* were taken from a specimen killed in corrosive sublimate, the remainder of the series from specimens killed in picro-acetic acid. The latter fluid is the better preservative for the chromatin at least during the early stages.

An ovum such as is readily found in the peripheral portion of the ovary or migrating through the body-cavity is shown in Fig. 6 *a*. Those in Fig. 6 *b—d* have just attached themselves to the peritoneal epithelium. In all these cases the nuclei of the accessory cells are distinctly visible at either end of the young oocytes, but there is no longer any trace of a cell-limit between the cytoplasm of the accessory cells and that of the ovum. The cell-bodies of the three cells appear to fuse and form one oval or elliptical trinucleate cell. The deeply staining nucleolus in each nucleus remains distinct for some time; that of the ovum enlarges rapidly.

At first (Figs. 7, 9 and 10) the chromatic skein of the germinal vesicle, or oocyte-nucleus, is quite distinct and appears to form a continuous filament of uniform thickness throughout (Fig. 7). Later this skein resolves itself into a series of caryomicrosomes (Figs. 9 and 10). Finally (Fig. 8) the skein passes into the reticular stage leaving a more or less open space around the eccentric nucleolus.

During these stages the accessory nuclei grow apace and their boundaries become more difficult to trace. This is due in part to the fact that at the poles of the oval trinuclear mass the nuclear outlines reach the cell-boundary and appear to fuse with it, while in the opposite direction they reach the walls of the germinal vesicle. Hence there is only a limited region in which the membrane of the accessory nucleus may still be detected (Fig. 8).

As the ova grow the cytoplasm becomes denser and acquires a greater affinity for the haematoxylin and carmines. Eggs in this stage are shown in Figs. 11—14. In all of these — excepting Fig. 14

which represents a transverse section of an ovum — the contours of the accessory nuclei are still visible on either side of the germinal vesicle. They have become extended and have taken on the same appearance as the reticular cytoplasm. Within the germinal vesicle the stain fails to differentiate the chromatic from the achromatic reticulum, so that I can affirm nothing concerning the condition of the chromatin in this stage. Not infrequently the growing ova take up spermatozoa from the body-cavity and appear to digest them. This is shown in Fig. 13, where the fragments of the head of a spermatozoon are easily recognized by the regular series of chromatic discs. This process, of course, can have no relation to fecundation, but appears to be due to a phagocytic tendency on the part of the young ova. The ova of *Myzostoma*, as I shall show in another paper, are never fertilized till they are discharged into the water, no matter how numerous the mature and active spermatozoa which may occur with them in the body-cavity.

In the stages which succeed those just described all traces of the accessory nuclei have disappeared. Their outlines become indistinguishable from the general cytoplasmic reticulum of the ovum. This reticulum, at first very obscure, becomes more sharply accentuated and has more distended meshes, as the egg approaches maturity. Its affinity for stains is impaired and the spaces between the meshes of the reticulum seem to fill with a clear liquid (Fig. 15).

## 2. *Myzostoma circinatum* n. sp. (Pl. 10 Fig. 18).

A single specimen of this interesting species was found clinging to the convex surface near the base of one of the arms of an undetermined species of *Pentacrinus*. The locality given on the Challenger label is »station 214« (south of the Philippines). The Myzostome was of a drab color and about 5.5 mm long. The flattened body was proportionally much thinner than that of *M. cirriferum*. Its edges were rolled up to a considerable extent so that their exact outlines could not be determined without injuring the specimen. They bear long cirri, presumably 10 on either side. The suckers were large and distinct. The tips of the parapodia were circinate and each parapodium bore a pointed cirrus on the mesial surface of its base.

*M. circinatum* at first sight closely resembles v. GRAFF'S *M. wyvillei* & *thompsoni* ('84 b, Pl. 6 Figs. 1 and 2), the only other described species

with circinate parapodia, but the following differences, some of which I believe to be of specific value, may be pointed out. The body of *M. wyville-thompsoni* is only 2.3 mm long and 1.7 mm broad. v. GRAFF's figure shows that the parapodia are relatively much larger and provided with more powerful hooks than those of *circinatum*. The most striking difference, however, is the absence of cirri at the bases of the parapodia in v. GRAFF's species. *M. wyville-thompsoni* is from the same locality as my species, but it occurs on different hosts, viz. *Metacrinus costalis* and *M. angulatus*.

The series of sections which was made from the specimen of *M. circinatum* revealed a most unsatisfactory histological preservation. This of course was to be expected in a specimen which had lain in alcohol since the days of the Challenger expedition. Nevertheless it was possible to determine that the structure of the reproductive organs was essentially the same as those of *M. cirriferum* in stage 9. There were two ovaries on one side of the intestine and only one on the other. Probably the single ovary originally consisted of two which had become closely applied to each other. In minute structure the ovaries agreed in every respect with those of *cirriferum*. The young oocytes could be readily distinguished from the deeply staining accessory cells adhering to their surfaces. Most of the testicular cells were nearly or quite mature, and huge masses of spermatozoa were found in cavities of the parenchyma on either side of the intestine. I was unable to find the vesiculæ seminales and the penes, so that I am in doubt as to the manner in which the spermatozoa find their way into the water. The testes may, perhaps, dehisce into the body-cavity and allow the spermatozoa to pass out of the orifice of the uterus.

### 3. *M. glabrum*, Leuck.

Like *M. cirriferum* this species has been repeatedly described and figured (SEMPER '57, v. GRAFF '77, BEARD '84, etc.). It occurs on the disc in the immediate vicinity of the mouth of *Antedon rosacea*<sup>1</sup>, attaching itself in such a way that its extensible pharynx may be inserted into the mouth of its host. Very frequently the larger specimens of *M. glabrum* bear smaller individuals on the

<sup>1</sup> According to v. GRAFF ('87 pag. 2) *M. glabrum* is parasitic also on *Antedon petasus*, Düb. and Kor.



anterior edges of their backs. These smaller individuals have been rightly regarded by v. GRAFF and others as the young of the same species. BEARD's observations on these young, which it pleases him to call »complemental males«, will be considered in the sequel. Here I am concerned only with an account and interpretation of my own observations.

The ovaries of *M. glabrum* are a single pair of deeply staining oval masses, one on either side of the intestine in the middle of the body. In horizontal sections the general appearance of these organs is that of Pl. 10 Fig. 20 *ov.* Each mass is not solid like an ovary of *M. cirriferum*, but permeated with narrow and irregular spaces. The true relations of the ovaries to the body-cavity and circumjacent organs are best studied in transverse sections (Fig. 19). The ovaries are seen to consist of deeply staining cavernous invaginations of the uterine wall on either side of the intestine. The spaces which permeate them are continuous with the lumen of the uterus (*ut*) and its ramifications, the main branches of the »ovaries« of other authors. The minute structure of an ovary is shown in Fig. 21. In this figure it is readily seen that the organ is really a sudden and pronounced thickening of the peritoneal epithelium (*p.ep*) lining the »uterus« (body-cavity) and its ramifications. The thickening takes on the appearance of an invagination because its central portions are traversed by the spaces above described. These spaces, as will be seen, probably arise by the breaking away of cells in certain portions of the ovarian mass. The organ clearly consists of two kinds of cells, the larger and paler elements being oogonia or oocytes, the smaller and more deeply staining elements the accessory cells. In the specimen figured a number of spermatozoa (*sp*) have migrated from the body-cavity into the ovarian crypts. In the ovaries of many specimens — especially during the younger stages — the oogonia may be seen dividing. I have reproduced several such cells in Fig. 22. It will be observed that the accessory cells are already attached to the dividing oogonia. The divisions are evidently about to result in the formation of more oogonia or oocytes. I have not been able to determine how these new oogonia or oocytes acquire their accessory cells — whether by a division of the original accessory cells, or by attracting to their surfaces some of the deeply staining cells which occur so abundantly in all parts of the ovary. The solution of this problem is by no means easy, for not only are all the cells of the ovary very small and closely applied to one another, but the

karyokinetic figures are often poorly preserved and periodic in their appearance.

Towards the free periphery of the ovarian mass the cells are already arranged in triplets, each of which consists of an oocyte with a smaller accessory cell on either side. An examination of Fig. 23 *a—g* will show that the stages in the setting free of these triplets, their attachment and growth agree very closely with the corresponding stages of *M. cirriferum*. The accessory cells are assimilated by the growing oocyte, or ovum in the same manner. The last remnants of these cells are traceable only to the deeply staining stage of the ovum (Fig. 23*f*). In the earlier stages (Fig. 23 *c—f*) several irregular and deeply staining granules are found scattered through the cytoplasm especially towards the poles. These may be, for ought that can be determined to the contrary, the disintegrating masses of chromatin belonging to the nuclei of the accessory cells. The granules are not seen in the stage represented in Fig. 23*g*.

When a series of individuals of *M. glabrum* of different sizes was carefully sectioned and studied the following facts in the growth and structure of the reproductive organs were ascertained:

Stage 1. 0.175 mm long. There is a distinct and rather spacious body-cavity in this stage. The diverticula of the intestine are very short, however, being mere hollow buds.

In the region of the ovary there is a small accumulation of peritoneal cells (young oogonia) which are indistinguishable in appearance from the spermatogonia, a few of which are found in the ventral parenchyma.

These spermatogonia are not always clearly distinguishable from other non-sexual cells which are still relatively large and have a somewhat embryonic appearance.

Stage 2. 0.25 mm long. The body-cavity has grown smaller, the gut-diverticula somewhat longer. This decrease in the extent of the body-cavity in this stage is to be attributed to the proliferation of the spermatogonia which, I believe, first arise from the peritoneum lining the floor of the body-cavity and thence proliferate downwards into the ventral parenchyma between the insertions of the parapodia. The masses of spermatogonia thus formed appear to push up against the floor of the body-cavity and tend to obliterate its lumen. Many spermatogonia are dividing in this stage, but the majority are in the resting stage. A very few spermatocytes have been formed and have begun to divide, but none of the male

reproductive elements have as yet advanced beyond this point. The ovaries are in the same condition as in stage 1; they are mere flattened accumulations of young oogonia, or modified peritoneal epithelial cells on either side of the intestine.

Stage 3. 0.3—0.35 mm long (Pl. 11 Fig. 25). The intestinal diverticula extend out on either side beyond the insertions of the parapodia, but are still quite simple. The body-cavities on either side above these diverticula are only just fusing in some specimens in the median line above the intestine to form the »uterus«. The thickened portion of the body ventral to the intestine and its branches is full of proliferating male elements — many actively dividing spermatogonia and spermatocytes and a goodly number of mature spermatozoa. The ovaries are somewhat larger than in the preceding stages, but the two kinds of cells which are so characteristic of these organs in a later stage are not yet clearly seen, although the beginning of such a differentiation is perhaps already indicated by a difference in the size of the nuclei. Myzostomes in this stage are thus functionally male.

Stage 4. 0.375 mm long. The intestinal diverticula are developing further ramifications. The body-cavity has been obliterated with the exception of a very small space surrounding the ovaries. These are somewhat larger, but otherwise in about the same condition of development as in the preceding stage. The total volume of the testicular follicles has increased considerably, and there are a great number of mature spermatozoa.

Stage 5. 0.5—0.8 mm long. The body-cavity has become larger about the ovaries, but is not apparent elsewhere in the sections. The ovaries have increased in volume and the two kinds of cells, the oogonia and accessory cells, stand out clearly; the latter often staining very deeply in this stage. Instead of being smooth as in the preceding stages, the surface of the ovary becomes somewhat irregular and small cavities begin to invade the hitherto solid tissue of the organ. These cavities are large and distinct in specimens 0.8 mm long.

The greater portion of the Myzostome's body is now filled out with the testicular cells in all stages of division and metamorphosis into the spermatozoa. There are mature spermatozoa in abundance, both in the recesses of the ventral parenchyma and in the cavities of the vesiculæ seminales. A few testicular follicles have also made their appearance in the parenchyma dorsal to the intestinal rami-



fications, and like those of the ventral parenchyma present all the stages in the multiplication and maturation of the male elements.

Stage 6a. 1 mm long. Specimens in this stage are found like those of the five preceding stages attached to the backs of older individuals. The intestinal diverticula now extend into the thin lateral edges of the body and have acquired further ramifications.

In the peripheral portions of the ovaries which have now the adult form, the triplet-cells are seen breaking away and migrating into the body-cavity, which has extended further towards the lateral edges of the body along the dorsal surface of the intestinal diverticula. In some of the specimens a few of the oocytes have begun their growth while still in the ovary (compare Pl. 12 Fig. 56o). The male reproductive cells are still increasing in bulk and number.

Stage 6b. 1 mm long. The specimens have migrated from the backs of the older Myzostomes and have attached themselves to the disc of the *Antedon*. Sections reveal almost the same conditions as in the specimens of Stage 6a. The body-cavity is becoming larger and a few loose triplet-cells are found floating in it near the ovary.

Stage 7. 1—1.5 mm long. In this stage there is a further enlargement of the body-cavity. The conditions of the female reproductive organs may be readily studied in horizontal sections of specimens 1.5 mm long, like the sections represented in Pl. 11 Fig. 24. Here the ovary contains several dividing oogonia (*oog*) and the triplet-cells may be seen breaking away from the irregular margins of the organ. These cell-clusters (*o.m*) may be traced as they float through the ramifications of the body-cavity in every direction, till they attach themselves to the peritoneal epithelium. In some places they have begun to grow into ova together with their accessory cells.

The appearance of a cross-section of a specimen 1 mm long and which, like the preceding specimen, has already settled on the disc of the Crinoid is shown in Pl. 10 Fig. 19. There is an appreciable relative decrease in the size and extent of the testes. The ova, of which quite a number have taken up their abode in the body-cavity, show a tendency to settle on the dorsal peritoneum. They very soon become so numerous as to assume polygonal outlines from mutual pressure. None of these ova have as yet reached maturity. During their growth the peritoneal epithelium grows in between them and appears to surround them with follicles of flattened cells. These follicular partitions may in some cases arise from the

accessory cells, but I do not believe this to be the case. I am certain that the ova do not originate from the peritoneal epithelium of the body-cavity diverticula, as BEARD ('94) and others before him have claimed.

A cross-section through the ovary of the right side of Fig. 19 is shown, as it appears under a higher magnification, in Fig. 21.

Stage 8. 2.5—3.5 mm long. The body-cavity has reached its ultimate limits and is full of ova in all stages of growth. In this stage the »uterus« may be packed full of ripe ova ready to be discharged from the uterine orifice, which in this species is situated on the dorsal surface of the body near the cloacal opening. The testes, though reduced, are still voluminous; there are many mature spermatozoa, some of which have passed into the body-cavity, while others fill the vesiculæ seminales. The ovaries are well developed, but I have found no karyokinetic figures to indicate a continued proliferation of oogonia. Doubtless triplet-cells still continue to be given off into the body-cavity, and probably this emigration of oocytes with their attendant cells may take place throughout the life of the animals either continually or intermittently. For obvious reasons this emigration is more difficult of demonstration than that which takes place when the body-cavity is still empty, or nearly empty. In this stage the animal is a functional hermaphrodite.

Stage 9. 3.5—4 mm long. The body-cavity appears to be very large, because the ova which have distended it during their growth have been largely discharged into the water and the slower influx of ova from the ovaries is far from occupying as much space as the original batch. Most of the ova which are still found clinging to the peritoneal walls of the body-cavity are well along towards maturity. In this stage the animal is really a functional female, since the testes are nearly or quite exhausted. One often find a few ripe spermatozoa floating about in the body-cavity. It would seem that the animal does not live long after this stage which is attained by many individuals about the last of March. After this date I found very few mature individuals on the specimens of *Antedon* which I examined. This matter, however, requires further investigation at the hands of those who may have an opportunity of studying the species during the ensuing months of the spring and summer.

The series of stages of *M. glabrum* here described will be found to differ in no important particular from the series of *M. cirriferum*

given above: *M. glabrum* is dioecious from the time its reproductive organs first appear, and like *M. cirriferum* it is functionally male in early life, then functionally hermaphrodite and finally functionally female in its senile stages. The correlation of the migration to the disc of the *Antedon* and the development of functional hermaphroditism is not by any means perfect, since it is possible to find functional male individuals on the disc of the *Antedon*, and incipiently hermaphrodite individuals still attached to the back and sides of the older *Myzostomes*. But in general it may be said that the change from the functional male to the functional hermaphrodite occurs when the animal shifts its position to the disc.

#### 4. *M. alatum*, v. Graff.

In form and habits this species closely resembles *M. glabrum*. My observations were made on half a dozen specimens obtained from the discs of a few *Antedon phalangium*, Müller. The young are found attached to the anterior dorsal surface of the older individuals. The ovary and testes are almost exactly like those of *M. glabrum*, so that I may dispense with a special description and figures. The young individuals are functionally male, the larger ones functionally hermaphrodite. I have not seen any functionally female specimens, but doubt not that they occur.

PROUHO's observations ('92) on this species, though incomplete in some particulars, were evidently made on more material than I have been able to secure, and as they offer very valuable support to my interpretation of the sexual phases of the *Myzostomidae*, I may quote them here.

He says: »On trouve, en effet, très fréquemment, sur le dos du *M. alatum*, de soi-disant mâles complémentaires, au nombre de un ou deux, rappelant exactement ceux qui ont été décrits par M. BEARD chez le *Myzostoma glabrum* et que M. v. GRAFF avait eu probablement raison de considérer comme des jeunes. Or une série d'observations m'a montré, sans aucun doute possible, que les individus fixés sur les dos du *Myzostoma alatum* hermaphrodite sont de petits *Myzostomes* de son espèce qui, mâles dans leur jeune âge, avec spermatozoïdes bien développés et conduits déférents pareils à ceux de l'adulte, grandissent et acquièrent, en grossissant, des ovaires identiques à ceux de l'hermaphrodite qui les supporte, et cela sans abandonner les dos de ce dernier.«



The latter part of this quotation is worthy of particular attention. PROUHO did not see the true ovaries and what he designates as such are the »ovaries« of other writers, viz. the masses of eggs accumulated in the branching body-cavity. PROUHO's remarks are of interest because they show that in *M. alatum* the migration to the disc of the *Antedon* may be delayed till the animals are plainly hermaphrodite.

I have had no difficulty in finding the true ovaries, one on either side of the intestine, in a small individual attached to the back of an adult *M. alatum*. The structure of these organs is too much like that of the ovaries of *M. glabrum* in the corresponding period of growth (stage 7) to require special description.

This peculiar habit of the young specimens settling on the older ones is not confined to *M. glabrum* and *alatum*. It occurs also in *M. horologium*, v. Graff, parasitic on *Actinometra jukesi* and *A. strata*, as may be concluded from v. GRAFF'S Pl. 1 Fig. 14 ('84 b). In describing the species at pag. 28 he says: »The sexual organs resemble those of the last mentioned species (*M. glabrum*) and the young are attached to the body of the adult in the same way.«

Three of the species studied by NANSEN ('85), viz.: *Myzostoma gigas*, Lütken, *giganteum*, Nansen, and *carpenteri*, v. Graff, also agree with the above mentioned species in carrying the young. NANSEN also infers, and I quite agree with him, that the same habit may occur in most sedentary species, like *M. chinesisicum*, v. Graff, *testudo*, v. Graff, *echinus*, v. Graff, and *compressum*, v. Graff.

##### 5. *M. platypus*, v. Graff.

This interesting species was described and figured by v. GRAFF ('87, pag. 13 and 14, Pl. 3 Figs. 7 and 8 and 9—12) from a single specimen taken from a leather-like uncalcified cyst on a specimen of *Actinometra nobilis* from Samboangan. v. GRAFF refrained from sectioning the type specimen and confined himself to a description of its external characters. On looking over the specimens of *Actinometra nobilis* in the S. Kensington Museum I happened upon one which had the disc and bases of the arms covered with soft elliptical cysts. Nine of these cysts were opened and each was found to contain a single large specimen of *M. platypus*. Eight of the specimens were sectioned in the hope of finding differences in the development of the reproductive organs, but unfortunately all of them were almost exactly of the same age.

The dorsal and ventral aspect of one of the specimens is represented in Pl. 11 Figs. 26 and 27. The body is triangular in outline, the lateral edges being reflected dorsally like the brim of a tricorn hat. Of the three sides one is anterior and bears the dorsally reflected pharynx, while the two others are lateral. The edges of the three folds are furnished with the usual 20 cirri. The ventral surface is embossed with a number of peculiar thickenings. There is a longitudinal series of four raised and flattened lines extending along the mid-ventral line (Fig. 27z). In one specimen the second and third of these four thickenings were confluent. v. GRAFF has given a good description of the 10 parapodia; each of which bears at its base a large heartshaped and more or less flattened thickening. The penes (*pen*) are unusually large and well-developed. They are reflected dorsally along the sides of the body as a pair of thickwalled and somewhat tapering tubes. The suckers, too, are excessively developed and project considerably beyond the surface of the body. All of these structures, suckers, cordate thickenings, penes and linear median thickenings give the ventral surface of the animal a sculptured or chiseled appearance.

Sections showed that all of the specimens were in the functionally hermaphrodite phase with much reduced or evanescent male organs. The transverse section, of which Fig. 28 represents a little more than one half, passes through the middle of the body cutting on either side a penis (*pen*), the mid-ventral thickening and third pair of parapodia (*pr*). As in many other cysticolous species the great bulk of the body consists of parenchymatous tissue. The intestine and its branches (*int* and *int.r*) are accompanied by rather narrow ventral and dorsal ramifications of the body-cavity (*coe*). In these latter ramifications the ova are found, either mature and floating freely in the lumen or attached to the walls and in different stages of growth.

The ovaries (*ov*) are readily found, owing to their great affinity for stains, and may be regarded as representing a type intermediate between the ovaries of *M. cirriferum* and *glabrum*. The thickening of peritoneal epithelium from which each of the ovaries originates is not depressed into the underlying parenchyma as in *M. glabrum*, but projects into the lumen of the body-cavity as in *cirriferum*. At the same time the thickening is split into several irregular lobes or masses like those seen in the ovaries of *M. glabrum*. The ovaries of *M. platypus*, however, differ from those of all other *Myzostomes*

hitherto described in lying ventral to the intestinal ramifications (see the upper part of Fig. 28)<sup>1</sup>. The minute structure of the ovary is like that of other species. Oocytes and accessory cells are readily distinguished by their size and staining, though both of these elements are more minute than their equivalents in the preceding species.

In Fig. 28 a few testicular follicles (*ts*) are seen embedded in the parenchyma beneath the terminal coelomic ramifications in the upturned lateral portion of the body, and also in what probably represents the lumen of the penis.

Since the specimens of *M. platypus* were all taken from the same Crinoid and were all in very nearly the same stage, I can of course make no definite statements concerning the sexual phases through which this species may pass. Utilizing, however, the facts which I have collected from other species, I infer that the stage of *M. platypus* described above, must correspond to the late hermaphrodite stage of *M. cirriferum* and *glabrum*. Had the specimens been killed somewhat later in the year, I doubt not that they would have been found to be purely female, without any traces of testes. Perhaps at this time young specimens in the male phase would have been found in the cyst of the *Actinometra*.

#### 6. *M. belli* n. sp.

Of this species, which I take great pleasure in dedicating to Prof. F. JEFFREY BELL, three specimens were studied. They were taken from hard calcareous galls at the bases of the arms of *Pentacrinus alternicirrus*. Each gall contained but a single Myzostome. The Crinoids were collected at Station 214 (south of the Philippines) by the Challenger Expedition.

The three parasites were whitish in color and varied in length from 2.25—2.5 mm. Dorsal and ventral views of one of the specimens are shown in Pl. 11 Figs. 31 and 32. The lateral edges of the body are reflected dorsally till they nearly meet. A few imperfectly developed cirri are observable towards the anterior ends of the lateral edges near the protruding tip of the pharynx, and five pairs of small pointed parapodia are readily distinguished on the ventral aspect. I failed to find any traces of a penis or of suckers either

<sup>1</sup> This figure has been inverted by the lithographer.



in surface views or in sections. This simplification of structure extends also to the internal sexual organs. All three specimens were in about the same phase of reproductive activity. Curiously enough these specimens, notwithstanding their enclosure in the thickwalled cysts and long sojourn in alcohol, were in a most excellent state of preservation.

Pl. 11 Fig. 33 represents a cross-section of one of the specimens through the middle of the body. The crescentic outline of the section is sufficiently explained by a glance at the surface view in Fig. 31. The posterior end of the retracted pharynx and the tips of the intestinal ramifications (*int.r*) which run forward into this region of the body are cut transversely. The spacious body-cavity in which the intestinal ramifications lie, is filled with mature or nearly mature vesiculated ova (*o*). At first I had great difficulty in finding the ovaries, because I sought for them where they are found in other species, viz. dorsal to the main branches of the intestine and near the center of the body. They were finally found in all three specimens as two deeply staining cell-masses beneath the intestine some distance from the mid-ventral line and very close to the ventral wall of the body (*ov*). Under a higher magnification (Pl. 11 Fig. 34) the pale oocytes and deeply staining accessory cells were very easily resolved. Near the edge of the mass the typical triplet-cells were seen floating in the body-cavity or already applied to the peritoneal epithelium and beginning their growth. A study of the consecutive sections shows that the ovaries are attached to the bases of a pair of septa at a point where these latter merge into the parenchyma of the ventral body-wall. In Pl. 12 Fig. 38 I reproduce a section passing through the insertion of an ovary. It will be seen that it does not differ in any important particular from the ovary of *M. cirriferum*.

While the ovaries of *M. belli* have taken up a lateral and ventral position nearly corresponding to the position of the testes in other species, the testes of this peculiar form are found in a position which recalls that of the ovaries of other species, viz. dorsal to the intestine and its main diverticula and in the middle of the body. The whole mass of the testes (*ts*) where it projects into the body-cavity is divided into three lobes by two dorso-ventral septa. The median mass is the largest and projects into that portion of the body-cavity which other investigators have called the »uterus«. In the testicular masses the minute cells may be observed in all stages of spermatogenesis. The extremely small mature spermatozoa pass

out into the body-cavity, where they may be detected among the maturing ova and still coiled up within small masses of a plasmatic substance (*sp.*).

In one of the three specimens the testes are much reduced, and this leads me to infer that they may ultimately disappear completely when the last spermatogonia have developed into spermatozoa, and that a purely female phase may supervene in the life of *M. belli*. This inference gains in probability with the observations on the next species to be described. I deem it very probable that in an earlier stage the species may be protandric like *M. cirriferum*, *glabrum* etc.; at least there are no facts to stand in the way of such a supposition.

#### 7. *M. cryptopodium* n. sp.

Of this species I have seen only a single specimen taken from a smooth pea-shaped calcareous cyst on the arm of a specimen of *Metacrinus interruptus*, Carp. The label was marked »Indian Museum, Calcutta«. The Myzostome was terra-cotta colored and 3.5 mm long. Lateral and dorsal views of the specimen are shown in Pl. 11 Figs. 35 and 36. Like *M. belli*, *M. cryptopodium* has the lateral portions of the body reflected dorsally, but this reflection is more complete, involving also the postero-lateral edges. The two edges which overlap dorsally have a few feeble rudiments of cirri anteriorly. I could find traces of only two pairs of suckers, corresponding to the third and fourth pairs of other species. The ventral surface is marked on either side (Fig. 35) by five deep furrows, the most anterior being the shortest, the most posterior the longest and deepest. Sections show that the small parapodia are concealed each at the bottom of one of these furrows.

A comparison of a cross-section (Fig. 37) through the middle of the body with the corresponding section of *M. belli* represented in Fig. 33 is very instructive. The posterior end of the retracted pharynx (*ph*) is shown where it protrudes into the cavity of the intestine. The intestinal ramifications (*int.r*) are more capacious and much less subdivided at their tips than in *M. belli*. The body-cavity (*coe*) into which the intestinal ramifications extend appears at first sight to be much more extensive, but this is due to the smaller number of ova which it contains. In the neighboring sections a few indistinct traces of testes were found in the same position as the testes of *M. belli*. The large and very distinct ovaries (*ov*) are ventral to the main

intestinal ramifications and are attached to the bases of the dorso-ventral septa, one on either side. Even under the low magnification with which the section was drawn, the cespitose arrangement of the oocytes and their accessory cells could be made out; under a higher magnification the ovarian nature of these structures was perfectly manifest.

I regard the specimen as presenting the female (hysterogynous) stage in the development of the reproductive organs subsequent to that observed in the three specimens of the closely allied *M. belli*. Further histological details could not be made out on account of the rather poor preservation of the specimen.

*M. cryptopodium* is allied to v. GRAFF's *M. pentacrini*, as will be seen by comparing my description and figures with v. GRAFF's description ('84b, pag. 62—64) and figures (Pl. 11 Figs. 12—14). In *M. pentacrini* the parapodia are not concealed in pockets but project from the surface, although their bases »lie in shallow cavities«. »Suckers are entirely absent« in v. GRAFF's species and the margin of the body when unrolled »is covered with short cirri«. v. GRAFF also says that »the ramification of the intestinal coeca was very distinct; it is more abundant in this species than in any other« (cf. v. GRAFF's Pl. 12 Fig. 11). *M. cryptopodium* on the other hand has fewer terminal coeca than any species in which these organs have been described. Moreover *M. pentacrini* »is like the above mentioned species [*M. deformator*] hermaphrodite, but differs from the typical free-living forms, in that the male generative opening and testes are only developed on one side, on the other there are only small rudiments of them, and the space generally occupied by these organs is filled with the highly-developed ovarian follicles«. The length of *M. pentacrini* is only 1.7 mm.

The cyst formed by v. GRAFF's species is also very different from that of *M. cryptopodium*. The cyst of the latter species is large and globular like that of *M. tenuispinum* (vide v. GRAFF's Pl. 13 Fig. 14) and contains only a single Myzostome. *M. pentacrini* »does not produce real cysts upon the arms of its host, but only swellings which gradually disappear«. Two to three individuals may inhabit one cyst, but when this is the case they are separated from one another by partitions.



8. *M. eremita* n. sp.

Three very poorly preserved specimens of this species were examined. They were taken from galls on a Challenger specimen of *Metacrinus moseleyi*, Carp. The original label alludes to Pl. 44 Fig. 1 of CARPENTER'S work on the Crinoids of the Challenger Expedition and gives »Station 214« (south of the Philippines) as the locality. Each cyst is a slight thickening and resembles somewhat the cyst of *M. pentacrini*. It implicates only 3 or 4 joints of the arm and the basal segments of the adjacent pinnules as in that species. The irregular opening of the cyst is sharply defined and the outer surfaces of the affected joints are irregularly granulated. Each cyst contains but a single Myzostome which is of a drab color. One of the somewhat distorted specimens is shown from the dorsal and ventral side in Pl. 12 Figs. 39 and 40. These figures show that the dorsal reflection of the edges of the body is far from being as pronounced as in other cysticolous species. The cirri are small or wanting, except in the vicinity of the pharynx. On the ventral surface the small pointed parapodia are distinctly seen. I could find no indications of penes or suckers.

The preservation of the specimens was so bad that I could do very little with the sections.

Specimen No. 1, measured 0.75 mm. In it I could detect traces of the testes, but there were no ova in the body-cavity.

Specimen No. 2, measured 1 mm. A few distinct but very young ova were found in the body-cavity; also a few masses of spermatogonia in karyokinesis.

Specimen No. 3, measured 1.25 mm. There were a few young ova in the body-cavity, but no traces of testes could be found.

All these specimens were evidently young and this is also indicated by the small size of the cysts and possibly also by the feeble reflection of the edges of the body. The intestinal ramifications were few in number. A pair of nephridia could be traced out, as in all the other species which I have examined.

The meager and unsatisfactory data here recorded acquire significance only from a comparison with the next species to be described, *M. pulvinar*. I believe that the three specimens of *M. eremita* which I have seen very probably represent three successive stages in the transition from the male to the female phase.

There is a remote possibility that the species here described from such poor specimens may belong to one of v. GRAFF's species. The young individuals of the cysticolous species differ so widely from the adults that it is impossible to refer it to any of the described species; nor is *Metacrinus moseleyi* recorded among the hosts of the species described by v. GRAFF.

#### 9. *M. pulvinar*, v. Graff.

v. GRAFF (84a, 84b, pag. 41—42) first described this remarkable species from a single specimen »found upon the peristome of *Antedon phalangium* Müll., dredged in the Minch from 60—80 fathoms, Aug. 14, 1869 by H. M. S. „Porcupine“«. The specimen was 2.7 mm long and 3.2 mm broad. In the main v. GRAFF's description is correct, although one of the figures, representing the dorsal aspect of the Myzostome (Pl. 3 Fig. 21) shows that the specimen was distorted. This distortion is not perceptible from the ventral side (Fig. 22). v. GRAFF considered the species to be allied to *M. radiatum* — a relationship which I believe must now be considered very doubtful.

A very considerable advance in our knowledge of the structure and habits of this species has been made by PROUHO. Besides calling attention to the existence of rudimental suckers in *M. pulvinar* — organs which v. GRAFF failed to discover — he has shown that the animal does not live upon the peristome of *A. phalangium*, but that it is entoparasitic<sup>1</sup>. He says ('92, pag. 847): »il habite le tube digestif de son hôte, dans lequel il est enfoncé assez profondément pour être invisible de l'extérieur. Le Myzostome occupe la presque totalité de la première partie du tube digestif de la comatule (oesophage et sac stomacal) et est situé de telle sorte que son extrémité antérieure est tournée vers le pôle aboral. Il s'appuie par sa face ventrale, fortement convexe et portant les dix parapodes, sur l'épithélium digestif de la comatule, tandis que sa face dorsale concave, regardant l'orifice buccal de cette dernière, forme une gouttière qui donne passage aux courants alimentaires, courants qui nourrissent à la fois l'hôte et son parasite. La disposition en gouttière de la face dorsale du *Myzostoma pulvinar* explique comment celui-ci, malgré

<sup>1</sup> BEARD ('94, p. 403) speaks of this as »one of the encysted species«. This is an instance of the care with which he has read PROUHO's paper and my own preliminary note ('94, p. 181).

ses dimensions considérables, n'obstrue pas complètement le tube digestif de la comatule.»

V. GRAFF says nothing about the sex of the specimen which he examined. PROUHO however distinctly affirms that *M. pulvinar* is dioecious, with a »dimorphisme sexuel bien accentué«. The specimen which V. GRAFF described corresponds to the female of PROUHO. The male is thus described by the French author: »Le mâle ne mesure que 1 mm de longueur sur 0.8 mm de largeur; il est accroché aux téguments de la femelle sur laquelle il peut se déplacer assez rapidement. Il est aplati, elliptique, rappelant par sa forme les Myzostomes libres. Son tube digestif n'est pas ramifié, mais montre, de chaque côté, les amorces des trois ramifications que présentent tous les autres Myzostomes; sa bouche, située tout près du bord marginal, est ventrale. Il possède deux testicules, un de chaque côté du tube digestif, munis chacun d'un canal déférent débouchant sur la face ventrale.«

PROUHO's remarks show unmistakably that *M. pulvinar* closely resembles some of the cysticolous species described by V. GRAFF (*M. cysticolum*, *tenuispinum*, *willemoesii*, etc.) in presenting large female and small male individuals.

My own observations on this species are based on some 30 specimens taken in the Bay of Sorrento. About half of these would correspond to PROUHO's males, the remainder to his females. The living females are of a beautiful coral red color, sometimes inclining to yellowish; the males are white and somewhat translucent. I have been able to confirm PROUHO's notes on the habits of this species in every particular. I have, however, frequently seen the scoop-shaped posterior end of the female Myzostome protruding from the Crinoid's mouth like a little red tongue.

The female specimens which came under my notice measured 2.75—3.5 mm in length and 3.75—4.5 mm in breadth. One of these specimens is represented in dorsal and ventral view in Pl. 12 Figs. 41 and 42. Fig. 41 shows two males (*juv*) attached near the cloacal orifice (*an*), which is situated on the dorsal surface, and another on the postero-lateral edge of the body. These males when magnified (Fig. 43; ventral view) appear like typical Myzostomes of another species. They measure 0.5—0.85 mm. In most cases only a single male is borne by a female.

The association of these Myzostomes in pairs at once recalls the similar conditions in *M. glabrum* and *M. alatum*, and although the two



individuals thus associated are very dissimilar in the entoparasitic species, it occurred to me that they might nevertheless be different developmental stages of the same species. This opinion was advanced in my preliminary paper ('94). I have since obtained sections which leave no doubt as to the correctness of my contention. This will appear from a consideration of the following stages.

Stage 1. 0.5—0.8 mm long. Individuals in this stage have the appearance of Pl. 12 Fig. 43. They are found on the dorsal or lateral surfaces — usually the former — of the tongue-like caudal end or hiding under the reflected lateral and anterior edges of the large specimens. They are not so firmly attached as the young of *M. glabrum* but are capable of shifting their position quite rapidly, as PROUHO has observed, on the densely ciliated integument of the subjacent Myzostome. In transverse sections (Fig. 46) passing through the middle of the body, there is no difficulty in distinguishing the intestine (*int*) which is perfectly straight and without ramifications as yet, a small unbranched body-cavity (*coe*) corresponding to the future »uterus«, well-developed parapodia provided with powerful hooks (*st*), and a cylindrical ganglionic mass (*nv*) lying beneath the intestine. Embedded in the parenchyma on either side of the body is a large solid mass of testicular follicles (*ts*) closely resembling those of the so-called male of the cysticolous *M. murrayi* (cf. v. GRAFF 84b, Pl. 15 Fig. 11*t*). In more advanced individuals of this stage the small cells of these follicles are seen to be in active karyokinesis. Each testicle has a very short efferent duct opening on the surface. The penis, if present at all, must be exceedingly small. Masses of very minute spermatozoa embedded in a plasmatic substance are often seen protruding from the male openings as indicated in the figure. The plasmatic substance probably dissolves away in the water, as has been observed in other species, and sets the wriggling spermatozoa free. In this stage no traces of ovaries were to be found, and the individuals are really males, although it is probable that some of the peritoneal cells forming the walls of the uterus are already set apart as young oogonia. This point I have not as yet been able to determine satisfactorily.

Stage 2. 0.8—0.825 mm long. I have found only two specimens of this stage among my limited amount of material, but they are of the utmost importance.

The younger specimen (Fig. 47) measuring 0.825 mm in length has essentially the same outline in cross-section as the specimen

represented in Fig. 46. The ventral surface is quite flat, the dorsal convex, at least towards the margins. The section Fig. 47 does not quite pass through the middle of the body. At one side just above the intestine, which is only beginning to send out diverticula (*int.r*), a small mass of cells (*ov*) represents the first visible anlage of one of the ovaries. I admit that my interpretation of this organ may be open to some doubt, although the fact that it appears on one side of the body first is really no serious objection.

In the other specimen, however, which, though older than the one just described, is nevertheless somewhat shorter (0.8 mm), the conditions are too clear to admit of misinterpretation. The most valuable section through this specimen is represented in Fig. 48. The contour of the section should be noted and compared with the contour of Fig. 47: it shows the beginning of a depression in the mid-dorsal line and an incipient reflection of the lateral edges of the body. The testes (*ts*), which are relatively smaller and more compact than in the preceding stage (Fig. 46), are evidently on the way to disappearing. Over the intestine, which shows the first traces of an evagination on either side, the »uterus« is distinctly seen. It is double in this region, but in sections further towards the posterior end of the body the two cavities fuse to form a single unpaired lumen. The two cavities in the figure are nearly filled with a mass of cells (*ov*) which under a higher power (Fig. 49) leave no doubt, whatever, as to their ovarian nature. The oocytes (or oogonia) are large and clear and stand out in strong contrast to the small deeply staining accessory cells which lie between and among them. The general tufted, or cespitose arrangement of the cells is like that in the ovaries of *M. cirriferum* and *belli*. At the periphery of the organs, especially on one side, young clusters of oocytes with adhering accessory cells are breaking away from the ovarian mass and falling into the cavity of the uterus.

This stage of *M. pulvinar* would correspond, so far as the female reproductive organs are concerned, to stages 4 or 5 of *M. cirriferum*, but the male organs of the entoparasitic species are in a stage which would probably lie between stages 9 and 10 of *M. cirriferum*.

Stage 3. 1.7 mm long. This stage I have not seen, but PROUHO was fortunate enough to find a specimen which must belong here. He describes it very briefly: »Les deux sexes doivent s'associer de très bonne heure, car j'ai observé une jeune femelle de 1.7 mm

de longueur qui portait sur son dos un mâle de 0.7 mm. Cet individu femelle ne présentait encore aucune trace d'ovaires mais avait déjà la forme caractéristique de l'adulte.« This observation is valuable, because it indicates the size of the animal when it attains its peculiar adult shape. The ovaries were undoubtedly present, but were overlooked by PROUHO. The oocytes were probably migrating to their points of attachment in the ramifications of the »uterus« (body-cavity), but had not yet grown to a sufficient size to attract PROUHO'S attention. The testes had probably completely disappeared.

Stage 4. 2.75—3.5 mm long. Individuals of this length have the appearance of Pl. 12 Figs. 41 and 42 and in turn bear individuals which are in stages 1 and 2. Sections show that the testes have completely disappeared, so completely that I have found it impossible to discover in the parenchyma any traces of their former location. The intestine (*int*) sends out on either side three thin main branches (not cut in the section figured) which terminate in small diverticula in the upturned lateral portions of the body. The intestinal ramifications are accompanied and enveloped by corresponding ramifications of the coelom (*coe*) (»uterus«, body-cavity).

The two ovaries (*ov*), though much more massive than in stage 2, still retain their primitive position and may still be separated by a median vertical septum as in the younger stage (Fig. 48). Their position is in strong contrast to that of the ovaries of *M. belli* and *cryptopodium*. The ramifications of the body-cavity contain many ova in all stages of growth, the younger ones being attached to its peritoneal lining, the older ones floating freely in its lumen. In *Myzostomes* older than the one from which Fig. 44 was drawn, the mature ova fill the »uterus« and its six main branches. The cytoplasm of the mature ova has the same vesicular appearance as in *M. belli*. A considerably magnified ovary of one of the specimens in this stage is shown in Fig. 45. It is split up into irregular lobes, but still shows distinctly the intermingled pale oocytes and deeply staining accessory cells.

This fourth and last phase of *M. pulvinar* is purely female and corresponds to the final phases of *M. cryptopodium*, *cirriferum* and *glabrum*. Further comparison of *M. pulvinar* with these and other species will be undertaken in the general part of this paper.



10. The Parasites of *Myzostoma*.

The species of *Myzostoma*, though themselves parasitic, are infested in turn with parasites. In NANSEN's fine paper ('85, pag. 63 Pl. 8 Fig. 25) there is a brief account of a tape-worm *Cysticercus* which he discovered in the alimentary tract of *M. graffi*; to this parasite he gives the name *Taenia myzostoma*. I have not happened on this or any other *Taeniae*, in looking over my sections, but I have found two new parasites, an *Amoeba* and a species of *Distoma*, both of which may be briefly described.

*Amoeba myzostomatis* n. sp.

Under this name I would describe, at least provisionally, a peculiar amoeba-like form — possibly the young of some Gregarine — which occurred in great numbers in the body-cavity of a large *M. glabrum*, the sections of which were stained with iron-haematoxylin and Orange G. The body-cavity was distended with young and nearly full-grown ova. Among these — five of which I reproduce in Pl. 12 Figs. 52—55 — occurred the amoeboid organisms. In most cases the uniformly staining and rather shrunken body of the parasite was produced into a long fine point which had penetrated the cytoplasm of an ovum. In a few instances a single *Amoeba* had two points, each entering the body of an adjacent ovum (Fig. 54). The cytoplasm of the ova thus attacked contained large granules which took up the haematoxylin with avidity. These granules were larger and more numerous than those which occur in normal ova of about the same stage (cf. Pl. 10 Fig. 23). A region of the cytoplasm immediately surrounding the point of the *Amoeba* was free from these granules, of the same orange stain as the parasite and exhibited a peculiar radiation, not unlike the radiation of an astrosphere at the pole of a karyokinetic spindle (Fig. 52 and 54). The point did not completely fill out the indentation which it had made in the cytoplasm of the ovum. This is seen in Fig. 55 where both puncture and point are cut transversely. This condition is very probably due to a shrinkage in the protoplasm of the *Amoeba* occasioned by a loss of water during preservation.

Occasionally Amoebae were found which were not in the act of puncturing the ova. Two of these which appear as rounded masses of protoplasm are represented in Fig. 56 (*am*). Each contained, be-

sides a number of deeply staining irregular granules, a pale round body, which I hesitate to interpret as a nucleus although it is certainly remarkable that no other structure comparable to a nucleus could be found in these amoeboid organisms when they had been treated with such an excellent nuclear stain as HEIDENHAIN'S iron-haematoxylin.

*Distoma myzostomatis* n. sp.

From 1 to 5 of these parasites were found in each of the sectioned specimens of *M. platypus*. They usually occurred in the parenchyma of the wall of the pharynx near its anterior end and were all without exception young specimens. Two of these parasites which happened to be sectioned in a favorable plane are shown in Pl. 12 Fig. 51. The upper parasite in the figure is cut sagittally, the lower horizontally. The two suckers (*ac.o* and *ac.v*) and the pharynx (*ph*) lying between them are distinctly seen. The region between the two suckers is encircled with a girdle of dark pigment (*pg*) which was constant in all the specimens. It invades the deeper tissues of the body as shown in the upper parasite. It was also possible to detect rudiments of the reproductive organs (?*gd*) and of the excretory system (*neph*). In some cases a small piece of the pharyngeal parenchyma of the host had been drawn into the median sucker of the Distome, as shown in the upper parasite of Fig. 51 (*g*).

These data are, of course, too brief to be of any service in determining the life history of this Distome, which must be an interesting one, living as it does in the tissues of a host which in turn lives in the tissues of a second host, a singular case of emboîtement, or scatulation — a Trematode within a Myzostome, a Myzostome within a Crinoid.

## Part II. General Considerations.

### a. Historical and Critical.

In the minds of the older authors, LOVÉN ('42), SCHULTZE ('54), O. SCHMIDT ('57), and SEMPER ('57) there was no doubt concerning the sex of the Myzostomidae. The common European species, in those days the only species known, were at once set down as hermaphrodites — an inference which was, of course, perfectly justified by the observation that both ova and spermatozoa were formed in the same individual.

A modification of this early view was introduced by v. WILLEMOES-SUHM ('75) in a letter to v. SIEBOLD from the Challenger Expedition. In this letter he announces the discovery of encysted Myzostomes. In each cyst, or gall were found »stets zwei Myzostomen<sup>1</sup>, ein großes Individuum, das viel dicker ist als irgend welche, die ich früher frei auf den Armen des Seesternes fand, und ein kleines, das etwa nur ein Fünftel des vorigen misst, ganz dünn und platt. Das ist Alles, was ich bis jetzt als sicher annehmen kann, da ich die dickeren Exemplare noch nicht genauer untersucht habe. Es liegt aber sehr nahe, an die sogenannten Männchen und Weibchen von *Distoma Okenii* in den Kiemenhöhlen von *Brama Rayi* zu denken und anzunehmen, dass auch hier das eine Thier sich namentlich für die männliche, das andere für die weibliche Thätigkeit entwickelt, jedenfalls ist es interessant zu sehen, dass *Myzostomum* sich ganz wie gewisse Trematoden (*Monostomum faba*, *Distomum ferox* etc.) paarweise encystiren kann, ein Fall, der bei den Myzostomen an den europäischen Küsten bisher meist beobachtet worden zu sein scheint«. This interesting observation was, so far as the sexual relation of the two encysted Myzostomes was concerned, only a shrewd guess, since v. WILLEMOES-SUHM, according to his own statement, had not been able to study the internal anatomy of his specimens.

A few years later v. GRAFF ('77) in his monograph of the genus accepted the view of the older authors and gave a very good account of the reproductive organs. Like some of his predecessors he observed small individuals of *M. glabrum* attached to the anterior dorsal region of the larger ones, and he correctly interpreted the former as the young of the latter.

The unusual position of the young individuals was supposed to be due to a desire on their part to get as near as possible to the food current passing into the mouth of the Crinoid. They were supposed to attach themselves to the disc of the Crinoid on reaching a certain size. v. GRAFF did not study the sex of the young individuals.

In another paper ('83) v. GRAFF gave the first account of the sexual phases in cysticolous forms (*M. cysticolum*, *inflator* and *Murrayi*), and in a somewhat later contribution ('84b), describing the fine series of specimens obtained by the Challenger Expedition, he gives a

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<sup>1</sup> This species was afterwards described by v. GRAFF as *M. tenuispinum* ('84b, pagg. 68—70).



fuller account of these same species and adds several others. In all some ten gall-producing species were described. The sex is mentioned in seven of these. Two of them (*M. pentacrini* and *deformator*) are hermaphrodites and appear to agree with the free-living species except in the unilateral development of the testes. In one species (*M. cysticolum*) v. GRAFF found two individuals, one large and the other very small, inhabiting a single cyst. In the small specimen only male organs were seen; in the large one he found female organs with vestiges of testes. In four other cysticolous species (*M. tenuispinum*, *willemoesii*, *inflator*, *murrayi*) there were also two individuals in each cyst, a large and a small one. Only male organs were found in the former and only female organs in the latter. v. GRAFF therefore regarded these as dioecious species, but his mind seems hardly to have been definitely made up on this subject, as shown by the following remark ('84b, pag. 11—12): »More abundant materials are required before the question about the life-history of the Myzostomida cysticola can be definitely answered, but my investigations permit me to state that the following is in all probability correct.

The male and female being found associated in a common cyst and increasing in size with the growth of the cyst, shows that they perforate the arm-joints or pinnules of their host together. The growth of the cyst is of course caused by the presence of the parasite; the female deposits her eggs within the cyst, and the young embryos, after they have abandoned the cyst and lost their ciliated coat, associate together in pairs, and bore their way through the arm-joints. In both the sexual development begins with the appearance of testes (cf. *M. brevicirrum*), but in the female the testes degenerate and disappear entirely, or leave but a minute rudiment (*M. cysticolum*) when the ovaries make their appearance in addition<sup>1</sup>.«

<sup>1</sup> v. GRAFF's supposition that the young Myzostomes associate in pairs and together take part in forming a gall seems to me hardly plausible. Judging from my observations on *M. glabrum* and *pulvinar*, both of which show a distinct tendency to occur in pairs, each consisting of a senior and junior individual, 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 thereupon become the senior partner of another young Myzostome, and so on. According

The *M. brevicirrum* alluded to in this passage is a free-living species of which v. GRAFF says in another place ('84b, pag. 43): »Since in individuals of 0.24 mm diameter the vasa deferentia and the seminal vesicles are filled with spermatozoa, whereas the eggs are but little developed, it may be concluded that the male apparatus is earlier developed than the female.«

These two passages taken together with v. GRAFF's earlier observations on the young of *M. glabrum* show how closely he came to the true interpretation of the hermaphroditism of the Myzostomidae. It is indeed strange that he failed to detect the red thread of proandry which might have been conceived to explain the apparently very heterogeneous sexual conditions of the group.

In the same year as v. GRAFF's final observations on the Cysticola, appeared BEARD's dissertation on the life-history and development of *Myzostoma* ('84). So far as the sexual phases are concerned, BEARD's observations are confined to a single species, *M. glabrum*. The small individuals on the larger ones were observed, but BEARD says of them (pag. 569): »they are not young ones but fully developed males, usually with numerous fully developed and functional spermatozoa. In fact *M. glabrum* is not as all previous observers, including the latest Prof. GRAFF, have considered, a simple hermaphrodite, but is hermaphrodite with fully developed and highly organized males.« In these small individuals, which he calls »complemental males«, BEARD found a »total absence of all trace of female organs«. It is in vain that we search this paper for the feeblest fact to prove that these males are »fully developed«, that they do not grow beyond the stage in which BEARD found them. A deceptive argument from analogy with the Cirripedia takes the place of fact, and we are brought at the end of the paper by a kind of hocus pocus, not uncommon in morphological writings, to the far-reaching conclusion that hermaphroditism in general is derived from gonochorism and not vice versa as most authors maintain. 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

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to this view all the cysticolous Myzostomes of a given species would not be cyst-producing but only those which, instead of entering the orifice of a preformed gall in their juvenile stage, happen to settle between the arm-joints or contrive to work their way into the calcareous skeleton of the Crinoid.

v. GRAFF's rather guarded remarks on these species in the paper to which BEARD evidently refers ('84 a).

BEARD's interpretation of the small individuals as »complemental males« was accepted by NANSEN ('85), who succeeded in finding them also in the three species which he studied. NANSEN, however, dissents from BEARD's general conclusion regarding the origin of hermaphroditism in the Metazoa.

In a short paper of recent date ('92) PROUHO undertook to show that the small individuals attached to the large hermaphrodite specimens of *M. alatum* are really young hermaphrodites in which the female organs have not yet developed, and he goes on to say: »Je n'ai pas encore la preuve que les mâles complémentaires du *M. glabrum* acquièrent, eux aussi, des ovaires, mais ce que j'ai observé chez le *M. alatum* me porte à le croire.« From his observations on *M. pulvinar* he concluded that this species is dioecious. He tabulates the Mediterranean species of *Myzostoma* thus:

|  |                       |
|--|-----------------------|
| »Type hermaphrodite . . . . .                        | <i>M. cirriferum</i>  |
| »           »           protérandre . . . . .        | <i>M. alatum</i>      |
| »           »           avec mâle complémentaire (?) | <i>M. glabrum</i>     |
| »   dioïque avec mâle pygmé . . . . .                | <i>M. pulvinar</i> «. |

Such startling sexual variations occurring within the limits of a single genus can lead to only one of two reflexions: either we must have here a very unusual instability of sex, or there must be something radically wrong about the accepted accounts of *Myzostome* anatomy. Most authors have tacitly accepted the former alternative and have placed too implicit confidence in their interpretation of the reproductive organs. A more careful study of these organs, especially of the female organs, puts the whole question in a different light. All preceding authors have been led astray by regarding the general peritoneal epithelium or general parenchyma as giving rise to the ova, whereas these elements are produced only by a very restricted portion of the peritoneal epithelium, which may be readily compared with the ovaries of Annelids, Vertebrates, etc. Even recent authors like BEARD and PROUHO would probably agree with BRAUN who, in a resumé of the work done on *Myzostomes* up to 1888, defines the ovaries thus (pag. 213): »Die Ovarien stellen 7—8 Paar verästelte, zwischen den Darmblindsäckchen und Hoden gelegene Schläuche dar, die sich manchmal bis zum Scheibenrand erstrecken und alle seitlich an einem gemeinschaftlichen, median verlaufenden, weiten Canal ansitzen, dem Uterus.« The true condition of affairs must have been



suspected by LANG who writes in his text book ('88) concerning the reproductive organs of Myzostomes (pag. 265): »Bei den geschlechtsreifen Thieren erfüllen zahlreiche Eizellen haufenweise das Parenchym zwischen den Darmästen, vorwiegend auf der Rückenseite. Diese Eimassen werden als Ovarien gedeutet. Es ist aber möglich, dass sie nur aus den von den wirklichen Eierstöcken gelieferten Eiern bestehen. Die Herkunft und Bildungsstätte der Eier ist wenigstens noch nicht sicher erkannt<sup>1</sup>.«

My attention was attracted to the ovaries while studying the oogenesis of *M. glabrum*. Starting out with the view of preceding authors I sought for the earliest stages of the ova in the peritoneal epithelium lining the body-cavity, but I failed completely to find any traces of proliferation or of karyokinetic figures in the cells of this layer — a failure which was all the more striking, because I had sectioned many young Myzostomes in which the ova were evidently rapidly increasing in number. It was during this search that I happened to find the two peculiar deeply staining masses of minute cells on either side of the intestine near the center of the body. These masses proved to be a pair of organs which NANSEN ('85) alone of all previous observers had noticed. The Norwegian zoologist saw a single pair of these structures in *M. giganteum* and two pairs in *M. graffi* »on the dorsal side of the stomach«. He goes on to say that »these organs are situated in more or less open branches issuing from the uterus and consist of crowds of small cells with dark staining nuclei and nucleoli. I have found ova close to these organs. I consider these organs to be traces of the primordial ovaries which have, however, degenerated, the epithelium of the body-cavity acquiring the function of producing ova.«

NANSEN found these organs also in the »complemental males« of *M. giganteum*, *gigas* and *carpenteri*. This, he thinks, is no objection to their being rudimental ovaries, since in these cases they lie in evaginations of what is obviously the rudimental uterus. The occurrence of these two rudiments is interpreted as a remnant of a former hermaphrodite condition. NANSEN believes that he has seen egg-cells among the small cells of these organs, of which he gives no very accurate cytological description, but which he nevertheless represents correctly as they appear under a low power in his plates

<sup>1</sup> The spacing is my own.

(Tab. 2 Figs. 6, 15 and Tab. 9 Fig. 23). In the description of the figures they are called »problematic organs«, and there are many indications both in the Danish and English text to show that he was far from having reached a definite conclusion respecting the structure and function of these organs.

Sections of well preserved specimens of *M. glabrum* convinced me that NANSEN'S »problematic organs« were in no respect rudimental, and the identity of the triplet-cells, of which the organs consist, with the youngest stages of the ova in the body-cavity soon led to their interpretation as the only true ovaries of the Myzostome; a conclusion fully borne out by a subsequent study of their origin from local proliferations of the peritoneal epithelium and the not uncommon occurrence of karyokinetic figures in their cells (proliferating oogonia).

In 1895 I published a brief preliminary account of my work on the Mediterranean species and showed how the discovery of the true ovaries supplied the very point needed to reduce the apparently complicated and heterogeneous relations of the sexes to a condition of hermaphroditism uniform throughout the Myzostome group but with a varying prominence of the protandric and hysterogynous stages. Although I had made no observations on the cysticolous species I ventured to extend my conclusions to these forms, since the sexual phases of the entoparasitic species *M. pulvinar*, which agrees closely with the extreme *Cysticola*, seemed to be capable of the same interpretation as those of the free-living species. That this extension was sufficiently justified, is proved by the observations on *M. pulvinar* recorded in the first part of this paper.

Without waiting for my final account of the sexual phases of the Myzostomes, BEARD ('94) has assailed my position with great confidence -- reiterating his unshaken faith in the »complemental male« hypothesis which he advanced a decade ago. He adds a few observations made since his dissertation was published.

In order that this ghost of a »complemental male« which has disturbed the whole subject of the sexual conditions in the Myzostomes, may at last be definitely laid, I would add to the observations contained in the first part of this paper the following considerations which, I believe, will do away with all the objections so studiously brought forward against my views.

1) BEARD'S observations on the sexual phases are confined to a single species (*M. glabrum*). He seems not to have taken the trouble to

examine different stages of the more typical and commoner *M. cirri-ferum*, and although I showed in my preliminary note that this species is protandric and furnishes the clue to the sexual conditions in the other free-living forms, he does not once allude to these observations. Why should this species, which is undoubtedly protandric, be quietly ignored in a discussion which has for its first object to determine whether the hermaphroditism of *Myzostomes* is or is not protandric?

2) I should like to know where BEARD has ever shown that his so-called complemental males do not grow beyond the stage in which he found them. Certainly a few months' sojourn at Naples is quite inadequate to show any such thing for a slowly growing form like *M. glabrum*, and since »complemental males« are of such very rare occurrence in the animal kingdom, the burden of proof must lie with him who denies that the small individuals ultimately develop into the large hermaphrodite and female specimens. This demonstration might be dispensed with only if it could be shown that the organization of the complemental male differed to such an extent from that of the larger hermaphrodite that the latter could not be supposed to pass through a stage like the former. And even in this case, those who are acquainted with the possibilities of growth and metamorphosis would hardly rest satisfied with mere assertion.

3) As a matter of fact, there is absolutely nothing in the organization of the so-called complemental male which prevents it from being a stage through which the large hermaphrodite might pass. Indeed, we must assume that it is very similar, if not identical, with a stage through which the hermaphrodite must pass. It is a fact, easy of observation, that in the embryos and young of the Metazoa in general the nervous system is relatively more voluminous than in the adult. This we find to be the case with the nervous system in the so-called complemental males of *M. glabrum* when compared with the nervous system of the large hermaphrodites<sup>1</sup>. It is also easy to observe that within this series of different-sized individuals which would be regarded by BEARD as complemental males, the body-cavity (»uterus«) and intestine pass from simple median tubes to ramified structures, thus leading by gradual steps to the earliest conditions of these organs in the hermaphrodites.

<sup>1</sup> BEARD appears to have observed this, although the truth of his remark ('85, pag. 570) that »in the males the nervous system seems to be richer in ganglion cells than in the hermaphrodite« may well be doubted.



The same holds good also of the »lateral oviducts« of NANSEN, or nephridia, as I prefer to call them. It may be confidently put down as a fact that all the characters in which the so-called complementary males of *M. glabrum* and allied species differ from the hermaphrodites are simply the characters of younger individuals and not by any means necessarily or even probably those of another sex.

4) One of BEARD'S main objections is a curious bit of reasoning. At pag. 401 he says: »WHEELER is in error in his supposition that all the youngest specimens on the disc are larger than those seated on hermaphrodites. It is quite easy to find individuals on the disc of *Antedon* as small and smaller than the supposed males, and a comparison of the two, i. e. of very small hermaphrodites from the disc and of males from the backs of hermaphrodites has supplied evidence strongly supporting my former conclusions.«

For the purposes of comparison a series of males were taken and sectioned and a corresponding set of what were presumably young hermaphrodites from the disc were treated in the same way, the size of the individual being estimated by the number of sections of a given thickness ( $\frac{1}{113}$  mm). BEARD sectioned 8 males which »yielded 66, 70, 78, 79, 90, 97, 128 and 151 sections respectively, while the 12 hermaphrodites furnished 93, 94, 97, 97, 100, 112, 138, 138, 140, 152, 160 and 168 sections«.

And this is »evidence« that the males cannot be merely young hermaphrodites! Two perfectly patent errors in this »evidence« — an error in method and one in common sense — seem not to have revealed themselves to BEARD. In the first place, does BEARD imagine that during the fixing and embedding process all *Myzostomes* retain exactly the same size which they had in life, or contract in such a uniform manner as to make the counting of sections a reliable method of measurement? Is he quite sure that he has overlooked no young ova in the body-cavity of the »males« from 97—151 sections in length? And then, in the second place, even granting that the two series may overlap — and I do this willingly, being quite at a loss to know where I ever »supposed« that »all the youngest specimens on the disc are larger than those seated on the hermaphrodites« — what has this overlapping to do with the question at issue? Obviously nothing at all, unless BEARD wishes to maintain the absurdity that all the individuals of a given species of animal at the moment of reaching sexual maturity are convertible into exactly the same number of microtome sections of  $\frac{1}{113}$  mm in thickness! The morpho-

logist may well deserve the blame — not to say contempt — of those who deal with the wide and fundamental questions of variation when he has to resort to such assumptions as this »to bolster up an argument which is otherwise untenable«.

5) It is interesting to note that BEARD has spent no time looking for those hermaphrodites which have fewer than 93 sections, and still such must exist if his hypothesis is to be accepted. Where are they? BEARD has taken the pains at pag. 402 to draw up a table to show that the hermaphrodites of *M. glabrum* are far more abundant than the males. If this is the case — and again I do not doubt the fact — we should expect to find at least as many hermaphrodites as males among the stages of 66—93 sections. But no one has ever seen hermaphrodites of this size, and the reason is very simple: the hermaphrodites of this size are in the protandric stage!

BEARD claims that the »complemental males«, if really only young hermaphrodites, »ought to be more abundant than is actually the case«. I cannot see how this must follow. The life of the functional hermaphrodite is in all probability much longer than that of the protandric stage. Hence, other conditions being equal, the number of surviving hermaphrodites at any given time must be greater than the number of protandric young. This numerical ratio of adults to young even in the breeding season undoubtedly obtains in many animals which produce but few young or when, as in parasites like the Myzostomes, the chances of the survival of the young beyond the earliest stages are comparatively small.

6) BEARD records the following observation, which agrees with PROUHO's observation on *M. alatum* (see pag. 243). He says (pag. 402): »Sometimes a small form was found seated on the side wall, instead of on the back of a large hermaphrodite, and such specimens, which thus did not occupy the normal position of a male, invariably turned out to be hermaphrodite.« Considered carefully this observation tells against BEARD's hypothesis, for what are these young hermaphrodites doing on the old ones? Certainly the same cause which induces the so-called males to attach themselves to the large specimens will explain the presence of the young hermaphrodites in a similar situation<sup>1</sup>. Hence there is not even a difference in at-

<sup>1</sup> I cannot attach any importance to the difference between the side and the »normal« position of the small individuals, since these can shift their positions at will.

tachment left between the young hermaphrodites and BEARD'S complementary males.

V. GRAFF believed the attachment of the young Myzostomes to the outer or dorsal region of the larger specimens to be due to a desire to get as near as possible to the food current entering the Crinoid's mouth. This view was rejected by BEARD on what appear to me to be very insufficient grounds. While I accept V. GRAFF'S view as probably correct, I believe that there are also other causes which induce the young to settle on the backs of the old specimens. I deem it very probable that the young, when they give up their pelagic life, may find it difficult to insert their small and weak parapodial hooks into the tough skin of the Crinoid's disc and consequently choose the softer dorsal integument of the older Myzostomes. Furthermore it is not improbable that the rapid current-producing movement of the cilia covering the backs of the old hermaphrodites may favor the respiratory and nutritive conditions in the young individuals.

7) BEARD'S remarks about the organs which I have called the ovaries (NANSEN'S »problematic organs«) resolve themselves into so many purely gratuitous assertions, and they show very clearly that he has never studied these organs at all carefully. At page 402 (foot note) he says of them: »these may quite possibly be rudimentary or 'accessory' testes in the male«. Why it should be necessary to invoke even the possibility of their being »accessory« testes is far from apparent, except for the purpose of throwing doubt on my interpretation. And here I would dispose of the notion of their being rudimentary organs, a view which BEARD evidently appropriated from NANSEN, and found very useful in conducting his argument. The only grounds that can be brought forward to indicate a »rudimentary« or »vestigial« character are the relatively small size of the organs and of their component cells. Their small size is no proof that they are not ovaries, as a comparison with the Oligochaeta shows. As well might we regard as rudimentary the two small bodies which occur in but one segment of the earthworm, and the ovarian nature of which has never been doubted, owing to the fact that the ova do not leave these organs till they are large enough to be recognized as ova<sup>1</sup>. If they broke away from the ovary in a younger stage

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<sup>1</sup> Miss KATHARINE FOOT has kindly sent me some specimens of earthworm ovaries with measurements of the worms from which they were taken.



these bodies would probably have long been regarded as problematic or rudimental. For have not the true testes of the Oligochaeta been similarly overlooked and this term repeatedly and even recently applied to the vesiculae seminales?

Moreover, as I have shown, the ovaries develop and grow till the Myzostome has reached its full size and thenceforth show no signs of the diminution commonly seen in rudimental or vestigial structures.

The small size of the cells cannot be taken as an indication of a rudimental condition of the organ, since nearly all the tissues of the Myzostome consist of very small cells. The karyokinetic figures so often found in the ovarian cells long after they have disappeared from the other tissues and in relatively late stages of the animal's growth, flatly contradict NANSEN'S and BEARD'S supposition.

Then, too, BEARD must know that it is always more difficult to prove that an organ does not than that it does function. In this case also the burden of proof lies with him who denies.

In his haste to point out that my interpretation is inadequate BEARD appears to have lost sight of the fact that he has never yet shown that the general peritoneal epithelium of *Myzostoma* may give rise to ova; and that in the absence of figures his assertions could not pretend to any greater weight than those which I advanced in my preliminary paper.

8) BEARD makes the statement (pag. 403): »Many of the extreme cysticolous forms have been shown to be dioecious.« Where has this been shown? Certainly v. GRAFF, who has given us almost the only observations which we possess on the Cysticola has never »shown« this. All of the so-called dioecious Cysticola described by v. GRAFF are quite as readily interpreted as protandric and hysterogynous hermaphrodites.

9) BEARD'S insinuation that my prediction concerning *M. pulvinar* was only made »to bolster up an argument which is otherwise untenable« calls for no comment after what I have said of this species in the present paper.

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In a *Lumbricus terrestris* 170 mm long, the ovaries were only 1.25 mm long, and in a specimen of *Allolobophora foetida* 100 mm long, the ovaries did not exceed 1 mm in length. In a *M. glabrum* measuring 3 mm in length, each of the ovaries measured about 0.1 mm, so that the length of the ovaries of the Myzostome compared with the length of the body is more than 30 times as large as those of the earthworm.

10) The fancied analogy between the Myzostomes and Cirripedia adduced by BEARD in his first paper and again repeated in his latest contribution, has no value as proof. »Comparaison n'est pas raison.« If mere analogy is to be given any weight at all, my view would certainly be the more plausible, since protandry among hermaphrodite animals is far more frequent than the occurrence of complementary males (see pag. 290).

BEARD'S remarks concerning the origin of hermaphroditism in general will be referred to in the sequel. Here enough has been said to show that his assertions, far from being »redolent of the true Darwinian spirit« as they were to FRITZ MÜLLER ('85), may be more aptly compared to an ignis fatuus. Not only have they completely failed to throw any new light on the sexual conditions of the Myzostomes, but they have baffled and misled subsequent observers. The view which I still maintain has at least the merit of reducing all the apparently diverse sexual conditions of these peculiar parasites to a single law — a more or less pronounced dichogamy. *Simplex sigillum veritatis.*

#### b. The Relations of the Myzostomidae to the Chaetopod Annelids.

The observations recorded in the first part of the present paper have an important bearing on the interpretation of some doubtful points in the general anatomical structure of the Myzostomes and hence also on the natural affinities of the group to other Invertebrata. This chapter is, therefore, in one sense a digression from my theme, but in another sense it may be taken as indirect evidence in favor of the foregoing interpretation of the sexual conditions.

The Myzostomes have been relegated by different authors and at different times to the Trematodes, Crustacea, Tardigrada or Annelida Chaetopoda. METSCHNIKOFF ('66) and BEARD ('85) have adduced cogent reasons for placing them among the Chaetopod Annelids; the former regarding them as an ectoparasitic group of Chaetopods, the latter with more limited definition as a family of the Errantia. Two of the principal authorities on the Myzostomidae, v. GRAFF and NANSEN, have never accepted this view. VON GRAFF ('78 and '84 b) would unite the Myzostomidae, Linguatulidae and Tardigrada in a group, Stelechopoda, to be inserted between the Annelids and Arthropods. NANSEN ('85, pag. 80) is »inclined to

regard the Myzostomidae as a peculiar distinct group belonging to the Annelids, related to the Chaetopods, but also showing a tendency to some of the Arachnids (Linguatulida, Tardigrada, and perhaps Pycnogonida) and Crustaceans. For the reasons which have induced these different authors to adopt their respective views I can only refer to their papers.

It will be admitted on all sides that the structure of the reproductive organs and their relations to the coelom are important diagnostic characters, and it has been mainly due to a faulty or insufficient interpretation of these and some other organs (nephridia, parapodia, »suckers«) that some of the most strikingly Chaetopod characters of the Myzostomidae have not been generally recognized. It is for the purpose of corroborating the view advanced by METSCHNIKOFF and helping to establish a permanent resting place for this hitherto nomadic group that I subjoin the following considerations.

1. The Relations of the reproductive organs — the testes and especially the ovaries — to the body-cavity. The interpretation of the »uterus« and »ovaries« of other authors as a ramifying body-cavity into which the ova fall and in which they grow to their full size, at once recalls the condition seen in the Polychaeta. This body-cavity is quite distinct in the youngest Myzostomes which I have studied, and its temporary occlusion is due simply to an inward growth of the parenchyma in the portion of the body ventral to the intestine. This growth appears to be caused by the rapid accumulation of male reproductive cells in this region of the body. When the ova begin to escape from the ovaries the body-cavity again reappears and becomes at first coextensive with and then more extensive than the superjacent intestinal ramifications. The ovaries are merely one, or two (*M. cirriferum*) pairs of thickenings in the peritoneum lining this body-cavity and may be compared without difficulty to the ovaries of Chaetopods.

The position of the ovaries in most species of *Myzostoma* — viz. dorsal to the ramifications of the intestine — at first sight appears to be a difference of some importance, but species like *M. belli*, *cryptopodium* and *platypus*, where the ovaries are ventral to the branches of the intestine, show in this respect a greater resemblance to most Chaetopods. The manner in which the young oocytes detach themselves from the ovaries, pass into the body-cavity and there grow to their full size, is clearly a Chaetopod character. That they do



not float about freely during their growth, but are stowed away in masses in the diverticula is a secondary condition easily accounted for.

There are greater but by no means insuperable obstacles in the way of a comparison of the testes of *Myzostomes* with those of *Chaetopods*. In the youngest stages of *M. glabrum* examined, the spermatogonia could be traced to the cells of the peritoneum. During their proliferation these spermatogonia do not project into the body-cavity like the oogonia of many species, but into the parenchyma, which soon encloses them in masses, very much as the ovarian stroma encloses the PFLÜGER'S columns of the Vertebrate, thus cutting them off from the peritoneum. Notwithstanding this separation from their place of origin, the male reproductive elements, when they become mature, are in many species set free into the body-cavity, whence they may leave the body through the female genital opening. Even in forms like *M. glabrum* and *cirriferum*, which have vasa deferentia and special male openings through the penes, many spermatozoa find their way into the body-cavity and escape with the ova through the orifice of the »uterus«.

In forms like *M. belli* and probably also *M. cryptopodium*, where the vasa deferentia and penes have been lost, all the spermatozoa must pass out through the body-cavity like the ova. In these cases the typical *Chaetopod* condition has probably been reacquired secondarily.

2. The structure of the ovaries. In their minute structure the ovaries of *Myzostoma* are readily compared with those of other *Chaetopoda*. In both groups two kinds of cells are early differentiated — the reproductive cells proper (oogonia and oocytes) and what I have called the accessory cells. The latter are nothing more nor less than the »Nährzellen« of other authors!

A very striking similarity to the condition seen in *Myzostoma* is exhibited by the Polychaete *Ophryotrocha puerilis*, as described simultaneously by BRAEM ('93) and KORSCHULT ('93). The descriptions of both authors agree except in a few minor details. Of the two kinds of cells which may be distinguished in the ovaries of *Ophryotrocha*, the oocyte is larger and clearer, the Nährzelle somewhat smaller and more granular. These cells always separate from the ovary and pass out into the body-cavity in pairs. At first the twin cells do not differ much in size; but the nucleus of the Nährzelle is richer in chromatin than the germinal vesicle. Soon the Nährzelle

is seen to have outstripped the oocyte in volume, but it is not long before the conditions are reversed, the oocyte growing much more rapidly than the Nährzelle. Finally, when the egg-cell has attained the limit of its growth, the Nährzelle is found clinging to one point of its surface as a small deeply staining body. According to KORSCHULT the Nährzelle ultimately disappears (»verschwindet«), but BRAEM, who is more explicit, says that it separates from the full grown egg and »vielleicht wird der Rest der Nährzellen noch zum Theil von der Haemolymphe verdaut, zum anderen Theil, nämlich in so fern er für den Organismus nicht weiter verwendbar ist, wird er durch die Segmentalporen nach außen entfernt. In der Schleimhülle, welche die frisch abgelegten Eier umgiebt, konnte ich die ausgeworfenen Nährzellen mit Bestimmtheit nachweisen«.

In another Polychaete, *Tomopteris*, each egg-cell when it leaves the ovary to pass into the body-cavity is accompanied by a mass of 7 smaller cells, which do not detach themselves till the growth of the ovum is completed. These smaller cells were regarded as Nährzellen by VEJDOVSKY ('78), but according to CHUN's more recent and complete account ('88) the 7 smaller cells are to be regarded neither as Nährzellen nor as ultimately giving rise to ova. Waiving for the present any discussion of the function of these cells, I believe that they are undoubtedly the morphological equivalents of the accessory cells of *Myzostoma* and the Nährzellen of *Ophryotrocha*.

A very interesting case of the association of egg and Nährzellen has been observed by ANDREWS ('91) in *Diopatra*. In the ovary of this Polychaete the egg is attached to two long and tapering strings, each of which consists of a single series of compressed cells. The tapering tips of the strings are inserted in the ovaries, while their somewhat broader ends are attached either to opposite poles or later on to adjacent surfaces of the oocyte. »Eventually, such cell-loops (Fig. 5) break away even at the tips, and then float off in the body-cavity liquid, each with a growing centrally placed ovum . . . . The strings fall off after the ovum is 300  $\mu$  in diameter, and do not appear to diminish before then, but to drop off intact, though this requires reinvestigation.«

SPENGLER ('79) has given an excellent account of the growing egg of *Bonellia*. In this case the accessory cells which accompany the ovum during its growth are of three kinds: 1. a spherical mass of cells not unlike a blastula, and containing 2. a single central cell. This mass of cells, the »Zellenknopf«, is attached to one end of the

growing oocyte and both bodies are invested with 3. a layer of flattened peritoneal cells. The latter form a pedicel which at first anchors the egg and Zellenknopf to the wall of the ventral blood-vessel, but which finally ruptures and allows the egg to float out into the body-cavity. The central cell degenerates and ultimately the whole Zellenknopf together with the investing peritoneal layer falls away from the ovum; at least SPENGLER records the fact (pag. 370), »dass man gelegentlich in der Leibeshöhlenflüssigkeit Zellenballen antrifft, welche die größte Ähnlichkeit mit einem Zellenknopfe haben; ich zweifle nicht daran, dass es in der That von den Eiern abgelöste Zellenknöpfe sind«.

In another Gephyrean, *Thalassema*, if we may accept an observation of SEMPER quoted by LUDWIG ('74), the conditions seem to be much simpler and more like those observed in *Ophryotrocha*; the Zellenknopf being reduced to a single cell. LEYDIG ('49) long ago described and figured a mass of cells attached to the egg of the Hirudinean *Piscicola* and evidently comparable to the Zellenknopf of *Bonellia*. LUDWIG, too ('74, pag. 67 and Taf. 1 Figs. 9 and 10), called attention to similar accessory cells in *Pontobdella* and *Branchellion*.

All the Chaetopods here considered agree in possessing Nährzellen which accompany the ovum into the body-cavity and only leave it, when it is nearly or quite full-grown. In number and arrangement, however, these cells vary greatly in the different species, from the simple condition seen in *Ophryotrocha* and *Thalassema* to the elaborate Zellenknopf of *Bonellia* and the long cell-strings of *Diopatra*. Probably an investigation, undertaken with this particular purpose in view, would bring to light in many other Chaetopods still other peculiarities in the number and arrangement of the accessory cells. Be this as it may, however, the described forms differ from the accessory cells of *Myzostoma* in two respects: 1. in *Myzostoma* there is an accessory cell at either pole of the oocytes, 2. the accessory cells of *Myzostoma* are soon worked into the cytoplasm of the growing oocyte and not ultimately cast off into the body-cavity after prolonged association with the ovum. These differences seem at first sight to be very important and seriously to invalidate the homology which I am maintaining, but the following considerations show that such is not really the case. In the first place I am not perfectly sure that all the oocytes of *Myzostoma* have two accessory cells; in several instances I have found only one, and, while I am inclined to believe that the other cell may be concealed behind the



ovum, it is quite possible that it may be altogether absent. In these instances the appearance of the cell-group is strikingly like that of the oocyte with its Nährzelle in *Ophryotrocha*. It may be noted, moreover, that there is really a bipolar arrangement of the Nährzellen in *Diopatra* and that it is only necessary to imagine each of the cell-strings of that Terebellid reduced to a single cell to have the condition seen in *Myzostoma*. The difference between *Myzostoma* and *Diopatra* would be no greater than that which obtains between the two Gephyreans *Bonellia* and *Thalassema*. In the second place I can see no reason for abandoning the homology on the ground that the accessory cells are not cast off. There is this difference between Polychaeta and *Myzostoma* that in the latter the growing eggs are stowed away in compact masses in the diverticula of the body-cavity, whereas in the former they can usually move about more freely. Hence there is really no opportunity for the accessory cells to leave the ova, and it would seem quite natural that they should be appropriated as food<sup>1</sup>.

Nährzellen are known to be of very general occurrence in the Arthropoda. They have long been known to occur in Crustacea, especially in *Sacculina*, where they have been repeatedly described (GERBE '69; ED. VAN BENEDEN '69, 70 a, 70 b; BALBIANI '69; PÉREZ '78; DELAGE '84); v. SIEBOLD has observed them in *Apus* ('71), WEISMANN in *Daphnia* ('85) and BRAUER in *Branchipus* ('92). In Insects they have been very carefully studied by KORSCHOLT ('86) to whom the reader may be referred for a full account of the subject. The trophic function of the Nährzellen can hardly be doubted in Arthropods where these cells are consumed by the oocytes, but it is more difficult to understand in Annelids, where the egg presents a far greater surface to the nutrient fluids of the body-cavity than to the Nährzelle. In many Polychaeta, too, the Nährzellen appear to be absent, although the growth of the ovum seems to be completed quite as easily as it is when they are present. These considerations show that a discussion of the views of the different authors, concern-

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<sup>1</sup> I must confess that although I have taken great pains to ascertain the fate of the accessory cells, there is still a possibility that they are not all appropriated by the oocytes. One often finds small, flattened and deeply staining cells which form follicle-like partitions between the ova. Whether these arise from some of the accessory cells or from the parenchyma and peritoneum, I am unable to say.

ing the origin in the ovary and the function of the Nährzellen cannot be profitably undertaken at the present time.

3. Nephridia. Recent students of the Myzostomes have described a pair of somewhat convoluted tubules, each beginning with an opening into the body-cavity (»uterus«) just back of the ovaries and passing ventrally and posteriorly to open into the cloaca. These tubules were perhaps seen by SEMPER, although in his Fig. 5 Tab. 4 they are represented incorrectly so far as their relations to the cloaca are concerned. They were also seen and figured by V. GRAFF ('77) in cross-sections, but strangely enough he appears to have regarded them as intestinal diverticula. He denies the existence of the tubules which SEMPER interpreted as the oviducts. The best description of the tubules in question is given by NANSEN ('85, pag. 78 Pl. 1 Fig. 11 *ovd*, Fig. 8, Pl. 9 Figs. 10 and 23) who calls them lateral oviducts, to distinguish them from the unpaired median oviduct, the backward continuation of the »uterus«. NANSEN found the epithelium of each lateral oviduct to be much ciliated (Pl. 1 Fig. 26) and of a secretory nature, for »mucous globular secretions of variable size are often observed in it, vide Pl. 7 Fig. 25a«. These oviducts are also shown in NANSEN's Fig. 20, 20a, 21 Pl. 9.

I have had no difficulty in finding the »lateral oviducts« of NANSEN in the Myzostomes which I have studied, and in tracing the tubules from their openings into the body-cavity to their openings into the cloaca. NANSEN's description is in general correct, but I cannot agree with his interpretation of these tubules as oviducts. Although he figured a number of ova in the tubules in his diagrammatic Fig. 8 Pl. 1, I have never yet been able to find a mature and normal ovum in them. Sometimes a few immature and obviously decomposing ova may be found, but quite as often there are mature spermatozoa, and for this reason they might with equal justice be regarded as spermducts. When the Myzostomes are full of ripe eggs, a very little pressure will cause them to expell their ova in a pink cloud from NANSEN's median oviduct, i. e. the opening of the »uterus« dorsal to the cloacal orifice, but sections of such pressed specimens show that none of the ova have passed into the tubules through the funnel-like openings, as might be reasonably expected if these tubules were really oviducts. On the other hand the secretory character of the tubules may be readily inferred from the small globules which stain very deeply in haematoxylin and which are scattered through the cytoplasm of the gland-like epithelium of the tubules and through their lumen. This

secretory character of the tubules together with their whole structure and arrangement leads me to regard them as true nephridia — and it is strange that NANSEN did not come to the same conclusion<sup>1</sup>.

In the different species which I have sectioned there is considerable variation in the opening of the nephridia, both at their posterior or cloacal nephropores, and at their anterior ends (nephrostomes). The two nephridia may have separate nephrostomes, or may unite to form a single funnel opening into the body-cavity. Similarly the two nephridia may unite to form a single tube, or end-piece, which opens into the cloaca, or they may remain distinct and have separate openings into the cloaca. The conditions in each of the nine species are here very briefly given:

*M. cirriferum*. Distinct nephrostomes; a long unpaired end-piece opening into the anterior ventral end of the capacious cloaca (Fig. 5).

*M. circinatum*. Distinct nephrostomes; nephropores paired, opening into the ventral portion of the cloaca. This species agrees with NANSEN's figure of *M. giganteum* ('85, Pl. 1 Fig. 5).

*M. glabrum*. Single nephrostome; the nephridia run for some distance side by side just ventral to the intestine, then fuse to form a long end-piece which opens into the anterior ventral end of the capacious cloaca. In some specimens the secretion-granules are very irregular and angular and stain very deeply.

*M. alatum*. Single nephrostome; unpaired end-piece as in *M. glabrum*. The nephridia contained immature and decomposing ova, normal mature spermatozoa and mucous-like granules.

*M. platypus*. Single nephrostome; separate nephropores opening into the cloaca rather far apart. The cilia covering the nephrostomes and extending along the ducts to their openings into the cloaca are unusually long and distinct in this species<sup>2</sup>.

<sup>1</sup> I had adopted this view long before the appearance of the paper in which it was announced by BEARD ('94, pag. 403).

<sup>2</sup> In some species cross-sections of the tubules show a cob-web like reticulum extending across the lumina — an appearance also frequently seen in the mesonephric tubules of some Vertebrates (Amphibia). It is very difficult to decide whether this appearance is due to the presence of cilia glued together by the reagents or to the frayed out ends of the gland-like cells of the tubules. The cilia when distinct — and they are always very distinct in the nephrostomes and nephropores — are all directed backwards, showing that the cur-



*M. belli*. In this species I failed to find the nephrostomes; there is an unpaired end-piece, which does not open into the cloaca, but on the surface of the body through a papilla lying just ventral to the cloacal orifice. As the uterus opens just above the cloaca, there are three ciliated apertures in this species, close together. In all three specimens the nephridia were full of mature spermatozoa evidently on their way to the exterior.

*M. cryptopodium*. Single nephrostome; the ducts open on the surface by means of an unpaired end-piece which perforates a papilla just under the cloacal orifice.

*M. eremita*. As nearly as I was able to make out, the conditions in this species are like those in the two preceding.

*M. pulvinar*. Distinct nephrostomes; the unpaired end-piece is short and narrow and opens on a distinct papilla which projects into the lumen of the cloaca.

*M. belli* and *cryptopodium* tend to show that the nephridia originally opened on the surface of the body as in other Chaetopoda. In some species the unpaired end-piece has moved forward secondarily and acquired an opening into the cloaca. In still other species the nephropores have not fused, but have nevertheless undergone the same shifting forward. This shifting is perhaps to be explained by the extent to which the ectoderm is infolded in the embryo to form the cloaca, but this question cannot be decided till a careful study has been made of the alimentary tract and its relations to the insertions of the nephridia in as many species of *Myzostoma* as possible. The results of such a study could not fail to throw an interesting side-light on the obscure morphology of the Malpighian tubules in the Arthropoda.

In *M. belli* the nephridia still retain the spermiducal function which they have in many Chaetopods. The position of the nephrostomes just back of the ovaries recalls the condition seen in many Chaetopoda; although the oviducal function has been transferred to the median unpaired opening of the body-cavity.

The occurrence of but a single pair of nephridia is, of course,

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rent must pass through the tubules from the body-cavity to the exterior. Hence the view that the tubules may be respiratory in function has no foundation whatsoever.

no objection to the view here advocated, since several Annelids have only a single pair of these organs. Moreover the Myzostomes have in all probability undergone a very great reduction in the number of segments, and we should, of course, expect a concomitant reduction in the number of pairs of nephridia.

4. The segmental sacs (»suckers«). These prominent organs have not escaped the attention of any of the more careful students of the Myzostomidae, but hitherto all attempts at an interpretation of their morphological significance have failed. Many authors have regarded them as suckers, but observation of the living animal readily shows that they have no adhesive function, and the name is only another instance of the misleading nomenclature which has been employed in naming the organs of the Myzostomidae.

The best and most recent description of the segmental sacs is given by NANSEN ('85, pag. 42—44 and 76—77). I quote from his English resumé (pag. 76): »What previous writers have called »suckers« are not really such, but ciliated glandulous sacks, as illustrated in Pl. 8 Figs. 19 and 20. There are no muscular walls such as GRAFF has described. The inner walls consist of a glandulous tissue, with large cells situated in one, or several layers; this tissue is covered by a ciliated cuticle, which is striated by the cilia penetrating into the tissue, vide Figs. 19 and 20. Only a few muscular fibres occur in the walls of the sacks, and those are usually dorso-ventral muscles which penetrate through the glandulous tissue and are secured to the cuticle by their extremities, vide Fig. 20*m*. In *M. glabrum*, the glandulous tissue is separated from the surrounding connective-tissue by a cuticle, on whose exterior side several muscles are situated, and I have not observed such a clearly defined cuticle in the other species examined. In the surrounding connective-tissue, vacuoli frequently occur. Among the glandulous cells, connective-tissue nuclei can be seen; this is especially the case in *M. graffi* and *M. giganteum*. — The openings of these sacks are, more or less, prominent in the various species, and the thickness of their oval margins also varies very much, vide Pl. 8 Figs. 19 and 20. The form of the opening is in some species circular (e. g. *M. cirriferum*, Fig. 22), and in others oval (e. g. *M. giganteum*, Fig. 21). The openings are provided with sphincters, which vary in development in the various species; in some species they are few in number, and thick (e. g. *M. cirriferum*, Fig. 20*sph*), whilst in other species they are more numerous, but are then less developed in thickness (e. g. *M. giganteum*, Fig. 19).

Round the openings radial fibres also occur whose function is to act as dilatares, vide Fig. 18 *m*, *m'*; Figs. 21 and 22.α

NANSEN is inclined to regard the segmental sacs as modified nephridia. The obvious objection that they have no communication with the body-cavity, he attempts to remove by referring to the antennal and shell-glands of Crustacea. He would regard the large cells forming the walls of the sac as glandular and believes that they secrete the mucous-like granules (vide his Fig. 19 Pl. 8) which he finds in the cavity of the sac and among the cilia covering its cuticular lining. He does not allude to a further objection to his view, viz. the obviously ectodermal origin of the segmental sacs.

Although my own study of the segmental sacs is still far from being completed, I have thought it best to give in this connection a brief sketch of their occurrence, structure, etc., reserving a fuller and more accurate account for future publication. The organs in question occur in nearly all, if not in all species of *Myzostoma*, but the extent to which they may be developed, is highly variable. In general they may be said to be largest in the free-living species and reduced to mere rudiments or altogether absent (?) in the cysticolous and entoparasitic forms. But that their reduction is not due exclusively to cysticolous habits is shown by *M. platypus*, which has the largest and most elaborate segmental sacs hitherto observed in any Myzostome. On the other hand, in the active *M. cirriferum* the sacs are scarcely as well developed as in the sluggish species like *M. glabrum* and *alatum*. The extent to which the organs may vary in structure will be seen from the following description of four species, which really present four distinct types of segmental sac:

*M. platypus*. v. GRAFF who first described this species was impressed with the large size and odd appearance of its »suckers« and suggested that a careful investigation might »yield some answer to the questions raised by NANSEN in regard to the function and morphological import of these organs«. Among my many sections I have found several which show the histological structure of the sacs fairly well — notwithstanding the rather poor and protracted preservation.

Each of the 8 sacs projects as a flat-topped circular tubercle above the general level of the ventro-lateral surface of the animal's body. The center of the tubercle is formed by a smoothly rounded boss, surrounded and partly enclosed by a thick sphincter-like ring, the surface of which is furrowed by two concentric circular grooves



and thus divided into three flange-like rings, the median of which is the most prominent (Pl. 11 Fig. 27). A longitudinal section through a sac (Fig. 29) shows that the organ is readily reducible to the form of sac found in *M. cirriferum* and other species (cf. NANSEN'S '85, Fig. 20 Pl. 8). The central boss may be pushed out of the orifice of the sphincter-like ring just as the flattened or concave floor of the organ may be everted in *M. cirriferum*. Scattered testicular follicles (*ts*) and even some of the terminal ramifications of the intestine may extend into the parenchyma of the base of the sac. Numerous refractive bright yellow granules (*y*) are found in the boss and the middle flange of the sphincter-like ring.

The complicated structure of the boss is shown under a high magnification in Fig. 30. In this figure, which shows only a portion of the section, a number of layers may be distinguished running parallel to the surface of the boss. The outermost layer is a distinct cuticle (*ct*) which very probably bears cilia in the living animal. Beneath it lies a much thicker zone (*str*) with alternate bands of more and less deeply staining fibres. This zone is limited internally by a thin layer of delicate fibres running parallel to the surface cuticle. Then follows a broader band bounded in turn by transverse fibres with small deeply staining nuclei. Radial lines traverse this zone and are continued inwards through the zone of small nuclei into the contours of huge elongated cells, which take up the greater portion of the section. The nuclei of these cells (*n.gl*) form a more or less irregular zone beyond which the cytoplasm is filled with the deep yellow granules. Under the higher magnification the granules appear as concretions with irregular but rounded outlines. The larger granules seem to consist of clusters of smaller granules. Each granule or concretion seems to be surrounded by a narrow pale space. In some cells a few of the granules may extend out beyond the nuclear zone. Long and very attenuate and more deeply staining cells with small deeply staining nuclei (*sm*) are interspersed between the large cells. The attenuate cells, which I take to be smooth muscle fibres — the retractors of the boss — are seen in Fig. 29 extending back into the parenchyma from the middle of the boss. I failed to resolve the inner ends of the large cells which merge into the parenchyma cells constituting the base of the organ. Through this parenchyma smaller yellow granules are scattered.

If the yellow granules occurred only in the large cells of the boss, we might perhaps see our way to a solution of the function

of the sac as a kind of gland, but granules of exactly the same kind are deposited, often in conspicuous masses, in the outer parenchyma of the sphincter-like ring (Fig. 29), in the cordate elevations at the bases of the parapodia and in other portions of the animal's body. This, together with the fact that these granules seem never to be excreted from the body, leads me to suspect that they are pigment granules.

*M. glabrum*. In sections the retracted sacs of this species appear as spherical or pear-shaped bodies with walls so thick that the cavity is obliterated or reduced to an irregular ramifying slit between the folds of the walls. The walls themselves consist mainly of large succulent cells which undoubtedly correspond to the large gland-like cells of *M. platypus* and which in some iron-haematoxylin specimens are full of very fine black granules. These granules, however, resemble densely aggregated cytomicrosomes rather than the secretion-granules of gland-cells. Peripherally the succulent cells are covered with a dense striated cuticle, which probably bears rigid cilia in the living *Myzostome*. To this cuticle are attached the radial muscle fibres that run between the large succulent cells and function as retractors of the walls of the sac. In sections stained with iron-haematoxylin these fibres are often colored black, while the intervening cells stain much more faintly. When the sac is everted it forms a somewhat irregularly folded fungiform elevation on the surface of the body.

*M. cirriferum*. In this species the sacs are flattened and have a distinct cavity and much thinner walls than in the preceding species (vide NANSEN's Fig. 20 Pl. 8). The rigid cilia covering the cuticular lining of the sac are very distinct, while the large cells of the walls are much vacuolated. These vacuoles are probably produced by the sudden withdrawal of the water from the succulent cells during preservation. The retractor and sphincter are correctly represented by NANSEN.

*M. pulvinar*. In this species the sacs were said to be absent by v. GRAFF ('84b), but PROUHO has succeeded in detecting them ('92). In hardened specimens they are readily found as small white spots not far from the reflected edge of the body in the dorsal (morphologically ventral) surface (Pl. 12 Fig. 41). In sections each spot is seen to correspond to a small pit or dimple which is covered with rigid cilia. Beneath the dimple the parenchyma or, more probably what corresponds to the remains of the large succulent

cells of the other species, is reduced to a number of vacuoles between which runs a coarse net-work. Beyond this I was unable to make out any structure in these rudimental organs.

What is the function of these segmental sacs? From their ectodermal origin they may be glandular, sensory or respiratory in function. Their structure is obviously ill-adapted to respiration, so that this possibility may be excluded. It is much more difficult to decide between the two remaining functions.

When I first saw these organs, I was inclined to accept NANSEN's view that they are excretory or secretory in function. Not having seen the nephridia at that time, I proceeded to test the validity of the Norwegian zoologist's view by placing a number of specimens of *M. glabrum* for 24 hours in sea-water containing powdered carmine. By the end of that time the sacs stood out as four deep red spots along either side of the body, and I at once concluded that the carmine had been taken up through the intestine and deposited in the walls and cavities of the sacks. A single series of sections, however, soon proved to me that I was entirely mistaken; there was a small amount of carmine in the intestine and its branches, but none whatever in the cytoplasm of the large succulent cells forming the walls of the sacks. The cavities of the sacks and the spaces between the folds of their walls were full of carmine, but it had been drawn in from the outside, probably by a movement of the cilia surrounding the sacs and by the inversion of the sacs themselves. This experiment was repeated several times. In many cases the animals would not swallow the carmine, but their suckers would take it up nevertheless. These experiments, besides showing that the sacs are probably not nephric organs, will explain the presence of the mucous granules of NANSEN in the cavity. These are very probably only secretions of the true nephridia or feces which have been taken in from the outside. If a *M. glabrum* be placed on its back and the orifices of its segmental sacs carefully examined with a lens, one will often see a few granules of matter thrown out of a sac, especially when it is about to be everted. These granules I take to be the same as those figured by NANSEN.

The second alternative, viz. that the segmental sacs may be sense-organs, seems to me to be more plausible. I take them to be in all probability the homologues of the lateral line organs (Seitenorgane) which have been described in many Chaetopods (Capitellidae, EISIG '79,'87; Polyophtalmidae, E. MEYER '82; Amphi-



ctenidae, E. MEYER; Glyceridae, EISIG '87; Naidae, SEMPER '76; VEJDOVSKY '84). The facts which seem to me to favor this homology are the following:

1) The sacs of the Myzostomidae are metameric and lie lateral or dorsal to their respective parapodia like the Seitenorgane of Capitellidae.

2) The segmental sacs like the Seitenorgane are eversible and provided with a special set of retractor muscles (EISIG's Haarfeld-retractor).

3) The general structure of the segmental sacs is not unlike that of the »Seitenorgane« as described and figured by EISIG. In both cases the well-developed cuticle covering the surface of the organ is provided with cilia which are easily destroyed by reagents and are very probably not motile, but sensory in function. The large gland-like cells in the sacs may be in reality ganglionic — at least they closely resemble the cells which NANSEN regards as parapodial ganglia. If this is the case, they would probably correspond to EISIG's »Körnerzellen«. It may also be remarked that EISIG found yellow granules in the Seitenorgane of Capitellids, and we have seen that yellow granules also occur in the segmental sacs of *M. platypus*.

The all-important point in the homology, viz. the presence of a nerve supplying the large cells of the segmental sac, I have not yet been able to establish; but it should be remembered that it is no easy task to detect the nerve which supplies the lateral line organ of the Chaetopods. Unfortunately it did not occur to me while at Naples that the segmental sacs might be sensory, and so the opportunity of employing methylene blue and GOLGI's method on fresh material was allowed to escape.

EISIG has extended the homology of the »Seitenorgane« of Chaetopods to the lateral line organs of Vertebrates. It seems to me that it may be extended also to certain organs in the Arthropoda. Certainly in the embryo *Limulus* the organs designated as sensory by PATTEN ('89, '90) and KINGSLEY ('90, '92, '93) have a striking superficial resemblance to the segmental sacs of *Myzostoma*. The exact nature of these organs is extremely doubtful, and the difficulty of deciding between the same alternatives which have just been discussed, is apparent in KINGSLEY's paper. After speaking of these organs in 1890 as »plainly sensory«, they subsequently become »more

probably glandular<sup>1</sup>. Both PATTEN and KINGSLEY agree, however, that one pair of these organs (viz. the fourth) gives rise to the so-called »dorsal organs« of *Limulus*. This fact is of interest, for if these organs in *Limulus* be really embryonic lateral line organs, we may yet be able to trace out the phylogenetic history of such enigmatical structures as the paired »dorsal organs« of *Mysis*, the paired lobulated outgrowths on either side of the head in the embryo *Asellus*, etc.

The fact that in *Myzostoma* there are five pairs of parapodia, but only four pairs of segmental sacs, naturally leads to the question as to what has become of the missing pair of sacs. The answer to this question I believe we need not go far to seek: the third pair of the original five pairs of sacs has been converted into the so-called penes. These are more or less prominent papillae lateral to and near the bases of the third pair of parapodia. Each papilla is perforated by a ductus ejaculatorius which widens proximally into a vesicula seminalis. The latter receives the mature spermatozoa from the vasa deferentia and these in turn from the ramifying testicular follicles<sup>2</sup>.

Bizarre as the development of a male reproductive organ from a lateral line organ may appear at first sight, I am nevertheless unable to see any great difficulty in such a change of function. It is in fact easy to see how the bottom of an eversible sac might acquire an opening into the body-cavity under the pressure of a great accumulation of spermatozoa; the sac would then become reduced to a mere conduit. The histological difficulties are not insuperable, for the large infolded ectodermal cells which form the walls of the ductus ejaculatorius may be homologized with the large succulent cell forming the walls of the segmental sacs. Another fact which supports the view here advocated is the correlative variation of the segmental sacs and penes in different species of *Myzostoma*. In *M. platypus* e. g., where the sacs are extremely large, the penes also attain to extraordinary dimensions, whereas both sets of organs become

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<sup>1</sup> Cf. also KINGSLEY's remarks at pag. 538, '90; pag. 51 and 52, '92, and pag. 222, '93.

<sup>2</sup> It is hardly correct to call the papillae penes, since the Myzostomidae do not copulate. Even in *M. platypus*, where these organs are enormously developed, they are apparently only intended to be thrust through the orifice of the gall to disseminate the spermatozoa in the sea-water.

rudimental or obliterated concomitantly in some cysticolous and entoparasitic *Myzostomes* (e. g. *M. pulvinar*).

BEARD ('84) has given a very different interpretation of the male ducts from the above. After attempting a reduction of the oviduct (i. e. the median dorsal opening of the body-cavity) to a pair of nephridia, he goes on to say (pag. 566) that the »two male ducts are much more easily referable both from position and structure to segmental organs which still open into the body-cavity«. While the reduction of the oviduct to a pair of nephridia hardly requires serious consideration, the homology of the male ducts with nephridia is not so easily refuted. As BEARD himself, however, now interprets NANSEN'S lateral oviducts as nephridia ('94), he would probably abandon these earlier homologies, unless, indeed, he should assume that two pairs of nephridia have been retained in the *Myzostomidae*.

5: Parapodia and Cirri. The resemblance of the cirri and parapodia of *Myzostoma* to the homonymous structures of the Chaetopoda has often been pointed out, and I should not here allude to the subject, were it not to call attention to two structures which have not been sufficiently considered by preceding authors and which make the resemblance still more striking. The first structure is the ventral cirrus of the parapodium. This I believe to be present in at least two, and possibly in three, species of *Myzostoma*. In *M. circinatum* the small, pointed and somewhat curled cirri inserted on the inner bases of the parapodia (Pl. 10 Fig. 18) are in all probability typical ventral cirri, readily homologized with the ventral cirri of Polychaeta. In *M. platypus* (Pl. 11 Fig. 27) the heart-shaped elevations with broad bases of attachment are probably only another form of ventral cirri, which, curiously enough, seem to have undergone a modification comparable to that of the dorsal cirri (elytra) in Chaetopods like *Lepidonotus* and *Tomopteris*. I also deem it probable that the peculiar pedunculate cups at the bases of the parapodia in *M. calocotyle*, v. Graff may represent a third form of ventral cirri. v. GRAFF ('84b, Pl. 3 Figs. 25 and 26) regarded them as »suckers«, but I find it very remarkable that segmental sacs should occur, not between and some distance dorsal to the parapodia, but attached to the bases of the parapodia. Moreover v. GRAFF figures five of these cup-like organs on one side of the body!

That the twenty cirri which fringe the edge of the disc-like body in most *Myzostomes* are to be regarded as homologues of the



dorsal cirri of Chaetopods, is highly probable. If, then, we take into consideration the segmental sacs and their homology with the dorsal cirri of neural parapodia — a theory advanced by EISIG ('87) and supported by his own observations and those of EHLERS ('64) and CLAPARÈDE ('68) on species of *Glycera*, in which it is possible to trace the gradual reduction and transformation of the cirri into organs like those of the lateral line — we have the following homologies between the Chaetopoda and Myzostomidae:

| Chaetopoda                                    | Myzostoma                       |
|---|---------------------------------|
| ventral cirrus . . . . .                      | ventral cirrus (usually absent) |
| neural parapodium . . . . .                   | parapodium                      |
| lateral line organ . . . . .                  | segmental sac                   |
| (modified dorsal cirrus of neural parapodium) |                                 |
| haemal parapodium . . . . .                   | absent                          |
| dorsal cirrus . . . . .                       | two or more dorsal cirri.       |

The second point to which I would call attention, concerns the secretion of the hooks, reserve hooks and supporting rods of the parapodia in *Myzostoma* as compared with the secretion of the setae in Chaetopods. The minute structure of the hooks etc. in *Myzostoma* is thus described by NANSEN ('85, pag. 77): »The hooks are not, as GRAFF states in his monograph, hollow, but consist of two layers; an outer, somewhat homogeneous layer and an inner one composed of fibrous substance. The outer layer has a yellow colour and is very slightly staining; it is very thin at the base of the hooks, but increases, gradually, in thickness towards the extremity, and the acuminate extremities of the hooks become formed, thus, almost exclusively by this layer, and acquire, also, a more intense yellow colour, especially in the more developed hooks. The inner fibrous mass consists of colourless fibres, which are thickest in the center of the hook and, on transverse sections, exhibit a distinct hexagonal form, vide Pl. 7 Fig. 19. Towards the outer layer these hexagonal fibres become so minute that they are with difficulty distinguishable. This fibrous mass is, usually, vividly stained by colouring reagents. The structure of the supporting rod is similar to that of the hooks, and the manubrial plate is composed of the homogeneous yellow substance of the outer layer.«

This description, which I am able to confirm from my own observation, shows clearly that there is no essential difference between

the minute structure of the *Myzostome* and *Chaetopod* seta<sup>1</sup>. Such being the case we should expect to find a great similarity in the structures which secrete the setae in both cases. It is well known from the researches of LEYDIG (*Phreoryctes* '65, pag. 256); CLAPARÈDE (*Terebella* '73); PERRIER (*Lumbricus* '74, pag. 347); SPENGLER (*Echiurus*, *Bonellia* '80, pag. 478—484); VEJDOVSKY (*Dendrobaena*, *Lumbricus* etc. '84) and EISIG (Capitellidae '87, pag. 575—576) that each seta is secreted by a single large cell situated in the fundus of the seta-sac. In all *Chaetopods*, so far as known, this »Basalzelle« has more or less the form of a plano-convex lens with its flat side covering the truncated proximal end of the seta which its cytoplasm gradually secretes. In *Myzostoma* also each of the modified setae is secreted by a single large cell, but this cell, instead of having the form of a plano-convex lens, is pear-shaped and hangs by a thin pedicel to a much flattened disc-like plate of cytoplasm covering the truncated end of the seta. One of these cells is seen at *st.c* in Pl. 11 Fig. 25. The constant association of these cells with the setae, their large size and characteristic glandular appearance, leaves no doubt that they are the homologues of the »Basalzellen« of *Chaetopods*. These pear-shaped setiparous cells are figured by NANSEN, and he says at pag. 77: »I have frequently observed at the upper extremity of the supporting rods large unipolar cells, with their prolongations directed towards the extremity of the rods (Pl. 7 Fig. 22 *a.b*), but I have been unable to determine in what manner these prolongations terminate, or what is their physiological function.«

PERRIER observed in the earthworm ('74, pag. 347) and EISIG in Capitellids ('87, pag. 576) certain appearances in the nuclei of the basal cells which led them to infer that the nucleus is concerned in the process of secreting the seta. The position of the rather small nucleus in the broadened bulb-shaped end of the basal cell in *Myzostoma*, and its distance from the secreting cytoplasmic plate does not favor PERRIER's and EISIG's view, but a careful study of the nucleus and cytoplasm will have to be undertaken before any definite statement can be made on this point.

6. The strong *Chaetopod* affinities of *Myzostoma* are further shown by their resemblance to the *Polychaeta* of the genus *Spinther*. v. GRAFF has called attention to the resemblances in the closing paragraph of his interesting monograph of the

<sup>1</sup> The similarity is clearly recognized by EISIG '87, pag. 576.

genus ('88, pag. 61). Both *Myzostoma* and *Spinther* have arisen from Polychaete ancestors, but both have taken to parasitism — *Spinther* to living on Sponges and *Myzostoma* on Crinoids — with the result of an interesting parallelism in structure. Although *Spinther* has retained a greater number of segments (from 12 in *S. miniaceus* to 52 in *S. arcticus*) than *Myzostoma*, both forms have tended to depart from the elongate Annelid type and to assume a flattened form and more radial symmetry. In *Spinther* the reproductive orifice lies in the mid-dorsal line just above the anus and the intestine sends out a pair of diverticula in each segment except in the posterior end of the body. »Endotheliale Septa zwischen den einzelnen Segmenten sind nicht vorhanden und nur die zwischen den Darmdivertikeln verlaufenden dorsoventralen Muskelbündel stellen eine unvollständige Kammerung des Leibesraumes dar.« The parapodia with their hooked setae and dorsal cirri, and the general appearance of the body-cavity with the sexual products accumulated in the portion dorsal to the intestine recall the conditions seen in *Myzostoma*. *Spinther* has no nephridia according to v. GRAFF, and he has not succeeded in finding the ovaries and testes, although it is possible that certain clusters of large »indifferent cells« in the ventral portion of the body-cavity between the intestinal diverticula and between these and the integument may be the organs in question.

### Résumé and Conclusion.

For the sake of a more graphic expression of the sexual phases of *Myzostoma* I give two diagrams, Pl. 12 Figs. 57 and 58; the former representing the conditions in species like *M. cirriferum* and *glabrum*, the latter in *M. pulvinar* and probably many of the *Cysticola* which have been supposed to be dioecious. To begin with Fig. 57, the whole triangle *akm* may be taken to represent the whole of the reproductive system from its first appearance in the embryo, or trochophore (at *a*) to its development in the adult, when it may be represented by the line *km*. The unshaded triangle *abc* may be regarded as the sexless, neutral, or undifferentiated condition of the reproductive cells (gonoblasts) and the two parts of the line *bc*, viz. *bo* and *oc* as the ultimate division into spermatogonia on the one hand and oogonia on the other. The dark triangle *boh* represents the male, the paler trapezium *cokm* the female organs. The lighter region *boed* of the male triangle represents the period preceding the appearance of the



mature spermatozoa, the deeply-shaded triangle *beh* the gradually diminishing male organs after the appearance of mature reproductive cells. Similarly the region *cofgm* would represent the period preceding the appearance of the first mature ova, the triangle *fkjg* the period of maturity. As there are very probably many immature ova still present in the ovaries and body-cavity at death, I have extended this region to *gm* in the line *km*. Thus four distinct phases may be recognized in the life of these Myzostomes:

- 1) A phase of sexual neutrality, or indifference.
- 2) A protandric phase extending from the appearance of the first ripe spermatozoa to the appearance of the first ripe ova (♂).
- 3) An androgynous or functionally hermaphrodite phase extending from the appearance of the first ripe ova to the disappearance of the last ripe spermatozoa (♂♀).
- 4) A hysterogynous phase extending from the disappearance of the last spermatozoa to the disappearance of the last ripe ova — an event which is very probably not attained at the time of the animal's death (♀).

A comparison of this schema (Fig. 57) with Fig. 58 shows at a glance the peculiarities of forms like *M. pulvinar*. The same methods of shading indicate the morphologically equivalent regions in both diagrams. In *M. pulvinar* the male phase is very short and terminates at *h* before the retarded appearance of the first mature ova at *f*; so that this species lacks a functionally hermaphrodite stage corresponding to ♂♀ in the schema of *M. glabrum*, and there intervenes a period during which the animal grows, but does not produce ova or spermatozoa. Hence, when a number of specimens are examined, this sharp separation of the male and female phases in time has the same superficial appearance as the separation in space in gonochoristic forms with dwarf males<sup>1</sup>.

The genus *Myzostoma* is by no means exceptional in presenting this form of dichogamy, viz. the sequence of protandry, functional hermaphroditism and hysterogyny: an exactly similar asynchronism

<sup>1</sup> *M. pulvinar* is certainly peculiar in exhibiting two well-marked periods of sexual maturity during its life-time. In this respect it resembles the cases of dissogony which occur among the Ctenophora. In *M. pulvinar* the periods are functionally unisexual, in the Ctenophora functionally hermaphrodite.

and sequence in the ripening of the sexual products has long been known to occur in many other hermaphrodite Metazoa<sup>1</sup>.

How is this asynchronism in the maturation of the sexual products to be explained? Some authors, approaching the phenomenon from the physiological side, would regard it as due to an unequal distribution of nutriment to the reproductive organs: during one period

<sup>1</sup> Omitting all reference to the general statements concerning dichogamy to be found in our standard text-books of Zoology, I give here a list — probably very incomplete — of the cases which I have been able to gather from special papers, for the purpose of showing the wide distribution and frequency of the phenomenon. Several of the references have been drawn from recent papers by PELSENEER ('94) and MONTGOMERY ('95):

**Porifera:** *Spongilla* (C. KELLER '78); *Aplysilla* (v. LENDENFELD '83, pag. 261).

**Cnidaria:** *Hydra* (ECKER '53; MARSHALL '82, pag. 669).

**Platyhelminthes. Acoela:** *Convoluta* (CLAPARÈDE '61, pag. 128); **Rhabdocoela:** *Graffilla* (BÖHMIG '86, pag. 315; v. IHERING '80, pag. 147); *Promesostoma* and *Macrostoma* (v. GRAFF '82, pag. 127); *Stenostoma* (J. KELLER '94, pag. 377 and 398); **Tricladidea** (HALLEZ '79, pag. 43); *Bipalium* LOMAN ('88); **Polycladidea** (LANG '94, pag. 1091); **Trematoda** (ERCOLANI '82, pag. 43); **Cestoda:** *Solenophorus* (ROBOZ '82, pag. 263); **Nemertini:** *Pro-rhynchus* (v. KENNEL '83; MOORE '95); *Tetrastemma* (MARION '74); *Stichostemma* (MONTGOMERY '94 and '95).

**Nematoda:** *Allantonema* (LEUCKART '87); *Filaria* (ZUR STRASSEN '91, pag. 439).

**Annelida. Polychaeta:** *Ophryotrocha* (KORSCHOLT '93); **Myzostomidae:** *Myzostoma* (PROUHO '92; WHEELER '94).

**Mollusca:** *Limnaeus* (EISIG '69); *Agriolimax agrestis* and *melanocephalus* (BABOR '94); *Cymbulia* (LEUCKART '54); *Cymbuliosis* (PECK '90); *Desmopterus papilio* (CHUN '89); *Clione limacina*, *Clio striata*, *Lobiger*, *Eolis*, *Elysia* (PELSENEER '94); *Entoconcha* (J. MÜLLER '52); *Neomenia* (WIRÉN '92); *Solenopus* (KOREN & DANIELSSEN '77); *Ostrea edulis* (DAVAINE '53; P. J. VAN BENEDEN '55).

**Echinoderma:** *Asterina gibbosa* (CUÉNOT '88; LANG '94, pag. 1091); *Synapta*, *Anapta*, *Chirodota* (LANG '94, pag. 1091); *Amphiura squamata* (LANG '94, pag. 1091).

**Crustacea.** Cymothoidae: *Neroëla*, *Cymothoa*, *Anilocra* (BULLAR '76 and '77; PAUL MAYER '79); Cryptoniscidae (KOSSMANN '84).

**Chordata:** *Myxine glutinosa* (CUNNINGHAM '87 and NANSEN '88); *Chrysophrys* (BROCK '78).

Protogyny, or the opposite sequence in the maturation of the sexual products, i. e. the earlier maturation of the female and later maturation of the male cells, is very rare in the animal kingdom. The only cases which I have met with are those cited by PELSENEER ('94) and MONTGOMERY ('95), viz. the Turbellarian *Microstoma lineare* (RYWOSCH '87 and '89), the Pulmonates *Limax maximus*, *Malacolimax tenellus* (BABOR '94) and *Agriolimax laevis* (BABOR '94 and BROCK '86) and the Tunicate *Salpa* (KROHN '46). A similar preponderance of the protandrous over the protogynous sequence has been observed in flowering plants.

of the hermaphrodite's existence the reproductive system may receive less, during another period more nutriment. Hence the animal will produce first spermatozoa and then ova. This dichogamy, especially in parasitic animals, is assumed to depend also on another factor, viz. the necessity of producing an immense number of ova and spermatozoa, for the vicissitudes of parasitic life are so great that only a few of the many eggs can ever reach their full development. Therefore the animal must begin very early and continue throughout life to produce reproductive elements. And although perhaps provided with an abundance of food, much of this must be utilized in the processes of growth and only a small residuum is available for the production of the less expensive reproductive elements, the spermatozoa. As the animal approaches its adult stature, however, and growth is nearly completed, it can spare more material for the production of the more expensive yolk-laden ova.

Other authors are inclined to believe that dichogamy, being obviously conducive to cross-fertilization, has therefore been produced by natural selection from chance variations in the time of maturation of the reproductive cells. The advantages of cross-fertilization appear to have been demonstrated in some cases, but a fact which I have often observed in *M. glabrum* — viz. that the eggs are fertilized as readily with the spermatozoa of the same individual and develop as rapidly and normally as eggs fertilized with the spermatozoa of other individuals — leads me to believe that the above mentioned physiological causes are the fundamental ones, and that the advantages which may in some cases result from dichogamy are accessory. In other words: cross-fertilization may be the consequence of physiological causes of a nutritive character, and this consequence may not be inevitable, as is shown in some cases (*M. glabrum* and the yuccas among plants), where the functional male and functional female stages of the same individual coincide or overlap, and thereby admit of self-fertilization.

In this connection it is, perhaps, admissible to add a few remarks on a question concerning which there is still considerable difference of opinion among zoologists, the question as to whether hermaphroditism or gonochorism is phylogenetically the more primitive condition in the Metazoa. The majority of zoologists maintain that the Metazoa were originally hermaphrodite and that the dioecious forms have been derived from these by the suppression of one set of reproductive organs, the female individual



having lost its male organs, the male the female organs which it originally possessed. The opposite view, viz. that hermaphroditism is a secondary condition brought about by the acquisition of the organs of the opposite sex in animals originally dioecious or gonochoristic, has been advocated by BEARD ('84), FRITZ MÜLLER ('85) and DELAGE ('84), and more recently by PELSENEER ('94) and MONTGOMERY ('95). To these investigators, especially to BEARD and FRITZ MÜLLER, the Myzostomes appeared to be very important, since they were supposed to present the transitions from gonochoristic to hermaphrodite forms through species with »complemental males«. These last were naturally supposed to represent the evanescent rudiments of a sex whose essential organs had been, so to speak, grafted on to the reproductive organs of the female individual. In species like *M. cirriferum* the male individuals were supposed to have been completely eliminated.

NANSEN'S objections to this view ('85, pag. 79 and 80), together with the facts recorded in the present paper, show clearly that the Myzostomes can no longer be used as evidence of the derived nature of hermaphroditism. I do not by any means believe that this withdrawal of the Myzostomes is a death-blow to the general hypothesis of BEARD and FRITZ MÜLLER; on the contrary, the evidence still remaining, especially that contained in the latter author's paper and in PELSENEER'S interesting contribution, has considerable weight and is calculated to shake our faith in the older and wider spread doctrine of the phylogenetic derivation of gonochorism from hermaphroditism<sup>1</sup>.

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<sup>1</sup> The advocates of this older view have always laid considerable stress on the hermaphrodite characters of the embryos of gonochoristic animals. This subject, it seems to me, is in urgent need of thorough and critical reinvestigation. The facts themselves are far from being satisfactorily established, and the use of terms is often very loose and unscientific. To give only two instances: the stage of sexual neutrality or indifference in the embryos of gonochoristic animals is often called hermaphrodite. But we are not justified in using this term to describe the undifferentiated sexual Anlage which may be converted under certain conditions, as yet very imperfectly known, into a male and under other conditions into the female reproductive organ. This is perhaps as great an absurdity as to say that water is a compound of ice and vapor, because the liquid is convertible under certain fixed and well known conditions into a solid, and under other conditions quite as definite, into a gas. WATASÉ ('92), too, has called attention to this error.

Then again, several authors, confounding sex and heredity, speak of the cleavage cells of the egg and even of the cells of the adult organism as herma-

MONTGOMERY ('95) has made use of dichogamy in solving this same question. Referring to protandry and protogyny, at pag. 531 he says: »Now we have found that in each phase, the products of the one sex develop earlier than the products of the other sex; accordingly, judging from the well known biogenetic law, that the ontogeny repeats (to some extent at least) the phylogeny, we may logically conclude that the Hermaphroditism of the Metazoa, which present one or another of these phases of sexual development, has been secondarily acquired.« And further on (pag. 531), he becomes more explicit: »There now arises the question: in which sex has the hermaphroditic state been superimposed? In the case of protandric hermaphrodites, since here the male stage appears first in the ontogeny, one must suppose that it has been imposed on the male — that ova have appeared in the testicle, and the individual has thus become hermaphroditic. Similarly, in all cases of Successive Hermaphroditism<sup>1</sup> with perhaps the exception of *Microstomum lineare*, we may consider that here too the Hermaphroditism has been imposed on male individuals. In proterogynic forms on the contrary, the Hermaphroditism has probably been imposed on the female, since here the female stage appears ontogenetically first.«

This is the first attempt to apply the »biogenetic law« to the question at issue, and as such it may not be without interest in these days when some morphologists apply it to everything indiscriminately, and others are becoming more and more cautious in its application. But whatever may be the value of this law in other cases, I believe that it had best have been left unapplied in the present instance. MONTGOMERY overlooks the fact that the animals he is considering are all along hermaphrodite from the first bifurcation of the original sexual Anlage in embryonic life to the time of disappearance of the last spermatozoa — and that hence dichogamy is merely a difference

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phrodite (MARSHALL '93, pag. 15; MACFARLANE '93, pag. 273 et al.) when they mean that these cells contain morphological elements derived from both parents. Thus they virtually say that the soma of a unisexual organism is hermaphrodite, a statement which illustrates inadmissible looseness in the use of the term. Sex being the faculty of producing eggs or spermatozoa, the ovum or spermatozoon as such cannot be said to have sex.

<sup>1</sup> MONTGOMERY's distinction of three forms of hermaphroditism — successive, protandric and protogynic — is somewhat misleading. The occurrence of both ova and spermatozoa in the same gonad or in different gonads in the same individual does not affect the main question, since both ova and spermatozoa have in either case a separate origin from undifferentiated sexual cells.

in the time of maturation of the reproductive cells, and not in the time of the appearance of the two sexual Anlagen themselves. Therefore protandry and protogyny may very well be due to causes of a purely physiological nature — such as those above referred to — and hence fall within the category of phenomena which we are in the habit of calling cenogenetic. It is, indeed, quite conceivable that the maturation sequence may be the very reverse of the phylogenetic sequence. At any rate, I feel convinced that the maturation sequence cannot be used as a safe criterion for determining whether the male or female forms the original basis for a particular case of hermaphroditism.

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## Explanation of the Plates 10—12.

### Reference Letters.

|   |   |
|---|---|
| <i>ac.n</i> nuclei of accessory cells.  | <i>o</i> ovum.  |
| <i>ac.o</i> oral sucker.                | <i>o.a</i> ovum just attached (to peritoneal epithelium).                                 |
| <i>ac.v</i> ventral sucker.             | <i>o.m</i> ovum migrating through the body-cavity.  |
| <i>am</i> parasitic Amoeba.             | <i>oog</i> oogonia dividing.  |
| <i>an</i> anus.                         | <i>o.ut</i> orifice of the uterus.  |
| <i>c</i> food-particles.                | <i>ov</i> ovary.  |
| <i>cl</i> cloaca.                       | <i>ov.a</i> anterior ovary.   |
| <i>coe</i> coelom (body-cavity).        | <i>ov.p</i> posterior ovary.  |
| <i>cr</i> cirrus.                       | <i>p</i> parapodium.  |
| <i>ex.p</i> excretory pore.             | <i>par</i> parenchyma.  |
| <i>f</i> fissures in the ovary.         | <i>pen</i> penis.   |
| <i>gd</i> gonad.                        | <i>p.ep</i> peritoneal epithelium.  |
| <i>gr</i> deeply staining granules.     | <i>pg</i> pigment.  |
| <i>int</i> intestine.                   | <i>ph</i> pharynx.  |
| <i>int.ep</i> intestinal epithelium.    | <i>pst</i> boss of the segmental sac of <i>M. platypus</i> .                              |
| <i>int.r</i> intestinal ramification.   | <i>q</i> pharyngeal tissue drawn into the ventral sucker of <i>Distoma myzostomatis</i> . |
| <i>juv</i> young <i>Myzostome</i> .     | <i>r</i> ring enclosing the boss of the segmental sac.                                    |
| <i>ll</i> lateral edges of the body.    | <i>sep</i> septum.  |
| <i>mm</i> manubrium.                    | <i>s.m</i> smooth muscle cells.   |
| <i>ms</i> muscles.                      |   |
| <i>neph</i> nephridium.                 |   |
| <i>n.gl</i> nuclei of gland-like cells. |   |
| <i>n.n</i> zone of small nuclei.        |   |
| <i>nv</i> ventral ganglion.             |   |

|   |  |
|---|--|
| <i>sp</i> mature spermatozoa.                   | <i>ts</i> testes.  |
| <i>spc</i> spermatocytes dividing.              | <i>ut</i> » uterus «.  |
| <i>spg</i> spermatogonia.                       | <i>v.s</i> vesiculae seminales.                                  |
| <i>spg.p</i> spermatogonia dividing.            | <i>ver</i> small wart-like projections of the dorsal integument. |
| <i>st</i> seta.                                 | <i>y</i> yellow concretions.                                     |
| <i>st.c</i> gland-cell which secretes the seta. | <i>z</i> thickening in the mid-ventral line of                   |
| <i>str</i> striated zone.                       | <i>M. platypus</i> .   |
| <i>s.v</i> ventral body-wall.                   |  |

## Plate 10.

- Myzostoma cirriferum* Figs. 1—17; *M. circinatum* Fig. 18; *M. glabrum* Fig. 19—23.
- Fig. 1. Median portion of a horizontal section through the region of the ovaries of a *M. cirriferum* 1.25 mm long. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .
- Fig. 2. Median portion of a horizontal section through the region of the ovaries of a *M. cirriferum* 1 mm long. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .
- Fig. 3. Transverse section through the middle of the body of a *M. cirriferum* 0.6 mm long. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .
- Fig. 4. Transverse section through the anterior pair of ovaries of a *M. cirriferum* 1.75 mm long. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .
- Fig. 5. Median sagittal section of a *M. cirriferum* 1.75 mm long. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .
- Fig. 6 a—c. Stages in the early growth of the ovum of *M. cirriferum* (corrosive subl. hardening). ZEISS hom. immer.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 7. Five young ova of the same species, hardened in picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 8. A young ovum of the same species. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 9. Somewhat older ovum of *M. cirriferum*. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 10. Ovum in about the same stage as Fig. 9. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 11. Older ovum still showing the enlarged contours of the accessory nuclei. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 12. Young ovum with two nucleoli. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 13. Older ovum with pieces of a spermatozoon in its cytoplasm. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 14. Older ovum with two nucleoli. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 15. Mature ovum. Picroacetic acid. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 16. Transverse section of a *M. cirriferum* 0.35 mm long. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 2 = 530  $\times$ .
- Fig. 17. Next section to the one represented in Fig. 16. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 2 = 530  $\times$ .
- Fig. 18. *Myzostoma circinatum* n. sp. seen from the ventral surface. 10  $\times$ .
- Fig. 19. Transverse section through the region of the ovaries of a *M. glabrum* 1 mm long and attached to the disc of the *Antedon*. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .



- Fig. 20. Horizontal section through the region of the ovaries in a specimen of *M. glabrum* 1.25 mm long. Specimen attached to the disc of the *Antedon*. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100  $\times$ .
- Fig. 21. Transverse section through one of the ovaries of Fig. 19 enlarged. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 1 = 385  $\times$ .
- Fig. 22 a—e. Five oogonia of *M. glabrum* dividing. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .
- Fig. 23 a—h. Seven stages in the development of the oocyte of *M. glabrum*, hardened in corrosive sublimate. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 3 = 730  $\times$ .

## Plate 11.

*M. glabrum* Figs. 24 and 25; *M. platypus* Figs. 26—30; *M. belli* Figs. 31—34;  
*M. cryptopodium* Figs. 35—37.

- Fig. 24. Horizontal section through the ovary and adjacent body-cavity ramifications of *M. glabrum*, showing the migration and attachment of the ova. Length 1.25 mm; specimen from the disc of the *Antedon*. ZEISS obj. D.; oc. 3 = 325  $\times$ .
- Fig. 25. Transverse section through the middle of the body of a specimen of *M. glabrum* 0.35 mm long, attached to the back of an older *Myzostome*. ZEISS obj. D.; oc. 3 = 325  $\times$ .
- Fig. 26. Dorsal view } of *M. platypus*. 10  $\times$ .
- Fig. 27. Ventral view } of *M. platypus*. 10  $\times$ .
- Fig. 28. Transverse section through the middle of the body of *M. platypus*. GUNDLACH obj. 1 inch; ZEISS oc. 3 = 45  $\times$ .
- Fig. 29. Sagittal section of one of the segmental sacs of *M. platypus*. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 2 = 65  $\times$ .
- Fig. 30. Portion of the boss of the sac represented in Fig. 29 more highly magnified. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 2 = 530  $\times$ .
- Fig. 31. Dorsal view } of *M. belli*, n. sp. 10  $\times$ .
- Fig. 32. Ventral view } of *M. belli*, n. sp. 10  $\times$ .
- Fig. 33. Transverse section through the region of the ovaries in *M. belli*. GUNDLACH obj.  $1\frac{2}{3}$  inch; oc. 2 = 65  $\times$ .
- Fig. 34. Transverse section of an ovary of *M. belli*. ZEISS obj. E.; oc. 2 = 390  $\times$ .
- Fig. 35. Lateral view } of *M. cryptopodium*, n. sp. 10  $\times$ .
- Fig. 36. Dorsal view } of *M. cryptopodium*, n. sp. 10  $\times$ .
- Fig. 37. Transverse section through the region of the ovaries of *M. cryptopodium*. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 1 = 50  $\times$ .

## Plate 12.

- M. belli* Fig. 38; *M. eremita* Figs. 39 and 40; *M. pulvinar* Figs. 41—50; *Distoma myzostomatis* Fig. 51; *Amoeba myzostomatis* Figs. 52—56.
- Fig. 38. Section through the ovary of *M. belli*. ZEISS obj. E.; oc. 2 = 390  $\times$ .
- Fig. 39. Dorsal view } of *M. eremita*, n. sp. 10  $\times$ .
- Fig. 40. Ventral view } of *M. eremita*, n. sp. 10  $\times$ .
- Fig. 41. Dorsal view of an adult specimen of *M. pulvinar* with two young attached at *juv.* 10  $\times$ .
- Fig. 42. Ventral view of the same specimen showing one young individual attached. 10  $\times$ .

- Fig. 43. Young *M. pulvinar* (functional male) taken from the back of a large specimen and mounted in balsam. 13 $\times$ .
- Fig. 44. Transverse section of a *M. pulvinar* 2.5 mm long, through the region of the ovaries. GUNDLACH obj. 1 inch; ZEISS oc. 3 = 45 $\times$ .
- Fig. 45. Transverse section of one of the ovaries of Fig. 44 enlarged. ZEISS obj. D; oc. 2 = 240 $\times$ .
- Fig. 46. Transverse section through a young *M. pulvinar* (functional male) 0.7 mm long, in which there are as yet no traces of ovaries or nephridia. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 2 = 65 $\times$ .
- Fig. 47. Transverse section through a young specimen of *M. pulvinar* 0.825 mm long. Ramifications of the intestine appearing. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100 $\times$ .
- Fig. 48. Transverse section through a young specimen of *M. pulvinar* 0.8 mm long. Hermaphrodite stage. GUNDLACH obj.  $1\frac{2}{3}$  inch; ZEISS oc. 3 = 100 $\times$ .
- Fig. 49. The ovaries of Fig. 48 enlarged. ZEISS hom. immers. obj.  $\frac{1}{12}$ ; oc. 2 = 530 $\times$ .
- Fig. 50. Transverse section through the intestine of a young *M. pulvinar* 0.825 mm long, showing the nephridia. ZEISS hom. immers.  $\frac{1}{12}$ ; oc. 2 = 530 $\times$ .
- Fig. 51. Piece of a section through the pharynx of *M. platypus*, showing two young specimens of *Distoma myzostomatis*. ZEISS obj. D.; oc. 2 = 240 $\times$ .
- Figs. 52—55. Sections of eggs from the body-cavity of *M. glabrum*, showing *Amoeba myzostomatis* in the process of perforating them. ZEISS hom. immers. obj.  $\frac{1}{12}$ ; oc. 3 = 730 $\times$ .
- Fig. 56. Section of the ovary of *M. glabrum*, showing two free Amoebae. ZEISS hom. immers. obj.  $\frac{1}{12}$ ; oc. 3 = 730 $\times$ .
- Fig. 57. Diagram to illustrate the sexual phases of *M. glabrum* and allied species. For explanation see pages 288 and 289.
- Fig. 58. Diagram to illustrate the sexual phases of *M. pulvinar* and the cysticolous Myzostomidae. For explanation see page 289.

University of Chicago, Ill., U. S. A., June 1<sup>st</sup>, 1895.



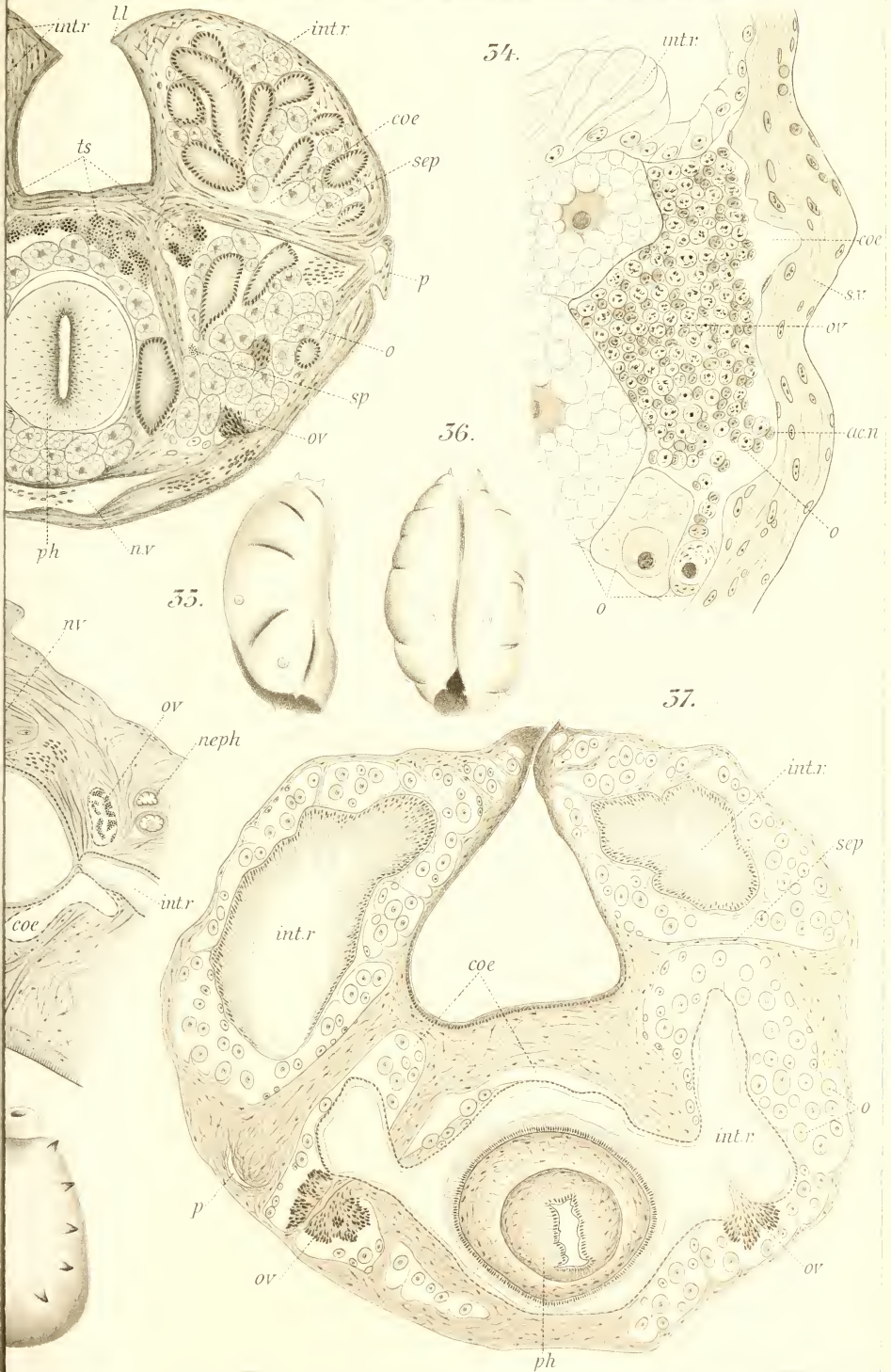




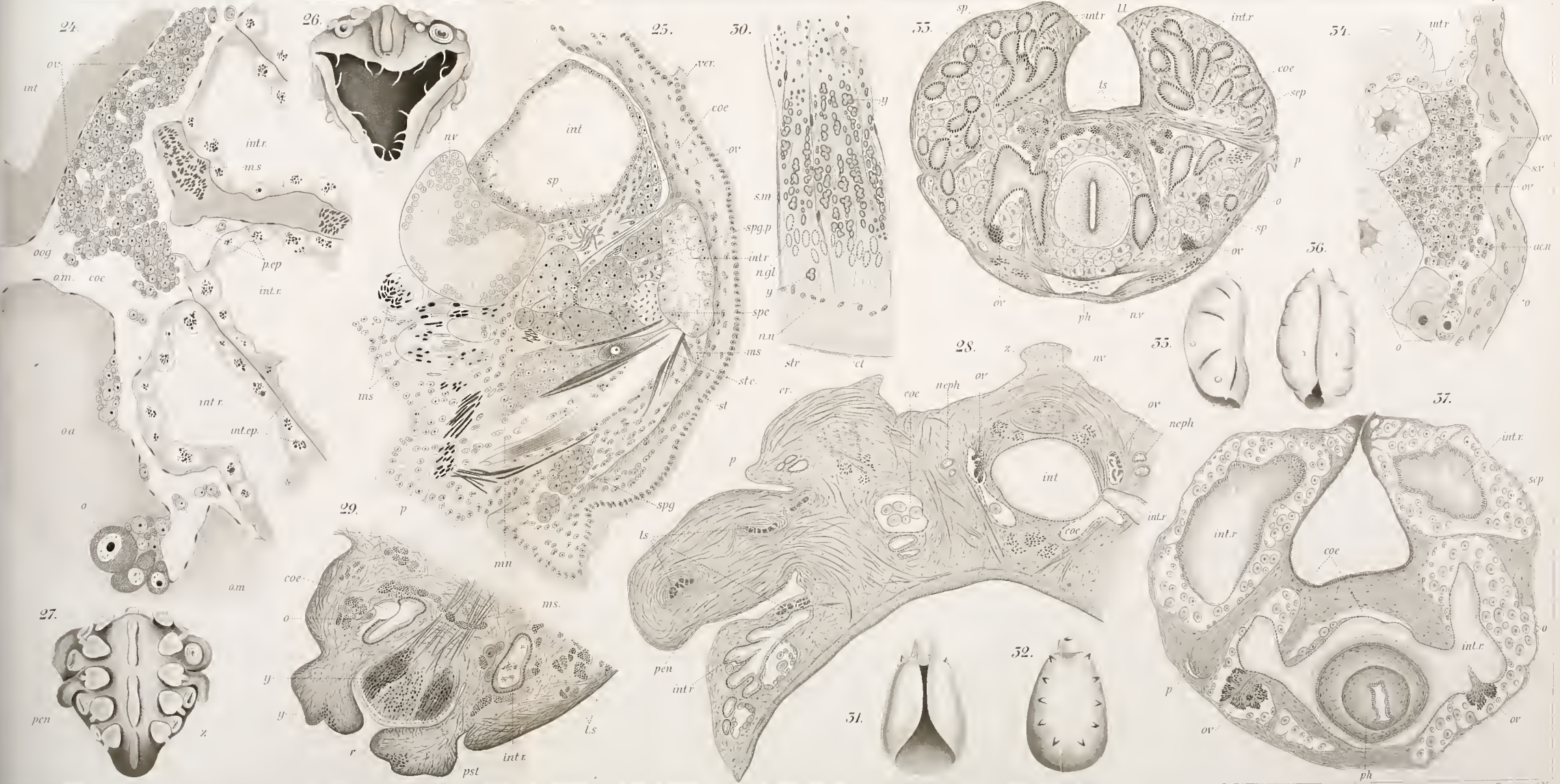






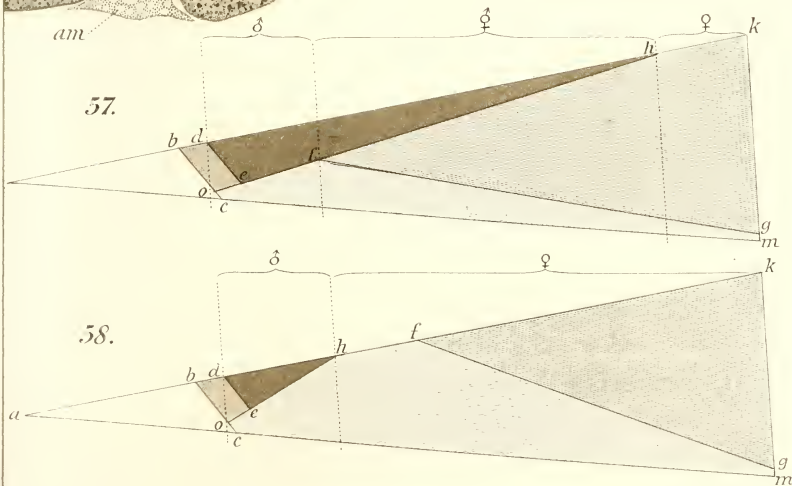
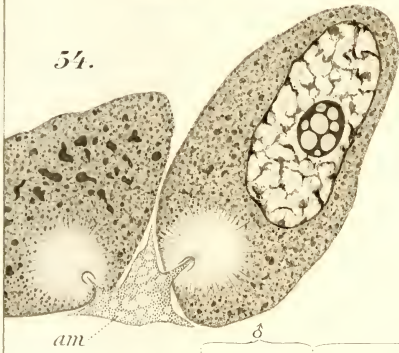
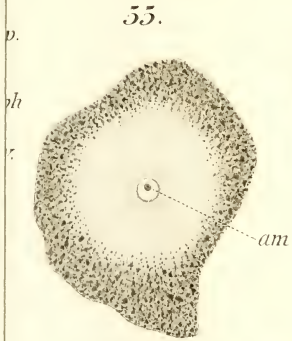
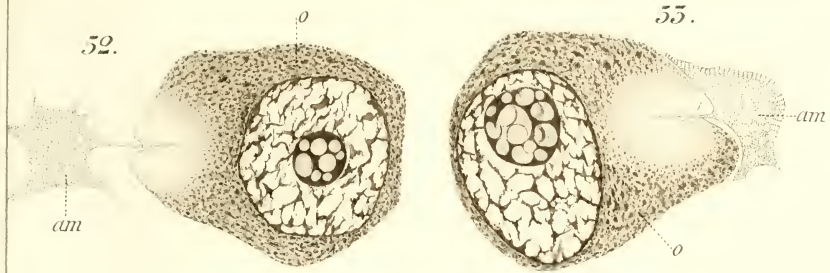


















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Autor(en)/Author(s): Wheeler William Morton

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