ART. VI.—*Tubularia Not Parthenogenous*; by Prof. HENRY JAMES CLARK, of Harvard University, Cambridge, Mass.

It is with no small degree of pleasure that I announce the discovery of the *eggs* of the Tubularians. During the middle of October I had in my aquarium the three most common species, of this group, on our shores, viz: *Tubularia indivisa* Lin. (*T. Couthouyi* Ag.) *Thamnocnidia coronata* Ag. (*Tubularia coronata* Abild., *Thamnocnidia spectabilis* Ag.) *Parypha calamaris*? (*P. crocea* Ag., *Tubularia calamaris* Van Ben.?). In each of these I have traced the development of the *egg*, from its inception to

the time of its escape, as a hydroid form from the medusoid genital. I do not wonder that the egg has eluded the observation of naturalists thus far, for so faint are its outlines that it might be put down as one of the tests of a first class objective. Although I had obtained glimpses of it with a Tolles' $\frac{1}{2}$ inch objective, yet it was not until I applied a $\frac{1}{4}$ inch objective, of the same optician, that I gained a clear and unmistakable view of this long sought body. Thus we are relieved of what once seemed to be the anomaly of a male, on the one hand, producing a perfect fecundating material, and, on the other hand, a female producing young without a corresponding fertilizable egg.

In order to make the mode of development of the egg fully comprehensible, I must prelude the description by an account of some other discoveries which I have made in regard to the muscular system of Hydroids. It has long been a matter of speculation among physiologists and zoölogists as to what is the basis of contraction in these animals; and some indeed have given themselves up to the idea of a contraction of the individual cells of the walls, imagining themselves to be warranted in this belief by the supposed example of the so-called unicellular Infusoria. Not discovering the true muscular layer, they have mistaken the effect for the cause; seeing the cells of the walls of a Hydroid diminishing during the contraction, and enlarging during the expansion of the animal, they have supposed that the individual cells were the instruments which effected their own changes; whereas they were only the subjects of a power which reigned among them. As long ago as 1843, Quatrefages (Ann. Sc. Nat., vol. 20,) got a glimpse of the muscular system of one of the Hydroids, *Hydractinia* (*Synhydra* Quatrf.); but his story is so mingled with what is, without much doubt, incorrect, that it would be impossible to generalize from his observations.

I made my first satisfactory determination of the position of the muscular system of Hydroids in *Coryne*, ("*C. mirabilis*" Ag.) more than a year and a half ago. The discovery is noted thus in my journal, "March 14, 1862. Between the outer and inner walls (of the hydraform *Coryne*) of the body and tentacles, there is a layer of longitudinal fibrillated *muscular bands*.—The cells of the core of the tentacles are arranged about an imaginary axis in three ranks, that is, the breadth of three cells occupies the whole circumference of the tentacles; and the so-called axial column is composed of the interstitial granules at the inner ends of the cells."—In the following month my journal runs thus. "April 13, 1862. Walked to Boston and collected *Tiaropsis* ("*T. diademata*" Ag.), *Bougainvillia* ("*B. superciliaris*" Ag.), and *Sarsia*, (*Coryne mirabilis*" Ag.). The muscular system, of *Tiaropsis*, *Bougainvillia*, and *Sarsia*, is a layer of circular and a layer of longitudinal

*fibrillæ*¹ lying between and behind the innermost and middle walls of the disc." Thus I had verified the existence of a muscular system in both the Hydroid and its medusogenitalia. I would also mention in passing that in the hydraform *Scyphostoma* of *Aurelia aurita* ("A. flavidula" Ag.), which I had raised from eggs and kept in my aquarium for eighteen months, I detected, last January, a similar, longitudinally fibrillated layer of muscles, between the outer and inner walls of the stem, disc, and tentacles. In the proboscis, disc and base of the tentacles, and in the four equidistant columns, or pilasters, which project into the digestive cavity, this muscular layer is separated from the inner wall by a *gelatiniform layer* of varying thickness. In the four pilasters the gelatiniform layer is a solid core which thins out suddenly, at the top of the stem, to a slender cord, and in this form it continues to the bottom of the stem of the *Scyphostoma*. I have already published a detailed account of the muscular system of the adult medusoid form of this species in Agassiz's Contributions to the Natural History of the United States, vol. iv, p. 61. I would also refer to the May number of this Journal, page 347, note 5, for a minute account of the gelatiniform layer of this medusa. In regard to the development of the muscular system of *Aurelia*, I would so far modify my opinion as to say that the fibrillæ are developed from a substratum of interstitially originating formative cells, which are metamorphosed, after the well known method, into contractile threads. I hope I may be pardoned for this divergence from the base upon which I began, because I hope thereby to disclose the more general prevalence of this myological feature in the morphology of *Acalephæ*.

During my studies upon the development of the eggs of the

¹ The presence of a muscular system in Hydro-Medusæ was long ago detected by Wagner, Sars and others; but they gave no details of its structure or position. Later, Huxley described the system in Siphonophoræ, as being in the outer wall. We owe to Allman the credit of having first pointed out, in the hydraform, the nature and true position of the muscular system. He says, (Anat. and Physiol. of Cordylophora, Phil. Trans. 1853, p. 372), "It consists of numerous longitudinal fibres, which are in close contact with the inner surface of the ectoderm." "Similar fibres may be witnessed in *Coryne*, *Syncoryne*, and other marine Tubulariadae," &c. The most elaborate attempt upon this subject is that of Agassiz. His description of the muscular system of *Hippocrene*, *Sarsia* and *Tiaropsis*, in his monograph, on the *Acalephæ* of North America, Mem. Am. Acad., 1849, and repeated, in part, in his "Contributions to the Natural History of the United States," iv, 213, is a representation of an effect for a cause; as he has uniformly described the wrinkles of the walls, produced by contraction, as *muscular fibres*; and everywhere the cells of either the innermost or middle wall are described as "*contractile cells*" of the muscular layer. The truth is, the muscular layer is composed of *fibrillæ*, which, I have every reason to believe, are developed by a direct arrangement from the interstitial blastema, simply through the intervention of the *formative-cell process*, and not by a disintegrative metamorphosis of fully organized cells. In the section on *Coryne* in Agassiz's "Contributions," there is so great an incongruity between the description of the structure of the last stages of the young medusoid, and what follows upon the anatomy of the adult form, that one is forced to believe that the two parts of the investigation were made by different observers. Certainly no diversity of age could produce this.

Tubularians I have found it impossible to understand the mode of origin of the ovigerous layer without taking into account the development and varying position of the muscular layer. In the hydroids of these three Tubularians, there intervenes an excessively thin, longitudinally fibrillated muscular layer between the outer and inner walls of the stem, disc, tentacles, and branching stems of the genitalia; and whenever the latter pululate to form a genital sac, a medusoid, all the cellular and muscular elements enter into the operation, and thus there arises at first a highly contractile, triple walled hernia, the outer wall of which consists of a single stratum of broad cells, each containing a large nucleus; the middle wall, or stratum, forms the muscular layer; and the innermost wall is made up of a single layer of very large prismatic cells. This is the first stage of medusoid development. Hardly, however, has the bud declared itself before the ovigerous layer begins to develop. This is done in a very simple manner; at the end of the bud, the inner wall, and with it the muscular layer, recede from the outer wall, and leave between them a space which is occupied by a distinct, peculiarly colored substance, which is no less than the incipient ovigerous layer. Contemporaneous with the origin of this layer the eggs appear; and in fact they may be said to form nine-tenths of the bulk of this stratum, the remainder constituting the intercellular blastema, such as I think is the original basis of all cell development. The eggs, although they eventually become very numerous, are at first only very few in number, perhaps five or six, and compare in size with the cells of the outer wall of the bud. The very distinct Purkinjean vesicle occupies about one-third of the diameter of the ovum. As the space between the walls of the bud increases, it gradually assumes a spheroidal form, and as it is constantly filled by the ovigerous layer, the latter also becomes globular. Surrounding this space we have on one side the outer wall at the end of the bud, and on the other side, the inner wall, lined by the muscular layer, assuming a cup-shaped form. Gradually and during the process of growth the edge of the cup becomes narrowed, and by degrees closes over the intervening space occupied by the ovigerous layer, and shuts the latter off from the outer wall. By this process that part of the muscular layer which lines the cup and directly embraces the ovigerous layer is cut off from that part of its continuation which lies beneath the outer wall. In this condition the end of the medusoid is constructed thus: proceeding from without inwardly, we have an outer wall, an outer muscular layer, an inner cellular layer formed by the closing over of the edge of the cup, an inner muscular layer surrounding a fifth stratum which is the ovigerous layer.

Only one step more is now required to perfect the morphological plan of development of this organ, and that is brought

about by a simple hollowing out of the ovigerous stratum, so that, instead of remaining a solid mass, it becomes as it were a lining to the muscular layer, which embraces it. Thus in an end view of the bud we would have a hollow sphere made up of five concentric layers, succeeding each other as enumerated above. This is essentially the typical form of the meduso-genitalium of the Tubularians; for whatever changes occur in the later days of growth, no new morphological features are instituted.

The development of the radiating and circular tubes in *Tubularia* is merely a hollowing out of channels in the middle wall of the bud; and the formation of a proboscis in all three of the species of Tubularians is simply through a development of a protuberance, from the bottom of the cup, in such a manner that a part of the ovigerous layer, or innermost wall of the meduso-genital, becomes the outer wall of the proboscis; the subjacent muscular layer, which originally embraced it, becomes apparently inverted in its relations, and in its turn lies beneath this wall; and lastly, what was formerly the outer wall at the bottom of the cup becomes the inner wall of the proboscis.

The only difference, if it can be called a difference, between this meduso-genital and the more highly developed free forms of such as *Hybocodon*, *Corymorpha*, *Bougainvillia*, *Lizzia* and *Coryne*, is that the latter do not develop eggs in their ovigerous layer, or as it has been called in them, the outer wall of the proboscis and the innermost wall of the bell, until a much later period.² The mode of development of all the walls is alike in the

² *On the walls of the most highly developed medusoid.*—The immense gelatiniform mass which constitutes such a large proportion of the bell of these free forms—or even of some of those which remain fixed at the latter end of the breeding season, as in "*Coryne mirabilis*,"—is merely an extraordinary increase of the interstitial blastema of the two adjoining, outer and middle walls, between which it develops as these recede from each other. In the younger stages of the medusoid, the gelatiniform substance exhibits an irregular fibroid structure, with a few multi-caudate cells, and granules here and there; but in the adult period it is exceedingly difficult to detect any fibrillation. This is always the last layer formed in the process of development, and with it we have the highest kind of meduso-genitalia. In this condition the bell of a medusoid, for instance "*Coryne* (*Sarsia*) *mirabilis*," is constituted thus: 1st, there is the outer wall, *ectophragma*; 2d, the gelatiniform layer, *chondrophys*; 3d, the outer muscular stratum, *ectomyoplax*, which presses closely upon the middle, 4th, wall, *mesophragma*; 5th, the inner muscular layer, *endomyoplax*; and 6th the innermost wall, *endophragma*. In the proboscis,—*manubrium*, Allman,—we have, 1st, the outer wall, *ectophragma manubriale*; 2d, the muscular layer, *myoplax manubrialis*; and 3d the inner wall *endophragma manubriale*. In the velum all the layers, except the chondrophys, exist, and follow each other as in the bell proper. In the tentacles there are but three strata, viz. 1st, the *ectophragma*, 2d, the *myoplax*, which is continuous with the *ectomyoplax* of the bell, and 3d, the *endophragma*, in continuity with the *mesophragma* of the bell. Now in the fully-formed meduso-genital of the above mentioned Tubularians, *T. indivisa*, &c., only the chondrophys is wanting. The terms *ectoderm* and *endoderm* I gladly adopt for, yet would restrict to, the outer and inner walls of the cœnosarc of the hydraform; but as it would seem to be a misapplication of terms to call the "middle wall," of the meduso-genital or gonophore, a *derm*, I apply to it the name *mesophragma*, i. e. median wall or partition, and to the outer and inner walls of the same, to carry out the idea, the terms *ectophragma* and *endophragma*.

former and the latter; *there is but one type of development in the medusoids of all the Hydroids*. This is what my observations within the past two years have led me to believe. The further development of the young of the Tubularians proceeds in an unequal degree for the different individuals, some of them grow much more rapidly than others, and finally, becoming separated from their matrix, move freely in the cavity of the genital organ, until their tentacles are developed so as to present *the same one-sided cylindrico-claviform outlines as the parent*, and then they escape into the open sea. Thus they succeed each other until the ovigerous layer is totally bereft of all its progeny, and nothing but a faintly granular blastema is left to represent the outer wall of the proboscis, and its continuation the innermost wall of the bell. I would add finally, that in the males of these Tubularians, not even excepting Parypha, the meduso-genitals are identical in form, structure, and development with those of the females.