

Notes on some Hydromedusae from the Bay of Naples.

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With plates 21 and 22.

The following 'notes' on a few Hydromedusae obtained at Naples during the spring and summer of 1903 comprise a series of observations upon several species, some of which are believed to be new, others more or less rare, and all of more than ordinary biological interest. It is believed that the account submitted may have some value both as to the morphological and faunal facts concerned as well as a contribution toward a clearer knowledge of some hitherto disputed problems.

Pachycordyle Weismanni sp. nov.

During the month of May I obtained several colonies of an interesting hydroid which in many respects seems closely allied to *Pachycordyle napolitana* Weismann, but which will be seen to have some sharp differences. The colonies were obtained from the Bay of Naples at comparatively small depths and all inhabiting the shell of a living snail, *Fusus rostrata*. The hydroids live fairly well in the aquarium, having been kept under observation for as much as a week at a time. During this time several medusae were liberated, thus affording opportunity for critical study of the entire life history of the species, excepting that of the embryo. As intimated above, the hydroid seems to live 'fairly' well in the aquarium. It was, however, evident that with successive days under this changed environment there was more or less decline in vigor, both of the hydroid and developing medusae, for the first medusa, which was born during the first day in the aquarium, exhibited a vigor and activity

quite lacking in those born several days later. The colony continued to live, however, and medusae were liberated during an entire week, at the end of which time the hydroids were killed and preserved for subsequent study of morphological details here-in-after described. Most of the material was fixed in alcoholic-corrosive solutions, and in 10 % solutions of formalin in sea-water.

It may be remarked, incidentally, that of the preserved material some was worked up soon after preparation, and other portions after my return several months later, and with an experience similar to that which I have elsewhere mentioned, namely, that better results were obtained from the newly prepared material than from that long preserved. This I believe may be regarded as a general rule having few exceptions so far as coelenterates are concerned. Sections were in almost all cases stained by means of HEIDENHAIN'S iron-haematoxylin, followed in some cases by Bordeaux-red, with excellent results.

Systematic.

The genus *Pachycordyle* was instituted for a hydroid found by WEISMANN at Naples, and described by him in his monograph¹. It is unnecessary to cite in detail his description of the hydroid except on certain points involved in comparisons.

As I have noted above, the general features of the present hydroid have much in common with that described by WEISMANN. The one feature in particular which would seem to sharply distinguish the two is the fact that WEISMANN'S species is recorded as having only sessile gonophores while in the present case, as already cited, the gonophore is a free medusa, however, a short-lived one.

It should be noticed in this connection that WEISMANN'S specimens were all male, while strangely enough in the present case I was only able to obtain female colonies. Whether this circumstance of itself affords room for doubt as to the specific difference of the two may be open to some question, of course, tho so far as my observations have gone, as a rule where the medusa is free in one sex of a given species it is almost invariably free in both. I have elsewhere shown² that occasionally specimens of *Pennaria tiarella* are found in which many of the female medusae discharge their

¹ Die Entstehung der Sexualzellen bei den Hydromedusen. Jena 1883 pag. 87.

² Amer. Natural. Vol. 34 1900 pag. 391.

eggs without becoming free, tho I have not noticed this feature among male colonies.

It should also be said that in the species under consideration the gonophores in their earlier stages of development show every aspect, whether of form or structure, of sessile sporosae. But since these come to maturity within a few days it would seem as if WEISMANN could hardly have failed to distinguish the development of the medusa and its probable birth. Moreover, he describes the gonophore as having a ramified spadix. While this may be the case during early development, in the mature medusa it has entirely disappeared. Whether here again the difference of sex may involve difference of structure must remain an open question, at least for the present.

Incidentally it may be worthy of remark that WEISMANN'S specimens were obtained from considerable depths, '40 meters', and from the shell of a species of *Murex*, while as noted above the present specimens were all found on a shell of another genus and at small depths.

While owing to the fact that only one sex has been available for these comparisons and from which to formulate diagnostic definitions there may naturally remain some doubt as to the distinctness of the species, I am, however, strongly convinced of its specific independence, and venture to propose for it the name *Pachycordyle Weismanni*, in honor of the author of the genus and his distinguished contributions to hydroid morphology.

Specific Diagnosis.

Trophosome: Colony arising from a delicate, reticulated hydro-rhiza. Hydrocaulus sparingly branched, from 3—8 mm high. Perisarc somewhat dense, not extending beyond the base of the hydranth, dull yellowish brown in color. Hydranths club-shaped, with sub-conical hypostome. Tentacles from 8—16, filiform, becoming delicate and thread-like when fully expanded (Pl. 21 Fig. 1).

Color: Hydranth body orange or reddish, hypostome whitish.

Habitat: Upon the shell of *Fusus rostratus*.

Gonosome: Medusa buds borne on side of stem, rarely on lateral branches, pear-shaped as they approach maturity, seldom more than two or three on a single polyp, the entire gonophore enclosed within a sheath of perisarc (gonangium?). The medusa escapes from the capsule by rupturing or dissolving the distal end, after which the

capsule may often be found in a partially collapsed condition upon the stem or branches.

Medusa piriform, with prominent apical projection. Size 2 mm high by 1.3 mm broad. Velum narrow, velar opening very small. Manubrium rather large, conical and devoid of peduncle. Bell very transparent, with scattered nematocysts over the exumbrellar surface. Radial canals lacking, marginal canal simply a fissure of varying size between the layers of ectoderm with vestiges of entodermal lining near the margin. Tentacles entirely lacking. The medusa is devoid of color except on the manubrium, which varies from orange to dark brown. Mouth wholly lacking. When first liberated the medusa swims with a short, jerky motion, tho of limited vigor, a few contractions appearing to exhaust the little creature. Eggs are discharged almost immediately after the birth of the medusa, the life of which is very ephemeral, not exceeding one or two hours (Fig. 2).

Origin of the Germ Cells

Concerning the origin of the germ cells my observations upon this species agree in most points with those of WEISMANN on the related species, in so far as actual conditions are concerned. He finds these cells in the entoderm, and there only, yet rather insists upon the probability of their descent from ectoderm cells, while as yet in an indistinguishable stage. His specimens being all male in which, as he says, the primitive germ cells are small and correspondingly difficult of recognition, affords some plausibility for his contention, tho he likewise makes similar claims concerning the ultimate source of egg cells in other genera.

These speculative deductions are without any support from my own observations, tho as already noted, they were restricted to female colonies entirely and therefore cannot of course be claimed to prove those of WEISMANN to have been wholly in error. In the species under consideration the germ cells originate in the entoderm and are not found elsewhere at any time during their growth or maturation. As is very well known, the size and character of the egg cells render them easily distinguishable even at a comparatively early period in their development. In sections of the hydroid stem in both long and cross series and stained by various methods I have found no evidence of their occurrence other than in the entoderm.

Moreover, these sections failed likewise to afford any evidence of WEISMANN'S so-called "Keimzone". While eggs are found usually in greater numbers in the immediate region of the gonophore buds, as might be naturally expected, than in other portions, still they are found in not inconsiderable numbers at points more or less remote from this region, both above and below.

As a rule the egg cells are found in the deeper portions of the entoderm, tho not unusually they are found to occur likewise on the surface as shown in Fig. 3. Occurring in greater numbers in the region near the origin of the gonophore, and possibly also inciting its development, they seem to be carried into the bud during its formation and development. It would seem, however, that there is a migration of egg cells directly into the gonophore from adjacent portions of the stem, since it hardly seems probable that the large numbers which finally occupy the gonophore could have originated in immediate contact with it. Such a migration is well known in many other hydroids and may be accepted as occurring here, tho no direct evidence of it has been observed in the course of the present research. With the growth of the gonophore there seems to be a segregation of eggs into groups, or nests, about which there are developed follicular folds of the entoderm, as shown in Figs. 4, 5, in some cases entirely enclosing them. Others continue to lie in close contact with the entoderm lamella and finally form the superficial layer in the free medusa.

Development of the Gonophore.

As already intimated, the gonophore arises as a bud from the side of the stem, or more rarely upon a branch. It is at first indistinguishable from an ordinary hydranth bud, involving a direct evagination of both ectoderm and entoderm. The presence of eggs in immediate contact with it usually reveals its true character. From the first and throughout its entire development nematocysts are found in the ectoderm and multiplying during development furnish the nematocyst clusters of the exumbrella of the medusa. In iron haematoxylin preparations they stain a deep black during early development, as may be noted in several of the figures.

At first the gonophore is a simple club-shaped organ, as shown in several of the figures, but soon takes on a typical pear-shaped aspect, as shown in Fig. 5. At about this time there seems to be a cessation of the process of ovarian migration into it and very soon

the proximal portions seem to constrict to form the pedicel of the gonophore. Somewhat later the constriction cuts off the gonophore from direct communication with the enteron of the stem, as shown in Fig. 6. Coincident with these changes there appear at the distal end of the organ, which up to this time has been simply a typical two-layered sporosac, a proliferation of ectoderm cells, the dissolution of the middle lamella and the ingrowth of the ectodermic plug to form the so-called bell-nucleus (Glockenkern), as shown in Fig. 4. The presence of numerous karyokinetic figures, as well as the micro-chemical reactions of the cells betoken the intense activity of the growing tissue. At first the bell-nucleus is rather globular in form. Very soon, however, it assumes an oval outline and continues to flatten and extend laterally in all directions. With this flattening of the structure there is reestablished the supporting lamella, a layer of entoderm is formed between it and the bell-nucleus, so that the latter comes to lie between the outer layer and the inner which contains the eggs. Coincident with this development and gradual extension of the bell-nucleus there has been a differentiation of its cells. Along its entire inner surface there has been differentiated a single layer of cells, forming in section a delicate chain-like series extending the entire length of the growing band, as shown in Fig. 5.

This growth and differentiation continues, gradually extending as a delicate sheet, laterally and proximally, the inner chain-like series forming an extremely delicate ectodermal membrane over the outer egg layer, the other layer of ectoderm forming the lining of the sub-umbrella of the medusa and overlying the thin layer of entoderm, to which reference was made above. This process continues till about half of the interior cavity of the gonophore is thus supplied with a double layer of ectoderm, one covering the eggs, which in the mean time have become somewhat evenly distributed over the developing manubrium, the other constituting the lining of the bell, as just mentioned, and as shown somewhat diagrammatically in Fig. 7.

With the completion of this ectodermic investment there occurs, apparently, both an expansion of the lateral walls of the gonophore to approximately the shape of the future medusa, and also a contraction of the entodermic walls into a more nearly cylindrical and conical shape, thus giving rise to the manubrium already referred to. This contraction to form the manubrium is apparently a purely

mechanical process due, in part at least, to a reduction of the entodermic cellmass which has been involved in the transformation of a considerable portion of these epithelial cells into purely nutritive cells concerned in the growth of the eggs. Abundant evidence of this is found in the manifest signs of degenerative metabolism occurring throughout the entire mass. In many cases the cellular character had been lost entirely, in others it had been greatly modified. Figs. 4 and 7 show something of these changes.

With these phases of development completed the medusoid features may be said to be well established, though velum, tentacles, and canal systems are lacking. Only the first of these organs is finally developed. Tentacles are wholly absent; the bud-like projections shown at *m* in Fig. 7 are but sectional aspects of the bell margin, which as is shown in Fig. 2 of the fully developed medusa, is thick and rim-like. The velum is formed shortly before the birth of the medusa by a double fold of ectoderm, as shown in Fig. 7 *v*. This fold is apparently continuous over the entire velar end of the medusa, until shortly before birth, when a circular opening is formed by what seems to be an absorption of the central cells.

Of the canal system there is little to be said, since it is at best quite rudimentary. In Fig. 7 *c.c* is shown what in general position and form may be considered as the marginal canal. In no case have I been able to find traces of radial canals. In certain specimens sections would show a deeper fission of the entoderm layers at the junction of the apical projection and the lateral walls of the umbrella, and in others an extension of the marginal canal upwards, but there was no communication between the two. Furthermore, the manubrium is permanently mouthless, so that the medusa is apparently doomed to an ephemeral existence as an independent organism. And such is indeed the case. Of many specimens liberated from hydroid colonies in the aquarium none lived for more than an hour or two at most, as indicated in an earlier connection.

The apical projection is bulb-like, very thin and hollow as shown in Fig. 7. It is lined internally by an extremely delicate and tenuous layer of entoderm, the presence of which only becomes demonstrable under the highest powers of the microscope. The ectoderm layer over this region is likewise very thin, though more easily distinguished than the former.

As the medusae approach the period of liberation numerous orange-colored pigment granules appear in and among the entoderm

cells of the manubrium, particularly in the median and terminal portions, giving to the loose tissue a distinctly brownish color. A careful study of the origin and development of these granules compels the conclusion that they are results of waste metabolism, or in other words, excretory products. When attention is directed to the fact that the entodermal epithelium of this region has been the center of active metabolism incident to the growth of the eggs from the time the gonophore bud became functionally disconnected from the body of the polyp, and that in their stages of growth these entoderm cells through cytomorphosis became essentially nutritive cells, the foregoing conclusion is only what might be naturally expected.

In connection with these observations it had occurred to me that possibly certain of these pigment granules might find their way into the growing eggs along with nutritive matter absorbed from the entoderm cells, but a careful examination failed to show that this was the case. Furthermore, since the pigmentation of the eggs occurs chiefly as they attain full growth, and coincident with the metabolism involved in the phases of maturation, I incline to believe that it is due in this case, as in the former, to pigment granules evolved through similar cytoplasmic metabolism. This view is strengthened by the fact that in the present case, as well as in others well known, the color of the eggs differs from that of the manubrium, to a greater or less extent.

In a recent contribution¹ I have directed attention to the relation of excretory processes to coloration among certain of the lower invertebrates, and the facts here cited afford additional evidence in support of the general proposition.

LENDENFELD², in a critical paper on *Eucopeella* has briefly referred to the probable relation of the brownish pigment present in the radial canals of the medusa to excretory processes. He expressly says, "Diese Pigmentmassen gleichen denen, die in dem Entoderm der Nährthiere vorkommen, durchaus und glaube ich dieselben ebenfalls als Excretionsstoffe deuten zu sollen. Die Masse der Excretionsstoffe richtet sich natürlich nach der Lebhaftigkeit des Stoffwechsels und es wird deshalb nicht Wunder nehmen, wenn gerade in den Radialkanälen der lebhaft wachsenden Medusenknospen sich solche Stoffe anhäufen."

¹ Science Vol. 19 1904 pag. 132.

² Zeit. Wiss. Z. 38. Bd. 1883 pag. 545.

As will be seen from the foregoing account, we have here a medusa which is either extremely degenerate, or one of very primitive type. Its development within a chitinous capsule (gonangium?), associated with the sporosac-like history of the gonophore would seem to suggest the latter alternative. So far as I am aware the development of Anthomedusae within gonangia is quite rare if not wholly anomalous. The unique gonophores of *Dicoryne* are probably of very different character and significance.

In 1883 LENDENFELD (op. cit.) described a new hydroid and medusa, *Eucopella campanularia*, which apparently sustains a relation to the Campanularidae similar to that of the medusa herein described to the Tubularidae. The medusae of these forms have much in common, such as shape, size, rudimentary organs, etc.

Moreover, in the origin of the eggs, their migration into the gonangium which later gives rise to the medusae, the nutrition of the eggs and the general character of their later history, the correspondences between the two are very interesting. LENDENFELD's description of *Eucopella* also confirms the suggestion of a preceding paragraph that these are probably both generalized, or primitive types of medusae, in which the origin of the eggs, apart from, and prior to the organization, of the medusa, points to a condition similar to that found in such hydroids as *Hydractinia*, *Clava*, etc. in which there is nothing more than a sporosac within which the eggs develop after their origin in the body of the animal and later migration into these specialized nutritive capsules.

As the eggs approach maturity two rather marked changes are more or less apparent, one involving the character of the cytoplasm, the other that of the nucleus. In their earlier history the egg cytoplasm consists of a more or less viscid matrix through which is distributed a finely granular matter, the whole forming a somewhat homogeneous body. With the assumption of the spherical shape and typical size (about 0.9 mm), the cytoplasm becomes more predominantly granular in character and at the same time there appears in many cases a tendency toward vacuolation. I have elsewhere¹ called attention to a similar condition in the eggs of *Pennaria* at about this period in their history and the same thing has been noted by METSCHNIKOFF² and others. In *Pennaria* it had seemed

¹ Arch. Entwicklungsmech. 18. Bd. 1904 pag. 462.

² Embryologische Studien an Medusen. Wien 1886.

to me to be associated with maturation and fertilization phenomena, but the latter feature must be eliminated in the present instance, since in the absence of male specimens it was obviously out of the question. Whether any of the immediate phases of maturation may have been involved is likewise open to doubt, since I was unable to demonstrate any of the ordinary features of this process, either in living eggs or in those sectioned and stained. Intimately associated with these changes were nuclear modifications of a more or less remarkable character. Prominent among them is the dissolution of the nuclear membrane which occurs shortly before the birth of the medusa and the discharge of the eggs. Following this there occurs a marked decrease in the mass of the nuclear substance, probably due to the loss of nuclear sap, or a dispersal of matter through the cytoplasm, so that the nucleus measures only about half that of the ovarian egg. Of still greater importance is the change which occurs in the chromatin network of the nucleus, which appears to wholly disintegrate and to disperse through the cytoplasm. Not the slightest trace of chromosomes or chromatin substance can be demonstrated in the nuclei or cytoplasm at the time of the liberation of the medusa. The nucleus itself, greatly reduced in size, may still be seen as a definite area of very homogeneous texture, but indefinitely merging into the surrounding cytoplasm, there being no trace of nuclear membrane.

Prior to these later nuclear changes is another involving the nucleolus, which during the earlier ovarian history is a body of conspicuous character and strong staining qualities. In sections of eggs of about the conditions shown in Fig. 8, or sometime prior to the complete dissolution of the nuclear membrane and perhaps inciting it, it is quite common to find nucleoli migrating bodily from the nucleus into the cytoplasm where they seem later to disintegrate and mingle with it. In several sections double nucleoli were found in a single nucleus, as shown in Figs. 8 and 9. In almost every case of this sort one of these bodies appeared appreciably smaller than the other, and often somewhat distorted in shape, as may be observed in the figures just cited.

Vacuolation of these nuclei was not an infrequent phenomenon. It usually consisted of one, or rarely two, slightly refractile vesicular bodies occupying an excentric position in the nucleolus. Careful search was made for evidence of directly dividing nucleoli, but without success. The occurrence of two in a given instance is probably

due to the degeneration of the one and the formation of another *de novo* before the first had escaped from the nucleus.

Whether the phenomena herein considered lend further force to the previous suggestion that the vacuolation of the cytoplasm of the eggs was probably due to changes associated in some way with maturation, or whether they may not rather be interpreted as expressions of cytoplasmic activities, or phases of metabolism similar to those previously considered, may be somewhat problematical, and must so remain for the present, since my material is neither sufficiently varied nor abundant to justify further speculations or conclusions.

Tubularia mesembryanthemum Allm.

The conflicting accounts of the development of this hydroid which have been given by earlier investigators, particularly CIAMICIAN¹, METSCHNIKOFF (op. cit.), and BRAUER² led me to make some observations upon living specimens, and also to collect material from which to review certain of the problems involved, such as the mode of cleavage, formation of the germ layers, etc.

While from the living specimens I was able to follow the later history of the embryo, its final escape from the gonophore and some aspects of its independent life, it was not practicable to follow out with any degree of satisfaction the details of cleavage. This was done by means of sections of the gonophores made in several planes, supplemented in some measure by the preparation of entire gonophores stained and mounted as transparent objects, much as had been done in the case of living material.

The preserved material was submitted to one of my students, Miss HOWLAND, who under my direction cut and stained the sections and traced the phases of maturation and cleavage, and some of the aspects of the later embryo.

The differing accounts as to the origin of the germ cells given by CIAMICIAN and WEISMANN, and that of BRAUER seem to be rather a difference of interpretation than of fact. The germ cells have been found both in the ectoderm of the peduncle of the gonophore as BRAUER contends and in the ectoderm and entoderm of the spadix

¹ Zeit. Wiss. Z. 32. Bd. 1879 pag. 323.

² Ibid. 52. Bd. 1891 pag. 551.

as had been maintained by CIAMICIAN and later confirmed by WEISMANN. I am inclined to regard both as true; or in other words, that the germ cells probably arise rather indiscriminately in both positions, though in some specimens rather predominantly in the one region and in others equally pronounced in the other region. As I have elsewhere shown this to be the case with species of *Eudendrium*, it is unnecessary to more than mention the matter in this connection. It would seem that in this species we have a hydroid in which the differentiation of the body cells of the two layers is physiologically less sharp than in others.

The growth of the egg is quite similar in most respects to that of other species of *Tubularia*, such as *larynx*, as described by DOFLEIN¹, and *crocea*, as described by ALLEN². It has not been possible to confirm BRAUER's view that those germ cells which are to give rise to eggs are sharply differentiated before they come into the gonophore, or during their migration thitherward. On the other hand the view of DOFLEIN that their impulse toward active egg development is the result largely of position and nutrition in the gonophore seems by far the more probable, and is in general agreement with similar facts in the case of other species.

Of the large number of germ cells which crowd the mature gonophore a comparatively few, perhaps three or four, assume the character of ova at any one period of development. Their growth results from the active absorption of their less fortunate fellows, as has been shown in many other cases, as by ALLEN and DOFLEIN, previously cited, and by the present writer in the case of *Pennaria* (op. cit.).

As in the case of most Tubularians, after the development and liberation of one series of embryos other of the primordial germ cells proceed to grow as the former had done, and thus the process continues for several generations. The case is very different, of course, in species with free medusae, like *Pennaria*. Here the eggs are all discharged at about the same time and the medusa dies shortly after; hence most of the germ cells are consumed in the growth of the first series of eggs. The same is probably true in most short-lived medusae, but with many others, successive generations of eggs are produced during the entire breeding season.

¹ Zeit. Wiss. Z. 62. Bd. 1896 pag. 61.

² Biol. Bull. Chicago Vol. 1 1900 pag. 291.

The differences as to the exact means by which the growing eggs appropriate the surrounding germ cells which characterize the accounts of CIAMICIAN, BRAUER, and DOFLEIN, seem to me to be similar to others already cited as to the region where they originate, etc., namely, a difference of interpretation and definition, rather than of fact. As I have shown in the case of *Penmaria tiarella* and *carolini*¹, so it seems with species of *Tubularia*, there may be differences as to points of detail. In some cases the egg may engulf the germ cells bodily, later reducing them to a fluid condition; while in others this reduction appears to take place before absorption. But whether before or after, it must ultimately depend upon some process of reduction substantially digestive in character before final assimilation is accomplished. The only other alternative to the supposition is that of mere fusion of the protoplasm of the one with that of the other without any assimilative changes whatsoever. That this is not the case would seem to be proved by the fact of the persistence of these so-called pseudocells or nuclei within the eggs during the entire history of growth, and even that of development, as is well known by those who have concerned themselves with the subject. Apparently the disintegration, or reduction of these nuclei takes place much less rapidly than does that of the cytoplasm of the germ cells, so that they may be distinguished within vacuoles of the growing, or developing eggs long after their first incorporation.

Maturation and Fertilization.

Concerning these phenomena there is little to add to the earlier researches of CIAMICIAN and BRAUER. It has not been possible to confirm the observation of the former that during the process of maturation the eggs become more or less conical on the side from which the polar bodies are extruded. Since, however, his observations were made, in part at least, upon living eggs, while, upon this phase of the subject, my own observations have all been upon preserved material, there may be no definite contradiction. It would seem to me doubtful, however, whether any appreciable change of form could be observed upon eggs enclosed in fixed gonophores within which they are usually closely packed.

BRAUER's account is much fuller and more definite than is that

¹ Arch. Entwicklungsmech. 18. Bd. 1904 pag. 457.

of CIAMICIAN. Concerning his accounts of maturation my own observations are mainly confirmatory. As to fertilization, however, I have not been able to obtain cytological details quite comparable with those described by him. Concerning nuclear phenomena associated with these processes my observations confirm in considerable degree those which I have elsewhere described in connection with the development of *Pennaria* and *Eudendrium*. There is the same migration of the nucleus to the periphery of the egg, the dissolution of the nuclear membrane, and the same apparent dissipation of the nuclear substance throughout the cytoplasm of the egg, followed later by its apparent reorganization just prior to the first signs of cleavage.

Cleavage.

It is perhaps concerning this phase of the life history that most dissension has arisen. CIAMICIAN was the first to critically study its development, and in doing so directed his observations largely to the aspects presented by the living eggs. This he did by cutting off clusters of gonophores and studying them under the microscope. But as he confesses, the various contractions of the several parts of the gonophores and the resulting movements and readjustments so shift the position of the eggs that it is extremely difficult to obtain accurate observations.

He concluded that cleavage was unequal, the first and third furrows being at right angles to each other and meridional, the second equatorial and from within outward. In later cleavages there is a more rapid division of the cells at the animal pole, these later growing over the blastomeres of the vegetative pole by a process of epibole and enclosing the latter which later form the entoderm.

This conclusion has been frequently called in question by later observers. BALFOUR¹ claimed that an examination of segmentation by means of sections failed entirely to confirm CIAMICIAN's results. COXX² has likewise failed to find any evidences of epibolic gastrulation in another species of *Tubularia*, and from this has undertaken to discredit CIAMICIAN's conclusions. As is well known from later observations different species at times show very considerable va-

¹ Comparative Embryology, 2^d Edition, 1885, Vol. 1 pag. 154.

² Z. Anz. 5. Jahrg. 1882 pag. 483.

riation in matters of cleavage, particularly among hydroids, and COXX's contention is not therefore, valid as an objection.

The researches of BRAUER, however, leave little doubt that on this point CIAMICIAN was evidently mistaken, and my own observations tend to confirm this conclusion. BRAUER maintains that cleavage in this species takes place by two sharply different processes, namely, first, by a more or less regular mode of fairly equal cleavages during the two meridional furrows, later ones being more or less unequal and irregular. In the second mode cleavage involves the nuclei only, which proliferate independent of the cytoplasm, forming a multinucleate egg, after which there follows a cleavage of the egg into as many cells as there are nuclei. In this process there may be considerable variety. It may occur when there are but few nuclei, four or six, or it may not begin until there are sixteen, or perhaps more.

My own observations upon this point, while confirming in a measure those of BRAUER, do not warrant any such sharp conclusion as to the distinctness of these processes. One may find a regular cleavage into two and four cells, etc., and he may also find an internal nuclear proliferation, in some cases indeed, many more nuclei arising than BRAUER has indicated, before cell organization and cleavage take place. But I have not been able to sharply differentiate these modes. They often graduate imperceptibly into each other, indeed, may be found occurring in the same egg, though this is not common. I am inclined therefore, to consider them as only varying phases of cleavage conditions more or less common among Coelenterates, particularly among Hydromedusae. This is notably the case with *Pennaria*, as I have recently shown, and as ALLEN (op. cit.) has shown in the case of *Tubularia crocea*.

As illustrating somewhat more clearly than is possible by merely verbal description I have included a few sketches made by Miss HOWLAND in connection with a study of sections already referred to.

In Fig. 9 is shown an egg in which nuclear proliferation is under way, but in which no signs of cleavage are present. This condition may continue somewhat indefinitely, as already suggested, till finally a syneytium is formed, very much as in the case of *Pennaria* (op. cit.), and as shown in Fig. 11, from which by a graduated process of cell organization and differentiation the germ layers are finally established, as shown in a later paragraph.

In Fig. 10, is shown a section of another egg in which likewise the nuclear conditions are very similar to those of Fig. 9, but in the present case evidences of cleavage are present as shown at regions marked *c.pl.* Here there is apparently no close relation between nuclear activity and that of the cytoplasm. This again is quite in keeping with conditions well known in other cases.

In Figs. 12—23 are shown a series of simply outline sketches illustrating the striking irregularity of cleavage in a large proportion of these eggs. Figs. 12—17 (Pl. 21) show the first six sections in a series of twelve of a single egg. The sections begin evidently at the animal pole, if we may assume polarity in these eggs, as only in the first four sections are nuclei present, the later sections showing only the large and very unequal blastomeres of the vegetal pole. In Figs. 18—23 (Pl. 22) are shown likewise a similar series of another egg, but in this case the sections are vertical instead of horizontal, as in the previous case. In this case the six sections are the central ones of a series of fourteen, and show the gradual progression of cleavage from the animal pole, the other remaining undivided.

It is probably from observations upon similar cleavage phenomena that CIAMICIAN conceived the presence of an epibolic gastrulation, an interpretation quite likely to be made where surface views chiefly are under consideration. But as shown in sectional series it is just as evident that BALFOUR's contention against such a process is indisputable.

Formation of the Germ Layers.

Concerning the origin and formation of the germ layers in this and related species views have been hardly less conflicting than on points already considered.

According to CIAMICIAN, as previously suggested, an epibolic gastrula is formed. This seems so obviously improbable, and moreover, so lacking in evidence as to demand little attempt at refutation. It is not difficult to recognize conditions in cleavage which might easily be construed from superficial aspects as comparable with this form of gastrulation, but many hundreds of sections of eggs in all stages of development have not afforded the slightest evidence of such a process.

According to METSCHNIKOFF¹ a true morula is formed. 'The cells of the morula appear to be identical in structure and consequently to show no difference between ectoderm and entoderm. Only after the number of embryonal cells has become quite considerable do the elements lying at the periphery form a connected layer, which is differentiated from the inner parenchyma mass by a sharp contour.'

BRAUER maintains that cleavage results in a coeloblastula, the entoderm arising by multipolar delamination from the cells of the blastula. While the embryo at this stage appears morula-like, he maintains that it is really a bilamellar embryo, with both germ layers established, though not yet sharply differentiated.

So far as my own observations go they tend to confirm the conclusions of METSCHNIKOFF, though in some degree agreeing also with phases of BRAUER's conclusions. I have found no evidence in support of the view that the germ layers are established during early cleavage, as BRAUER has claimed, nor that they result chiefly from a delamination of any sort, whether primary or secondary, unipolar or multipolar. That a morula-like condition often results from the more regular type of cleavage there can hardly be serious doubt. On the other hand it is often just as evident that a syncytium is formed, especially in cases of nuclear proliferation. Here the differentiation of the germ layers is brought about by a slow and graduated process of cell organization and adjustment. The conditions found in this species resemble in many respects those which I have described in *Eudendrium* and *Pennaria*. For a considerable time after the ectoderm is fairly established, the entodermal mass continues as a more or less homogeneous aggregation of cells in an undifferentiated condition. Finally the cells adjacent to the ectodermal lamella assume a more or less columnar shape, form a continuous series, and thus give origin to a definitive entoderm. Coincident with these changes, or shortly following, the inner mass of cells show signs of disintegration, become vacuolated and tend to liquefy, thus giving rise to the gastric cavity of the embryo.

Later History of the Embryo.

Concerning the formation of the actinula there is little to be added to the account given by CIAMICIAN. The embryo becomes

¹ Embryolog. Studien an Medusen 1886 pag. 69.

more disk-shaped, tentacles bud from the margins of the disk, and continue to grow in length, the embryo becomes entirely free in the cavity of the gonophore and later escapes as a typical actinula, differing in no essential respects from those of other well known species of *Tubularia*.

The actinula is not ciliated and has therefore no special organs of locomotion. On escape it is wholly at the mercy of the waves, or currents for distribution. In the aquarium it usually sinks close by the parent colony, often indeed falling among them, and seems to fix itself promptly upon any object with which it comes in contact, even the stems of parent hydroids. A careful inspection of colonies of hydroids which were discharging actinulae in the aquarium revealed the presence of young polyps in various stages of growth, from those apparently but recently attached, to specimens of considerable size, and of such maturity that gonophore buds were beginning to develop. It was not unusual to find several of these attached to a single stem, as shown in figure 24 (Pl. 22). As will be noted these young polyps show a definitely annulated perisarc over the entire length of the stem, whereas in the adult condition the perisarc is wholly devoid of this feature.

These observations recalled others of a similar character made upon *Corymorpha pendula*, a brief account of which I have elsewhere recorded¹. There were in these cases conditions which seemed to indicate the probability that the small polyps attached to the bases of the hydroid might be independent organisms, and if so perhaps a new species, and they were provisionally so designated, under the name of *T. parasitica*, as indicative of their presumed relation to the larger organism. It is unnecessary to go over in detail the grounds which seemed to justify this conclusion. Suffice it to say that the total annulation of the perisarc of the small polyps, the deeply insinuated rhizoidal attachment, and the presence of gonads were among the more obvious and apparently distinctive characters, which seemed to point toward their specific independence.

The observations above recorded concerning the history of the polyp of *T. mesembryanthemum*, and also a brief note by TORRY² concerning similar observations on the young of *Corymorpha palma* incline me to reconsider my earlier views concerning the case of

¹ Amer. Natural. Vol. 36 1902 pag. 549.

² Hydroids of Pacific Coast. in: Publ. Univ. California Z. Vol. 1 1902 pag. 38.

C. pendula. In so doing, however, it should be noted that the attachment of the polyps in the two cases is very different. In the case of *C. pendula* there is a deep insinuation of the finger-like roots within the perisarc of the base of the hydroid, and usually low among the rhizoidal filaments of the adults, while in the case of *T. mesembryanthemum* the attachment of the young is purely superficial, and occurs at any place upon the stem.

Perigonimus napolitanus sp. nov. (?)

Of the twelve known species of *Perigonimus* but two have been recorded from the Bay of Naples, namely, *P. linearis* Alder, by DU PLESSIS¹ in 1880, and *P. cidaritis* WEISMANN², in 1883. WEISMANN has contended that DU PLESSIS was mistaken in ascribing his species to *P. linearis*, believing it to be that which he has described as new under the last of the above named species.

During two different times, in 1894 and again in 1903, I have sought to identify one or both these species among the Naples hydroid fauna but have not succeeded. A hydroid taken from the same habitat, namely, the spines of the sea urchin, *Dorocidaris papillata*, in 1894 and at first thought to be the species recorded by DU PLESSIS, was found to lack characters distinctive of the species as described by ALDER and moreover lacked also characters enumerated by WEISMANN, particularly as to size, number of tentacles, etc. both of the hydroid and medusa. WEISMANN's species has been described as 9 cm high and to have 20 tentacles. The medusa differs from those of most species in having 4 marginal tentacles, and well developed oral tentacles with tufts of netting organs.

HARTLAUB³ has called attention to the unusual characters of WEISMANN's medusa and has suggested that they might reasonably be assigned to a different genus, or even to a different family, so far as their fundamental characteristics are concerned.

When, in addition to this, one reflects that hydroids of commensal habits, such as is the case with most or all the species of *Perigonimus*, are usually of small size, and when furthermore it is

¹ Mitth. Z. Stat. Neapel 2. Bd. 1880 pag. 146.

² Entstehung d. Sexualzellen bei d. Hydromedusen. Jena 1883 pag. 117.

³ Zeit. Wiss. Z. 61. Bd. 1896 pag. 161.

recalled that WEISMANN describes the perisarc of *P. cidaritis* as only a thin, slimy covering, the height of the slender stemmed hydroid, 9 cm, is of itself most remarkable. So far as I am aware, no species yet described has a height of more than about 8 mm, except *P. muscoides*, in which the height is doubtfully given as 2 to 3 inches.

Concerning the characters and affinities of *P. linearis* there has always been more or less doubt. It was originally described by ALDER as *Atractylis linearis*, and was later referred by ALLMAN¹ to the genus *Perigonimus*, but with a confession of grave doubt as to its real affinities, not having himself seen the species. I have previously expressed some doubt as to the occurrence of this species at Naples. Specimens from the collections preserved at the Zoological Station and marked *P. linearis*(?), have proven to be quite a different hydroid. And though I have sought during two summers, as intimated above, to secure the species it has not been found.

Upon the two different occasions previously cited I have obtained a hydroid which is undoubtedly a species of *Perigonimus*, but have not been able to identify it with either of the species above mentioned, nor with any other hitherto described. It was taken first in June, 1894, and again in April, May and June, 1903. In both cases the hydroid colonies were vigorous and large, but no gonads were present, a fact which would seem to suggest that the breeding season had probably past, or perhaps had not yet arrived. WEISMANN found his species in March, at which time gonophores were present. My own observations cover a period from March 6 to July 30, so that it would seem strange not to find some colonies bearing gonophores, yet such have been the facts in the present case.

In both instances the habitat of the colonies conforms well with that of members of the genus generally, namely, a commensal one. The hydroids were found in a few cases upon the shell of a shallow water gasteropod, but in most abundance and in best condition upon the margin of the carapace and upon the legs of a common crab, *Carcinus maenas*. It is an interesting coincidence that the species which it most resembles in general aspects, *P. jonesii*, of Long Island, N. Y., has a similar habitat on the spider crab, *Libinia emarginata*. This commensal habit of *Perigonimus* is a most interesting one, though not peculiar, since it is shared by a considerable number

¹ Monogr. Gymnoblasic Hydroids. London 1871 pag. 329.

of well known cases, such as *Hydractinia*, *Podocoryne*, etc. But in *Perigonimus*, a genus comprising perhaps the largest number of species among Gymnoblasteae, so far as detailed information is available it seems that almost without exception the species are essentially commensal.

In common also with most known species the one here under consideration has a gelatinous perisarc, which covers the entire colony from the hydrorhiza to the body of the hydranths, and covering the latter to the bases of the tentacles, though not in any appreciable degree extending to the tentacles, as seems to have been the case with WEISMANN's species. There can hardly be reasonable doubt that the mucus-like covering is a definite secretion by the hydroid itself, and homologous with the chitinous perisarc common to hydroids generally.

A character in the present species is the long, slender, stem-like branches which arise at sharp angles from the stems and grow quite long without signs of giving rise to hydranths. There seems to be evidence that eventually hydranths arise from their tips, but it is not conclusive, as in only a few cases have newly formed hydranths appeared upon them.

The following are the more distinctive diagnostic characters of the species, which seems to be new, and for which the name *P. napolitanus* is proposed: —

Trophosome (Pl. 22 Fig. 25): Hydrocaulus composed of numerous stems, variously branched, some of the latter without hydranths, all branches arising at sharp angles from the main stems or branches, entire hydrocaulus arising from a net-like hydrorhiza, and attaining a height of from 4–8 mm. Hydranths elongate, more or less fusiform, with conical hypostome, and with a single whorl of rather stout tentacles, 7–12 in number. Entire colony provided with an indefinite, gelatinous perisarc, extending over bodies of hydranths to close beneath the circle of tentacles. Perisarc sometimes dense and somewhat chitinous in older portion of stems and hydrorhiza, and of dull brownish color. Gelatinous perisarc often studded with foreign particles, diatoms, etc., which thus give to the colony a rough, or fuzzy appearance, as shown in fig. 25.

Gonosome: wholly unknown.

It is worthy of mention in this connection also, that I took on May 4. 1903, a hydroid which, barring the absence of gonophores, bore a close relation to *P. repens* Wright, and is probably identical

with that species. As in the former species, and as just mentioned, no gonophores were present, rendering impossible full determination of the identity suggested. A careful comparison of the hydroid with the descriptions and figures of HINCKS leaves little doubt in my own mind, and if later observations of the species when the medusae are present shall confirm this view it will extend the range of distribution of the species to Mediterranean waters, as CALKINS¹ report of it in 'Hydroids from Puget Sound', has extended its distribution to Pacific waters.

Gemmaria implexa Alder.

In 1880 DU PLESSIS (op. cit.), records the occurrence of the medusa of this species at Naples during the month of March, and makes the very interesting remark that the specimens taken differed from typical medusae of the species in having 4 complete marginal tentacles instead of 2. »Encore cette méduse diffère-t-elle par quelques points de celle qui a servi de type aux descriptions qui existent dans les ouvrages anglais. Ainsi cette méduse présente 4 tentacules marginaux complets au lieu de deux seuls comme l'indique ALLMAN«.

DU PLESSIS makes no reference to the hydroid and presumably he had only the medusa taken in the 'Auftrieb', which leaves the question of identity an open one, at least in part, and particularly so in that his medusa had the unusual number of four tentacles.

On May 13, I obtained a small colony of the hydroid from which in a short time after having placed it in the aquarium a medusa was liberated, and within the following day several others. During the month I obtained about a dozen additional colonies of hydroids and placing them in separate aquaria obtained from most of them free medusae, which lived apparently quite normally for nearly a fortnight, thus affording ample time for critical observations as to growth, habits, etc. In Pl. 22 Fig. 27 is shown a sketch of the entire colony, and in figs. 28, 29, are shown also sketches of individual hydranth, and medusa.

As to habitat all the colonies obtained by me were found upon the live shells of small lamellibranch molluscs, apparently belonging to the genera *Nucula* and *Corbula*. According to HINCKS and ALL-

¹ Proc. Boston Soc. N. H. Vol. 28 1899.

MAN the habitat varies from tide pools to considerable depths, and on fragments of rocks, shells, etc.

While conforming in most respects to the diagnoses given of the species by HINCKS and ALLMAN (op. cit.) in some few points there are differences, though not to my mind of any considerable importance. As to size HINCKS gives the height of the hydroid as from 12 to 20 mm, while according to ALLMAN it averages about 6 mm. In my own specimens the height varied from 3 to 6 mm in the expanded condition. It would seem that HINCKS must have had very unusual specimens, or that in some way his figures are incorrect.

A point of most difference is that concerning the location of the gonophores on the hydranth. According to both the previously named observers these bodies arise low upon the body of the hydranth and in a single, or sub-verticillate cluster. I have found them arising in several clusters or even singly, at any point or portion of the hydranth, and quite as frequently near the oral as the basal region of the body. They are borne on short pedicels, frequently in clusters of from two to four on the same peduncle.

The Medusa. At birth the medusae are sub-spherical and average about 0.6 mm in diameter, and have two well developed tentacles, which arise from large bulbous bases on opposite sides of the body, each tentacle provided with numerous stalked nematocysts. As noticed in a previous paragraph, they live well in the aquarium, but do not appear to grow to any appreciable extent. The largest specimen measured 0.8 mm in height by 0.7 mm in breadth. The general aspects of the little creature are shown in fig. 29, but no figure can delineate the elegant grace and beauty which it exhibits when floating languidly with tentacles extended, like delicate streamers fringed with an exquisite embroidery of stalked batteries of nematocysts, to a length of ten times the diameter of the bell, or quivers in magic undulations as the limpid creature pulses itself through the water. Little wonder is it that, observing something of its exquisite features that prince of earlier observers, MCCRADY, as expressing his sense of the beautiful, ascribed to the genus the name *Gemmaria*, the little gem!

As ALLMAN has well remarked, one of the most unique among the several characters of this medusa is that of the numerous, stalked capsules of nematocysts which fringe the tentacles. From near the basal bulbs to their very tips, the tentacles are irregularly covered

with these interesting organs. To this author's graphic description of them (op. cit. p. 225), it is unnecessary to add. In but few particulars do my own observations differ in any material respect from his. In the first place my specimens have not shown the abrupt ends of the tentacles which he has figured. As will be noticed from the figure already cited, the tentacles usually have attenuated distal portions as shown. Again the body of the tentacles is more or less roughened or rugose, due to the irregular projections of the ectoderm cells in pseudopod-like processes. And finally I have not been able to observe the peculiar vibratory shimmerings of the pedunculated nematocyst capsules to which he has referred. In repeated observations directed to the detection of just this phenomenon I have as often failed to distinguish it. Possibly it is only an occasional phenomenon, arising perhaps under special conditions which may not have been present in the case of my specimens, or possibly it may be lacking entirely in some cases. I am in full accord with ALLMAN as to the essentially 'sarcodal' nature of the peduncles of the netting organs, as well as to their irritability and contractility. It seems to me that the rugose appearance of the tentacles is likewise due in part to essentially the same ectosarcal activity of the cells of the ectoderm, which seem to thrust out and retract pseudopod-like processes of varying shapes and sizes and in part to the netting organs with which they are studded. Vesicular cavities in the entoderm of the tentacles are frequently to be seen, within which are exhibited exquisite displays of Brownian activity among minute pigmentary granules. The same phenomena also occur in the irregularities of the walls of the radial canals.

As will be seen in figure 29, there is an oval capsular enlargement arising at each perradius of the margin just over the radial canal, containing large nematocysts, the cnidocils of which may be seen as bristling projections from the outer surface. Usually those of the perradii bearing the tentacles are larger than those of the others.

The medusae are very transparent except for the brownish color of the manubrium, the delicate brownish pigment of the radial canals, and the reddish orange pigment of the basal bulbs of the tentacles.

The earlier reference herein to the medusae of this species observed by DE PLESSIS, which seemed peculiar in having four marginal tentacles, recalls the fact that the medusa originally described

by McCrady¹ and for which he established the genus, had likewise four tentacles. In 1900 Mayer² obtained a hydroid at the Tortugas which he described as the trophosome of the species, *G. gemmosa*, the medusae of which when first liberated had but two tentacles, nor did others appear.

The question naturally arises, whether in these cases we may have a different species, or whether the medusae of the same species occasionally vary as to the number of tentacles. The latter seems to me the more probable alternative. It is well known that medusae of different species, or even of different genera, often resemble each other so closely as to appear to be identical. Hartlaub, for instance, as cited in a previous connection, has shown this to be the case in several instances which need not be reviewed in this connection. Such is apparently the case also with the medusae of *Gemmaria* and *Corynitis*. I am strongly convinced, however, that in this case we have to do, not with two distinct genera, but with different species of the same genus; for it has never seemed to me that there are differences between the two which are sufficiently marked to justify generic distinction. And what is true in this case is probably true in many others of similar sort. This is doubtless due in large measure to the fact of the separate and independent life of the two organisms, hydroid and medusa. When we shall have worked out critically the ontogeny of the several species, much of the apparent anomaly will doubtless disappear.

Corydendrium parasiticum Cavolini.

Among the many species of hydromedusae which have long engaged the interest and observations of naturalists, few if any, surpass the one here under review. It was originally described by Cavolini³ in 1785 under the name of *Sertularia parasitica* in a small monograph upon the Naples fauna, which for painstaking observations and clear interpretation may well rank as a classic of its time. After its original description it remained for nearly three quarters of a century little, if at all known to students of the group, though it is at present a fairly familiar object among its congeners

¹ Gymnophthalmata of Charleston Harbor. 1857.

² Bull. Mus. Harvard Coll. Vol. 37 1900 pag. 35.

³ Memorie Polypi Marini. Napoli 1785.

of the Neapolitan fauna. It was first studied by the present writer in 1894 and again during the summer of 1903, at which time it was obtained in various stages, from small, single polyps growing among the remains of old and mostly dead colonies of *Eudendrium* and *Pennaria*. This fact naturally recalled the belief of CAVOLINI that it was parasitic upon the former of these hydroids, one of the few points in its original description in which the Neapolitan naturalist was undoubtedly mistaken, as WEISMANN has proven, and as I have also been able to confirm, in that finely developed colonies have been obtained wholly free from any association with *Eudendrium*, or other hydroid, growing indeed upon fragments of rock, etc.

ALLMAN¹ in describing this hydroid, knowledge of which was derived entirely from CAVOLINI's description, expressed somewhat emphatic doubt upon several points of habit, structure, etc. Among them is that of its parasitism referred to in the preceding paragraph. Another had reference to its life history, ALLMAN claiming that it would undoubtedly be found to have a free medusa stage, and further that the claim of CAVOLINI to have traced the origin of eggs and embryos was as undoubtedly erroneous as he believed the other features to have been. He says concerning this point 'It is far more probable that the egglike bodies are parasitical organisms than that they have any direct relation with the hydroid'. He is likewise in error as to the fasciated condition of the stems of the hydroid.

It remained for WEISMANN² to show that ALLMAN's contentions were, with the exception of that referring to parasitism, without foundation in fact.

My own observations have confirmed those of WEISMANN on these points without exception.

WEISMANN's account of the essentials of structure, habits, etc., is so full and admirable that it is unnecessary to undertake here to review or repeat it. What follows has to do almost wholly with matters of development, concerning which WEISMANN records little beyond such aspects as come within the province of his particular problem, namely, the origin of the sex-cells.

¹ A Monograph of the Gymnoblasic Hydroids. London 1871 pag. 263.

² Die Entstehung der Sexualzellen bei den Hydromedusen. Jena 1883 pag. 35 etc.

I very much regret that owing to the quality of material and its incompleteness I shall not be able to go into any considerable details as to cytological aspects of maturation or fertilization, though so far as I have been able to observe there seems to be nothing unusual in these respects.

The germ cells arise in the entoderm of the stem and later segregate within follicular pouches where they are nourished and complete their growth, the follicles themselves growing and becoming correspondingly larger, and more or less hydranth-like, but without trace of tentacles, each however having at maturity a protruding head, the end of which becomes ruptured for the extrusion of the eggs. WEISMANN has published admirable illustrations of these features. (Cf. op. cit. Pl. 14, Figs. 1 and 2; Pl. 15, Figs. 3, 4, 5.) The eggs seem to be discharged singly and fertilization probably occurs during this time, following which they become surrounded by a definite firm membrane within which cleavage and the development of the embryo takes place. WEISMANN believes that all the eggs of a given gonophore are discharged at about the same time and that their cleavage and subsequent development proceed simultaneously. In this, however, I am unable to concur. Many cases have come under my observation in which considerable variation in the condition of development of a given cluster of eggs is quite evident. This may be readily seen in preparations of entire gonophores, but is strikingly demonstrated from sections of gonophore clusters. In Figs. 30 and 31 are shown camera sketches of sections of two eggs of the same cluster, in the one case the embryo having reached the period of definite ectodermal differentiation, while the other is only in an early cleavage stage. As compared with other known cases this difference must imply at least a range of from fifteen to twenty hours, and I have no doubt that others of still wider divergence are not lacking. WEISMANN's citation of the noteworthy approximation to simultaneous development is, however, well made. It is certainly quite unusual to find among hydroids with fixed sporosacs so near an approach to this condition as that under consideration. It resembles more the conditions prevalent in shortlived medusae, like those of *Pennaria*, or *Pachycordyle* as described in a preceding section of this paper. The resemblance is the more striking since there is not the remotest approach toward a medusoid character in these simple follicular sporosacs.

Cleavage begins, as WEISMANN has shown, very soon after the

discharge of the eggs from the summit of the gonophore. As a rule it seems to be remarkably regular and equal, a condition probably facilitated by the essentially free and independent disposition of the eggs about the conical apex of the gonophore. While during the earlier phases of cleavage the entire egg appears to be involved, in some specimens there appears to be a condition of independent nuclear proliferation similar to that found in many species of *Tubularia*, among which that cited in a previous section of this paper is an instance. Cleavage finally results in the formation of a solid morula, or in some cases a morula-like embryo having something of a syncytial character, it being impossible to distinguish any definite cellular organization, but rather a multinucleate embryo, such as is well known among not a few *Hydromedusae*.

Formation of the Germ Layers.

Concerning the ectoderm attention has already been directed to its appearance at a comparatively early period in development. Fig. 31 is one from an embryo which has just begun to assume the piriform shape of the planula. In this it is as yet barely possible to clearly distinguish the columnar shape of typical ectoderm cells of an embryo at this stage. The ectodermal nuclei are definite and large, and for the most part superficially disposed. At a somewhat later period the ectoderm becomes finally and definitely differentiated, and the entire embryo more planula-like, apparently approaching birth. Still I have not found any intrinsic differentiation among the ectoderm cells themselves, such, for instance, as nematocysts.

Concerning entoderm formation I am unable to specify. The entodermal mass shown in Fig. 31 continues essentially unchanged, probably up to and beyond the time of the birth of the planula, a condition not uncommon among *Hydromedusae* generally. The nuclei continue to proliferate, but without corresponding cytoplasmic activity, at least during the distinctively embryonic development. Differentiation of the entoderm probably takes place by a gradual process of cellular organization of the entodermal mass, parts of which undoubtedly serve, as in other well-known cases, as nutritive substance till the larva finally attaches itself and assumes the polyp stage, while the cellular elements become organized into a definitive entoderm.

Podocoryne conchicola (Philippi), in part.

Since the original description of *Podocoryne carnea* by Sars¹ in 1846 its distribution has been recorded over a large portion of the northern Atlantic on both eastern and western coasts, and several new species have been described.

During the spring and summer of 1903 the present writer had occasion to examine several colonies of what appeared to be perfectly typical species of *Podocoryne carnea* Sars. An examination of the medusae, large numbers of which were set free in the aquaria, showed them to differ from this species in the rather remarkable fact that they possessed only four marginal tentacles at birth, whereas medusae of the other species have uniformly eight at the time of birth or very shortly following. So far as I am aware, only one species of *Podocoryne* has a medusa whose tentacles are only four in number, namely, *P. aculeata* Rud. Wagner, and in this species all are quite rudimentary and continue so. The specimens here under consideration seem to have four tentacles, and only four. Medusae were kept in the aquaria for several days, indeed as much as a week, during which time the sexual products were matured and discharged, but in not a single case was there the sign of additional tentacles. I was, moreover, assured by Dr. Lo Bianco, who is familiar with the fauna of this region, that this medusa never has more than the four primary tentacles, so far as he had observed.

In his account of British Hydroid Zoophytes HINCKS² includes among the species of *Podocoryne*, *areolata*, originally described by ALDER as *Hydractinia areolata*, whose medusae are characterized by the presence of from one to three unequally developed tentacles in each interradial interval, in addition to the four primary periradial tentacles. So far as I am aware this is the only known species whose tentacles number more than eight.

HAECKEL³ under the generic name *Dysmorphosa* describes four species, namely, *carnea* Sars, *fulgurans* A. Agassiz, *minima* Haeckel, and *octostyla* Haeckel, and these are all characterized by the presence of 8 tentacles, the interradial group usually arising slightly

¹ Fauna Littor. Norvegiae 1846.

² British Hydroid Zoophytes. London 1868.

³ Das System der Medusen. Jena 1879.

later than the primary, or perradial, and remaining somewhat smaller in size. So characteristic does HAECKEL regard this feature that he has designated it as one of the generic characters of these medusae.

GROBBEN¹, however, has published a somewhat detailed account of *Podocoryne carnea*, one feature of which was the presence of but four tentacles on the medusae. These medusae are represented, moreover, as bearing sexual products, a fact which would certainly imply approximate maturity, and therefore justify the further inference that no additional tentacles appear. GROBBEN's figures have been variously copied into text-books, monographs, etc., but so far as I have been able to discover, no particular note has been made of the apparent anomaly, that all earlier accounts, including, those of SARS, KROHN, HINCKS, ALLMAN, and later of HAECKEL as just cited, give to the medusa the usual eight marginal tentacles. So far as I am aware, nothing has been said as to the probability of this fact being due to the existence of at least a distinct variety, if not indeed of a distinct species.

HAECKEL (op. cit.), has indeed expressed some doubt as to whether there might not be a distinction in the Mediterranean species in the following words: — "Es ist möglich, daß die mediterrane Form von der nordischen echten *D. carnea* specifisch zu unterscheiden ist, in welchem Falle der ersteren der ältere, von ihrem Entdecker gegebene Name: *Dysmorphosa conchicola* verbleiben kann."

WEISMANN has likewise expressed a doubt of a similar sort, as possibly accounting for apparent discrepancies between his version of the origin of the sex-cells and that of DE VARENNE as to the same subject.

From these citations, as well as from the foregoing account, it may be clearly seen that in all probability we have in the Naples form a distinct species, and indeed, on the basis of HAECKEL's System, even a distinct genus. The latter, however, may be at once dismissed as wholly inadmissible, as the mere presence of a few more or less tentacles would not, in itself, justify any such separation. Moreover, when one comes to compare the hydroid colonies of the Naples species with those of other localities there is not the slightest doubt as to their very close relationship. ALLMAN himself says they are indistinguishable from typical *P. carnea* Sars. Incidentally, it may be noted in this connection that ALLMAN's doubt

¹ Sitzungsab. Akad. Wien 72. Bd. 1875.

as to the presence of the so-called spiral zooids among this species, it not sustained. Both WEISMANN and GROBBEN have shown their presence, and I have found them in every colony examined.

It had occurred to me during the progress of my observations that possibly the tetranematous condition of the medusae of the Naples species might be due to some incidental, or local cause. I therefore examined specimens from various localities, both male and female, but found in every case that the medusae showed the same absolute constancy in this feature. An examination of more than one thousand specimens failed to detect any variation in this respect.

I feel therefore confident that we have here a distinct species, and acting on the suggestion of HAECKEL, previously quoted, I propose for it the name *Podocoryne conchicola*, restoring the specific designation of PHILIPPI¹, who in 1842 described a hydroid under the name *Dysmorphosa conchicola*, which has since been considered by many to have been identical with *Podocoryne carnea* Sars. ALLMAN has, however, doubted the reliability of PHILIPPI's description, and furthermore the widespread use of Sars' name throughout the literature should give pause to any attempt to readjust the matter at present.

The following diagnostic characters are distinctive of the medusa, no occasion arising in my judgment for a redescription of the trophosome, which differs in no significant way from that of typical *P. carnea* Sars (a slightly larger size perhaps, being the only point of difference observed, and that not constant): —

Medusa (Pl. 22 Fig. 26): bell nearly hemispherical, slightly higher than broad, size, 0.8 mm high by 0.7 broad; velum rather wide; manubrium quadrate in shape, with four oral arms which are tipped with clusters of nematocysts; marginal tentacles 4, perradially disposed, and not becoming more numerous with age; when swimming the tentacles usually coiled closely against the bell as shown in Fig. 26, when resting on the bottom of the aquarium or floating sluggishly, tentacles usually extended at right angles to main axis of body; basal bulbs of tentacles rather prominent, and with brownish pigment, though no definite ocelli; outer surface of bell sparingly dotted with nematocysts; gonads borne in four series on the base of the manubrium. Bell very transparent and colorless, except at

¹ Arch. Naturg. S. Jahrg. 1842 pag. 37.

base of tentacles as mentioned above; the base of the manubrium is likewise slightly brownish.

As a final note I desire to acknowledge my obligations to the Zoological Station for material used in the foregoing descriptions, and my grateful appreciation of the unfailing courtesy of the Director and other members of the Staff.

Explanation of Figures.

Plate 21.

- Fig. 1. Entire colony of hydroid, *Pachycordyle Weismanni*. $\times 3$.
- Fig. 2. Medusa of same. Greatly magnified.
- Fig. 3. Longitudinal section of stem and gonophore bud, showing egg-cells in entoderm.
- Fig. 4. Similar section through gonophore of later stage, showing bell-nucleus *Glk*.
- Fig. 5. Similar section of slightly later stage, showing follicular groups of ova, and development of ectoderm of medusa.
- Fig. 6. Optical section of medusa about the time of isolation from the coenosarc of stem.
- Fig. 7. Section of mature medusa at time of birth. *m.* marginal rim; *v.* velum; *c.c.* circular canal?
- Fig. 8. Section through medusa bud some time prior to maturity, showing nutritive entoderm at *ent*, various nuclear features, etc.
- Fig. 9. Section of egg of *Tubularia mesembryanthemum*, showing multinucleate condition before cleavage. *n.* nuclei; *ps.c.* pseudocells; *g.w.* wall of gonophore.
- Fig. 10. Section of an egg similar to fig. 9, with lines of incipient cleavage at *c.pl*.
- Fig. 11. Later stage of multinucleate egg, syncytium.
- Figs. 12—17. Outlines of first six sections of an egg, only four of which showed nuclei.

Plate 22.

- Figs. 18—23. Similar series, median six sections in a series of fourteen, showing progressive cleavage from animal to vegetal pole.
- Fig. 24. Young polyps attached to stem of parent hydroid.
- Fig. 25. Colony of hydroid, *Perigonimus napolitanus*. $\times 10$.
- Fig. 26. Medusa of *Podocoryne conchicola*, showing position of tentacles during active movements of medusa.
- Fig. 27. Colony of *Gemmaria implexa* on shell. $\times 3$.

- Fig. 28. Single hydranth of same. more highly magnified, showing medusa buds at *m*.
- Fig. 29. Medusa of *G. implexa*, greatly enlarged, showing general shape of medusa, aspect of tentacles, stalked nematocyst capsules, etc. Only one tentacle drawn complete.
- Fig. 30. Section of egg of *Corydendrium* in early phase of cleavage.
- Fig. 31. Section of early embryo of *Corydendrium*, with ectoderm, *ect*. Undifferentiated entodermal mass *ent*. comprising the center.
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