On the Structure and Affinities of Mnestra parasites Krohn; with a revision of the classification of the Cladonemidae.

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With plates 2 and 3.

An account of the anatomy and affinities of *Mnestra* was the primary purpose of the present paper; but, during the progress of the work it gradually became apparent that the commonly accepted classifications of the Cladonemidae would be subjected to an undue strain by the foreible introduction of the genus, and that therefore a modified scheme of classification of this family was needed.

It is to be hoped that a more searching investigation of the other Cladonemid genera and especially of the Haeckelian genera may soon be made.

The present research would have been impossible for me had it not been for the facilities afforded by the Naples Zoological Station. Once more I gladly avail myself of an opportunity of thanking my good friends, the Officers of the Stazione Zoologica for their never failing courtesies to me, as well as to my fellow countrymen who have occupied Oxford and British Association Tables at their Aquarium.

Historical.

The discovery of *Mnestra* was one of the aehievements of the three naturalist friends GEGENBAUR, KÖLLIKER and HEINRICH MÜLLER during their sojourn at Messina for the purpose of becoming more

nearly acquainted with the marine fauna of the Mediterranean. In the autumn of 1852 and in February and March 1853 a number of specimens of *Phyllirhoë bucephala* were captured, which were encumbered with a remarkable appendage hanging from the anterior third of the ventral margin of the body.

This "glocken-förmige Anhang" was first chronicled in 1853 by HEINRICH MÜLLER who suggested that it might possibly be an adhering medusa. In the following year it was again described in somewhat greater detail by H. MÜLLER and GEGENBAUR who published the drawing reproduced in figure 37, but although these distinguished observers alluded to the presence in the "Anhang" of refractile bodies resembling nematocysts, they did not venture to give it either a name or a position in the animal kingdom.

In the meantime however KROHN fully recognising an affinity with the Gymnophthalmous medusae of Forbes, had endorsed its claim to be considered as the type of a new genus which he named after the Danaid $M_{V\eta \sigma \tau \rho \alpha}$. It should however be remarked that KROHN did not quite do justice to H. MÜLLER in writing: "Müller erklärt ihn sonach für ein Organ, dessen Function noch nicht ermittelt sei". This was not the case. In his first announcement of his discovery MÜLLER suggested that the "Anhang" was a "Qualle", but he also stated the case in favour of the organ theory and left the arbitration for a later observer.

In 1875 CLAUS drew attention to the presence of a deep notch in the margin of the umbrella (pl. 3 Fig. 36) and made a comparative study of the histology of the muscular tissue of the subumbrella.

HAECKEL in 1880 described *Mnestra* as a "tetracanale parasitische Craspedote" but felt himself unable to include it in his System. "Da bisher weder Gonade noch Otocyste beobachtet wurden, lässt sich ihre systematische Stellung nicht bestimmen." An opinion which was also held by CARUS in his Prodromus.

The present research was briefly described to the British Association in 1900 and it was then stated that in spite of the lack of observations upon the situation of the gonads, other anatomical features had been observed which indicate a close affinity between *Mnestra parasites* Krohn and certain genera of the Cladonemidae and which therefore enable us with some certainty to fix the position of *Mnestra* in the System. It is the object of this paper to give a fuller account of the anatomy and histology of this interesting medusa than has yet appeared.

Material.

During the spring of 1900 the prevailing westerly winds no doubt contributed to an unusually large number of *Phyllirhoë bucephala* and *Physalia* being captured in the Bay of Naples. Out of thirty-one individuals of *Phyllirhoë* taken between March 28 and April 20, nineteen, or more than half, had a *Mnestra* adhering to them.

My friend Dr. Lo BIANCO in the kindest way placed his store of spirit-preserved material from the Bay of Naples at my disposal for examination. The dates of capture were unfortunately not recorded but of forty-three full grown *Phyllirhoë* every one had or had had a *Mnestra* upon it.

A few microscope preparations made by the late Prof. KLEINEN-BERG of Messina, which were also submitted to me for examination, indicated in a not less convincing way that during certain seasons in the Mediterranean, it is exceptional to eatch a *Phyllirhoė bucephala* which has not got a *Mnestra* actually adhering to it, or which does not show some sign or scar at the spot where the *Mnestra* is usually attached.

So far as I am aware none of the several species of *Phyllirhoë* captured in seas other than the Mediterranean have been recorded as having been infested with the medusa. At present therefore we are justified in considering *Mnestra parasites* as peculiar to the Mediterranean.

Descriptive and Comparative Anatomy.

The *Mnestra* is attached to the *Phyllirhoë* by its manubrium which is relatively short. The blood of the host and apparently other cells also, constitute the nutriment of the medusa and are sucked through the channels in the manubrium into the gastral spaces.

The Umbrella.

The shape of the umbrella is more flattened than is usual among the free swimming Cladonemidae, but it is rarely as

depressed as in Clavatella prolifera, the creeping larva of Eleutheria. An important feature is the frequent presence of an in-pushing or "dimple" in the centre of the exumbral surface, from which, in typical cases, four centrifugal grooves proceed interradially to the margin. A similar grooving of the exumbrella is known in other Cladonemidae, especially during contraction e.g. Gemmaria sagittaria Ilek. Very frequently one of the grooves is so exaggerated as to notch the umbrella margin deeply; but the marginal notch is by no means so constant in its presence as to justify us in regarding it, with CLAUS, as diagnostic of the genus Mnestra. The marginal notch is shown in figs. 1, 2, 36, 39, 40, but was absent from some individuals. I have never seen a specimen with the four meridional grooves developed with such faultless radial symmetry as those drawn by Müller & Gegenbaur and Lankester (figs. 37, 38). All specimens examined by me were asymmetrical in some respect, and within certain limits exhibited a great variety of form and structure, a fact which is in great measure to be attributed to their sessile mode of life. It should however be stated that the symmetry of the velum and circular canal is not much affected by the asymmetrical deep grooves or notch upon the surface of the exumbrella.

The central in-pushing in the middle of the exumbrella (figs. 1, 42) is, I think, to be regarded as homologous with the umbral canal (Stieleanal) which places the gastric cavity of the developing Craspedote medusa in communication with the gastric eavity of the parent from which it has budded. If this interpretation be the true one, the in-pushing would be regarded by HARTLAUB as homologous with the umbral cavity (Scheitelhöhle) of *Eleutheria*.

The armament of the exumbrella.

The exumbrella is well armed with batteries of enidoblasts which are disposed in a ring all round the margin of the umbrella and along four perradial streaks which extend centripetally from the tentacle bases to the in-pushing in the centre of the exumbrella, and sometimes continue down into it. There is a considerable amount of variability in the exact distribution, width and length of these streaks. To these enidoblast streaks I have applied the name of enidaets¹.

¹ From xwôr, a nettle and 'axres a ray.

In some individuals, a cnidact may be longitudinally divided into two parts (fig. 1 radius 2), thus forecasting the condition desscribed by MAYER in the new species from Florida, *Ectopleura minerva*, in which two cnidacts proceed from each tentacle-base to the aboral pole. In *Mnestra* the streaks are broad near the tentacles, narrow near the aboral pole; a very constant feature seems to be a distinct broadening near the middle part of their course.

The nematocysts are in a high state of functional activity (fig. 8) and must be very effective as weapons of offence or defence. A theory to account for their retention in the sessile medusa will be considered below.

In the possession of a ring of enidoblasts round the margin of the umbrella, *Mnestra* is possessed of an organ rare amongst the Leptolinae, and it may well be considered as the first appearance of such a nettle ring or peronium as is to be found among the Geryonidae or Trachynemidae. In *Mnestra* however, all the nematocysts are in a state of offensive or defensive activity, whereas amongst so many of the Trachylinae, they are degraded into parts of a mere skeletal conglomerate. A similar marginal development of enidoblasts has been recorded in *Gemmaria implexa* and in *Clavatella* (= *Eleutheria*) both Cladonemidae.

The Tentacles.

The tentacles should be four in number, one at the end of each radial canal; but individuals with four in a state of complete development are very rare. One, two, three or even all four may be reduced. The majority of specimens had two adjacent tentacles reduced to mere knobs and many had three or even four reduced to this condition (figs. 36-40). It seemed to me that in some cases the reduction of the tentacles to knobs was a mark of old age.

A well developed tentacle of *Mnestra* is a compound hollow tentacle of the semipinnate type characteristic of the Cladonemidae (figs. 1, 14). The base is swollen and bulb-like; the distal portion is slender, tapering and very extensile, bearing a row of small, stalked club-shaped bodies along the entire length of the aboral side. These bodies (v. infra p. 43 and figs. 16, 17) contain enidoblasts and are undoubtedly homologous with the similar and similarly situated organs of several Cladonemid genera. For these organs the terms "Nebenfäden" and "tentaeulae" have already been

employed, but I should like to propose the more definitely descriptive name of *enidophors* for them as well as for kindred structures¹.

The bases of the tentaeles are much swollen and in some cases seemed to be provided with a pigmented patch which might be considered homologous with the ocellus of the Cladonemid genera.

The Velum and Subumbrella.

The volum notwithstanding the sessile habit of the animal is well developed, and so is the musculature of the subumbrella. When attached to the *Phyllirhoë* the *Mnestra* makes repeated swimming movements by contracting the velar and subumbrella eircular muscles; and even after separation from the host feeble spasmodic contractions will continue for some time, but owing partly to the small volume of the shallow subumbrella eavity, partly to the want of vigour in the muscular contractions, the efforts are insufficient for actual locomotion, even if the vigour of the contraction be artificially increased by stimulation.

The most probable explanation of the retention of the velar swimming muscles in a state of efficient contractility seems to be that they are required for some purpose other than that of locomotion. Although not admitting of absolute proof, there is ground for a reasonable conclusion that these muscles by their contraction, and the umbrella jelly by its elasticity, increase and diminish the size of the gastrie spaces. And thus a source of power commonly employed by medusae for swimming, seems to have become applied to a suctorial mechanism in *Mnestra* where organs of propulsion would be useless. In illustration of another case in which the alimentary system has been strengthened by the acquisition of an organ from the locomotor system, we may mention those Crustacea in the life history of which swimming appendages turn into masticatory organs.

The Gastrovascular System.

The gastrovascular system in its most typical condition is simple. There is a central stomach, four radial canals and a circular canal. The manubrium is invariably inserted into a pit on

^t These structures must not be confounded with the nematophores of the Plumularidae.

the ventral margin of the neck of the *Phyllirhoë* and is generally so firmly implanted that the manubrium will sooner be torn in two than let go its hold on the host. In one or two instances, I have thought I could detect an indication of oral lobes at the end of the manubrium, but the indication was too slight and the modification of the manubrium too great to support any definite comparison with *Gemmaria* in this respect.

The mouth and "ocsophageal" portion of the manubrium exhibits an extraordinary modification of structure, which although paralleled by what is known among certain Acrasped medusae, has not hitherto been described in any Craspedote form. The oral passage, instead of being freely open, has become blocked by a spongy growth of endoderm traversed by minute intercellular spaces, just as the central mouth of the Rhizostomae has been replaced by a multitude of tiny suctorial passages (red in fig. 41, shown in transverse section in fig. 19). It is a case of like cause producing like effect. Both *Mnestra* and the Rhizostomae have adopted a suctorial method of nutrition for which a spacious open mouth, perhaps for purely physical reasons, is not well adapted and has been replaced by a number of small passages. In Rhizostomae these passages are of a well defined nature, in *Mnestra* they are mere intercellular spaces in the endoderm.

The intercellular passages lead into a spacious axial cavity from which the radial canals lead on to the circular canal. The central cavity is usually irregular in shape and often has pouches communicating with it. The radial canals, though typically four, are variable both in number and distribution (figs. 39, 42). Two radial canals may unite and open by a common channel into the stomach; a fifth canal may appear between two radii etc. On the whole the variations in the arrangement of the radial canals seem to be more numerous than is usual amongst free swimming medusae, but it should be noted that in the closely allied *Eleutheria dichotoma* the number of radial canals seems also to be highly variable (HAECKEL).

A ciliated epithelium in the radial canals causes the contained liquid to flow in two opposite directions. Along the upper part of the canals there is a centrifugal current; along the lower part, the current is centripetal. Thus a very complete circulation is maintained.

Histology.

The Ectoderm of the Exumbrella.

The ectoderm for the most part consists of flattened polygonal cells with small round nuclei. It is generally easy to demonstrate that the cells are linked together by slender strands of protoplasm which bridge the relatively large intercellular spaces (figs. 3, 10). In some individuals which were examined in the living state, the cell outlines although retaining indications of a polygonal shape, were rounded and the slender protoplasmic connections were not to be seen (fig. 5): it is supposed that in these individuals the protoplasmic processes had been withdrawn either on account of old age or on account of bad health.

In the vicinity of the enidacts or streaks of enidoblasts upon the exumbrella, the ectodermal cells are of a peculiar form (fig. 10). While still retaining the polygonal character, they are more elongate than cells remote from a enidact. The cells are connected both with their neighbours and with the cells of the streak by attenuated processes of granular protoplasm which may be as much as three or four times as long as the cells to which they belong. These processes may be easily demonstrated in osmic preparations, in which too a few granules within the cytoplasm stain a conspicuous brown.

The Cnidoblast Streaks.

All round the margin of the umbrella and along the enidacts, the ectoderm is of a strikingly different character. Rising in slight relief from the exumbral surface, the cells of the streak are more elosely packed together and have smaller nuclei. Two sorts of cells are distinguishable — interstitial cells and enidoblasts (fig. 7).

The interstitial cells are in some parts delimited with well defined contours, but in others their nuclei lie in an undivided matrix of cytoplasm.

The enidoblasts are distributed somewhat irregularly along the streaks, which vary considerably in breadth. In the broader parts six or eight ranks of nematocysts fill the width; a single row of

nematocysts fills the narrower parts. The nuclei of the enidoblasts are easily distinguishable from those of the interstitial cells because they are flattened by close apposition to the nematocysts. Each enidoblast is provided with a enidocil; a drawing of a transverse section across a enidaet is shown in fig. 9.

The nematocysts when mature, respond readily to mechanical and chemical stimuli. The discharged threads are very thin at their free extremities, but are stouter at the proximal ends. The bases of the threads are armed with three or four reflected barbs (fig. 8).

The periphery of the umbrella is not so well supplied with thread cells as the streaks on the exumbrella. Cnidoblasts also occur upon the tentacles, especially on their bulbous bases.

The Ectoderm of the Tentacles.

The ectoderm cells are like the epithelio-muscular cells of many other Hydrozoa. Maceration preparations made by the classical method of the HERTWIGS, show that the epithelio-muscular cells are columnar in shape, with nuclei near their inner ends, vacuolated near their outer ends and provided with very fine muscular processes which in the living animal form a layer immediately outside the mesogloea.

Along the ab ral margin of certain of the tentacles is a row of cnidophors, stalked ovoid bodies shaped like the conidiophors of Uredineous Fungi (fig. 16). The knobs of these peculiar organs are composed of an outer envelope of numerous small ectoderm cells surrounding four enidoblasts (fig. 17). The stalks are wonderfully extensile like those of the somewhat similar organs among the Siphonophora. I could not ascertain the structure of the stalk to my satisfaction even with a 1/12 inch oil immersion lens, and the question of its being uni-or multi-cellular is left undecided. ALLMAN described the similar peduncles of *Gemmaria* as being "of true sarcode identical with that of Rhizopoda". When at full extension the stalks were four or five times as long as the terminal knob, but when contracted the lengths of stalk and knob became approximately equal.

The enidophor stalks like those of *Gemmaria implexa* Allman, under a low power, show an irregular contour. Under a high magnification the stalk is seen to be beset with minute processes which sometimes present a curious foliated appearance (fig. 17 a, f).

The withdrawal of the enidophors is not only effected by the diminution in length of the stalk and its consequent thickening, but also by the adoption of a spiral disposition (fig. 17 e), like the stem of a retracted *Vorticella*.

The similar enidophors in *Gemmaria* and *Pteronema* seem to be more plentifully supplied with nematocysts, and if drawings of them are to be trusted, are rather more pointed in shape. In *Gemmaria* moreover the enidophors are furnished with long vibratile cilia (ALLMAN).

Ectoderm of Subumbrella and Velum.

The cetoderm of the subumbrella is almost entirely composed of long fusiform muscle cells with elongate nuclei (fig. 11). The preparation shown in fig. 12 was made from an animal which had been kept alive in seawater tinged with soluble carmine. The muscle fibres remained unstained, but their nuclei became light pink and there appeared a number of round vacuoles of all sizes filled with carmine solution. The largest were larger than the nuclei, the smallest were extremely small.

The velum is also strongly muscular. It is composed of two layers of flattened contractile cells of a peculiar nature. CLAUS originally described such cells as part of the "Schirmmuskulatur", but in all specimens which fell into my hands, the cells of CLAUS occurred only in the velum, the musculature of the subumbrella being invariably composed of elongated cells like those described above. The illustration given by CLAUS (fig. 13) of a single cell seems to me to be a correct representation of a velar muscle cell. In shape, widest in the middle and tapering towards the ends; nucleus oval, with one or two nucleoli, in the broadest part of the cell; cytoplasm for the most part finely granular, but traversed with transversely striated fibrillae (myonemata) which occasionally branch, but on the whole run parallel to the major axis of the cell.

Mesogloea.

The mesogloea is structureless and devoid of immigrant cells. The mesogloea is fairly well developed in all regions of the body. A noteworthy feature is that it thins out and is absent in

the axial line of the medusa, so that there the ectoderm comes into contact with the endoderm of the gastric eavity.

In this respect *Mnestra* resembles such forms as *Eleutheria* in which a "Scheitelhöhle" or exumbral cavity is developed.

Endoderm.

The endoderm cells of the oral end of the manubrium have lost the usual epithelial structure, and as has already been mentioned, form a meshwork of spongy reticulated tissue which entirely fills the inside of the manubrium, as shown in the transverse section (fig. 19). In optical section this plug of reticular tissue strongly resembles the open meshwork of digestive cells which has been seen by many in other Coelenterata, e. g. LANKESTER and GÜNTHER in *Limnocodium*; but whereas in the latter case the endoderm is a mere inner lining to the manubrial canal, it forms a plug completely filling the cavity in *Mnestra*.

Spherical nuclei like those in the other gastric endoderm are situated at intervals in the strands of protoplasm which connect the cells with one another. Within the intercellular spaces of this cellcomplex may occasionally be observed small round corpuseles indistinguishable from small round corpuseles in the blood of the *Phyllirhoë* and also in the other gastro-vascular spaces of the *Mnestra*.

It is worthy of notice that in *Mnestra* cells seemingly devoted to digestion occur in the distal portion of the manubrium, whereas for the most part, in other medusae, such digestive cells line the proximal portion of the digestive cavity alone. This difference may be attributed to the difference in the food of free living and of parasitic medusae.

The rather irregularly shaped central gastric eavity is lined with a protoplasmic network containing many nuclei (fig. 20). The intercellular spaces in this region are much smaller and the protoplasmic strands are much thicker than in the manubrium.

Endoderm of radial and circular canals.

The endoderm at the junction of the radial canals with the stomach is of the nature of a ciliated pavement epithelium (fig. 21). The cells have spherical nuclei, irregular polygonal outlines and

are about twice as broad as high. I have not actually seen cilia upon them, but currents, rendered visible by particles suspended in the fluid, made it quite clear that the cells must be furnished with vibratile processes.

The epithelium of the circular canal is of a like nature. In transverse sections it would appear that the radial canals are encompassed by about 8 cells, whereas 6 are sufficient to go round the circular canal of smaller girth (figs. 11, 22).

Endoderm of Tentacles.

In the hollows of the tentacles the endodermal lining becomes thicker and the cells more columnar. Each cell has a flagellum. The nuclei are situated close to the attachment of the flagellum near the outer end of the cell (fig. 23). Many of the cells are vacuolated, a single large vacuole next the mesogloea in each, and some contain large spherical droplets which are stained brown in osmic preparations but are yellow in the live organism.

It will be noticed that the nuclei and vacuoles have the same relative disposition both in the endoderm and in the ectoderm. The nuclei are situated nearer to, and the vacuoles are situated further from, the axis of the tentacles.

In the reduced tentacles i. e. in those which do not bear enidophors but are reduced to mere stumps, the endoderm cells are of a taller form. On comparing the section through such a stumpy, reduced tentacle (fig. 24) with the section through a fully developed tentacle, part of which is shown in fig. 16, we are led to the conclusion that the total number of endoderm cells is very much the same in each of the two cases, although in the one case the endoderm cells are very closely packed together and contain few or no inclusions (vacuoles etc.), whereas in the other case the cells are much expanded and contain many inclusions. The endoderm cells in the enidophor, bearing tentacles are cushion-like and distended; those of the reduced tentacles are compressed. A possible explanation of this difference seems to me to be that the enidophorous tentacles are in need of some extra skeletal support for the proper performance of their functions. This support is afforded by the turgidity of the distended endoderm cells as is also the case in many other Hydrozoa.

Geographical Distribution.

Mnestra parasites has been recorded from Messina and the Bay of Naples. *Phyllirhoë* is an almost world-wide genus; its several species have been found to inhabit the N. and S. Pacific, the Indian Ocean and S. Atlantic as well as the Seas of Southern Europe. Yet if a sessile medusa infested such a large proportion of the exotic as of the Mediterranean individuals, it could hardly have escaped the notice of such accurate describers of *Phyllirhoë* as QUOY & GAIMARD, EYDOUX & SOULEYET, or MACDONALD. We are therefore justified in stating that the evidence is in favour of *Mnestra parasites* being confined to the Mediterranean and possibly adjoining seas.

The relation of the Mnestra to the Phyllirhoë.

Is the relation between *Mnestra* and *Phyllirhoë* one of parasitism or one of symbiosis?

All through the present paper, the opprobrious epithet "parasitie" has been avoided and the less inferible "sessile" has been employed. There is no doubt but that the adult *Muestra* like a vampire lives by bloodsucking and there also seems reason to believe that its young may be parasitic ab ovo; but may not the *Phyllirhoë* derive some advantage from the *Muestra* it bears?

The facts pertinent to the present discussion seem to be

- 1. That more than half of the *Phyllirhoë* examined were infested by *Mnestra*.
- 2. That the *Phyllirhoë* does not seem to be appreciably handicapped in its swimming powers by its burden.
- 3. That the *Mnestra* was never found attached to any part of a *Phyllirhoë* except to the "throat", upon the ventral margin of the body immediately beneath the junction of the oesophagus with the stomach.
- 4. That the exumbrella of the *Mnestra* is well equipped with nematocysts which on account of their position are useless for attack against the *Phyllirhoë*, but which have been observed to have been used with effect against another animal.

At what stage the *Mnestra* fixes itself to the *Phyllirhoë* is still a mystery, but a mystery which the facts come near to clearing up. Among the very youngest individuals of *Phyllirhoë*, a larger proportion seemed to be devoid of the medusa than was the case with the full grown individuals. The inference is that the *Mnestra* medusa or larva attaches itself to the *Phyllirhoë* after leading a free swimming existence of longer or shorter duration.

If this hypothesis be accepted, it follows as a necessary consequence that the numbers of young *Mnestra* must far exceed the numbers of *Phyllirhoë*, since but a small proportion can ever succeed in settling upon a *Phyllirhoë* in the open ocean. It also follows that the powers of reproduction of the *Mnestra* must be immensely increased as compared with the generality of medusae, and must, one would think, be greater than is usual even among many parasites. It is therefore most significant that all who have hitherto examined *Mnestra* should have failed to discover any trace either of sexual or asexual reproduction.

To repeat:

- 1. If our inference be correct that *Mnestra* passes through a free swimming stage of some duration, it follows that free swimming individuals should be very abundant.
- 2. Its method of reproduction should be much in evidence.

But, neither have free swimming *Mnestra* medusae been captured in considerable numbers, nor has the mode of reproduction of the sessile individuals been recorded.

Such considerations together with a knowledge of reproductive processes characteristic of parasites led me to the conclusion that the reproductive process of *Mnestra* might occur, not in the open sea but within the body of the *Phyllirhoë*. The migratory propensities of the germ cells of the Hydrozoa are universally acknowledged: is there any difficulty in imagining that germ cells which have originated in the manubrium of *Mnestra* are attracted by plentiful nutriment and wander into the nutrient liquids within the *Phyllirhoë*?

Stimulated by this speculation I immediately reexamined all available specimens of *Phyllirhoë*, and recognised in many, structures which bear the greatest resemblance to ova, spermatozoa and segmenting and dividing embryos (figs. 25—35).

In the younger specimens of *Phyllirhoë*, 7—11 millimetres in length, even though infested by *Mnestra*, I could find none of these phenomena, but in most (but not in all) of the older *Phyllirhoë* of 20 millimetres and more in length, the "young embryos" were very abundant, lying in the connective tissue of the molluse. Drawings of a few are given upon plate 3. In the early stages the cells are grouped regularly enough. The 2, 4 and 8 cell stages ¹ may all be easily found in certain individuals. At the 16 and 32 cell stages the "young embryos" are for the most part of irregular contour, ellipsoidal rather than spherical and with a cell or two projecting beyond the others here and there and thus marring the symmetry of the whole. The cells are mostly vacuolated. Further than the 32 cell stage I could not trace the young embryos, but in several stages they seemed to divide transversely.

In certain individuals of *Phyllirhoë*, there may be noticed local aggregations of tiny nuclei which stain well and which I believe may be the spermatozoa of the *Mnestra*. These nuclear aggregations occurred in the connective tissue in the neighbourhood of and rather posterior to the hermaphrodite glands of the *Phyllirhoë*. It is supposed that the sperm mother cells of the *Mnestra* wander to the position indicated and that the process of spermatogenesis occurs there. Fertilisation and the subsequent development would take place within the body of the *Phyllirhoë* of the embryo.

Unfortunately I cannot pretend that these conclusions are to be regarded as indisputable facts. The difficulties and possible errors of the correct interpretation of the phenomena are unusually great. We are justified in regarding the "developing embryos" and "spermatozoa" as being unessential and in a sense foreign to the *Phyllirhoë*, for they are not to be found in young or in all old individuals. It is easy to demonstrate that eells having the appearance of egg or sperm mother eells occur in great numbers at the point where the tissues of the *Mnestra* become continuous with the tissues of the *Phyllirhoë*, but it is not easy to give irrefragable proof that these cells wander to other parts of the *Phyllirhoë* and there give rise to the "spermatozoa" elumps or to the earliest stages of the "young embryos".

¹ It must be stated that in as much as it is not always easy to enumerate the exact number of cells in each embryo the numbers 8, 16, 32 must be taken as approximate only: or merely as descriptive terms to imply that the actual number of cells in the embryo is about that number.

Mittheilungen a. d. Zool. Station zu Neapel. Bd. 16.

I need hardly add that the difficulty of distinguishing a foreign eell of leucocyte appearance in the midst of molluscan connective tissue is very great.

The further history of the "young embryos" is unknown. It is possible that they may develope into planulae which make their way out of the Phyllichor either before or after its death, lead a free swimming existence for a time and finally settle upon other Phyllirhoë and grow into the mature Mnestra. Or, they may in the free state grow into medusae which settle upon the Phyllirhoë. In any case we are met with the difficulty of imagining how a small organism endowed with comparatively feeble swimming powers can succeed in attaching itself to a particular region of the surface of a much stronger swimmer. The "throat" of the Phyllirhoë is invariably marked by the special development of glandular cells, even in specimens which appear not to have been infested by Mnestra: it is possible that a secretion exuded from this region may attract the Mnestra. And certainly, if the Mnestra attached itself to most other parts of the Phyllirhoë, the swimming powers of the latter would be greatly impaired.

One observation would seem to indicate that in that particular case the *Mnestra* had only recently become attached to the *Phyllirhoë* and had led a free swimming medusa life until the said attachment. In April a *Mnestra*, firmly adhering to a *Phyllirhoë*, was captured, which had the shells of three pelagic organisms belonging to the family of the Tintinnoida in diverticula of its gastric eavity fig. 39). The shells agreed well with the illustrations of a variety of *Dictyocysta polymorpha* (Géza ENTZ. in: Mitth. Z. Stat. Neapel 6. Bd. pl. 14 figs. 3 and 4). Similar shells are described as having occurred frequently in the stomach of *Salpa* and so it is not surprising to find them in those of other pelagic animals.

The purpose of the complete armament possessed by *Mnestra* is not at first sight very clear. We cannot suppose that by its nettle batteries it is enabled to numb vietims and secure food for itself, since with its month firmly anchored to the *Phyllirhoë* it can neither procure nor devour prey. *Mnestra* is entirely dependent upon its host for nutriment and upon his movements for opportunities for the discharge of the nematoeysts.

It is true that some parts of the *Phyllirhoë* are within the range of a few of the thread-cells and that their discharge might have some stimulative effect upon the host, but the large exumbral batteries of the *Mnestra* can never be brought to bear upon the *Phyllirhoë*. Consequently, if these exumbral batteries serve any useful purpose, as their great efficiency indicates that they do, that purpose must be either offensive or defensive against other organisms than the *Phyllirhoë*; but on the other hand, owing to the position and sessility of the *Mnestra*, the batteries can only be brought into action with the connivance of the *Phyllirhoë*.

It is easier to suggest than to prove that the *Phyllirhoë* aets as if it were aware of the lethal weapon it earries on its neck. On one occasion only have I witnessed an action which would lend colour to this suggestion. The *Phyllirhoë* was slowly swimming along the bottom of a glass aquarium, and Perseus-like was holding its Medusa-head displayed. A young fish encountered the pair. It swam quietly along the side of the *Phyllirhoë*, but then on coming in contact with the *Mnestra*, immediately recoiled as if it had touched a dangerous object. However such an isolated observation as this cannot be accepted as more than a possible indication of the protection a *Mnestra* might be to the *Phyllirhoë*.

To sum up: --

Mnestra makes use of *Phyllirhoë* for the nutriment certainly of itself, and possibly of its germ cells and young embryoes.

Phyllirhoë may make use of *Mnestra* as a means of defence against enemies.

In consequence, the association is to be regarded as one of symbiosis rather than of parasitism and that therefore the specific name of *Mnestra parasites* does not give an entire indication of its relation to its host.

Affinities and Systematic Position.

In spite of the fact that we are still not quite certain about the place of development of the genital cells in *Mnestra*, yet we are sufficiently well acquainted with other characteristics of taxonomic value to assert definitely that it should be enrolled among

the Cladonemidae. The semi-pinnate, enidophor-bearing tentacles, the streaks of nematocysts and perhaps too the in-pushing in the centre of the exumbrella, if it be the vestige of a Scheitelhöhle, are all features familiar among Cladonemid genera.

But when we endeavour to more nearly define the relationships of *Mnestra* to the other genera of Cladonemidae we are met with difficulties which will only be removed when the results of a more searching investigation than has hitherto been made, of those other genera is before us. Then and not before will it be possible to write the phylogenetic history of the group with some pretence of accuracy.

All schemes for the classification of the Cladonemidae which have hitherto been proposed seem to me to have difficulties of their own. The reason for this is that within the limits of the group several quite peculiar organs have originated, organs which are not known in any other group of Anthomedusae. We have to deal with genera which differ very considerably in the grade of their organisation, and we have to take into account organs which may be phylogenetically related, or may have had an independant origin among allied organisms of which the chiefest mark of kinship is that they have a tendency to develop in certain ways.

A few of the chief facts with which the systematic zoologist is confronted and which he has to take into account in his classification are summarised in the following table.

Name of Genus	Ten: Number	acles Condition	Radial Canals	Erumbral cavity	Oral ten- tacles	Nemato- cyst tubes	Cnid- acts
Prerineira.	4	Sem.pinn.	Simple	Present	IJ	Ú	0
Zanelea	4	Sem.pinn.	Simple	Absent	0	0	4
Miestra	4-0	sem.pinn.	Simple	? Absent	Ú	0	4
Gonarie	2 oppos.	Sem.pinn.	Simple	Absent	Ŭ,	4	0
Ctenaria	2	Sem.pinn.	Forked	? Present	2.16	2	5
Eleutleria	4-6-5	Branched	Simple	Present	Û	0	0
Cladone a	5-10	Branche l	Forked	Absent	5 i	0	0
Dendrimema	-	Branched	Forked	Present	n	0	0
						_	

¹ I adopt HARTLAUB's number instead of the 4 of HAECKEL.

With the aid of such a table as this it is very easy to invent an artificial classification based upon one or two characters, but it is difficult to avoid violating what appear to be very close ties in respect of other equally characteristic structures.

In the system of HAECKEL, a primary division of the group was made according as to whether the radial canals are simple or forked, and as to whether the mouth is provided with oral tentacles Mundgriffel or not. The result was that a form *Ctenaria* with semipinnate tentacles was separated from the other forms with semipinnate tentacles and was associated with forms with branching tentacles, and vice versa *Eleutheria* was classed with the forms with semipinnate tentacles. But the chief objection which it is possible to raise against the Haeckelian system is that it depended primarily upon the fact of whether the radial canals fork or not, and therefore upon a character which recent observations on the variability of medusae have shown to be very variable among the individuals of a species. Such a variable characteristic should therefore not be chosen as the criterion of subfamilies.

In 1887 HARTLAUB having reinvestigated the anatomy of Eleutheria proposed another classification of the Cladonemidae upon a new basis - upon the presence or absence of a cavity of a peculiar nature used as a brood chamber between the stomach and the exumbrella. This cavity had long been known to occur in certain genera and was referred to by HAECKEL as the "Scheitelhöhle" or "Kuppelhöhle" or "Cavitas tholaris" and was considered by him to be homologous with that embryonic canal which originally connected the growing medusa with its hydroid parent. HARTLAUB contends that in Eleutheria the brood-chamber or "Scheitelhöhle" is in no way homologous with the "Stielkanal" of the young medusa but is a special organ lined with a peculiar epithelium, derived from the ectoderm, which serves the purpose of a marsupium and does not communicate with the gastric cavity but with the subumbrella cavity. Thus far the results of HARTLAUB are of the highest interest. but they do not justify his subsequent procedure in attempting to establish a classification of the Cladonemidae in which it is assumed without reinvestigation that the "Scheitelhöhlen" of Pteronema, Ctenaria and Dendronema, all genera described and figured by HAECKEL. are homologous with the very remarkable brood cavity of Eleutheria. For this assumption there is no evidence. except that HAECKEL is stated to have misunderstood the nature of the brood cavity of

Eleutheria. A more logical procedure would have been to have established a new position for the curious creeping *Eleutheria* and to have abstained from attributing to free-swimming genera an organ the existence of which in the sense of HARTLAUB, has never been demonstrated and of which the original describer has given a totally different interpretation.

Tentacles of the Cladonemidae.

Since in the classification of the Cladonemidae, about to be proposed, the structure of the tentacles is made a primary basis, a few remarks upon their structure may not be out of place. Two types are recognised, the semipinnate and the arborescent or branching. *Mnestra* affords us an example of the semipinnate tentacle with enidophors ranged all along the abaxial side; similar tentacles occur in *Pteronema*, *Zanclea*, *Gemmaria* and *Ctenaria*, save only that in the last mentioned genus the enidophors are filiform instead of being club-shaped.

The branching tentacle in its simplest form occurs in Eleutheria. The tentacle is divided into axial and abaxial branches, of which the abaxial branch ends in a capitulum of thread-cells, but the axial branch in the vounger stages (Clavatella) ends in a sucker, which is stated to be sometimes replaced by a capitulum of thread-cells in old individuals of Eleutheria. In Cladonema and Dendronema both the axial (sucker) branch and the abaxial (thread-cell-bearing) branch bear many secondary branches or ramuli. The branching is often of a dichotomous type. The abaxial branchlets mostly end in capitula of thread-cells and they are armed with little thread-cell batteries at intervals along their length. The abaxial portion of the tentacle is in fact very like a branching tentacle of the polyp Cladocorque which is also provided with numerous "capitate ramuli", or like the circumoral tentacles of the Margelidae. One of the first questions which occurs to the morphologist is: can it be shown that either the semipinnate or the branching type of tentacle is derived from the other, or that they are of independent origin?

I believed at first that it might be demonstrable that enidophors borne on the semipinnate tentacles might really be much reduced tentacular branches each armed with its little terminal capitulum of threadcells, and that consequently the semipinnate type should be regarded as the derivative of the arborescent type. Further

consideration has convinced me that this view is erroneous, that the two types of tentacle have had totally independent origins and that they are characteristic of the two subfamilies of Cladonemidac respectively.

The branching type of tentacle occurs in its simplest condition in *Elentheria*, the development of the more complex forms has been studied in the polyp (*Stauridium*) and in the young medusae of *Cladonema*, and in *Dendronema*. In all, the axis of the tentacle and of its branches is either "a continuous tube" lined with endoderm, or endoderm cells, and in the development of the *Cladonema* tentacle, the branches appear to arise on the axial side.

The semipinnate type of tentacle is characterised by the possession of enidophors which in all known forms consist solely of ectoderm and are developed upon the abaxial side of the tentacles.

This is certainly the case in *Mnestra*, *Gemmaria*, *Zanclea* and *Pteronema* and will very probably also be found to be the case in *Ctenaria* when that remarkable form is reinvestigated. The various stages through which the enidophor-bearing tentacle may have passed in the course of evolution are still to be found among the Anthomedusae. We assume that in the primitive type of tentacle, the enidoblasts were fairly uniformly distributed over the entire surface. The enidoblasts then seem to have become segregated into batteries as in *Sarsia*. The enidoblast batteries then became grouped along the abaxial side of the tentacle (*Ectopleura minerva* Mayer), then elevated upon contractile peduncles (*Ctenaria* [?]), and finally they became enclosed in cellular envelopes as in *Gemmaria*, *Mnestra* etc. It is interesting to note that *Gemellaria implexa*, the hydroid form of *Gemmaria*, has capitulate tentacles.

Nematocyst streaks (cnidacts) and nematocyst tubes.

There are two types of structure observable among the Cladonemidae which have never been proved to be homologous and which should therefore not be confused with one another. In one type the enidoblasts of the exambrella are arranged along radial streaks (enidacts) and lying on the outer surface of the umbrella are instantly available for purposes of offence. Cnidacts occur in several genera of medusae (e. g. *Ectopleura* with S) other than the Cladonemid genera *Zanelca*, *Mnestra* and *Ctenaria*.

In Gemmaria and Ctenaria there is a second type of nemato-

cyst-containing structure, here called a nematocyst tube. ALLMAN described 4 such in *Gemmaria* as "piriform chambers" extending from the circular canal and filled with small oval threadeells which can have nothing to do with the capture of prey, being sunk beneath the surface of the body. In *Ctenaria* there seem to be 2 such nematocyst tubes, and in *Willia* Forbes 24 small short saces of similar nature.

Until we have definite information to the contrary it is safer, judging from the appearance of the nematocyst tubes, to regard them as coecal endodermal outgrowths of the circular canal and as having no homological relation to the ectodermal streaks upon the exumbrella of *Mnestra* and *Zanclea*. Several cases in which nematocysts have developed from endoderm have already been described and so there is no a priori difficulty about that.

When we examine the classification proposed by HARTLAUB in further detail, we find that not only are *Ctenaria* and *Gemmaria* separated as in the Hacekelian system, but that *Pteronema* is alienated from *Zanelea* and *Gemmaria*, and *Dendronema* from *Cladonema*: i. e. it must be hypothecated that tentacular structures of identical nature have been independently evolved in two separate subfamilies. It is easier to believe that the nature of the "Scheitelhöhle" in HAECKEL's genera is not quite what HARTLAUB has assumed it to be.

I believe that the following scheme of classification will be found to be more in accordance with the statements which have been made concerning many points in the anatomy of Cladonemid medusae and will show clearly what is believed to be the relation of *Mnestra* to the other genera. It must however be clearly stated that no expression of opinion is intended in the scheme as to the homology or lack of homology between the Scheitelhöhle of *Eleutheria* and of other genera and the exumbral in-pushing in *Mnestra*.

Order Anthomedusae.

Family Cladonemidae Gegenbaur.

Anthomedusae with tentacles armed with enidophors, or branched. Radial canals 4-8 in number, simple or forked. Mouth either simple or provided with oral lips or oral tentacles (the sessile *Mnestra* excepted). Genital ridges $4|-8\rangle$, separate, upon the manubrium. Brood cavity, when developed, above the stomach.

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Sub-family 1. Pteronemidae.

Cladonemidae with unbranched tentacles armed with enidophors along the abaxial side. Radial canals 4, simple or forked.

Group α . Cnidophors stalked and knob-shaped. Radial canals simple. Oral tentacles absent.

I. "Scheitelhöhle" present as a brood pouch.

Pteronema Haeckel.

Tentacles 4; cnidacts on exumbrella absent.

II. "Scheitelhöhle" absent as a brood pouch.

Zanclea Gegenbaur.

Tentacles 4; cnidacts on exumbrella 4.

Mnestra Krohn.

Tentacles 4-0; cnidacts on exumbrella 4; sessile on *Phyllirhoë*.

Gemmaria Mc Crady.

Tentacles 2; enidacts on exumbrella absent, but 4 nematocyst tubes lie beneath the surface of the exumbrella.

Group 3. Cnidophors filiform. Radial canals forked. Oral tentacles present.

Ctenaria Haeckel.

Tentacles 2; cnidacts on exumbrella 8; tentacular pouches 2; "Scheitelhöhle" present.

Sub-family 2. Dendronemidae.

Cladonemidae with branched tentacles; the branches turned towards the mouth (axial) end in suckers, those turned away from the mouth (abaxial) end in batteries of nematocysts.

Group a. Axial and abaxial branches of tentacles are simple and undivided. Radial canals simple. Oral tentacles absent.

Eleutheria Quatrefages.

Scheitelhöhle, of peculiar structure, present; cnidacts absent.

Group β. Abaxial branches of tentacles branch dichotomously. Radial canals forked (usually). Oral tentacles present.

Cladonema Dujardin.

Oral tentacles 4, simple; Scheitelhöhle absent; Cnidacts absent.

Dendronema Haeckel.

Oral tentacles in 4 bundles, branched; Scheitelhöhle present; Cuidacts absent.

After drawing up this scheme for the classification of the Cladonemidae, I was pleased to find that it agrees with the short sketch of a natural system prepared by VANHÖFFEN and followed by DELAGE & HÉROUARD in so far as the division of the genera into Pteronemidae and Dendronemidae is concerned, but I cannot agree with the former in regarding the Cladonemidae as a subgroup

(Cladenomata, of the Pycnomerinthia or Oceanidae which have solid tentacles almost filled with large endoderm cells. My investigations on *Mnestra*, HAECKEL's drawings of *Gemmaria* and *Dendronema* and ALLMAN's description of *Cladonema* prove that these forms at any rate possess tentacles of the Coelomerinthic type i. e. contractile hollow tentacles with endodermal cells surrounding the lumen. On these and other grounds it would seem advisable to retain the Cladonemidae in a position of importance equal to that of the Codonidae and Oceanidae, as a third family of Anthomedusae in the System of VANHÖFFEN.

Conclusions.

In conclusion, it is believed that *Mnestra* owes its peculiar structure partly to the tendencies of growth which it has inherited from past ancestors and which it shares to a greater or lesser extent with other Cladonemidae, and partly to its sessile habit of life. In the first category I would include:

- 1. Such radial symmetry of parts as is discoverable in selected individuals.
- 2. 4 hollow tentaeles armed with stalked enidophors, in a series along the aboral margin.
- 3. 4 radial canals.
- 4. 4 perradial cnidacts upon the exumbrella.
- 5. A ring of cuidoblasts all round the margin of the umbrella.
- 6. The in-pushing in the centre of the exumbrella.

The characters supposed to be due to its sessile habit are:

- 1. Asymmetry of form.
- 2. Reduction of enidophor-bearing tentacles from the primitive number (4).
- 3. Irregularities in the development of gastric cavity, radial canals, enidacts and exumbral in-pushing.
- 4. Suctorial mouth.
- 5. Suppression of swimming powers.
- 6. The supposed migration of the germ cells into the body of the *Phyllirhoë* where fertilisation and development are believed to take place.

Vocabulary.

The literary pioneer who breaks ground new to his language is repeatedly confronted with the paueity or want of exactness of his vocabulary. HAECKEL in his report on the Deep Sea Medusae of the Challenger, has done his best to eurich the English language with many medusological terms, but even his comprehensive list leaves much to be desired when Cladonemidae have to be described.

Capitulum = "bouton urticaut", a battery of thread cells at the end of a tentacle cf. Coryne, Eleutheria.

Cnidact = "Nesselrippe" = "bandelette urticante", a radially disposed row of cnidoblasts upon the exumbrella.

- Chidophor = "Nebenfaden", "Nesselknopf", "tentacula", "pedunculated sac" ALLMAN, "Senkfaden" among Ctenophora, described on p. 43. It must not be confounded with "nematophore" Busk which is probably a modified Plumulariau hydroid.
- Exumbral canal = "Stielcanal". This may be homologous with the exumbral cavity.

Exumbral cavity = "Scheitelhöhle", "Trichterhöhle", "cavitas tholaris", and perhaps too the "brood chamber" of *Eleutheria*. Perhaps the word tholome might be used for this organ with international advantage.

Nematocyst tubes = "Senkfädentaschen" in Ctenaria. They occur also in Gemmaria.

Oral tentacles = "Mundgriffel".

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Explanation of the plates 2 and 3.

Abbreviations.

e.a enidaet.	nem nematocyst.			
e.e circular canal.	Ph the Phyllirhoë.			
e.ph enidophor.	r.c radial canal.			
eet ectoderm.	st stomach.			
end endoderm.	te tentacle.			
mn manubrium.	v velum.			

All drawings were made with a camera lucida. The high power drawings with ZEISS' 4 mm Apo. objective and compensating oculars 4 and 8.

Fig. 1. Mnestra parasites Krohn with two tentacles fully developed, as seen with the aboral side of the medusa, or the ventral aspect of the *Phyllirhoë* turned towards the spectator.

The central stomach, radial canals, velum etc. are seen by transparency.

Fig. 2. The same individual reft from the *Phyllirhoë* and viewed from its oral surface.

The aboral portions of the cnidacts are seen through the transparency of the jelly.

This individual *Mnestra* is abnormal in that one enidact is divided, and the radial canal diametrically opposite is bent, having obviously received some injury during the course of development.

- Fig. 3. Ectoderm cells on the exumbrella of a healthy *Mnestra*. Prep. KLEINEN-BERG's picrosulphuric and haematoxylin.
- Fig. 4. Ditto. Prep. Osmic acid.
- Fig. 5. Ectoderm cells on the exumbrella of a *Mnestra* believed to have been in bad health.
- Fig. 6. Ectoderm as seen in a living individual which had been living for 6 hours in seawater tinged with soluble carmine.
- Fig. 7. Cnidoblasts, with nematocysts and interstitial cells from a portion of a enidaet.
- Fig. S. A portion of a enidact with 2-3 rows of enidoblasts. The nematocysts have discharged their threads.
- Fig. 9. Transverse section across such a cnidact as is figured in Fig. 8.
- Fig. 10. Portion of exumbrella with the terminal portion of a cnidact seen partly in profile. Note the elongated processes which connect the neighbouring ectoderm cells with the enidact. Prep. Osmic acid.
- Fig. 11. Near the line of junction of the velum and the subumbrella are seen 5 nematocysts, belonging to the marginal ring of enidoblasts and the epithelium of the circular canal (c.c).
- Fig. 12. Musculature of the subumbrella.
- Fig. 13. Muscle cell from the volum (after CLAUS).

- Fig. 14. Portion of umbral margin, showing a well developed tentacle bearing enidophors, velum (*v*), radial canal (*r.e*) and enidact (*en*).
- Fig. 15. A similar view showing a reduced tentacle without enidophors.
- Fig. 16. Drawing of a bit of a tentacle partly in optical section to show its structure. The endoderm cells are laden with large brownish-yellow drops.
- Fig. 17. Drawings of enidophors.
 - a. Surface view.
 - b. In longitudinal optical section.
 - c, d. In transverse optical section.
 - e, f. Contracted stalks of cnidophors.
- Fig. 18. The manubrium of Mnestra inserted into the body wall of Phyllirhoë.
- Fig. 19. Transverse section across distal end of manubrium.
- Fig. 20. Endodermal lining of stomach.
- Fig. 21. Epithelial lining at junction of a radial canal and the stomach. In living specimens currents indicated the existence of vibratile processes upon this epithelium, probably as shown in Fig. 23.
- Fig. 22. Portion of a radial canal.
- Fig. 23. Endodermal lining of cavity at base of a tentacle.
- Fig. 24. Longitudinal section through a reduced tentacle showing the closely packed endoderm cells. Compare with Fig. 16. The circular canal *c.e* is shown in transverse section.
- Figs. 25—35 are all drawings of cells contained within the meshes of the connective tissue of *Phyllirhoë* to which *Mnestra* were or had been once attached. The structures in question have not been observed in *Phyllirhoë* which had never been infested by a *Mnestra*, and they are believed to be the sexual cells and developing young of the *Mnestra* which have wandered into the *Phyllirhoë*.
- Fig. 25. "Spermatozoa" of *Mnestra* clustered near a muscle fibre of *Phyllirho*". Two "ova" are shown in this preparation.
- Fig. 26 a, b. "Ova" of Mnestra, one is attached to a muscle cell of Phyllirhoë.
- Fig. 27. 2-cell stage "embryo" of Mnestra.
- Fig. 28. 4-cell stage "embryo" of Mnestra.
- Fig. 29, 30. 8-cell stage "embryos" of *Mnestra* lying among the connective tissue of the *Phyllirhoë*.
- Fig. 31, 32. 16-cell stage "embryos" of Mnestra.
- Fig. 33-35. Older "embryoes" of Mnestra.
- Fig. 36-42. To illustrate individual variations. Except Fig. 41 all are viewed from the oral surface, and the mouth and the subumbrella are turned towards the spectator.

Colours. Red: gastro-vascular system. Blue: enidaets and enidoblast ring near the circular canal.

- Fig. 36. After CLAUS' original drawing to show the marginal notch of CLAUS.
- Fig. 37. After Müller & Gegenbaur.
- Fig. 38. After an unpublished drawing by Prof. E. R. LANKESTER made at Naples, to show the quadriradial symmetry which was also characteristic of the *Mnestra* figured by Müller & GEGENBAUR.
- Fig. 39. One radial canal (IV) does not reach the central gastric cavity. Tentacles all reduced.

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Some Protozoa (*Dictyocysta*) were seen in the interior of this individual.

- Fig. 40. Gastrovascular system, normal. Cnidact I much more developed than the other three. Tentacles all reduced, but tentacle III more developed than the other three.
- Fig. 41. A young individual with 3 tentacles well developed. The medusa has turned itself inside out so that the exumbral surface has become eup-shaped. The distal end of the manubrium is widely extended over the surface of the *Phyllirhoë*. Four swellings were noticed one at each junction of a radial canal with the stomach: it is believed that these may indicate the point of origin of the gonads.
- Fig. 42. Tentacles all reduced. Cnidact of radius I discontinous. Gastrovascular system highly irregular, there being 6 radial canals one of which bifurcates. The black dotted line indicates the exumbral cavity or "Scheitelhöhle".

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