XI. The Croonian Lecture.—*Preliminary Observations on the Locomotor System of Medusæ.* *By* George J. Romanes, *M.A., F.L.S., &c.* *Communicated by Professor* Huxley, *LL.D., Sec. R.S., &c.*

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I. Structure and Movements of the Medusæ.

§ 1. *Structure of the Medusæ.*—Although it is not my intention in this preliminary notice to enter into the literature of my subject, it is nevertheless desirable to quote the well-known statements of Prof. L. Agassiz regarding the nature and distribution of the nervous system which he describes as occurring in the Medusæ. He says:—"There is unquestionably a nervous system in Medusæ, but this nervous system does not form large central masses to which all the activity of the body is referred, or from which it emanates. . . . . In Medusæ the nervous system consists of a simple cord, of a string of ovate cells, forming a ring round the lower margin of the animal, extending from one eye-speck to the other, following the circular chymiferous tube, and also its vertical branches, round the upper portion of which they form another circle. The substance of this nervous system, however, is throughout cellular, and strictly so, and the cells are ovate. There is no appearance in any of its parts of true fibres.

"I do not wonder, therefore, that the very existence of a nervous system in the Medusæ should have been denied, and should not be at all surprised if it were even now further questioned. I would only urge those interested in this question to look carefully along the inner margin of the chymiferous tubes, and to search there for a cord of cells of a peculiar ovate form, arranged in six or seven rows, forming a sort of string, or rather similar to a chain of ovate beads placed side by side and point to point, but in such a manner that the individual cells would overlap each other for one half, one third, or a quarter of their length, being from five to seven side by side at any given point upon a transverse section of the row; and would ask those who do not recognize at once such a string as the nervous system to trace it for its whole extent, especially to the base of the eye-speck, where these cells accumulate in a larger heap, with intervening coloured pigment forming a sort of ganglion; then, further, to follow it up along the inner side of the radiating chymiferous tubes which extend from the summit of the vault of the body, and to ascertain that here, again, it forms another circle round the central digestive cavity, from which other threads, or rather isolated series of elongated cells, run to the proboscis; they will then be satisfied that this apparatus, in all its complication, is really a nervous system of a peculiar structure and adaptation, with peculiar relations to the other systems of organs. . . . . and such a nervous system I have already traced in all its details, as here described, in the genera *Hippocrene* (*Bougainvillia*), *Tiaropsis*, and *Staurophora*" *.

As my own observations on the histology of the Medusæ are not yet complete, I do not intend to publish them on the present occasion; but I may nevertheless be permitted to remark, with reference to the passage just quoted, that the conclusion so positively enunciated concerning the function of the structures described has always appeared to me, as it has appeared to biologists in general, a conclusion that is certainly unwarranted by the facts. As the learned Professor himself insists, the cells to which he so confidently attributes a nervous character represent "a peculiar type of the nervous system, a type different from all those types which have yet been recognized in the animal kingdom;" and this fact alone, one would think, ought to have inspired extreme caution in founding deductions upon such a basis regarding a question of such high importance as is that concerning the presence of a nervous system in the class Hydrozoa. Whatever effect, therefore, the present paper may have in deciding this question, or in confirming the deductions of Prof. AGASSIZ, I wish to state, as emphatically as I can, that in my opinion these deductions were decidedly premature, and that hitherto the only legitimate attitude of mind to adopt towards the much-vexed question as to the presence of nerves in Medusæ, is that which is thus tersely formulated by one of the greatest living authorities upon the group:—"No nervous system has yet been discovered in any of these animals" †.

[POSTSCRIPT I.—Since this paper was presented to the Royal Society, Professor HUXLEY has been kind enough to direct my attention to an important memoir on the Medusæ, which I had not previously read. This memoir is by Prof. HAECKEL ‡, and in it he assigns special importance to his careful researches into the histology of the nervous tissues. The following is an epitome of his results, so far as they bear upon the subject of the present paper.

After stating the conflicting views held by AGASSIZ, M'CRADY, FRITZ MÜLLER, LEUCKART, KEFERSTEIN, EHLERS, CLAUS, and others concerning the existence of a nervous system in Medusæ, Prof. HAECKEL proceeds to state that his own observations with reference to this subject do not agree with those of any previous writers. These observations were chiefly made upon the *Geryonidæ*—a group of naked-eyed Medusæ which, according to this naturalist, present exceptionable facilities for demonstrating the presence of nervous elements by means of microscopical research. In their distribution these elements are described as forming a continuous circle all round the margin of the nectocalyx, following the course of the radial canals throughout their entire length, and proceeding also to the tentacles and to the marginal bodies. At the base of each tentacle there is

* Prof. L. AGASSIZ "On the Naked-eyed Medusæ of the shores of Massachusetts in their perfect state of Development:" see Memoirs of the American Academy of Arts and Sciences, new series, vol. iv. part ii. pp. 232, 233 (Cambridge and Boston: Metcalf and Co., 1850).

† HUXLEY, 'Classification of Animals.'

‡ Beiträge zur Naturgeschichte der Hydromedusen, von Dr. E. HAECKEL (Leipzig, 1865).

a ganglionic swelling, and it is from these ganglionic swellings that the nerves just mentioned take their origin. The most conspicuous of these nerves are those that proceed to the radial canals and marginal vesicles, while the least conspicuous are those that proceed to the tentacles. Cells, as a rule, can only be discerned in the ganglionic swellings, where they appear as fusiform and distinctly nucleated bodies of great transparency and high refractive power. On the other hand, the nerves that emanate from the ganglia are composed of a delicate and transparent tissue, in which no cellular elements can be distinguished, but which is longitudinally striated in a manner very suggestive of fibrillation. Treatment with acetic acid, however, brings out distinct nuclei in the case of the nerves that are situated in the marginal vesicles, while in those that accompany the radial canals ganglion-cells are sometimes met with.

It will be seen from this brief *résumé* that Prof. HAECKEL'S account of the distribution of the nervous tissues in Medusæ closely resembles that which had already been given by AGASSIZ, and from this it might be supposed that the one series of observations are confirmatory of the other. Prof. HAECKEL himself, however, is clearly of a very different opinion, and in several essential points his description certainly does not agree with that of AGASSIZ. For my own part, as I am able conscientiously to endorse all that Prof. HAECKEL says with regard to the extreme difficulty of distinguishing, in any of the species named by AGASSIZ, histological elements to which a nervous function might reasonably be assigned, I cannot help still thinking that the last-named observer must have been mistaken in his inferences concerning the tissue, which he says he observed without subjecting it to treatment of any kind. Possibly the structure which he describes may have been the optical expression of the thickness of the ectoderm in the region of the nutritive canals. Be this as it may, however, I cannot allow this postscript to appear without stating that in my opinion the microscopical researches of Prof. HAECKEL in this connexion are of much greater value than those of any previous observers; and this not only because of his deservedly high reputation as an histologist, but also because, judging from his figures, the tissues to which he ascribes a nervous function bear so close a resemblance to nervous tissue in general. Moreover, while this experienced microscopist is careful to state that even in the *Geryonidæ* it is no easy matter to distinguish the nervous elements, he also states (as already observed) that in this group these elements are much more readily distinguishable than in any other group of the naked-eyed Medusæ. For these reasons, therefore, I consider Prof. HAECKEL'S deductions from anatomical structure to physiological function as of a more legitimate, and so of a more trustworthy, character than were those of Prof. AGASSIZ; and when they are taken in conjunction with the remarkable verification which they receive from the experiments to be detailed in this memoir, they ought, I think, to be regarded as finally decisive of the long-disputed question as to the presence of a nervous system in Medusæ.]

§ 2. *Movements of the Medusæ.*—It is of course known to every one that the Medusæ are naturally locomotive animals, the various species swimming more or less rapidly by means of an alternate contraction and dilatation of the entire swimming-organ. It may not be so generally known, however, that these swimming-movements, although ordinarily rhythmical, are, at any rate in the case of some species, to a limited extent voluntary—using the latter term in the same sense as it is applicable to invertebrated animals in general. For instance, if *Sarsia* or *Aurelia*, &c. be *gently* irritated, the swimming-motions immediately become accelerated, and the acceleration persists for some time after the irritation has been withdrawn; but to secure this result the irritation must not be of such a character as an inanimate object might supply. Again, individuals belonging to some of the discophorous species of the naked-eyed Medusæ* exhibit peculiar movements on being alarmed; but I am not sure whether these are, as is most probable, purely involuntary, or performed with the view of affording protection to the more vital parts of the animal. Possibly the object may be to decrease the buoyancy of the nectocalyx, and so to escape from the source of injury by sinking through the water. In any case, however, it is necessary that I should here describe these movements, for I shall have occasion to refer to them later on. The movements in question, then, consist of a sudden folding together of the entire nectocalyx, consequent on an abnormally strong contraction of the swimming-muscles; and this contraction, besides being of unusual strength, is also of unusual duration. Thus the best idea of this movement will perhaps be gained by regarding it as a sort of spasm. The time during which this spasmodic contraction lasts is pretty uniform in different individuals of the same species; but it varies in different species from three to six seconds or more. In all cases the disappearance of the spasm is comparatively gradual, the nectocalyx re-expanding in a slow and graceful manner, instead of with the rapid motion characteristic of ordinary swimming. These movements only occur when the animal is being injured or threatened with injury.

II. Fundamental Observations.

§ 1. *Effects of excising the entire margins of Nectocalyces.*—Confining our attention under this heading to the naked-eyed Medusæ, I find that the following proposition applies to every species of the group which I have as yet had the opportunity of examining:—*Excision of the extreme margin of a nectocalyx causes immediate, total, and permanent paralysis of the entire organ.* Nothing can possibly be more definite than is this highly remarkable effect. I have made hundreds of observations upon various species of the naked-eyed Medusæ, of all ages and conditions of freshness, vigour, &c.; and I have constantly found that if the experiment be made with ordinary care, so as to avoid certain sources of error presently to be named, the result is as striking and decided as it is possible to desire. Indeed I do not know of any case in the animal kingdom where the removal of a centre of spontaneity causes so sudden and so complete a paralysis of the muscular system, there being no subsequent movements or twitchings of a reflex kind to disturb the absolute quiescence of the mutilated organism. The

* I adhere to FORBES's classification only because I have not happened to meet with any individual of the family Lucernariadæ.

experiment is particularly beautiful if performed on *Sarsia;* for the members of this genus being remarkably active, the death-like stillness which results from the loss of so minute a portion of their substance is rendered by contrast the more surprising.

From this experiment, therefore, I conclude that in the margin of all the species of naked-eyed Medusæ which I have as yet had the opportunity of examining there is situated an intensely localized system of centres of spontaneity, having at least for one of its functions the origination of impulses to which the contractions of the nectocalyx, under ordinary circumstances, are exclusively due. And this obvious deduction is confirmed (if it can be conceived to require confirmation) by the behaviour of the severed margin. This continues its rhythmical contractions with a vigour and a pertinacity not in the least impaired by its severance from the main organism; so that the contrast between the perfectly motionless swimming-bell and the active contractions of the thread-like portion which has just been removed from its margin is as striking a contrast as it is possible to conceive. Hence it is not surprising that if the margin be left *in situ* while other portions of the swimming-bell are mutilated to any extent, the spontaneity of the animal is not at all interfered with. For instance, if the equator of any individual belonging to the genus *Sarsia* (fig. 1, p. 276) be cut completely through, so that the swimming-bell instead of being closed at the top is converted into an open tube, this open tube continues its rhythmical contractions for an indefinitely long time, notwithstanding the organism so mutilated is, of course, unable to progress. Thus it is a matter of no consequence how small or how large a portion of contractile tissue is left adhering to the severed margin of the swimming-bell; for whether this portion be large or small, the locomotor centres contained in the margin are alike sufficient to supply the stimulus to contraction. Indeed if only the tiniest piece of contractile tissue be left adhering to a single eye-speck cut out of the bell of *Sarsia,* this tiny piece of tissue in this isolated state will continue its contractions for hours or even for days.

This observation, then, on the effect of removing the extreme periphery of nectocalyces, as it undoubtedly demonstrates the presence of an intensely localized system of locomotor centres in at least some of the Medusæ, and as it thus opens the way for a great amount of further experimental research—this observation I shall afterwards speak of as the fundamental observation. I very much regret to say, however, that, in consequence of my having been this year engaged in another line of experimental research which necessitated my constant residence in one locality, I have hitherto been able to make this fundamental observation only in the case of six genera of the naked-eyed Medusæ. As yet, therefore, it would be premature to predict with much confidence that subsequent experiments will prove the locomotor centres to be equally localized in the case of all the naked-eyed Medusæ. Nevertheless, as the genera which I have already submitted to the simple operation just described are genera which happen to present the most extreme differences as to form, size, and structure that occur among the true Medusæ, I think my results afford very good analogical grounds for expecting that future researches will prove the exclusive localization of spontaneity in the marginal rim of nectocalyces to be as constant a feature in the anatomy of true Medusæ as is the presence of the polypite, the tentacula, or the nutritive canals*.

Exception.—I must here record one exception to the numberless instances in which excision of the margins of naked-eyed Medusæ caused paralysis of the nectocalyces. This single exception occurred in a species called *Staurophora laciniata*, a species which, as I shall afterwards explain, I have made the subject of an investigation that necessitated the removal of the margins as the first step in each experiment. I have therefore removed the margin from scores of individuals belonging to this species, and have never met with any but this one exception to the general rule.

In this one exceptional case, after the entire margin had been removed, there were still three distinct centres of spontaneity remaining. One of these centres was situated in the muscular tissue near the periphery of the nectocalyx, and the other two in the substance of the greatly extended polypite that is characteristic of this animal, one centre being placed in each of the two opposite arms of the cross. On carefully excising these three points, with as small a portion of tissue adhering to them as possible, entire cessation of movement ensued in the nectocalyx, while the three severed parts persisted in their rhythmical contractions as long as I continued to observe them. Regarding this exception I have only to remark that it occurred in a somewhat aberrant form of the true Medusæ, and one which, in the unusual size of its nectocalyx, approached that which is usual in the swimming-organs of the covered-eyed Medusæ. It may also be observed that, looking to the type of animal life presented by the order, occasional exceptions of this kind might be expected to occur; and I am only surprised that within my experience they have proved themselves so rare.

§ 2. *Effects of excising the entire margins of Gonocalyces*†.—Turning now to the covered-eyed division of the Medusæ, I find, in all the species I have come across, that excision of the margins of gonocalyces produces an effect analogous to that which is produced by excision of the margins of nectocalyces. There is an important difference, however, between the two cases, in that the paralyzing effect of the operation on gonocalyces is neither so certain nor so complete as it is on nectocalyces. That is to say, although in the majority of experiments such mutilation of gonocalyces is followed by immediate paralysis, this is not invariably the case; so that one cannot here, as with the naked-eyed Medusæ, predict with any great confidence what will be

* The following are the species of naked-eyed Medusæ on which I have made the fundamental observation:—*Sarsia tubulosa* (SARS); *S. pulchella* (FORBES); *S. erythrops* (ROMANES); *Thaumantias inconspicua* (FORBES); *Bougainvillia* (*Hippocrene*) *superciliaris* (AGASSIZ); *B. gigantea* (?) (ROMANES); *B. fruticosa* (?) (ROMANES); *Staurophora laciniata* (AGASSIZ); *Tiaropsis diademata* (AGASSIZ); *T. indicans* (ROMANES); *T. polydiademata* (ROMANES); *T. oligoplocama* (ROMANES); *Stomabrachium octocostatum* (SARS).

† Although not in accordance with general usage, I extend this term to denote the swimming-organ of a covered-eyed Medusa. I do so because those terms which are more properly applicable to this structure are by some authors employed indiscriminately to designate the swimming-organs both of the covered- and of the naked-eyed divisions. Therefore, as it is most desirable for the purposes of the present memoir to avoid any ambiguity in this matter, I trust I shall be excused for thus violating the accepted terminology.

the immediate result of any particular experiment. Further, although such mutilation of a gonocalyx is usually followed by a paralysis as sudden and marked as that which follows such mutilation of a nectocalyx, the paralysis of the former differs from the paralysis of the latter in that it is very seldom *permanent.* After periods varying from a few seconds to half an hour or more, occasional, weak, and unrhythmical contractions begin to manifest themselves; or the contractions may even be resumed with but little apparent change in their character and frequency. The condition of the animal before the operation as to general vigour, &c. appears to be one factor in determining the effect of the operation; but this is very far from being the only factor.

These remarks apply to gonocalyces in general. It must now be observed, however, that these remarks do not apply in equal degrees to all the genera of the covered-eyed Medusæ which I have examined. In other words, if a number of individuals in each of several genera be subjected to the operation we are considering and the results tabulated, it will be found that the average degree of paralysis manifested by the individuals of the different genera is not uniform. For the sake of brevity, therefore, I shall choose a species belonging to each of the two genera which, within my limited experience, have shown the greatest differences in this respect; and by giving a somewhat detailed account of the manner in which the individuals composing these species behave under the form of mutilation described, I shall hope to convey a general idea of the manner in which individuals composing all the other species I have examined behave under similar circumstances—it being understood that all the other species I have examined occupy, in the particulars we are concerned with, a position somewhere intermediate between the two extremes which are described.

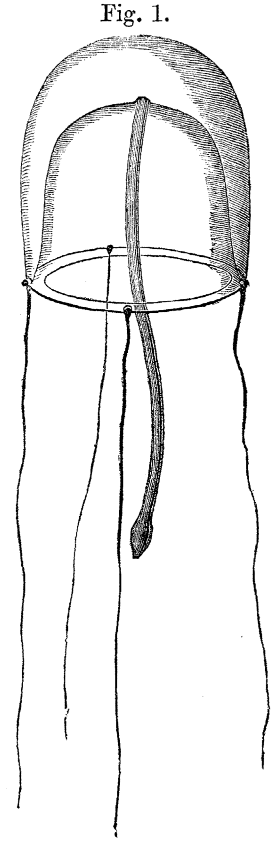
The species, then, to which I allude are *Aurelia aurita* and *Cyanœa capillata*, both exceedingly common forms. Of these species the first approaches nearest to the naked-eyed Medusæ in the concentration of its locomotor centres into the margin of the swimming-organ, while the second departs most widely from the naked-eyed Medusæ in this respect. It must be carefully noted, however, that in the case of these species, as well as in that of all the other species of covered-eyed Medusæ I have examined, the individual variations in these particulars are very great. Therefore, while describing these individual variations in the cases of *Aurelia aurita* and *Cyanœa capillata*, I wish it to be understood that the same remarks apply to all the species of the covered-eyed Medusæ which I have observed.

Excision of the entire margin of *Aurelia aurita*, inclusive of course of lithocysts, causes, in the great majority of cases, instantaneous and complete paralysis of the entire gonocalyx. In the minority of cases one or more supernumerary locomotor centres assert their presence in some part or parts of the general contractile tissue of the gonocalyx *immediately* after removal of its margin. The first of these two divisions admits of being again divided into two subdivisions. In the cases composing one of these subdivisions (and these are much the more numerous) additional centres of spontaneity become, so to speak, developed after the lapse of a greater or less interval of time; so that one cannot be quite sure, even for an hour after the operation, that the paralysis, however complete up to that time, will prove itself permanent. In the cases composing the other of these subdivisions, the paralysis, besides being instantaneous and complete, is also permanent, and thus in every way resembles the paralysis caused by the fundamental experiment in the case of nectocalyces.

Excision of the entire margin of *Cyanæa capillata* causes, in the majority of cases, instantaneous and complete paralysis of the gonocalyx; but this result is not of such comparatively frequent occurrence as it is with *Aurelia aurita.* Moreover, in the cases where supernumerary centres do not assert themselves immediately after the operation, they are almost sure to do so if the mutilated gonocalyx be left sufficiently long to recover from the shock caused by the operation. The period required before the first spontaneous contraction is given in such cases varies from a few minutes to an hour or more; but it is observable that if this period be prolonged, the subsequent contractions are almost sure to be of a feeble character with immensely long intervals between their occurrence—perhaps only one contraction being given in ten minutes or more, instead of between twenty to thirty contractions in one minute, as is characteristic of the unmutilated animal.

Upon the whole, then, although in all the species of covered-eyed Medusæ which I have as yet had the opportunity of examining the effects which result from excising the margins of gonocalyces are such as to warrant me in saying that the main supply of locomotor centres appears to be usually situated in that part of these organs, these effects are nevertheless such as to compel me at the same time to conclude that the locomotor centres of the covered-eyed Medusæ are more diffused or segregated than are those of the naked-eyed Medusæ. Lastly, it should be stated that all the species of covered-eyed Medusæ resemble all the species of naked-eyed Medusæ in that their members will endure any amount of section it is possible to make upon any of their parts, other than their margins, without their spontaneity being in the smallest degree affected.

Fig. 1.



Sarsia, × 3 times.

§ 3. *The effects of excising certain portions of the margins of Nectocalyces.*—The next question which naturally presents itself is as to whether the locomotor centres are equally distributed all round the margin of a swimming-organ, or situated only, or chiefly, in the so-called marginal bodies. To take the case of the naked-eyed Medusæ first, it is evident that in most of the genera, in consequence of the intertentacular spaces being so small, it is impossible to cut out the marginal bodies without at the same time cutting out the intervening portions of the margin. The genus *Sarsia*, however, is admirably adapted (as a glance at the annexed figure will show) for trying the effects of removing the marginal bodies without injuring the rest of the margin, and *vice versâ*. The results of such experiments upon members of this genus are as follow.

Whatever be the condition of the individual operated upon as to freshness, vigour, &c., it endures excision of three of its eye-specks without suffering any apparent detriment; but in most cases, as soon as the last eye-speck is cut out, the animal falls to the bottom of the water quite motionless. If the subject of the experiment happens to be a weakly specimen it will perhaps never move again: it has been killed by something very much resembling nervous shock. On the other hand, if the specimen operated upon be one which is in a fresh and vigorous state, its period of quiescence will probably be but short; the nervous shock (if we may so term it), although evidently considerable at the time, soon passes away, and the animal resumes its motions as before. In the great majority of cases, however, the activity of these motions is conspicuously diminished.

The effect of excising all the marginal tissue from between the eye-specks and leaving the latter untouched is not so definite as is the effect of the converse experiment just described. Moreover allowance must here be made for the fact that in this experiment the principal portion of the "veil" is of necessity removed; so that it becomes impossible to decide how much of the enfeebling effect of the section is due to the removal of locomotor centres from the nectocalyx, and how much to a change in the merely mechanical conditions of the organ. From the fact, however, that excision of the entire margin of *Sarsia* produces total paralysis, while excision of the eye-specks alone produces merely partial paralysis, there can be no doubt that both causes are combined. Indeed it has been a matter of the greatest surprise to me how very minute a portion of the intertentacular marginal tissue is sufficient, in the case of this genus, to animate the entire nectocalyx. Choosing vigorous specimens of *Sarsia*, I have tried, by cutting out all the margin besides, to ascertain how minute a portion of intertentacular tissue is sufficient to perform this function, and I find that this portion may be so small as to be quite invisible without the aid of a powerful lens. As it not unfrequently happens that in cutting out the extreme margin of *Sarsia* a minute part of the intertentacular tissue is left behind accidentally, I may here caution any one who repeats the fundamental observation upon this genus to be very careful in removing every atom of the marginal canal.

From numerous observations, then, upon *Sarsia*, I conclude that in this genus (and so, from analogy, probably in all the other genera of the true Medusæ) locomotor centres are situated in every part of the extreme margin of a nectocalyx, but that there is a greater supply of such centres in the marginal bodies than elsewhere.

§ 4. *Effects of excising certain portions of the margins of Gonocalyces.*—Coming now to the covered-eyed Medusæ, I find that the concentration of the locomotor centres of the margin into the marginal bodies, or lithocysts, is still more decided than it is in the case of *Sarsia*. Taking *Aurelia aurita* as a type of the group, I cannot say that, either by excising the lithocysts alone or by leaving the lithocysts *in situ* and excising all the rest of the marginal tissue, I have ever detected the slightest indications of locomotor centres being present in any part of the margin of the gonocalyx other than the eight lithocysts; so that all the remarks made upon this species in § 2, while we were dealing with the effects of excising the entire margin of gonocalyces, are equally applicable to the experiment we are now considering, viz. that of excising the lithocysts alone. In other words, but for the sake of symmetry I might as well have stated at the first, that in the case of *Aurelia aurita* all the remarkable paralyzing effects which are obtained by excising the entire margin of a gonocalyx are obtained in exactly the same degree by excising the eight lithocysts alone: the intermediate marginal tissue, in the case of this species, is totally destitute of locomotor centres.

I have in this section chosen *Aurelia aurita* as the type of the covered-eyed Medusæ, because, from the flattened shape of its gonocalyx, the differential experiment of cutting out lithocysts and intermediate marginal tissue respectively admits of being conducted in a fairer way than in the case of any other species of the group I have happened to come across; for, in the case of these other species, the form of the gonocalyces necessitated excision of large masses of contractile substance before all the tissue included between the lithocysts could be wholly removed. It therefore became impossible for me in these cases to determine how much of the paralyzing effect was due to removal of locomotor centres, and how much to possibly general shock. But although I was thus precluded from making any trustworthy experiments upon the effect of cutting out all the marginal tissue from between the lithocysts of these species, I was of course able to perform the converse experiment of cutting out the lithocysts alone. The result of numerous experiments of this kind is to satisfy me that, in all the species of covered-eyed Medusæ I have examined, the *chief* marginal supply of locomotor centres is aggregated in the eight lithocysts, although I am unable, for the reasons just given, to say whether or not the *exclusive* marginal supply of these centres is so aggregated. From this it will readily be gathered that, in all the species of covered-eyed Medusæ I have examined, the paralyzing effects of excising the lithocysts alone are most strongly marked, although, of course, from what has been said upon this group in § 2, it will be understood that the experimenter must be prepared to meet with all grades of individual variations in this respect. With regard to specific differences, it will now be apparent that *Aurelia aurita* is, of all the forms I have examined, the one that is most strongly affected by removal of its lithocysts, the paralysis of the gonocalyx thus caused being, in some cases, as permanent as it is total. In all the other species of covered-eyed Medusæ examined, I have found it a very rare thing to obtain permanent paralysis by excision of lithocysts. It may here be added that a portion of any size of contractile tissue left adhering to an excised lithocyst of any species of covered-eyed Medusa will very frequently be found to continue its rhythmical contractions after its severance from the main organism, while such is very rarely the case with any other portions of the marginal tissue when excised.

As the question concerning the presence of a nervous system in Medusæ has long been a warmly disputed one, it may perhaps facilitate its solution if I here observe that there is certainly no case in the whole animal kingdom where there is so great a disproportion between the mass of a ganglionic centre and that of the system which it is capable of setting in motion, as there is between the mass of a lithocyst and that of the gonocalyx which it animates. Thus, in order to obtain the exact proportions in the case of a medium-sized covered-eyed Medusid, weighing thirty pounds, I first removed seven of the lithocysts, and then observed that the eighth one continued to supply contractile impulses to the entire gonocalyx. I next cut out this lithocyst also, and having cleared it as much as possible of the adherent gelatinous tissue, weighed it. Observing further that the mutilated gonocalyx did not move for an hour after the operation (although previous to the operation it had been in active motion), I weighed this also, and obtained the surprising result, that the lithocyst had previously been animating a structure more than thirty million times its own weight! *

§ 5. *Summary of Division II.*—With a single exception to hundreds of observations upon six widely divergent genera of naked-eyed Medusæ, I find it to be uniformly true that removal of the extreme periphery of the animal causes instantaneous, complete, and permanent paralysis of the locomotor system. In the genus *Sarsia* my observations point very decidedly to the conclusion that the principal locomotor centres are the eye-specks, but that, nevertheless, every microscopical portion of the intertentacular spaces of the margin is likewise endowed with the property of originating locomotor impulses.

In the covered-eyed division of the Medusæ I find that the *principal* seat of spontaneity is the margin, but that the latter is not, as in the naked-eyed Medusæ, the *exclusive* seat of spontaneity. Although in the vast majority of cases I have found that excision of the margin impairs or destroys the spontaneity of the animal for a time, I have also found that the paralysis so produced is very seldom of a permanent nature. After a variable period occasional contractions are usually given, or in some cases the contractions may be resumed with but little apparent detriment. Considerable differences, however, in these respects are manifested by different species, and also by different individuals of the same species. Hence, in comparing the covered-eyed group as a whole with the naked-eyed group as a whole, so far as my observations extend I should say that the former resembles the latter in that its representatives usually have their main supply of locomotor centres situated in their margins, but that it differs from the latter in that its representatives usually have a greater or less supply of their locomotor centres scattered through the general contractile tissue of their swimming-

* This individual belonged to the species *Chrysaora hysoscella*. From analogy, however, I doubt not that if I had left the animal over night, next morning it would have exhibited feeble signs of spontaneity; for, as already observed, I have found it a rare thing to obtain thorough and *permanent* paralysis in any species of the covered-eyed Medusæ by the excision of lithocysts.

organs. But although the locomotor centres of a covered-eyed Medusa are thus, generally speaking, more diffused than are those of a naked-eyed Medusa, *if we consider the organism as a whole*, the locomotor centres in the *margin* of a covered-eyed Medusa are *less* diffused than are those in the *margin* of a naked-eyed Medusa; for, so far as my observations extend, I find that excision of the marginal bodies alone produces a greater comparative effect in the covered-eyed genera of Medusæ than it does in the genus *Sarsia*. But of course it is needless to say a much wider basis of observation than mine is required to establish this fact as applicable to the whole of the two groups of Medusæ. I may state, however, quite decidedly that in at least one species of the covered-eyed group (viz. *Aurelia aurita*) the only portions of the margin which are capable of originating spontaneous impulses to contraction are the eight lithocysts, and that in a very large majority of individuals belonging to this species excision of these minute bodies causes instantaneous and complete paralysis of the entire gonocalyx, which paralysis is sometimes also permanent *.

III. Stimulation.

§ 1. *Mechanical Stimulation.*—So far as my observations extend, I find that all Medusæ, after removal of their locomotor centres, invariably respond to every kind of stimulation. To take the case of *Sarsia* as a type, nothing can possibly be more definite than is the single sharp contraction of the mutilated nectocalyx in response to every nip with the forceps. The contraction is precisely similar to the ordinary ones that are performed by the unmutilated animal; so that by repeating the stimulus a number of times, the nectocalyx, with its centres of spontaneity removed, may be made to progress by a succession of contractions round and round the vessel in which it is contained, just as a frog, with its cerebral hemispheres removed, may be made to hop along the table in response to a succession of stimulations. The same remarks apply to all the species of covered-eyed Medusæ I have examined (though some species are more sensitive to stimulation than others): but in the case of many of the discophorous species of naked-eyed Medusæ these remarks must be somewhat modified; for, as previously stated, many of these species upon being irritated while still in an unmutilated state exhibit movements of a peculiar character quite distinct from the ordinary locomotor contractions; and now it must be added that in the case of all these species the mutilated nectocalyx does not, as in *Sarsia* and the covered-eyed Medusæ, respond to a strong stimulus by a single locomotor contraction (although they may do so in response to a weak stimulus), but it performs other actions that differ in different

* Although not covered by the title of this paper, it is desirable here to state that neither in the naked- nor in the covered-eyed Medusæ is the *polypite* affected in the smallest degree as to its motions by excision of the margin of the swimming-organ. For hours and days after the latter, in consequence of this operation, has entirely ceased to move, the former continues to perform whatever motions are characteristic of it in the unmutilated organism. Indeed these motions are not at all interfered with even by a complete severance of the polypite from the rest of the animal. In many of the experiments subsequently to be detailed, therefore, I began by removing the polypite, in order to afford better facilities for manipulation.

species, the action, however, in any given case always precisely resembling that which the unmutilated nectocalyx would have performed if irritated in the same way. Now *Sarsia*, in common with all the covered-eyed genera examined, when in the unmutilated state always endeavours to swim away from a source of irritation or alarm, and never performs any other motions; so that all the cases conform to this one simple rule:—*Every Medusa, when its centres of spontaneity have been removed, responds to a single stimulation by once performing that action which it would have performed in response to that stimulation had its centres of spontaneity still been intact.*

Different species of Medusæ exhibit different degrees of irritability in responding to stimuli; but in all the cases I have met with the degree of irritability is remarkably high. Thus *Aurelia aurita* is perhaps, of all the species I have experimented upon, the least sensitive to stimulation; yet if a narrow strip of tissue without any centres of spontaneity be taken from this animal and made to support in the air the weight of another strip which is spontaneously contracting, the slight amount of friction caused by the one gelatinous surface passing over the other upon each contraction of the uppermost strip is sufficient to determine a responsive contraction in the undermost strip. In some of the other species of covered-eyed Medusæ I have seen responsive contractions of the whole gonocalyx follow upon the exceedingly slight stimulus caused by a single drop of sea-water let fall upon the irritable surface from the height of one inch.

§ 2. *Electrical Stimulation* (A).—All parts of all the Medusæ I have examined are highly sensitive to electrical stimulation, both of the constant and of the induced currents. There is thus a large field for experimental research here opened up, and one upon which I have bestowed a considerable amount of labour. In now giving an abstract of some of the results hitherto yielded, it is only right that I should take the opportunity thus afforded of expressing my obligations and sincere thanks to my learned and highly esteemed friend Prof. BURDON-SANDERSON, but for whose prompt kindness in sending me all the electrical and various other apparatus in immediate answer to my numerous requests, it would have been impossible for me this year to have conducted, with any kind of completeness, the investigation which I undertook.

As just stated, both the severed margin, or system of locomotor centres, and the swimming-organ from which these have been removed respond to stimulation both of the direct and of the induced currents. There is an important difference, however, between the behaviour of the severed margin and of the mutilated nectocalyx with reference to these two kinds of stimulation; for while the former shows itself more sensitive to the induced shock than to the direct current, the reverse is true of the latter. That is to say, while the severed margin continues responsive even to weak induction-shocks after it has ceased to be affected either by make or break of the direct current, the mutilated nectocalyx continues responsive to make and break of the direct current after it has ceased to respond to the strongest induced shock, or even to Faradaic electricity with the secondary coil pushed to zero (one DANIELL'S cell in all cases). It is needless to observe how strongly this fact points to the ganglionic nature of the locomotor centres in the marginal tissues of Medusæ.

My observations were principally made upon the genus *Sarsia*; and the method I employed was to pass the platinum electrodes into the concavity of the mutilated swimming-bell while the latter was in the water, and then gently to raise the former until the contact between them and the tissue was seen to be sufficiently intimate. Similarly of course with the severed margin. I may here remark, for the benefit of those who may repeat this observation, that when the constant current is being applied to the mutilated bell the latter often contracts in a somewhat rhythmical manner. This is perhaps due to the hydrogen bubbles acting as stimulants to contraction, and in any case is certainly not to be regarded as *spontaneous* action. I may also state that minute crustaceans, by striking the mutilated bell, sometimes supply a stimulus to contraction. It is therefore desirable to conduct these experiments in filtered sea-water; and the same precaution of course should be taken when conducting the fundamental observation upon such swimming-organs as prove themselves highly sensitive to stimulation after removal of their locomotor centres.

(B) *Excitable tracts.*—The extreme sensitiveness of all the tissues of all the Medusæ to electrical stimulation affords us the means of ascertaining whether there is any localization of definite excitable tracts in these animals. As *Sarsiæ* are the most active of the Medusæ, and likewise the most delicately sensitive to electricity*, I have in this, as in other cases, taken the genus as the type of the group, and made it the subject of a more careful investigation than any of the other genera. In this preliminary paper, therefore, I shall confine myself, under this heading, to detailing my observations upon the genus *Sarsia* alone. The method I adopted was to slit open one side of the swimming-bell from base to apex, and then to lay it flat upon a glass slide with its inner surface uppermost. Having either cut off or turned back the polypite, I then placed the entire animal under the microscope on a slightly grooved object-glass, where I could keep it alive for a considerable time by moistening it at intervals with drops of sea-water. The stimulus I employed was always the induction-shock supplied by a single DANIELL'S cell and DU BOIS-REYMOND'S coil. The electrodes were fine needles passed through a small piece of india-rubber. The latter was firmly fixed to the stage forceps, which in turn was firmly fixed to a mechanical stage. In this way the object and the electrodes could be moved in any direction without altering their relative positions—a provision which made all the difference between the following observations being possible or impossible; for without this provision it would not have

* At whatever point the bell of *Sarsia* first responds to the induction-shock, it will generally be found that drawing out the secondary coil a quarter, or even an eighth, and very often only a sixteenth of an inch will make all the difference between a vigorous response and no response. Moreover this delicacy of appreciation, besides being thus very great, is also very constant: the excitability of the tissue is seldom found to vary in the least degree for a tolerably long time, although, of course, under the unnatural conditions in which the animal is placed, the excitability of its tissues begins at last gradually to diminish.

been practicable to get the electrodes adjusted accurately upon the various minute histological tracts of tissue, and at the same time to get them within the field of the microscope. The power I used was one-inch ROSS, and the strength of the induction-shock was of course regulated in the ordinary way.

The following are the results yielded by this method of investigating the distribution of excitable tracts in *Sarsia*; and it is interesting to observe how uniformly they coincide with the results obtained by section. I should like to observe, however, that some of the observations are attended with considerable difficulty (arising from escape of the current, conductivity of the gelatinous tissue, &c.); so that, although I have spent a great deal of time and trouble over this part of the inquiry, I desire it to be understood that I intend to confirm these observations more extensively next year.

The apex of the swimming-bell of *Sarsia* is much the least excitable portion of the animal; and from this point downwards to the margin there is a beautiful and uninterrupted progression of excitability, the latter being greatest of all when the electrodes are placed upon the string of cells described by AGASSIZ as nerve-cells. The actual proportions in one average case were as follow:—

(i) Electrodes on apex of inner bell. No contraction on strongest shock.

(ii) Electrodes a quarter of an inch from margin. Bell first contracted with secondary coil at 2 centims.

(iii) Electrodes one eighth of an inch from margin. Bell first contracted with secondary coil at 3 centims.

(iv) Electrodes one sixteenth of an inch from margin. Bell first contracted with secondary coil at 5 centims.

(v) Electrodes on the marginal canal. Bell first contracted with secondary coil at 9 centims.

Of the marginal tract of excitable tissue, the degree of excitability differs slightly in different parts. It is least when the electrodes are placed midway between the two eye-specks; it is somewhat greater when an eye-speck is included between the electrodes. The excitability is again slightly higher when one electrode is placed in an eye-speck and the other outside it. Still greater is the excitability when both electrodes are put into one eye-speck; and the excitability is greatest of all when care is taken to place both electrodes in that half of the eye-speck which is above the pigment-spot. In these remarks of course I wish it to be understood that the excitability is greater in the parts named than in other parts, when an equal amount of tissue is included between the electrodes in the case of both experiments constituting any comparative observation. The following are the ratios in an average case:—

{ (i) Electrodes between two eye-specks. Bell first contracted at $6\frac{1}{2}$ centims.
{ (ii) Electrodes with one eye-speck between them. Bell first contracted at $7\frac{1}{2}$ centims.

{ (iii) Electrodes with one eye-speck between them. Bell first contracted at 7 centims.
{ (iv) One electrode in an eye-speck. Bell first contracted at 8 centims.

{ (v) Both electrodes just outside an eye-speck. Bell first contracted at 8 centims.
{ (vi) Both electrodes in the eye-speck. Bell first contracted at 10 centims.

(vii) Both electrodes in the pigment part of an eye-speck. Bell first contracted at 8 centims.

(viii) Both electrodes in the vesicular part of an eye-speck. Bell first contracted at 12 centims.

With regard to the other parts of the nectocalyx, I have merely to state that there is a marked difference between the excitability of this organ when the electrodes are placed upon any one of the four radiating canals (and so upon the ascending nerve-chains described by AGASSIZ) and when the electrodes are placed upon the tissue between any of the canals. The ratio is generally about 9 centims. : $6\frac{1}{2}$ centims.

Thinking that this greater excitability of the bell when the electrodes were placed upon one of the radiating canals than when they were placed upon the intermediate tissue might possibly have been due to a slight escape of electricity, which in the one case would have become diffused over the muscular tissue of the bell, while in the other it might have been conducted to the marginal centres by a possibly high conducting-power of the radiating canal, I took the precaution of removing the margin altogether; but this did not modify the results.

I conclude, therefore, that in almost every particular there is, in the case of *Sarsia*, a perfect coincidence between the microscopical observations of Prof. L. AGASSIZ and the results yielded by the method of exploration by stimulus just described. Nevertheless I may here repeat what I said in the opening section, viz. that the inference so confidently drawn by that observer as to the function of the histological element he described was, as an inference, decidedly premature*.

(C) I must now describe a mode of section which would naturally fall under the next division of my subject, were it not for its great value in enabling us to conduct an important part of the inquiry relating to electrical stimulation.

* It is worth while to observe also, as showing the danger of drawing conclusions concerning function from histological observation alone, that although Prof. AGASSIZ was so positive regarding the localization of nervous tissue in the margins of Medusæ, he had no idea that the function of this supposed nervous tissue was so intensely specialized,—witness the passage already quoted, "There is unquestionably a nervous system in Medusæ, but this nervous system does not form large central masses to which all the activity of the body is referred, or from which it emanates."

There is another remark which may here be made. Prof. AGASSIZ somewhere observes that it is noteworthy how, in the naked-eyed Medusæ, the supposed nervous tracts follow everywhere the course of the nutritive system. Now, as my method of exploration by stimulus has yielded results confirmatory of Prof. AGASSIZ'S views in this respect, it becomes worth while to speculate as to whether the greater diffusion of the centres of spontaneity in the covered-eyed than in the naked-eyed group of Medusæ may not stand in some relation to the characteristically greater diffusion of the nutritive system in the one group than in the other. Certain it is that lithocysts always appear to stand in some peculiar anatomical relation to the nutritive canals, the latter sweeping round to meet the former (see Plate 32) and communicating through them with the external water. This, of course, may only be due, as GEGENBAUR supposes, to the lithocysts having some excretory function to perform; but now that these organs have been raised to the dignity of locomotor centres, and analogous centres have been proved to be similarly associated with nutritive tracts in the naked-eyed Medusæ, it is well to remember, in view of some deductions from the general theory of evolution, that this possibly non-accidental association of nutritive systems with the earliest indications of nervous systems may turn out to be an association of no small significance.

The mode of section is a very simple one, consisting merely in cutting round a greater or less extent of the marginal tissue, leaving one end of the resulting strip free and the other end attached *in situ*. Upon now irritating the distal or unattached end of this marginal strip, a wave of contraction may invariably be seen to start from the point at which the irritation is applied, and with some rapidity to traverse the entire strip. Upon arriving at the proximal or attached end of the strip, this contractile wave delivers its influence into the swimming-organ, which thereupon contracts in exactly the same manner as it does when itself directly irritated. Of course spontaneous contractions are continually originating in some portion or other of the severed strip; and these give rise to contractile waves and to contractions of the nectocalyx, just in the same way as do the disturbances originated by stimulus. In those species, however, of the discophorous naked-eyed Medusæ which respond to stimulation by the peculiar spasmodic movements of the nectocalyx already described, the difference between the effects upon the nectocalyx of contractile waves that originate spontaneously in the severed strip and those that thus originate in answer to stimuli is of a very marked character; for the spasmodic movements of the nectocalyx are as easily and as certainly evoked by irritating any part of the severed strip, as they are by irritating the substance of the nectocalyx itself.

From this description it will easily be seen that a Medusa thus operated upon supplies all the essential conditions for conducting the most important part of the investigation, so far as electrical stimulation is concerned, viz. that relating to electrotonus. We have already obtained ample evidence to warrant us in concluding that, if the organization of the Medusæ presents us with any thing that is analogous to nervous tissue at all, the periphery of the swimming-organ must be the position in which it is chiefly localized; so that even if these animals possess but the rudiments of a nervous system, a Medusa, when subjected to the mode of section just described, is for all practical purposes a nerve-muscle preparation.

If the intention of the experimenter be merely that of producing contractile waves, it does not signify upon what species of Medusa the form of section just described is practised; for whatever species happens to be chosen, the experiment is sure to be successful. But when the object in view is that of electrotonic investigation, it is desirable to exercise the utmost discretion in the choice of a suitable species. The one I have found most suitable is *Staurophora laciniata*; for this form presents all the qualities the experimenter can desire. Its size is sufficient to yield a foot or more of marginal tissue whereon to cause and test for electrotonus; its manner of folding together in response to stimulation is most decided; its endurance is considerable; and its sensitiveness to electrical stimuli is so great, that I have seen it respond to closure of the constant current supplied by a single DANIELL'S cell when all the plugs of the rheochord were firmly pressed in, and the travelling mercury cups were only drawn out one quarter of an inch.

When, therefore, I began my investigation upon this animal, I thought that the task of determining the questions before me would prove a comparatively easy one. Unfortunately my anticipations were not realized. The conducting-power of the gelatinous tissue (more or less of which is necessarily adherent to the marginal canal), the deleterious influence of the air upon the intrapolar portion of tissue which is necessarily exposed to it, the voluntary motions of the animal—these, and other elements of difficulty which I need not wait to specify, have proved so serious, that, although a great deal of labour has been expended upon this part of my subject, I do not yet feel myself justified in here giving a definite opinion with regard to it; and I have stated the foregoing details chiefly in the hope that the great importance of the inquiry may induce some other observer to assist me in conducting it. I may say, however, that I have obtained undoubted indications of a state of exalted sensibility in the extrapolar regions of the severed strip, although I am unable to say that I have obtained any satisfactory indications of a corresponding anelectrotonic state. I am not yet in a position to speak confidently with respect to PFLÜGER'S law*.

(D) Before leaving the subject of electrical stimulation, there are still a few further observations to detail.

(α) The excitable tissues of Medusæ in their behaviour towards electrical stimulation conform in all respects to the rules which are followed by the excitable tissues of other animals. Thus closure of the constant current acts as a much stronger stimulus than does opening of the same, while the reverse is true of the induction-shock.

(β) As before stated, different species of Medusæ manifest different degrees of sensitiveness to electrical stimulation, though in all cases the degree of sensitiveness is wonderfully high.

(γ) When the constant current is passing in a portion of the strip of a severed margin, the nectocalyx sometimes manifests uneasy motions *during the time the current is passing*. It is possible, however, that these motions may be merely due to accidental variations in the intensity of the current.

(δ) When the intrapolar portion of the severed margin of *S. laciniata* happens to be *spontaneously* contracting prior to the passage of the constant current, the moment this current is thrown in these spontaneous contractions often cease, and are then seldom resumed until the current is again broken, when they are almost sure to recommence. This effect may be produced a great number of times in succession.

(ε) *Exhaustion* of the excitable tissue of the nectocalyx may be easily shown by the ordinary methods. Exhausted tissue is much less sensitive to stimulation than is fresh tissue. Moreover, so far as the eye can judge, the contraction is slower and the period of latent stimulation prolonged.

(ζ) It is important to observe that the *tetanus* produced by Faradaic electricity is not of the nature of an apparently single prolonged contraction (except, of course, such among the naked-eyed Medusæ as respond to all kinds of stimuli in this way), but

* I may here observe that it was in one of my numerous electrical experiments upon *Staurophora laciniata* that the exception to the fundamental experiment mentioned in Division II. was noticed.

that of a number of contractions rapidly succeeding one another—as in the heart under similar excitation. This apparent absence of summation will probably require further treatment on some future occasion.

(η) I shall now conclude my remarks on electrical stimulation by describing a highly remarkable phenomenon, and one which I am quite unable to explain. I am persuaded, however, that it is a phenomenon well meriting the attention of physiologists. When the swimming-bell of *Sarsia* has had its margin removed, and so, as proved by hundreds of similar experiments, has been entirely deprived of its locomotor centres, nevertheless in response to electrical stimulation, instead of giving a single contraction to make or break, it may begin a highly peculiar motion of a flurried, shivering character, which lasts without intermission for periods varying from a few seconds to half an hour. I never but once saw a similar motion in the perfect animal, and this was in the case of a specimen which was dying from having been poisoned with iron-rust. The motion, I think, may be explained by supposing that the various parts of the muscle-layer are contracting without coordination; but why they should sometimes do this in response to stimulation, and why, when they do this, they should continue the action so long—these questions I cannot answer. In the case of so peculiar a phenomenon, however, it is necessary that I should detail all the facts I have been able to collect. I have never seen any similar or corresponding action performed by the paralyzed bells of other Medusids, and even in the case of *Sarsia* its occurrence is comparatively rare. When it does occur, however, it is always continuous; that is to say, it never spontaneously recommences after having once ceased. As already stated, the period of its duration is extremely variable; but when this period is long, it is observable that the shivering motions become feebler and feebler, until they eventually fade away into quiescence. The animal is then quite dead to all further stimulation. Beyond saying that the peculiar motions in question never originate independently of stimulation, I cannot give much further account of the conditions which determine their commencement. The following instances are quoted from my notes *in extenso*:—

"A healthy individual with centres removed, after failing to respond to either make or break of direct current, and after about a quarter of a minute's rest from a series of rapidly alternating makes and breaks of this current, began to shiver, and continued to do so for five minutes. Afterwards quite dead."

"Another healthy individual, after refusing to contract either on make or break of induced current for two or three times, began to shiver and continued to do so for twenty minutes. Afterwards quite dead. This individual had been used five minutes before for experiments with the direct current, to which it responded well and without shivering."

"Another healthy individual was left for some time after excision of margin, and then put into the well and submitted to induction-shocks. No contraction either on make or break with coil pushed to zero. On now trying direct current, without altering position of electrodes, violent contraction on make and also a decided one on break.

On again trying induced current, no contraction. On again trying direct current, strong contractions [thus far, of course, the behaviour of the tissue was normal, see above § 2 (A)], and after four or five of these, shivering began; this lasted for four minutes, and, when again quiescent, the bell again responded to make and break of direct current in the ordinary way."

Now all that can be gathered from these and similar notes is, that the shivering motion in question may be started either by the direct or by the induced current, and this in some cases when the bell has repeatedly refused to answer stimuli in the ordinary way. It may further be gathered from these notes that shivering is most likely to begin after the bell has received a number of shocks in succession. I must also state that it is almost certain to ensue upon slightly acidulating the water in which the mutilated bell is suspended. The shivering, if it begins under these circumstances, will then continue for some time even after the bell is restored to normal sea-water.

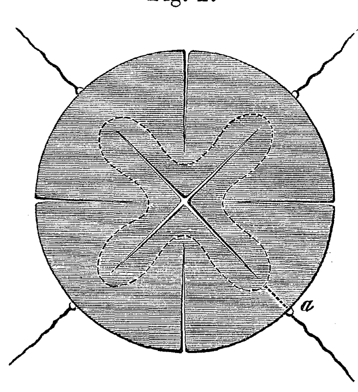
§ 3. *Chemical Stimulation.*—Under this heading I have very little to say, for the simple reason that the excitable tissues of Medusæ conform in every respect to the rules which are followed by the nervo-muscular tissues of higher animals. Both the severed locomotor centres and the mutilated swimming-organs, as well, I may add, as several polypites and tentacles, respond to applications of various acids, solutions of various metallic salts, alcohol, ether, glycerine, &c. It may here be stated that fresh water is quickly fatal to Medusæ, especially in the case of the naked-eyed group. This latter fact has been previously observed by AGASSIZ.

§ 4. *Thermal Stimulation.*—For the present I reserve my observations relating to this subject.

IV. SECTION.

§ 1. *Amount of section which the contractile tissues of Medusæ will endure without suffering loss of their physiological continuity.*—The extent to which the substance of the swimming-organs of Medusæ may be mutilated without undergoing destruction of their physiological continuity is in the highest degree astonishing. Again taking *Sarsia* as a type of the naked-eyed division, I shall here describe two modes of section which are the most trying that I was able to devise.

Fig. 2.



(*a*) Suppose the annexed diagram to represent *Sarsia* in projection, the lines being cuts. It will be seen that there are two systems of interdigitating cuts, with four radial cuts in each system. Those of the one system pass from the margin to two thirds of the way up the cone, while those of the other system pass in the form of a cross from the apex of the cone to two thirds of the way towards its base. It will thus be evident that a stimulus to contraction originating in any point *a* of the margin cannot radiate its influence throughout the whole contractile substance of the bell, except by traversing the zigzag course of the dotted line. Yet in the case of healthy specimens the spontaneous contractions are apparently as synchronous over the entire extent of the nectocalyx as they are when this organ is in an unmutilated state. Further, if the extreme margin of the nectocalyx be now removed, the paralyzed organ will respond to stimuli applied at any point just as readily and as simultaneously over its whole extent as it would do were there no system of interdigitating cuts present.

(*b*) The other mode of section to which I have alluded is that of a simple spiral. If the margin of *Sarsia* be removed in the form of a continuous thread with one end attached to the nectocalyx (as already described in the case of *Staurophora laciniata*), and if the section be then continued in the form of a spiral having two or more turns from the base to the apex of the cone, a wave of contraction, starting from any point in the original margin of the animal, passes into the spiral upon reaching its point of origin, and then runs round and round the spiral from the base to the apex of the cone. In vigorous specimens the course of the contractile wave is so rapid that, in a spiral of one turn, it requires a quick eye to perceive its true nature: to most persons the contraction appears simultaneous over the entire spiral, whereas it is really a successive wave. But in the case of non-vigorous specimens, or of a spiral having two turns, even a slow eye may perceive the true nature of the contraction. Some specimens of *Sarsia* endure more turns of the spiral than do others; but in all cases the animal will live for a long time in this corkscrew-like shape, performing its spontaneous contractions as pertinaciously as ever. As might be expected from the analogy of the experiment last described, if the marginal centres be removed altogether, the paralyzed spiral will respond to the weakest stimulus applied at its lower end or any other part of its course, and this as vigorously as if no spiral section had been performed. I may here observe, in passing, that of all the experiments upon excitable tissues with which I am acquainted, there is no single instance of a series of contrasts so astounding as are those exhibited by *Sarsia*—first darting hither and thither with the greatest spontaneity and vigour, then reduced to a state of absolute quiescence by the removal of an intensely localized system of locomotor centres, but yet remaining so keenly sensitive to stimulation throughout its entire extent, as shown by the modes of section just described.

(*c*) The gonocalyces of the covered-eyed Medusæ, being of a much larger size than are the nectocalyces of the naked-eyed Medusæ, present much greater facilities for conducting experiments in section. Of the species of the covered-eyed Medusæ which I have had the opportunity of examining, *Aurelia aurita*, on account of its flat shape, is much the best suited for this line of inquiry. I have therefore made this species the subject of a very extensive investigation. Under the present heading, however, it will only be necessary for me to describe three observations.

As already stated, the concentration of locomotor centres into the lithocysts of this species is more marked than in the case of any other species I have met with, notwithstanding individual instances frequently occur in which feeble locomotor centres are also scattered through the general contractile tissue of the gonocalyx. It will happen, then, that in any given case the chances are in favour of the individual experimented upon having most or all of its spontaneity aggregated, so to speak, in its eight lithocysts. If seven of these, therefore, be removed, all the spontaneous impulses to contraction must emanate from the remaining lithocyst. Indeed it may easily be seen that such is the case; for each pulsation of the gonocalyx is now of the nature of a double wave of contraction—the two waves starting simultaneously from the remaining lithocyst, each to run rapidly and equally in opposite directions, and so to meet at the point of the gonocalyx that is opposite to the lithocyst. Well, if this remaining lithocyst be made the point of origin of a spiral section which is carried round and round the flat-shaped disk, the result of course is a long strip of tissue, terminating at one end in the lithocyst, and at the other end in the remainder of the gonocalyx (see Plate 33*). A contractile wave proceeding from the lithocyst has now either to become blocked at some point in the length of the strip, or to traverse the whole length of the strip and deliver itself into the remaining contractile tissue of the gonocalyx. The conditions which determine the blocking of a contractile wave under these circumstances will be fully treated of further on: meanwhile it is enough to say that, as might be expected, the length and width of the strip are very important factors, but that, nevertheless, there are immense individual differences in the endurance of the contractile tissue under this form of section. The highest degree of such endurance that I have met with has been two and a half turns of the spiral (see Plate 33). The strip in this case was about an inch wide and nearly a yard long. I doubt not, however, that a wonder-seeker, by making a sufficient number of such experiments, could obtain results even more surprising.

(*d*) The second observation will be best appreciated by a glance at the accompanying woodcut (fig. 3), which is a drawing made from life of an individual submitted to radial

Fig. 3.

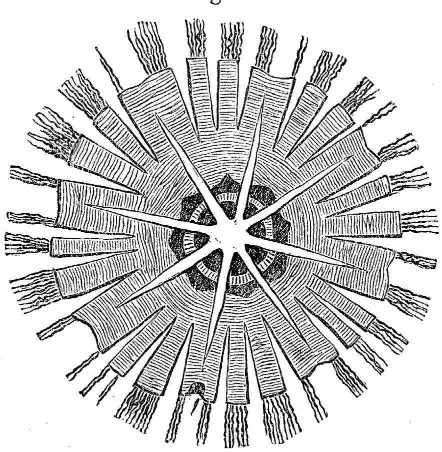
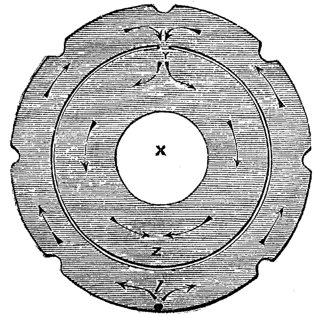


Fig. 4.



section in the way represented. The contractions emanating from the remaining lithocyst (*l*) passed through the entire gonocalyx with no appreciable diminution of vigor, so that I would have increased the severity of the section but for want of space.

* The central organs in this and in the preceding Plate are partly copied from Prof. L. AGASSIZ's representation of an allied species, and so are not perfectly accurate.

(*e*) The third observation will be readily understood from the annexed diagrammatic representation of *Aurelia aurita* (fig. 4). The central circle (x) stands for an open space cut out of the gonocalyx; the outer circle indicates the margin of the animal, with all lithocysts save one (l) removed; and the median circular line represents a cut. It will be seen that the effect of this cut is almost completely to sever the mass of tissue ($y\,z$) from the rest of the gonocalyx, the only connexion between them being the narrow neck of tissue at y. Yet, in the case to which I refer, the contractile waves emanating from l passed in the directions represented by the arrows without undergoing any appreciable loss of vigour. Upon completing the circular cut at y, the ring of tissue ($y\,z$) became totally paralyzed, while the outer circle of course continued its contractions as before. Now the neck of tissue at y measured only $\frac{1}{8}$ inch across, while the ring of tissue $y\,z$ when cut through and straightened out upon the table measured 1 inch across and 16 inches in length. That is to say, 16 square inches of tissue derived its impulse to vigorous contraction through a channel $\frac{1}{8}$ inch wide, notwithstanding the latter was situated at the furthest point of the circle from the discharging lithocyst which the form of the section rendered possible. It should be stated, however, that this experiment might be repeated a number of times without yielding a similar result. I regret that in this instance I did not try the effect of narrowing this neck of tissue still more; for, from the analogy afforded by numberless observations, I entertain but little doubt that some portion of this neck of tissue was pervaded by a very slender though very definite line of functionally differentiated tissue; and that if this line of differentiated tissue had not happened to be cut through in the narrowing of the connecting isthmus, the width of the latter might have been reduced to a half, a quarter, or even less, without impeding the passage of the contractile wave.

§ 2. (*a*) *Nature of the contractile tissues of swimming-organs.*—The last assertion leads us to this important part of our subject. Under this heading I propose to treat of the question, What is the nature of the general contractile substance of Medusæ? Is the contractile tissue of the swimming-organ pervaded by a definite system of sensory and motor tracts, so to speak, radiating respectively to and from the marginal centres? or is the contractile tissue of the swimming-organ of a more primitive nature, the functions of nerve and muscle being more or less blended throughout its substance? Now, for my own part, I deem this question the most interesting one with which the present paper is concerned; for the evolutionist, no less than the physiologist, will recognize its importance as of the highest. We have already obtained ample evidence of the fact that it is to the Medusæ we must look for the first decided integrations of tissue having, to say the least, something closely resembling a nervous function to subserve; and we have seen that these integrations appear in the form of intensely localized centres of spontaneity. It therefore becomes a matter of pressing moment to ascertain the manner in which the spontaneous impulses are transmitted from these centres and distributed throughout the contractile tissue of the swimming-organ—whether a definite system of lines of discharge becomes evolved *pari passu* with a definite system of centres of spontaneity, or contractile tissue can afford, so to speak, to retain more or less of its protoplasmic nature after spontaneity has become so far developed as to be localized in definite centres. In treating of this question, I will only resort to theory when compelled to do so by the facts.

From the observations already detailed it might well be concluded that the method of inquiry by section has already settled the question before us, seeing that this method has apparently reduced the hypothesis as to the presence of definite lines of discharge to an absurdity. A moment's thought will render obvious how very trying the spiral form of section already described (Plate 33) must be to any thing resembling a nervous plexus, while a glance at fig. 3 would seem to render the supposition as to the presence of any such plexus almost impossible. Nevertheless there is a weighty body of evidence to be adduced on the other side.

(*b*) Confining our attention to the species which, as already observed, is in every respect the best suited for sectional experiments, viz. *Aurelia aurita,* it is to be observed, in the first place, that it is the exception and not the rule for specimens to stand the spiral mode of section more than once round the swimming-organ without losing the physiological continuity of their tissues. Moreover different specimens exhibit extreme variations in their tolerance of this mode of section. Sometimes the contractile wave will become blocked when the contractile strip is only an inch long, while in other cases, as already stated, the wave will continue to pass through a strip more than thirty times that length; and between these two extremes there are all possible grades of tolerance. Now it seems to me that if the tissue through which these contractile waves pass is supposed to be of a functionally homogeneous nature, no reason can be assigned why there should be such great differences in the endurance of different individuals of the same species; while if we suppose that the passage of these contractile waves is more or less dependent on the presence of more or less differentiated lines of discharge, we encounter no difficulty; for it is almost to be expected that in such lowly forms of life such lines of discharge, if present, should not be constant as to position. In some cases, therefore, it would happen that important lines of discharge would soon be encountered by the section, while in other cases it would happen that such lines of discharge would escape the section for a longer distance. It is, indeed, almost incredible that any one line of discharge should happen to pursue a spiral course twice or thrice round the animal, and at the same time happen to be concentric with the course pursued by the section; but such an hypothesis is not necessary to account for the facts. All we have to assume is that there exists *a more or less intimate plexus* of such lines of discharge, the constituent elements of which are endowed with the capacity of vicarious action, and that in some cases the section happens to leave a series of their anastomoses in a continuous state. Doubtless even this assumption represents a state of things very difficult to believe; but I do not see that the numberless grades of individual variations already mentioned admit of being accounted for in any other way. Moreover I think that the difficulty of accepting this explanation will diminish if we cease to regard the hypothetical plexus as presenting the high degree of integration characteristic of a properly nervous plexus; but in this preliminary paper I cannot, without undue length, discuss this subject.

(*c*) The strongest evidence of definite lines of discharge being present, however, is yet to be adduced; and this consists in the following invariable fact:—*At whatever point in a strip that is being progressively elongated by section the contractile wave becomes blocked, the blocking is sure to take place* completely *and* exclusively *at that point.* Whereas up to the time that the incision reached quite up to that point the contractile waves showed no signs of meeting with any resistance in their passage from the severed strip to the rest of the gonocalyx, immediately after the incision is carried through that point the blocking of the contractile waves is total. Now, as I have tried this experiment a great number of times, and always tried it by carefully feeling the way round (*i. e.* only making a very short continuation of the cut after the occurrence of each contractile wave, and so very precisely localizing the spot at which the contractile waves ceased to pass into the gonocalyx), I can scarcely doubt that in every case the blocking is caused by cutting through a very slender line of tissue which was in some way or other differentiated from the surrounding tissue, and which, in virtue of its differentiation, had previously served to convey the contractile influence from the strip to the remainder of the gonocalyx. Why it should sometimes be so long before such slender lines of tissue are encountered by the section, or *a sufficient number* of them encountered to destroy the physiological continuity of the tissue, may well afford matter for surprise; but I must nevertheless assert my persuasion that, so far as my observations have yet gone, a legitimate deduction from them appears to be, that in every individual of this species (and so from analogy, as well as observations on other species, probably in all the Medusæ) these slender lines of differentiated tissue are present, that through their mediation the spontaneous impulses originating in the marginal centres are communicated to the contractile tissue of the swimming-organ, and therefore that these slender lines of differentiated tissue are functionally, if not structurally, nerves.

Although I intend for the present to reserve my observations on the histological part of the inquiry, I may here state, in passing, that I have hitherto failed to distinguish any structural modification of the tissue in the regions occupied by these supposed lines of discharge. On one occasion, when I made the radial incision on one side of the single remaining lithocyst, preparatory to making the circumferential incision necessary to procure a contractile strip, I was surprised to find that the entire gonocalyx, although previously contracting with vigour, became wholly paralyzed. Now the incision which I made was only half an inch long, and the effect it produced was amply sufficient to prove that the influence of the lithocyst had previously been communicated to the gonocalyx *from one side only.* I therefore concluded that somewhere within the small band of tissue half an inch long and quarter of an inch broad, which was included between the incision and the lithocyst, there must have been a line of discharge of sufficient size to convey the influence of the lithocyst to the entire gonocalyx. Yet upon staining this small portion of tissue with chloride of gold, I was unable to perceive any structural peculiarity that might be supposed to correspond with the functional peculiarity which it had previously exhibited.

(*d*) I have now to detail another fact of a very puzzling nature, but one which is certainly of great importance in its bearing upon the subject of the present section. When the spiral section is performed on *Aurelia aurita*, and when, as a consequence, the contractile waves which traverse the elongating strip become at some point suddenly blocked, if the section be stopped at this point it not unfrequently happens that after a time the blocking suddenly ceases, the contractile waves again passing from the strip into the gonocalyx as freely as they did before the section reached the point at which the blocking occurred. The time required for this restoration of physiological continuity is very variable, the limits being from a few seconds to an hour or more. Usually, however, the time required is from two to four minutes. This process of reestablishing the physiological connexions, although rapid, is not so instantaneous as is that of their destruction by section. In general it requires the passage of several contractile waves before the barrier to the passage of succeeding waves is completely thrown down. The first wave which effects a passage appears to have nearly all its force expended in overcoming the barrier, the residue being only sufficient to cause a very feeble, and sometimes almost imperceptible, contraction of the gonocalyx. The next wave, however, passes across the barrier with more facility, so that the resulting contraction of the gonocalyx is more decided. The third wave, again, causes a still more pronounced contraction of the gonocalyx; and so on with all succeeding waves, until every trace of the previous blocking has disappeared. When this is the case it generally happens that the strip will again admit of being elongated for a short distance before a blocking of the contractile wave again supervenes. Sometimes it will be found that this second blockage will also be overcome, and that the strip will then admit of being still further elongated without the passage of the waves being obstructed; and so on occasionally for three or four stages.

The same series of phenomena may be shown in another way. If a contractile strip of tolerable length be obtained with the waves passing freely from one end to the other, and if a series of parallel and equidistant cuts be made along one side of the strip, in a direction at right angles to the length and each cut extending across two thirds of the breadth of the strip, the chances are in favour of the contractile waves being wholly unaffected by the sections, however numerous these may be. But now, if another series of parallel and equidistant cuts of the same length as the first ones, and alternating with them, be made along the other side of the contractile strip, the result is, of course, a number of interdigitating cuts; and it is easy to see that by beginning with a few such cuts and progressively increasing their number, a point must somewhere be reached at which one portion of the strip will become physiologically separated from the rest. The amount of such section, however, which contractile strips will sometimes endure is truly surprising. I have seen such a strip 20 inches long by $1\frac{1}{2}$ inch wide, with ten such cuts along each side, and the contractile waves passing without impediment from end to end. But what I wish more especially to observe just now is, that by progressively increasing the number of such interdigitating cuts up to the point at which the contractile wave is blocked and then leaving the tissue to recover itself, in many cases it will be observed that the blocking is sooner or later overcome, that on then adding more interdigitating cuts the blocking again supervenes, but that in time it may again be overcome, and so on. It is, however, comparatively rare to find cases in which blocking is overcome twice or thrice in succession.

(*e*) Section is not the only way in which blocking of waves may be caused in contractile strips. I find that pressure, even though very gentle, exerted on any part of a strip causes a blocking of the waves at that part, even after the pressure has been removed. If the pressure has been long continued, after its removal the blocking will probably be permanent; but if the pressure has been only of short duration, the blocking will most likely be transitory. Even the slight strains caused by handling a contractile strip in the air are generally followed by a decrease in the rate of the waves, and sometimes by their being completely blocked. Other methods by which the passage of waves in contractile strips admits of being blocked will be alluded to further on.

(*f*) Such are some of the facts I have been able to collect bearing on the question concerning the physiological character of the general contractile tissues of the Medusæ. That these facts are of a somewhat paradoxical nature is evident; and whether or not there is any theory by which they admit of being satisfactorily reconciled is doubtful. I may say, however, that I think there is such a theory, and that I only refrain from publishing it at the present time because I think that at this early stage of the inquiry it is desirable, as much as possible, to avoid speculation.

V. Additional facts tending to prove the identity of the specialized marginal tissue of Medusæ with nervous tissue in general.

§ 1. *Sense-organs.*—It has long been thought more or less probable that the so-called "eye-specks" of Medusæ are rudimentary or incipient organs of vision; but I am not aware that any one has hitherto endeavoured to test the supposed probability by experiment. I say "supposed probability," because, in the absence of any structural resemblance to an ocellus, I do not see how speculation as to the function of these organs can be of any further value than a guess*. The guess, however, in this case happens to be correct.

* [Postscript II.—It is with considerable pleasure that I am now able to add the following very judicious and philosophical confirmation of this opinion by so high an authority as Prof. Haeckel:—"Die Deutung der Sinnesorgane niederer Thiere gehört ohne Zweifel zu den schwierigsten Objecten der vergleichenden Physiologie und ist der grössten Unsicherheit unterworfen. Wir sind gewohnt, die von den Wirbelthieren gewonnenen Anschauungen ohne Weiteres auch auf die wirbellosen Thiere der verschiedenen Kreise zu übertragen und bei diesen analoge Sinnesempfindungen anzunehmen, als wir selbst besitzen." Prof. Haeckel, indeed, inclines to the belief that the marginal vesicles which he examined are sense-organs of some kind; but this is a very different position

Having put two or three hundred *Sarsiæ* into a large bell-jar, I completely shut out the daylight from the room in which the jar was placed. By means of a dark lantern and a concentrating lens, I then cast a beam of light through the water in which the *Sarsiæ* were swimming. The effect upon the latter was most decided. From all parts of the bell-jar they crowded into the path of the beam, and were most numerous at that side of the jar which was nearest to the light. Indeed close against the glass they formed an almost solid mass, which followed the light wherever it was moved. The individuals composing this mass dashed themselves against the glass nearest the light with a vigour and determination closely resembling the behaviour of moths under similar circumstances. There can thus be no doubt about *Sarsia* possessing a visual sense.

The method of ascertaining whether this sense is lodged in the eye-specks was, of course, extremely simple. Choosing a dozen of the most vigorous specimens, I removed all the eye-specks from nine, and placed these together with the three unmutilated ones in another bell-jar. After a few minutes the mutilated animals recovered from their nervous shock, and began to swim about with tolerable vigour. I now darkened the room, and threw the concentrated beam of light into the water as before. The difference in the behaviour of the mutilated and of the unmutilated specimens was very

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to have occupied with regard to this matter from that which ventured upon bold assertions as to the specific function of these organs. Now, forasmuch as the above paragraph in the text was written without reference to Prof. HAECKEL's work, I should here like to add the remark that, in my opinion, his deductions concerning this matter differ from those of previous writers in the important particular that they were warranted by the facts of structure which he observed. Granting that he had satisfied himself as to the nervous character of the tissue he describes, and the peculiarly significant distribution of this tissue in the marginal vesicles which he figures appears to me certainly to justify his conclusion that "was die Deutung der Randkörperchen nach Feststellung dieses complicirteren Baues anlangt, so wird zunächst ihre allgemein gültige Stellung als *Sinnes-organe* dadurch nur befestigt." And it is of course needless to say that with the next succeeding sentences I fully concur. "Was aber die speciellere Feststellung der Sinnesqualität betrifft, so scheint mir diese dadurch nach keiner Richtung hin bestimmter bezeichnet zu werden. Im Gegentheil glaube ich, dass damit nur die wesentliche Differenz dieser Randbläschen von anderen ähnlichen Sinnesorganen niederer Thiere, z. B. von den meist zunächst damit verglichenen Gehörbläschen der Würmer und Mollusken, noch mehr bestätigt und ausdrücklich hervorgehoben wird. . . . . Noch weniger freilich als die von den meisten Autoren angenommene Deutung der Randbläschen unserer Medusen als Gehörorgane kann die von AGASSIZ und FRITZ MÜLLER vertretene Ansicht befriedigen, dass dieselben Augen seien. . . . . Alle diese Verhältnisse sind mit der Deutung der Concretion als 'Linse' und des sie umschliessenden Sinnesganglion als 'Sehnerv' durchaus unvereinbar."

It may not be unnecessary to say that, although the simple experiment above described effectually proves that the marginal bodies have a visual function to subserve, we are not for this reason justified in concluding that these bodies are so far specialized as organs of sight as to be precluded from ministering to any other sense. Therefore the results of the above-mentioned experiments cannot be held in any way to affect the judgment of Prof. HAECKEL:—"Und doch ist es viel wahrscheinlicher, dass hier wesentlich andere Sinnesempfindungen zu Stande kommen, von deren eigentlicher Qualität wir uns keine bestimmte Vorstellung machen können; wie es z. B. sehr wahrscheinlich ist, dass die Empfindung der Licht- und Schallwellen, für welche bei den höheren Thieren verschiedene Organe differenzirt sind, bei den niederen an ein und dasselbe Sinnesorgan, natürlich in unvollkommener Ausbildung, gebunden vorkommen." (For the quotations *vide loc. cit.* pp. 57, 58.)—Feb. 1876.]

marked. The three individuals which still had their eye-specks sought the light as before, while the nine without their eye-specks swam hither and thither without paying it any regard.

A further question, however, still remained to be determined. The pigment-spot of the eye-speck in Medusæ is, as AGASSIZ observes, placed *in front of* the presumably nervous tissue; and for this reason he naturally enough suggests that if the eye-speck has a visual function to perform, the probability is that the rays by which the organ is affected are the heat-rays lying beyond the range of the visible spectrum. Accordingly I brought a heated iron just ceasing to be red close against the large bell-jar which contained the numerous specimens of *Sarsia*; but not one of the latter approached the heated metal.

From these observations, therefore, I conclude that in *Sarsia* the faculty of appreciating luminous rays is present, and that this faculty is lodged exclusively in the eye-specks. My observations on the other genera of Medusæ in this connexion are not yet complete.

§ 2. *Effects of various Poisons on the Locomotor System of Medusæ.*—As this communication has now grown to an undue length, I shall reserve for a future paper many facts of great physiological interest regarding luminosity, general distribution of the supposed lines of discharge, coordination of the centres of spontaneity, rate of transmission of contractile waves in different genera and under various forms of section, &c., and shall conclude what I have to say at the present time by describing the effects of a few among the poisons I have tried upon the Medusæ, choosing those upon the list which most tend to prove the identity of the specialized marginal tissue of these animals with nervous tissue in general.

(*a*) The anæsthesiating influence of chloroform and ether is most decided. This fact, I find, has also been observed by AGASSIZ; and he remarks in effect that even if it stood alone it ought to be considered sufficient to demonstrate the presence of nerves in Medusæ. Without straining our deductive powers quite so far as this, I think that the marked influence of chloroform and ether upon the Medusæ may properly be taken as in some measure confirmatory of the doctrine which that great naturalist so strenuously upheld.

AGASSIZ appears to have tried the effect of chloroform only in the case of *Sarsia*. I may therefore state that in all the other genera I have experimented upon, both of the naked- and covered-eyed groups, the anæsthesiating influence of this substance is equally decided. This influence, moreover, is in every respect precisely similar to that which is observable in the case of the higher animals. Soon after a few drops of chloroform have been added to the water in which a vigorous medusid is contained, the locomotor pulsations of the latter become slower and slower in the time occupied by their execution, while the intervals of diastole become more and more prolonged. Concurrently with this slowing of the pulsations their strength naturally grows less and less vigorous, so that eventually the systoles are separated from one another by five or six times the normal interval, and when they occur are of the feeblest character. Soon after this stage has been reached the systoles altogether cease; and in a few seconds after they have done so the animal fails to respond even to the strongest stimuli; and this, be it remembered, is quite as remarkable a fact in the case of Medusæ as it is in the case of the higher animals. The time occupied by the whole of this process varies with different species; but it is always very brief, namely (speaking from memory) about fifteen seconds to a minute in the case of *Sarsia* and eighty seconds to two minutes in that of *Aurelia aurita*. But brief as is the time required for chloroform to assert its influence upon Medusæ, it is long as compared with the time required for its effects to pass off when the animal is again restored to normal sea-water. A specimen of *Sarsia* which has been completely anæsthesiated, and so to all appearance perfectly dead, resumes its pulsations a few seconds after being again immersed in unpoisoned water. There appears to be a relationship, however, between the time required for complete anæsthesiation and that required for complete subsequent recovery, for the recovery of *Aurelia aurita* takes a few seconds longer than does that of *Sarsia*. In all cases the recovery is progressive, the first pulsations being very feeble and the periods of diastole prolonged; but very shortly the pulsations resume their normal strength and frequency. The same animal may then, of course, be subjected to a repetition of the experiment, and this for an indefinite number of times.

(*b*) The anæsthesiating effects of morphia are as decided as are those of chloroform. I shall confine myself to describing the process of anæsthesiation in the case of *Aurelia aurita* in an extract from my notes:—"A very vigorous specimen, having twelve lithocysts, was placed in a somewhat strong sea-water solution of morphia. Half a minute after being introduced commencement of torpidity ensued, shown by contractions becoming fewer and feebler. In one minute the feeble impulses emanating from the prepotent lithocyst failed to spread far through the contractile tissue, appearing to encounter a growing resistance. Eventually this resistance became so great that only a very small portion of contractile tissue in the immediate neighbourhood of the lithocyst contracted, and this in a very slow and feeble way. Two minutes after immersion even these partial contractions entirely ceased, and soon afterwards all parts of the animal were completely dead to stimulation. Recovery in normal water slower than that after chloroform, but still soon quite complete. Repeated experiment on this individual four times without injury."

(*c*) The species I shall choose for describing the effects of strychnia is *Cyanæa capillata*, which is most admirably adapted for experiments with this and some of the other alkaloid poisons, from the fact that, in water kept at a constant temperature, its pulsations are as regular as are those of a heart. After *Cyanæa capillata* has been allowed to soak for ten minutes or so in a weak sea-water solution of strychnia, unmistakable signs of irregularity in the pulsations supervene. This irregularity then increases more and more, till at length it grows into well-marked convulsions. The convulsions manifest themselves in the form of extreme deviations from the rhythmical contractions so characteristic of *Cyanæa capillata.* Instead of the heart-like regularity with which systole and diastole follow one another in the unpoisoned animal, we now have periods of violent and prolonged systole resembling tonic spasm; and when the severity of this spasm is for a moment abated, it is generally renewed before the gonocalyx has had time again to become fully expanded. Moreover the spasm itself is not of uniform intensity throughout the time it lasts; but while the gonocalyx is in a continuously contracted state, there are observable a perpetual succession of extremely irregular oscillations in the strength of the contractile influence. It is further a highly interesting fact that the convulsions are very plainly of a *paroxysmal* nature. After the gonocalyx has suffered a prolonged period of convulsive movements, it expands to its full dimensions, and in this form remains for some time in a state of absolute quiescence. Presently, however, another paroxysm supervenes, to be followed by another period of quiescence, and so on for hours. The periods of quiescence are usually shorter than are those of convulsion; for while the former seldom last more than forty seconds or so, the latter may continue uninterruptedly for five or six minutes. In short, Medusæ, when submitted to the influence of strychnia, exhibit all the symptoms of strychnia poisoning in the higher animals. Death, however, is always in the fully expanded form.

(*d*) Curare has already been tried upon Medusæ, and is stated to have produced no effects; it is therefore especially desirable that I should first of all describe the method of exhibiting it which I employed.

Having placed the medusid to be examined in a flat-shaped beaker, I filled the latter to overflowing with sea-water. I next placed the beaker in a large basin, into which I then poured sea-water until the level was the same inside and outside the beaker, *i. e.* until the two bodies of water all but met over the brim. Having divided the medusid across its whole diameter, with the exception of a small piece of marginal tissue at one side to act as a connecting-link between the two resulting halves, I transferred one of these halves to the water in the basin, leaving the other half still in the beaker, the marginal tissue which served to unite the two halves being thus supported by the rim of the beaker. Over the minute portion of the marginal tissue which was thus of necessity exposed to the air, I placed a piece of blotting-paper which dipped freely into the sea-water. Lastly, I poisoned the water in the beaker with successive doses of curare solution.

The results obtained by this method were most marked and beautiful. Previous to the administration of the poison both halves of the medusid were of course contracting vigorously, waves of contractile influence now running from the half in the beaker to the half in the basin, and now *vice versâ.* But after the half in the beaker had become effectually poisoned by the curare, all motion in it completely ceased, the other, or unpoisoned half continuing to contract independently. I now stimulated the poisoned half by nipping a portion of its margin with the forceps. Nothing could be more decided than the result. It will be remembered that when any part of *Staurophora laciniata* is pinched with the forceps or otherwise irritated, the motion of the whole body which ensues is totally different from that of an ordinary locomotor contraction, all parts folding together in one very strong and long-protracted systole, after which the diastole is very much slower than usual. Well, on nipping any portion of the poisoned half of *Staurophora laciniata*, this half remained absolutely motionless, while the unpoisoned half, though far away from the seat of irritation, immediately ceased its normal contractions, and folded itself together in the very peculiar and distinctive manner just described. This observation was repeated a number of times, and, when once the requisite strength of the curare solution had been obtained, always with the same result. The most suitable strength I found to be 1 in 2500, in which solution the poisoned half required to soak for half an hour.

I also tried the effect of this poison on the covered-eyed Medusæ, and have fairly well satisfied myself that its peculiar influence is likewise observable in the case of this group.

It has further to be stated that when the poisoned half is again restored to normal sea-water, the effects of curare pass off with the same astonishing rapidity as is observable in the case of the other poisons which I have tried. Thus, although an exposure of half an hour to the influence of curare of the strength named is requisite to destroy the motor power in the case of *Staurophora laciniata*, half a minute is sufficient to ensure its incipient return when the animal is again immersed in unpoisoned water.

It is also to be observed that a very slight degree of *over*-poisoning paralyzes the transmitting system as well as the responding one; so that if any one should repeat my observation, I must warn him against drawing erroneous conclusions from this fact. Let him use weak solutions with prolonged soaking, and by watching when the voluntary motions in the poisoned half first cease, he need experience no difficulty in obtaining results as decided as it is possible for him to desire.

I think it would be difficult to overrate the importance of these results: to my mind they are perhaps the most interesting which are contained in this paper. They not only prove that curare poison is consistent in manifesting its remarkable property when applied to these the lowest forms of life that present the beginnings of a nervous system; but they prove what is far more important, that in animals which, as we have seen from other evidence, present us with the first indications of a nervous system, the latter appears to have already undergone a differentiation in its functions, such that it is capable not only of influencing contiguous contractile parts, but also of being influenced by distant excitable parts.

(*e*) I shall conclude all I have to say at the present time upon the subject of poisons by stating the interesting fact, that if any of the narcotic or anæsthesiating agents be administered to any portion of a contractile strip cut from the gonocalyx of *Aurelia aurita* in the way already described, the rate of the contractile waves is at first progressively slowed (I shall give the actual tracings in a future paper), and eventually their passage is completely blocked at the line where the poisoned water begins. Upon now restoring the poisoned portion of the contractile strip to normal sea-water the blocking is gradually overcome, and eventually every trace of it disappears. This experiment was suggested to me by Dr. BURDON SANDERSON*.

The contractile wave may be blocked by poisons in another way. A glance at Plate 33 will show that a circumferential strip cut from the gonocalyx of *Aurelia aurita* is pervaded transversely by a number of nutrient tubes, which have all been cut through by the section. At the side of the strip, therefore, furthest from the margin there are situated a number of open ends of these nutrient tubes. Now on injecting any of the narcotic poisons into one of these open ends, the fluid of course permeates the whole tube, and the contractile wave becomes blocked at the transverse line occupied by the tube as effectually as if the contractile strip had been cut through at that line.

A glance at Plate 32, again, will show that each lithocyst is surrounded by one of these nutrient canals. Upon injecting this canal, therefore, in a contractile strip, the effect of the poison may be exerted on the lithocyst more specially than it could be by any other method of administration. In view of recent observations concerning the effects of curare on the central nervous masses of higher animals, it may be worth while to state that a discharging lithocyst of *Aurelia aurita*, when thus injected with curare, speedily ceases its discharges. This fact alone, however, would not warrant any very trustworthy conclusions as to the influence of curare upon discharging centres; for it is within the limits of possibility that the paralyzing effects may here be due to the influence of the poison on the surrounding contractile tissue.

It is interesting to observe that if the discharging lithocyst be injected with chloroform, or a not too strong solution of morphia, it recovers in the course of a night, while with alcohol the first effects of the injection are considerably to accelerate the frequency and to augment the potency of the discharges; but the subsequent effects are a gradual diminution in the frequency and the vigour of these discharges until eventually total quiescence supervenes. In the course of a few hours, however, the torpidity wears away, and finally the medusid returns to its normal state.

VI. GENERAL SUMMARY.

There is very good analogical reason to expect that, in the case of the naked-eyed Medusæ, the exclusive localization of centres of spontaneity in the margins of nectocalyces will be found to be a very general, if not a constant, feature in the anatomy of the entire group. In six of the most divergent genera that occur in this group I have found it to be almost uniformly true that excision of the entire periphery of a nectocalyx is

* In conducting this experiment care must be taken not to exert the slightest pressure on any part of the strip (see IV. § 2 (*e*) p. 295). The method I adopted, therefore, was to have a vessel with a very deep furrow on each of its opposite lips. Upon filling this vessel to the level of these furrows with the poisoned water, and then immersing the whole vessel in ordinary sea-water up to the level of its brim, some of the poisoned water of course passed through the open furrows. The external body of water (*i. e.* the normal sea-water containing the animal) was therefore made proportionally very large, so that the slight escape of poison into it did not affect the experiment. On now passing the portion of the strip to be poisoned through the two opposite furrows it was allowed to soak in the poison while freely floating, and so without suffering pressure in any of its parts.

invariably followed by immediate, total, and permanent paralysis of the entire structure. I say *almost uniformly true*, for it will be remembered that in one individual instance three distinct centres of spontaneity remained after removal of all the marginal tissue. This individual instance occurred in a medusid belonging to the species *Staurophora laciniata*; and as this is the species which I found best suited for my experiments in electrotonus, I have had occasion to remove the marginal tissue from many scores of individuals belonging to it, and have never met with any but this one exception to a rule shown to be general by hundreds of experiments on the thirteen species named.

With the covered-eyed Medusæ the case is not so definite; for although centres of spontaneity unquestionably occur in the margins of all the members of this group which I have examined, these are not always, nor even generally, the only centres present. Looking to the order as a whole, so far as my experience extends, it is the exception and not the rule to obtain complete and permanent paralysis by excision of the marginal tissue of individuals composing this group. Considerable differences, however, are manifested by different species in this respect.

In *Sarsia* I find that a higher degree of paralyzing effect is produced by cutting out the four eye-specks alone than is produced by cutting out the intertentacular tissue alone; and I therefore conclude that the eye-specks are the principal seats of spontaneity. But they are far from being the *only* seats of spontaneity; for even the smallest atom of intertentacular tissue is sufficient, in the case of vigorous specimens, to animate the entire nectocalyx.

In none of the covered-eyed Medusæ examined have I found any evidence of the marginal tissue between the lithocysts being endowed with spontaneity. On the contrary, in the case of *Aurelia aurita*, which from its flat shape admits of fairer experimentation in this connexion than do any of the other genera examined, it is quite certain that all the spontaneity of the margin, and so, in most cases, of the whole animal, is concentrated in the eight lithocysts.

All Medusæ, after being paralyzed by the loss of their marginal centres, respond to all kinds of stimulation, and this by performing whatever action they would have performed in response to the stimulation employed had they been in their perfect state. Different species, however, manifest different degrees of irritability in their behaviour towards stimulation, although in all cases the degree of irritability is high.

Regarding electrical stimulation, both severed margins and the swimming-organs from which they have been taken are responsive both to the constant and to the induced current; but while severed margins remain responsive to weak induction-shocks after they cease to be affected by make and break of strong constant currents, the reverse is true of the mutilated swimming-organs; for, in the case of *Sarsia*, these remain responsive to make and break of the constant current even after they cease to respond to Faradaic electricity with the secondary coil pushed to zero (one cell).

The presence of excitable tracts has been proved in the case of *Sarsia* by means of electrical stimulation. The results are, that there is a progressive increase of excitability from the apex to the base of the nectocalyx, that the excitability is greater in the regions of the eye-specks than anywhere else in the course of the circular canal, and that it is greatest of all in the vesicular part of an eye-speck. Further, the radial canals present a higher degree of irritability than does the intermediate tissue.

A mode of section, which I need not again describe, renders it possible to experiment with the view of ascertaining whether or not the specialized marginal tissue of the Medusæ shows any indications of polarity while under the influence of the constant current. The inquiry, however, is attended with serious difficulties; so that at present I am only able to say that although I have sometimes obtained satisfactory indications of kathelectrotonus, I have never obtained the slightest indications of anelectrotonus. With respect to PFLÜGER'S law, notwithstanding I have spent a great deal of time over the subject, the evidence is too contradictory to be depended upon.

The contractile tissues of the Medusæ, in the comparative irritability they manifest towards make and break, upon the whole conform to the rules which are followed by irritable tissues in general.

The constant current during the time it is passing through a portion of the marginal tissue appears to have the power of inhibiting the spontaneous impulses to contraction which were previously originating in that portion; for so long as the current continues to pass, such spontaneous impulses sometimes cease in the intrapolar portion of the marginal tissue, and are renewed as soon as the current is broken.

Exhaustion of the contractile tissue may be easily shown by the ordinary methods, and in exhausted tissue, so far as the eye can judge, the contractions are slower and the period of latent stimulation prolonged.

The tetanus which is caused by Faradaic electricity is of the nature of a number of contractions following one another in quick succession with perceptible intervals between them.

Mutilated *Sarsiæ*, when stimulated by electricity or acidulated water, sometimes exhibit a highly peculiar and anomalous movement; but it is unnecessary to enter into all the details a second time.

With regard to chemical stimulation there is not much to say; for in none of the excitable tissues of the Medusæ have I found any exception to any of the rules which are conformed to by the excitable tissues of other animals.

My observations on the behaviour of the Medusæ in relation to thermal influences are omitted from the present paper.

Concerning the physiological properties of the general contractile tissue of swimming-organs, I confine myself in this paper to stating the results obtained by the spiral mode of section figured on Plate 33. These results are as follow. Different individuals of the species *Aurelia aurita* manifest great variations in the amount of spiral section they endure before the contractile strip becomes physiologically separated from the rest of the gonocalyx. In the majority of cases the contractile strip becomes physiologically separated from the rest of the gonocalyx before the spiral section has passed once round the latter. It is comparatively rare to find cases in which contractile waves continue to pass after the spiral incision has been carried twice round this organ; and it is still more rare to find cases of waves passing in specimens such as that represented in Plate 33, where the spiral section has made two and a half turns round the gonocalyx. When such cases as the latter do occur, if the specimen happens to be an ordinary-sized one, the contractile strip will be about a yard in length. On the other hand, cases may occur in which blocking of the contractile wave supervenes when the contractile strip is only an inch long; and in one case complete blocking of this wave was caused by the *radial* incision half an inch long, made on one side of a freely discharging lithocyst, *i. e.* before the *circumferential* incision was begun at all. But such extreme variations upon the side of intolerance of spiral section are as uncommon as are the extreme variations upon the side of tolerance. Now the fact that between these two extremes there are to be found all possible grades of tolerance, appears to warrant us in concluding that the contractile tissue of *Aurelia aurita* is not of a functionally homogeneous nature.

And this conclusion is very much strengthened by the additional fact that at whatever point in a contractile strip which is being progressively elongated by section the contractile wave becomes blocked, the blocking is sure to take place completely and exclusively at that point. This fact, it appears to me, can only be properly explained by supposing that more or less differentiated lines of discharge pervade the contractile tissue of the gonocalyx, and that the sudden and complete blocking of the contractile waves which invariably takes place at some determinate point during the progress of the section is due to the latter having at that point severed some important line of discharge, which had previously served to convey the influence of the lithocyst to the undivided parts of the gonocalyx. Nevertheless we must bear in mind that this deduction is supported by no histological evidence, and that it is, moreover, very difficult to reconcile with the fact that some specimens of *Aurelia aurita* endure so enormous an amount of the most severe forms of section without suffering loss of physiological continuity between any of their parts.

The deduction also appears difficult to reconcile with another fact, viz. that in some cases (which, however, are greatly in the minority) the blocking of contractile waves in spiral strips admits, after a time, of being overcome, the contractile waves again passing from the strip into the gonocalyx as freely as they did before the section reached the point at which the blocking occurred, and this occasionally two or three times in succession. I think, however, that there is a theory by which all these paradoxical facts may be reconciled; and so at the present stage of my inquiries I provisionally accept the hypothesis of there being present in the locomotor system of *Aurelia aurita* more or less definitely integrated lines of discharge. But, in making this statement, it is almost needless to add that I wish a marked distinction to be drawn between the certainty of the hypothesis and that of the facts from which it is deduced.

Blocking of contractile waves in strips may also be caused by making a system of interdigitating cuts in the strip itself, which system it is unnecessary again to describe. Blocking may also be caused by pressure exerted at any line which crosses the contractile strip transversely. In such cases the time during which the pressure lasts, and the intensity of the pressure while it does last, are the principal factors in determining the blockage of contractile waves, as well as the time during which such blockage will continue after the pressure has been removed. Various poisons also cause blocking of contractile waves, the obstruction to the passage of the waves being always very precisely restricted to the line in the strip where the poisoned water ends, or, if injections be used, where the injected poison is present. If a long portion of a contractile strip be immersed in the solution of a poison which will eventually cause a blocking of the waves, it is observable that for some little time before the blocking takes place the rate of transmission of the waves becomes progressively slowed.

The presence of a visual sense has been demonstrated in the case of the genus *Sarsia*, and its seat localized in the so-called eye-specks. It has also been proved that in this the first appearance of a visual organ in the animal series the rays by which the organ is affected are the properly luminous rays, and not the thermal rays beyond the luminous spectrum, as has been reasonably inferred from the position of the pigment-spot in relation to the other parts of the visual structure.

With regard to poisons, I confine myself on this occasion to briefly detailing the effects of only a few; and these effects are chosen for description in order to indicate the apparent functional identity of the locomotor centres of Medusæ, and of the relations which these centres bear to the contractile tissue of the swimming-organs, with the nervous tissue of all higher animals, and the relations which this bears to muscular tissue. Chloroform, ether, alcohol, morphia, strychnia, and curare all assert their several peculiar influences on the locomotor movements of the Medusæ, and this in all the particulars and with all the distinctness which is characteristic of their action on nervous tissues in general.

Received March 24, 1876.

POSTSCRIPT III.

On the 3rd of February, 1876, I received the following communication from Dr. LÜTKEN, of Copenhagen:—

"With reference to your interesting note in 'Nature,' November 12th, 1874, your attention is drawn to Dr. EIMER'S paper on the artificial divisibility &c. in *Aurelia aurita* and *Cyanæa capillata*, Würzburg 'Verhandlungen,' vi. (1874)."

The note here referred to is one which I sent to 'Nature' in September 1874, and which was published in November of that year. In this note I described the effects, on a species of naked-eyed Medusa, of what in this memoir I call the fundamental experiment*, and added a suggestion that such of the readers of 'Nature' as should have the opportunity of repeating this experiment on the other species of Medusæ during the summer and autumn months of 1875, should do so on as many species as possible. I have to regret that no one appears to have acted on this suggestion; but at the same time, I have to express my best thanks to Dr. LÜTKEN for the very valuable reference which he has supplied. Dr. EIMER'S paper clearly shows that he made the fundamental observation in the case of *Aurelia aurita* and *Cyanœa capillata* quite independently of my suggestion in 'Nature;' and Dr. LÜTKEN'S reference to this paper has been of special value to me from the fact that up to the time when I received it (viz. February 1876) no one in England appears to have been aware that Dr. EIMER had done any work in connexion with the nervous system of Medusæ. This ignorance is to be accounted for by the fact that the journal in which Dr. EIMER published his paper has but a very limited circulation in this country, while of the paper itself no abstract appears in the 'Centralblatt.'

The following is a full abstract of the results and opinions set forth by the paper in question.

In *Aurelia aurita* the author observed that excision of the lithocysts was usually followed by complete and permanent paralysis of the swimming-organ, while any tissue left adhering to a lithocyst continued rhythmically to contract "like the excised heart of a frog." He appears, however, to be decidedly of the opinion that the seats of spontaneity are not the lithocysts alone, but the entire crescent-shaped interruptions of the margin in which the lithocysts are lodged (see Plate 32). He arrives at this conclusion because he finds that by progressively lessening the amount of contractile tissue which is left adhering to an excised lithocyst, this amount may be reduced to a "tissue-zone" only a few millims. broad. This crescent-shaped zone, therefore, he always speaks of as the "contractile zone." Concerning the *character* of the contractions, Dr. EIMER is of the opinion that they are "usually involuntary," but that they are also in a certain degree subject to the control of the will.

The author next proceeds to detail some very interesting observations on the rate of the rhythm. He says, what is quite true, that although the pulsations of *Aurelia* are very rhythmical, they are frequently interrupted by pauses of longer or shorter duration. He says, further, that the duration of pauses bears a direct relation to the

* In some respects this description was not quite accurate, and for the following reason:—The observation was made towards the end of the summer of 1873 on some individuals of the species of *Slabberia conica*. I found that excision of the marginal bodies alone determined complete paralysis of the nectocalyx, and also, apparently, of the polypite. Next year I was unable to pursue the inquiry, but published the note in 'Nature' above referred to. Last year I continued the research, but did not happen to fall in with any specimens of *Slabberia*. From my observations on the nearly allied form of *Sarsia*, however, I am now inclined to believe that if my specimens of *Slabberia* two years before had been in a perfectly vigorous state, I should have found it necessary, in order to cause complete paralysis of the nectocalyx, to remove its *entire* margin, and not merely the vesicles alone.

previous number and strength of the pulsations. If the unmutilated animal be pricked with a needle, it endeavours to swim away from the source of irritation.

If the unmutilated animal be carefully watched while performing its locomotor contractions, it will be seen that the latter emanate from the margins of the crescent-shaped notches, *i. e.* from the "contractile zones;" upon every contraction the two sides of each zone approximate each other. Usually all the eight contractile zones contract together; but this is not always the case. Frequently the contraction originates in one or in several neighbouring zones simultaneously, and then propagates itself with lightning speed to all the others, which thereupon contract either simultaneously or in rapid succession. Thus the animal is no doubt able to steer itself in any direction it chooses.

From all this, then, it appears that a locomotor contraction of the umbrella may proceed from one, from several, or from all the zones simultaneously; but in no case can a contraction of one zone take place without being accompanied by a synchronous, or almost synchronous, contraction of all the others.

The number of contractions in a given time appeared to vary in an inverse proportion to the size of the animal. Upon excising all the contractile zones save one, the contractions were seen to emanate from this zone alone, and from thence to spread themselves all over the umbrella. On now excising this last remaining zone, all contractions suddenly ceased. Occasionally, however, there supervened several *irregular*, *inefficient*, and *feeble* contractions, which were of a more local nature. It was rarely that these contractions lasted for any considerable time; generally they ceased after a few moments, or at any rate after several hours: only in one case was it observed that they continued on the following day.

Immediately after this operation the animal usually remains motionless, as if suffering from shock, and it is only after an interval that it begins to make attempts at contractions. These attain a certain degree of vigour and then again decline. Mechanical stimulation, *e. g.* pricking the umbrella, causes in the mutilated organism responsive attempts at contraction; but sooner or later, after the spontaneity of the animal has been destroyed by excision of the contractile zones, the irritability of the contractile tissues disappears, and death of the tissues supervenes. Having placed three specimens of *Aurelia aurita* under similar conditions, Dr. EIMER removed all the lithocysts from one of them, all save one from another, and none at all from the remaining specimen. The specimen which had all its lithocysts removed began to show symptoms of decomposition (aufgelöst), while the other two specimens were still quite lively.

Next are detailed some experiments in bisecting specimens of *Aurelia aurita* through their whole diameter. It was observed that the shock which this operation entailed appeared to be more severely felt by the small individuals than by the large. It was also observed that in one experiment the two halves contracted independently, so that the number of contractions which were made in a given time by the one was no index of the number given in the same time by the other. On the day subsequent to the operation, however, both halves contracted pretty uniformly, and each half showed a tendency to assume a bell-shape. In consequence of this slight change of form, the two halves were now able to swim at all levels in the water, and were no longer obliged, as on the previous day, to lie at the bottom of the vessel. In spite of every care these two halves died on the third day, presumably from the want of food.

By counting the rate of the pulsations in entire animals, and then dividing these animals by radial incisions into halves, quarters, or eighths, in such a manner that each portion should contain at least one lithocyst, and, lastly, by counting the rate of the pulsations of the halves, quarters, or eighths, Dr. EIMER was able to satisfy himself as to the following very important fact:—The sum of the contractions performed by all the parts of a divided animal was, in a given time, equal to the number of contractions which had been performed by that animal before its mutilation. This rule, however, was liable to very frequent variations.

Portions thus severed and kept without nourishment manifest after a time a progressive retardation in the rate of their contractions. Want of fresh sea-water also has the same effect, producing the greatest irregularity in the rate, strength, and rhythm of the pulsations. Addition of fresh sea-water revives the animal even from a state of apparent death, when the contractions return to their normal strength and rhythm.

Dr. EIMER also made the following experiments in section. From the margin of *Aurelia aurita* he carried a radial incision of several millims. long, in order to test a view which he attributes to HAECKEL, viz. that all the nervous connexions in Medusæ are dependent upon a single peripheral ring. Of course he obtained negative results, and thereupon lengthened his radial section until it came within 8 millims., and in another individual within 6½ millims. from the ovarian pouch. He then found that at this point the two portions of the animal first became physiologically separated.

Next, in order to test AGASSIZ's view as to the presence of an upper nervous ring and the possibility in the former experiments of this ring having acted vicariously for the divided portion of the lower ring, Dr. EIMER made two radial incisions proceeding from the centre towards the circumference of the disk. He found, of course, that these sections might be carried to within quite a short distance of the margin before the portion of tissue which was included between them became physiologically separated from the rest of the umbrella.

Lastly, as a control experiment, the author cut out from the middle of an *Aurelia* measuring 10 centims. in diameter a circular mass measuring 7½ centims. in diameter, thus reducing the margin of the animal to the form of an open ring. This marginal ring continued, of course, to contract, and this at first more rapidly than usual. On the other hand, all spontaneity ceased in the other part of the animal after an interval of three hours. Dr. EIMER then submitted this open ring to a series of interdigitating cuts. He found that in no one of its parts was the physiological continuity of the tissue destroyed by the sections, although it seemed to him that the severer forms of such section tended partially to obstruct the passage of the contractile influence from one division to another—that the thinner the connecting link of tissue, the greater was the resistance which it offered to such passage. Therefore, in view of the fact that the physiological connexions only appear to be certain so long as the connecting portions of tissue are not narrowed down below a certain point, Dr. EIMER concludes in favour of a nervous plexus pervading the contractile tissues rather than in favour of the functional homogeneity of these tissues. He observes, however, very justly, that if such a plexus is present, its fibres must be capable in a high degree of vicarious action. Dr. EIMER states further, that the amount of tissue which proves sufficient to maintain physiological continuity between any two almost severed parts differs in different portions of the umbrella.

The paper concludes with several theories as to other possible functions which the lithocysts may have to subserve as well as that of locomotion, *e. g.* respiration and nutrition; but as these theories are not supported by any observations or experiments, it seems unnecessary to adduce them here. It therefore only remains to state that Dr. EIMER has satisfied himself as to the presence of nerve-cells and fibres in the region of the lithocysts, and that in his experiments upon excision of the contractile zones in *Cyanœa capillata* he obtained results which were perfectly conformable with those which he obtained in the case of *Aurelia aurita.*

I have entered thus at length into the contents of Dr. EIMER'S paper, because, as my work was throughout independent of his, it becomes the more important to state clearly the points in which we agree and the points in which we differ. It is a matter of satisfaction to me that, while the latter are but of subordinate interest, the former are throughout the more important.

First, then, as to the mere matter of priority, it may be well to state that, as Dr. EIMER'S work was done in September of 1874, I have a right to claim precedence, both as to observation and publication of what I have termed the fundamental experiment. On the other hand, Dr. EIMER has the right to precedence in the case of all his other observations. I shall now consider these observations *seriatim*; and if I appear to give undue prominence to the points in which I differ from Dr. EIMER, it is only because I thus hope to secure a still more perfect agreement in our future papers.

It will, of course, have been observed that Dr. EIMER'S view as to the exact seat of spontaneity in *Aurelia aurita* does not coincide with mine. He is careful to state that the ganglionic function is distributed all round what he terms the "contractile zone," *i. e.* the crescent-shaped interruption of the margin in which the lithocyst, together with its gelatinous hood, is situated (see Plate 32). On the other hand, I have stated it as my opinion that the lithocyst is alone the locomotor centre; and notwithstanding the account which Dr. EIMER gives of the experiments by which he sought to localize that centre, I still adhere to this opinion. Dr. EIMER'S experiments in this connexion were twofold:—1st, that of progressively lessening the amount of contractile tissue left adhering to an excised segment of *Aurelia aurita*; and 2nd, that of excising the lithocyst without injuring the "contractile zone." Of these two methods Dr. EIMER appears to lay most stress upon the first one; for he merely mentions the second method in a short footnote towards the end of his paper, and there states that he only tried it in a few cases. Yet to me it seems that for the object in view the second method is much more trustworthy than the first. I am well aware of the fact, pointed out by Dr. EIMER, that upon each contraction of a given segment of *Aurelia aurita* the two arms of the so-called "contractile zone" approximate each other, and that this gives rise to the appearance of spontaneous action on their part. I think, however, that this appearance is deceptive, being caused only by the absence of resistance at the interrupted part of the margin to the pressure exerted by the contraction of the immediately surrounding tissues. At any rate, so long as this possible explanation has not been thoroughly excluded by experiments conducted on the converse method of removing the lithocysts from between the arms of the contractile zone, so long, it seems to me, must the method we are considering be valueless. The question, then, must be decided by the converse method just alluded to, and by it alone. Now I have made experiments according to this method, and, so far as I remember, in every case, when sufficient care was taken to remove all the lithocysts, the contractile zone entirely ceased its contractions. And not only so, but by removing, with the aid of a well-pointed scissors, the little sac of crystals composing the central part of the lithocyst, without injuring the curious wing-like appendages by which this sac is partly surrounded, and, conversely, by removing in other specimens these wing-like appendages alone, without injuring the little sac of crystals—by these experiments I was able to satisfy myself that the whole spontaneity of the lithocyst appeared to be exclusively lodged in the minute sac of crystals referred to.

There is thus in this particular a direct contradiction between the results of Dr. EIMER's experiments and those of my own. I should therefore like to state that my experiments with reference to this subject were not made till near the end of the season, and so at a time when the only specimens I could procure were small and not very active. In view of this fact I intended to defer publishing any account of the experiments now detailed until I had an opportunity of confirming them on vigorous specimens; but a perusal of Dr. EIMER's statements appears to render it desirable for me to give an opinion now upon the point under consideration, although I confess that, for the reason just mentioned, I do so with some diffidence.

I fully agree with Dr. EIMER in his view that the contractions of *Aurelia aurita* are "usually involuntary," but that they are nevertheless to a certain extent subject to the control of volition. As stated in the beginning of this paper, I believe that different species of Medusæ are endowed in different degrees with the power of volition; and in this respect I should place *Aurelia aurita* at the head of all the covered-eyed species I have observed: its contractions are not of so purely *rhythmical* a nature as are those of *Cyanœa capillata*, &c.

But this leads us to the next observation mentioned by Dr. EIMER, viz. that the length of the pauses between any series of contractions bears a direct relation to the number and strength of the previous contractions. This is no doubt true as a general statement, and as such is what might have been anticipated; but I do not think that a number of observations would tend to establish any more precise relation. In the case of *Sarsia* the alternations between periods of rapid swimming and periods of complete repose are much more marked than in *Aurelia aurita*, to which Dr. EIMER'S tables refer; and I am sure that with them the rule in question can only apply in a very general way. It is to be observed that Dr. EIMER himself does not appear to place much reliance on particular applications of this rule.

I am able to confirm Dr. EIMER'S statements as to the various ways in which the lithocysts discharge their influence relatively to one another, and would only add the curious fact that very frequently one or more of the eight lithocysts appears to be temporarily or permanently prepotent over the others—the contractions always originating in it for a great number of times in succession.

Mere observation with the eye, however, is not sufficient to determine the interesting question as to whether or not there is any further coordination between the lithocysts than is brought about by the rapid passage of contractile waves from one to the other. I have accordingly made a large number of variously devised sections with the view of answering this question; but it would occupy too much space to detail them at present. I may state, however, that Dr. EIMER is quite right in his assertion that in no case can a contraction of one zone take place without being accompanied by a synchronous, or almost synchronous, contraction of all the others; and not only so, but in all my forms of section I find it to be universally true, that as soon as a contractile wave which starts from one lithocyst arrives at another (no matter how far off or how feeble the residuum of the contractile wave may be), the latter is immediately stimulated into activity, liberates a powerful discharge, and so originates a new wave of contraction. Thus, for instance, it is not difficult to obtain a series of lithocysts connected in such a manner that the resistance offered to the passage of the waves by a certain width of the junction tissue is such as just to allow the residuum of the contractile wave which emanates from one lithocyst to reach the adjacent lithocyst, thus causing it to originate another wave, which in turn is just able to pass to the next lithocyst in the series, and so on, each lithocyst in turn acting like a reinforcing battery to the passage of the contractile wave. But, as already observed, it does not fall within the scope of the present paper to discuss the subject of coordination among the locomotor centres of Medusæ. I may state, however, that there appears to be important differences between the discophorous naked-eyed Medusæ and the true Discophora in this respect; for in all the species of the former which I have as yet observed, the area of paralysis in the nectocalyx corresponds much more precisely with the line of ganglionic tissue which has been removed from its margin than it does in the case of the true Discophora.

I cannot quite assent to the description which Dr. EIMER gives of the contractions which sometimes supervene in the umbrella of *Aurelia aurita* when all the lithocysts have been removed. He describes them as "several *irregular*, *inefficient*, and *feeble* contractions of a local nature which rarely last any considerable time." This is no doubt partly true of some cases, but it is not true of all. I have frequently seen these after contractions as rhythmical (though this is rare), as effectual, and as powerful as those which had been previously supplied by the single remaining lithocyst. Moreover these contractions may usually be seen to emanate from some very localized portion of tissue, and from thence to radiate over the whole substance of the umbrella, just as the contractile waves which emanated from a single remaining lithocyst had previously done. On now cutting out this localized portion of tissue, the umbrella usually becomes again paralyzed, while the portion of tissue which previously animated it may be seen to continue its contractions after the manner of excised lithocysts. I did not pay sufficient attention to the number of hours after excision of the lithocysts during which these secondary movements continued, to admit of my speaking with confidence on this point; but so far as I can recollect my numerous experiments with this species, it is certainly not correct to say that these contractions "generally ceased after a few moments." My impression is that they *usually* last for several days. I agree with Dr. EIMER, however, that, as a general rule, the secondary movements in *Aurelia aurita* are not so persistent as the primary ones, and also that in this species, under some circumstances, insensibility to stimulation rapidly supervenes upon loss of spontaneity. This, however, is far from being always the case with *Aurelia aurita*, and is not even generally the case with some other species—*Cyanæa capillata*, for instance, continuing to respond even to slight stimulation *two or three days* after it has been completely paralyzed by the removal of its lithocysts, and this even though it be kept in a small jar without change of water. Again, if the lithocysts be left *in situ* and the animal be kept in a confined body of water, irritability will continue for days after all the usual indications of spontaneity have disappeared. Nevertheless, with but slight modifications, I have confirmed Dr. EIMER's experiment of placing different specimens of *Aurelia aurita* under similar conditions, removing the lithocysts of some and not of others, and observing that those individuals which had been operated upon died sooner than those which had not.

These experiments, however, and many others entailing similar precautions, I do not intend to publish until next year, when I hope to have the opportunity of conducting them in a more satisfactory manner.

I am also able to confirm Dr. EIMER's statements regarding the behaviour of bisected *Aureliæ*; and I think with him that it is not improbable that halves, quarters, or eighths of such Medusæ would, under suitable conditions, redevelop into entire animals.

Dr. EIMER's very interesting statement, to the effect that an *Aurelia* before its mutilation contracts twice, four, or eight times as rapidly as do its half, quarter, or eighth part after mutilation, is a statement which I am unable either to confirm or to dispute. I did indeed observe, in a general way, that the smaller segments of an *Aurelia* manifested a slower rhythm than the larger segments; but it never occurred to me to test for any constant relationship. Dr. EIMER, indeed, is careful to state that the relationship he points out is one that is liable to very frequent exceptions; but even if it were found only to apply to a tolerably large percentage of cases, it would be relationship full of interest to the physiologist.

It is needless to say that there is a complete agreement between Dr. EIMER and myself as regards the results of section.

Concerning Dr. EIMER'S histological observations, it is, of course, impossible for me to say any thing; for he neither figures nor describes the elements which he regards as nervous. They may therefore or may not correspond with appearances which I have myself observed.

It only remains to notice Dr. EIMER'S statement with reference to *Cyanæa capillata.* He says that the effects of the fundamental operation upon this species were precisely similar to the effects of it upon *Aurelia aurita*, whereas in my experience it was not so. As already stated, I found these effects to be *analogous*, but not *identical*—*Cyanæa capillata, as a rule*, being less frequently or less completely paralyzed by excision of its lithocysts alone than was *Aurelia aurita.* I can only explain this discrepancy between Dr. EIMER and myself by the fact which he states, viz. that he performed but few experiments on *Cyanæa capillata.*

In now concluding this somewhat elaborate postscript, I wish it to be understood that I have mentioned the various points in which Dr. EIMER and myself do not quite agree, only because I think it is for the benefit of the subject on which we are both engaged that such differences should be noted before the work of another year begins. In this way, when opportunity again affords, we may both be able to repeat such of our observations as are now rendered doubtful by want of complete accordance.

G. J. R.

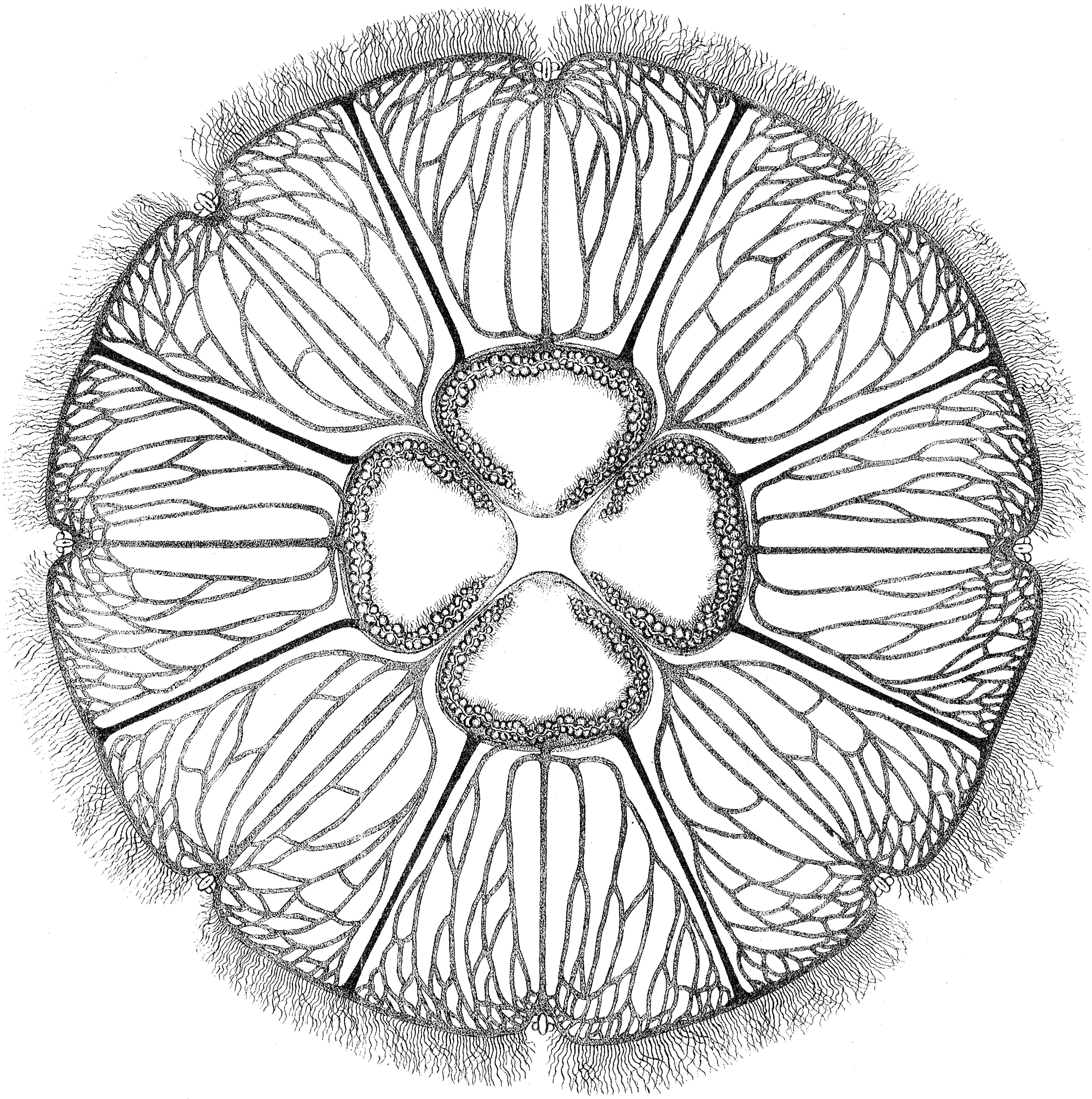
EXPLANATION OF THE PLATES.

PLATE 32.

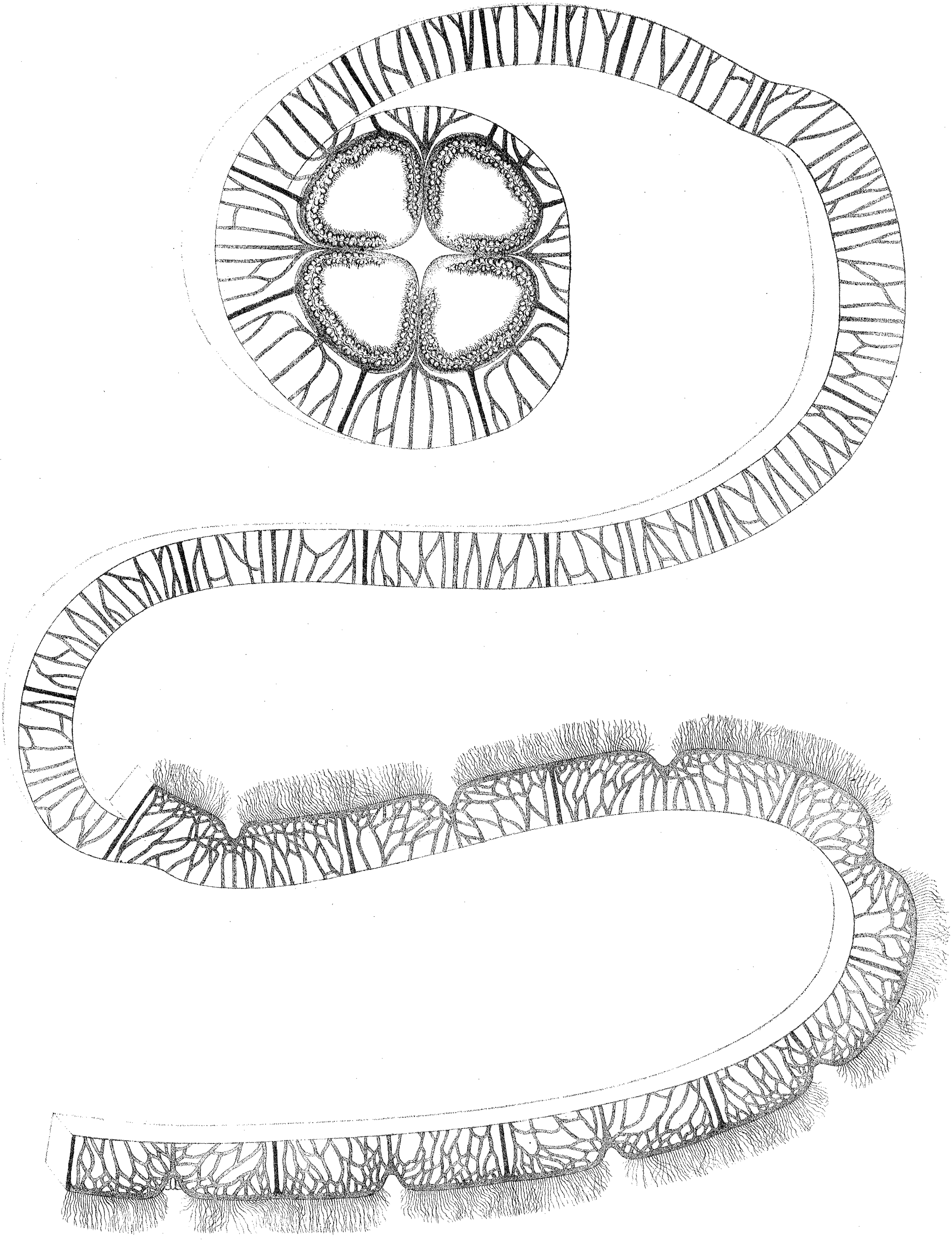
Aurelia aurita, $\frac{1}{2}$ nat. size. The animal is represented in full diastole, with its polypite removed. In some details the drawing is not quite accurate.

PLATE 33.

Aurelia aurita, with polypite and seven lithocysts removed, submitted to spiral section.



W. H. Wesley lith. W West & Co. imp.



W. H. Wesley lith. W. West & Co. imp.

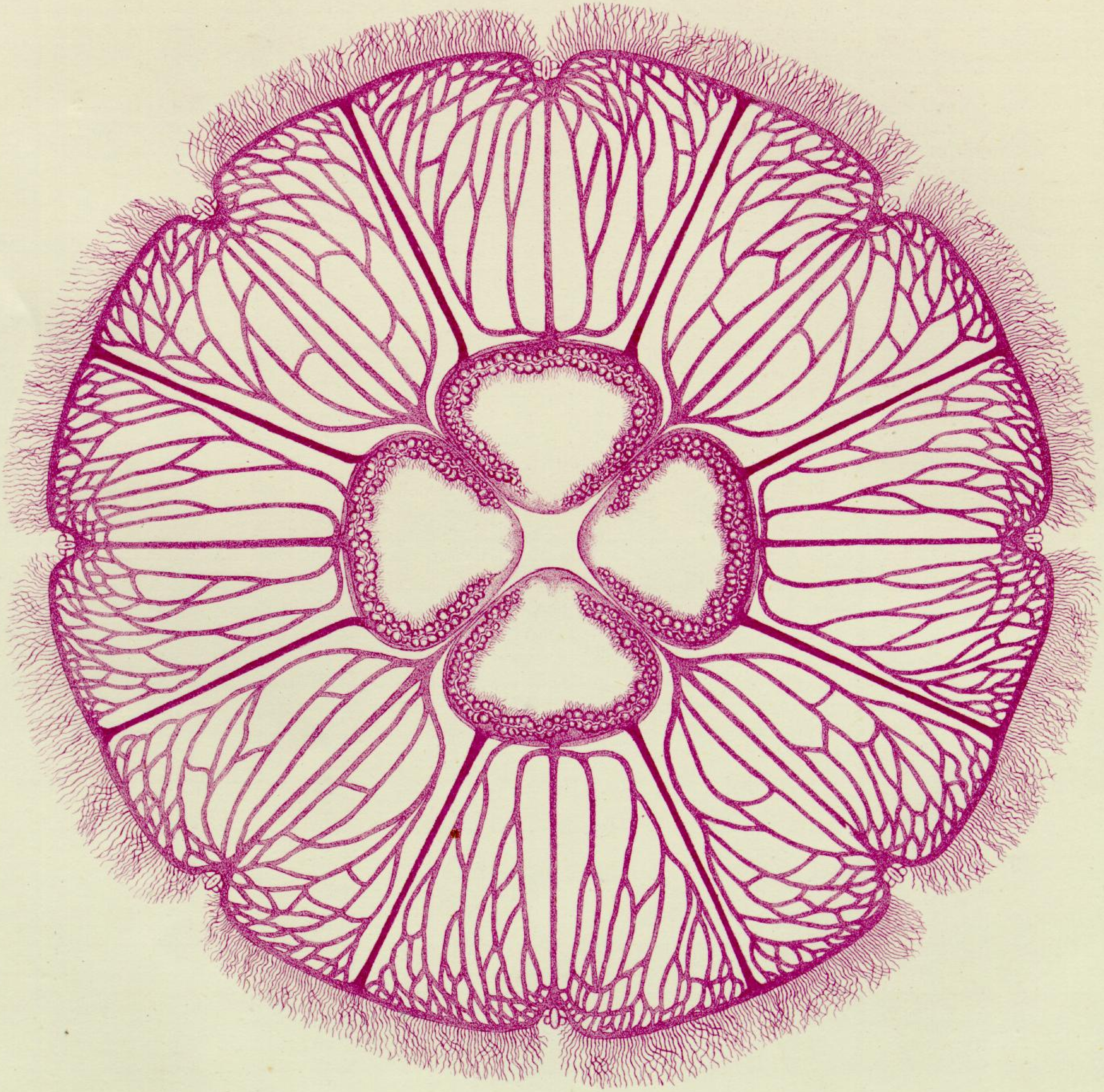


PLATE 32.

Aurelia aurita, $\frac{1}{2}$ nat. size. The animal is represented in full diastole, with its polypite removed. In some details the drawing is not quite accurate.

PLATE 33.

Aurelia aurita, with polypite and seven lithocysts removed, submitted to spiral section.