

VARIATION AMONG HYDROMEDUSAE.

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THE announcement of Bateson ('94), that "in the whole range of natural history there is no more striking case of the discontinuity and perfection of meristic variation than in the genus *Sarsia*, and the further proposition whether it is a mere coincidence that the specimens presenting this variation, so rare among the free-swimming Hydromedusae, should have been members of the same genus," directed my attention to this particular problem in conjunction with work upon this group of coelenterates which had engaged my attention for several years.

During the following years, therefore, collections of free medusae of several genera were made with a view to testing the problem raised by this observer. While as yet these collections are not extensive, except in a few genera, certain facts have been secured which may not be without value in their general bearing upon this as well as still broader problems of variation in general.

My collections have been restricted chiefly to the genera *Eucope*, *Obelia*, *Margelis*, *Pennaria*, *Gonionemus*, *Coryne* (*Sarsia*), and *Hybocodon*; the specimens of several others have been casually examined. Of the genera named, *Obelia* has not as yet been examined in sufficient numbers and detail to warrant any specific mention in this connection. And since these observations have been under way a paper by Agassiz and Woodworth ('96) on "Some Variations in the Genus *Eucope*" has appeared which so fully covers the facts involved in members of that genus, and are so coincident with my own, that no special details will be offered in connection with it, though the materials at hand are more abundant than upon any of the others.

What I shall have to offer in this paper, therefore, will be upon the other genera named, namely, Coryne, Gonionemus, Hybocodon, Pennaria, Nemopsis, and Margelis.

Coryne.

Of specimens of Coryne a comparatively few were available, though they were examined with unusual interest and care as belonging to the genus to which, apparently among the earliest, references to variation among Hydromedusae were made, and which called out the rather remarkable proposition of Bateson quoted in the opening paragraph of this paper. While the specimens were too few to warrant any definite conclusions, they nevertheless showed a most remarkable constancy in every morphological feature, not a single specimen exhibiting the slightest variation in any of the more conspicuous features, as tentacles, radial canals, manubrium, etc. If this constancy is as marked in different regions of distribution and for the large numbers cited by Bateson, it is not strange that he should refer to the matter in the terms quoted, as it would seem to be among the least variable of the free-swimming medusae of this group. It will at the same time show how very unsafe must be any such conclusion taken from so limited a range of observation.

Hybocodon.

Of the genus Hybocodon Ag. the number of specimens at my command has likewise been somewhat limited, slightly less than two hundred, still they have been sufficient to show some variation in certain features. This genus was instituted by L. Agassiz ('62), under which he included a Hydromedusa of very unique characters (*cf. Contribution to the Natural History of the United States*, Vol. IV, p. 243), one of which is the proliferous budding of medusae from the hydranth, which in turn give rise to secondary and many later specimens by a similar process of budding. (*Cf. op. cit.*, Pl. XXV, Fig. 13.)

The specimens which came into my hands were all preserved in formalin and had in consequence suffered considerable

distortion in the process, whereby minute variations of organs often became difficult of detection, yet I was able to demonstrate a fair degree of constancy in the general form of the medusa, its radial canals, tentacles, etc. I desire to direct attention to the number of tentacles. As stated by Agassiz, there seems to be a single long tentacle arising from the margin of the bell at the terminus of one of the radial canals, from the base of which arose later the proliferous medusae-buds, as shown in the figure already cited. From these secondary medusae other tentacles arose, giving to them the exact morphological equivalent of the primary or mother medusa. Hence, as several of these proliferous specimens budded off from the base of the primary tentacle, several tentacles would come to be clustered near the same point, giving the impression of a bunch of tentacles of the same nature. In several specimens in which the medusae-buds had not yet appeared, or could be detected as mere papilla-like bodies, these secondary tentacles were nevertheless well developed, and of a length frequently equal to that of the primary one. Now whether this be a variation, or whether it may not be rather fundamental, arising as a source from which the medusae are to spring, may perhaps be an open question, to be settled by a more critical examination of their development. Proceeding on the assumption before stated, I venture to cite it as a case of variation, though it may later be found to be rather the normal process.

The rather unusual character of this medusa, both in its origin and proliferous progeny, led me to suspect that it might exhibit more than the usual phases of variation; but in this I have been disappointed, except in the point just cited, — its constancy in almost every morphological detail being quite marked. As stated, however, in connection with observations upon *Coryne*, the limited number of specimens examined, and furthermore their distortion due to preservation, are barriers which should suggest reasonable caution in the formulation of any conclusion.

Pennaria. — Of this medusa I have had an almost unlimited number of specimens, having collected them during three

years devoted to the embryology of the species common in the waters of the Massachusetts coast, — *P. Tiarella* McCr. A critical study of these medusae is, however, rendered difficult and tedious owing to their minuteness and form. In size they are only about .8 mm. in diameter by about 1.5 mm. in length. The highly oval form renders difficult a study of the aboral surface and the junction of the radial, or chymiferous canals, — a point of considerable variability in many cases in other genera, notably *Gonionemus*, to be noted later. In a study of their morphology Smallwood ('99) has pointed out the variability in the structure and development of these canals. He has shown that in a considerable proportion of specimens there is a tendency to atrophy both in the radial and circumferential canals, especially the latter. These changes are not evident in a surface study of specimens, the pigmentation which marks their course being fairly constant. The principal variation to which I desire to direct attention in this connection is a physiological one, *viz.*, a rather marked variation in habit and activity. I have discussed elsewhere this feature ('00) and need only refer here in brief to those observations. As there pointed out, there seem to be two rather distinct features of habit; namely, a rather deep-water habit upon rocks, seaweed, piles, etc., and a surface habit upon eel-grass or similar support, which serves to bring the colonies to the surface, thus often in a low tide exposing them directly to the action of the midsummer sun and temperature.

Associated with these differences are correlated variations in the form and color of the colonies, or, as Bateson would designate them, "substantive variation." The surface or eel-grass varieties exhibit more distinctly the pinnatifid character which marks its specific peculiarity, due doubtless, in part at least, to the prone or floating disposition of the colonies. Associated also with this is the much higher coloration so conspicuous in these specimens, a variation extending not only to the perisarc of the colonies but also to the medusae and the eggs, which are rather bright orange, while those taken from the deeper waters are a pale, creamy white, with the slightest trace of pink in many cases.

Of the further physiological differences one of the most marked is that of the relative activities of the medusae of the afore-mentioned varieties; those of the surface habit exhibiting a much greater degree of activity and other vital phenomena. These, as previously pointed out, are extremely active, being liberated from the hydranths promptly upon maturity, swimming with great ease and freedom, and discharging the sexual products with great promptness. On the other hand those of the deep-water habit are passive, or even sluggish, — in many cases the medusae never becoming free from the hydranth, — discharging the sexual products with much less regularity and ease, and dying very soon after. These medusae are short lived at best and never increase in size after liberation from the hydroid. I would suggest the probable correlation of some of these features of variation with the degenerative tendency shown in both structural and physiological variations already noted, especially in the atrophy of the chymiferous canals.

A histological study of the tentaculocysts likewise shows degenerative tendencies, as does also the very rudimentary condition of the tentacles, which are barely distinguished as bud-like protuberances upon the margins of the bell.

In connection with previous work upon the development of *Pennaria*, attention was directed to variation in the rate of cleavage and subsequent development. This would seem to be a matter of considerable interest in connection with the fundamental problems of physiological variation. It is well known, of course, that cleavage is a phenomenon subject to considerable variation as to rate, due to variable conditions, and to some extent independent of sensible differences of environment. It seems to me, however, that in the case of *Pennaria* there are presented such marked extremes in this respect that it may well be considered as in some measure correlated with other features of physiological variation.

The variable rate in the later phases of larval development is also worthy of note. From data obtained during three summers of observation the range of time involved in the larval history varies from about two days up to about two weeks.

While in most cases these observations were made upon specimens under artificial conditions, namely, aquaria of variable sizes, etc., still the variations occurring were exhibited by larvae under identical conditions, such as they were.

Under the head of abnormalities in immediate connection with these observations, attention was also directed to certain variations in the morphology of the larvae and early polyps. Among these may be mentioned

1. Twin-planulae, — planulae with bifurcated ends, irregular bud-like outgrowths, etc. (*Cf. op. cit.*, Figs. 4–6, and 8, Pl. I.) It was suggested that they were probably due “to the intrinsic prepotency of hydroids to bud and branch.” While this is probably an explanation of the facts, that they exhibit interesting variations from the ordinary is not discredited on that account.

2. Attention was also directed to an interesting polyp form (*op. cit.*, Fig. 1 of text), which presented so marked a variation as to give rise to some doubt concerning its Pennarian affinities. In view of the rather large range of variability exhibited by the medusoid and larval persons already considered, I am still convinced that this is only a further illustration of the same principle. Indeed, I have during the present summer observed in other polyps reared under similar conditions the same variation from total annulations to less and less degrees. A few additional annulations of the hydroid perisarc is matter of no special surprise. A complete annulation of the early and plastic colony, while quite unusual, need not be regarded as improbable or especially strange.

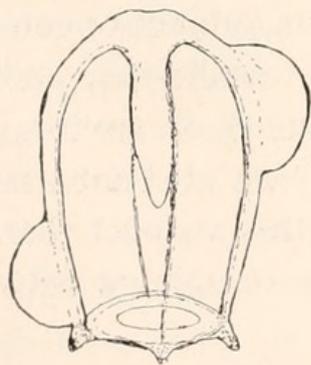


FIG. 1.

Another feature which may perhaps rather be designated as a monstrosity, or incidental excrescence, may be noted in this connection; namely, certain wartlike or pustular vesicles which often appear at various points on the exumbrella of the medusae. These are fairly represented in Fig. 1. The figure indicates relative positions where they are most likely to occur, though in no case have I noted more than one upon a given specimen. . . . A similar structure is referred to by Agassiz ('65) and

explained as due to distortion caused by the pressure of the ova within the bell. This I am convinced is a mistaken view, for I have noted it upon specimens both living and on those killed and preserved in formalin, in specimens with and without eggs. It seems, moreover, to be wholly restricted to the outer ectoderm only, in no case involving the inner ectoderm of the subumbrella. There is nothing indicative of the cause or character of these excrescences. Whether they are permanent or merely transient features I am not able to say, the short-lived condition rendering any determination difficult if not impossible.

Nemopsis.

Through the courtesy of Mr. Strong I had the privilege of examining a small collection of about one hundred specimens of *Nemopsis Bachei* taken in the tow off Tarpaulin Cove. The variations here seemed quite as evident as in *Eucope* and *Gonionemus*. Here again the variable features included radial canals, manubrium, gonads, and tentacles. Fully five per cent showed some feature of variation. About two per cent had but three radials and three gonads. One of these showed a definite correlation, including all the organs named above. One, however, of the trimerous forms had a fourth sensory bulb and tentacles, though these were less prominent than were the other three sets. The oral tentacles likewise shared in the correlation.

One specimen was a symmetrically pentamerous form with a perfect correlation of all the organs under consideration. Another specimen was quite as symmetrically hexamerous.

Several other specimens exhibited apparent symmetry in the number of gonads. Frequently one of the series showed the gonad of one canal very unequally developed as compared with the others. But while approaching sexual maturity, and in many cases fully so, it is of course impossible to say with certainty that the short gonad might not have shown further development with age. In any case it certainly showed variation as to *development*.

Concerning variation in the number and order of tentacles it is difficult to determine definitely, since in *Nemopsis* they constantly increase in number as the medusa grows, much as in *Margelis*. So while there appears to be considerable variation in the number and arrangement it may be rather due to variable development than to any actual meristic variation. The same may be true as to the order of appearance. The paired, capitate tentacles at the apex of the bulb appear uniformly first and seem to be fairly constant. The latter filamentous tentacles appear to arise in pairs successively toward the margins of the bulb. Since I was not able to follow this development in the stages of growth of the medusa it is impossible to determine definitely this point. So while there is upon the preserved specimens considerable want of symmetry in this respect, yet it may be due in part to slightly variable rates of development. No constancy was apparent in the matter, and it would seem therefore to be physiological rather than morphological.

Similarly there was apparently some variation as to the number and distinctness of the otocysts upon the sensory bulbs. Normally there is a single eye-spot at the base of each tentacle. But in many cases they were apparently absent. And while it is not impossible that they had been rendered indistinct by the formalin in which they were preserved, still it remains quite certain that marked differences were distinguishable among various specimens of similar size and preservation, and perhaps only critical histological examination will be adequate to finally determine this point, and this I have not been able to make.

Margelis.

Of these medusae more than five hundred specimens have been examined, most of which were quite young, having only the four pairs of marginal tentacles and four unbranched oral tentacles and measuring only about 0.5 mm. in diameter. Typically this medusa may be characterized as having a high hemispherical bell, four radial canals, at the distal or marginal ends of which four clusters of filiform tentacles arise. The bell is

thick, velum not specially prominent. Manubrium subconical, bearing four oral tentacles which divide dichotomously into small clusters of tentacles. Figs. 2-4 give good general impressions of the animal. The very minute size made necessary the constant use of the compound microscope in all the examinations.

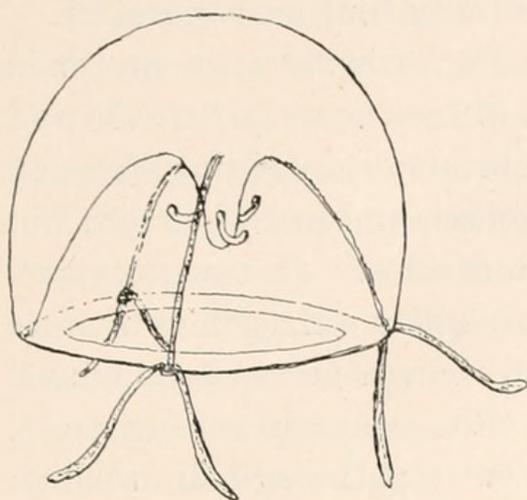


FIG. 2.

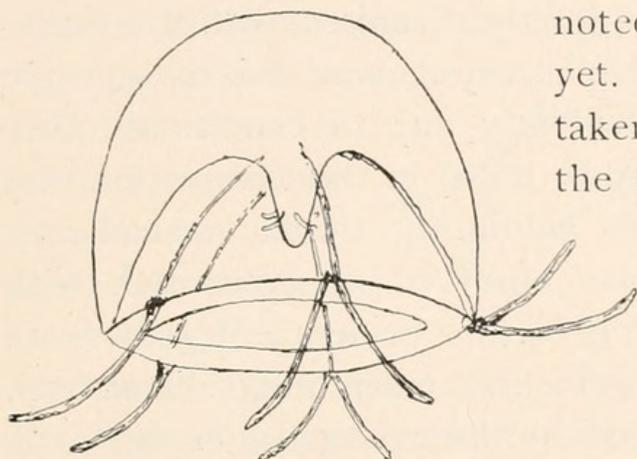


FIG. 3.

The variation in radial canals was usually correlated with that of the tentacles. In Fig. 2 is shown a trimerous specimen, in which there was a perfect correlation of all the organs, including oral tentacles (several specimens noted). In Figs. 3 and 4 is shown a pentamerous form, in which there appeared little meristic correlation.

For example, it will be seen that while five sets of tentacles correspond with the five radial canals, two had but a

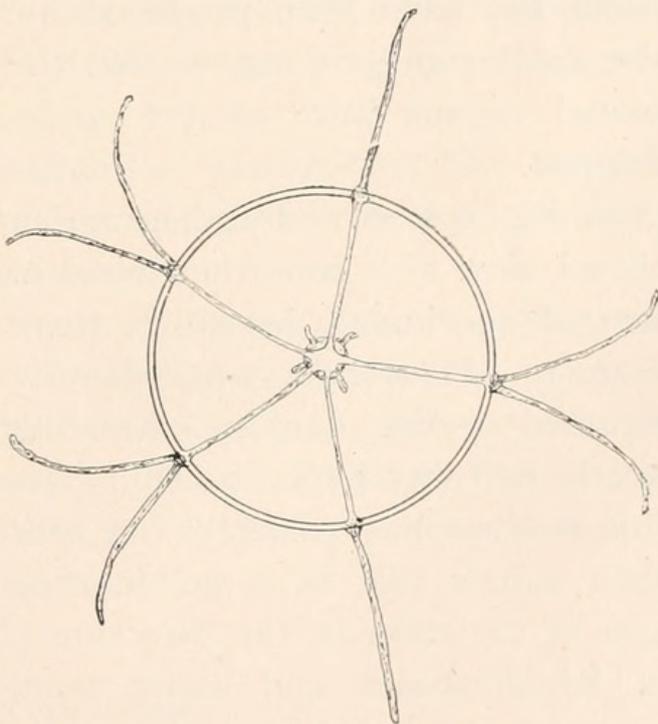


FIG. 4.

In general this medusa seems to be fairly constant in form, color, and organic symmetry. Only the radial canals, and tentacles — marginal and oral — were noted, no gonads being present as yet. Of the tentacles note was taken of the number of groups, the number of individual tentacles increasing in these with age. The total of all sorts of variations noted hardly exceeded two per cent.

single tentacle each, while the other three sets contained the normal (at this stage) number, two. A point not shown definitely in the figure is the fact of only four oral tentacles.

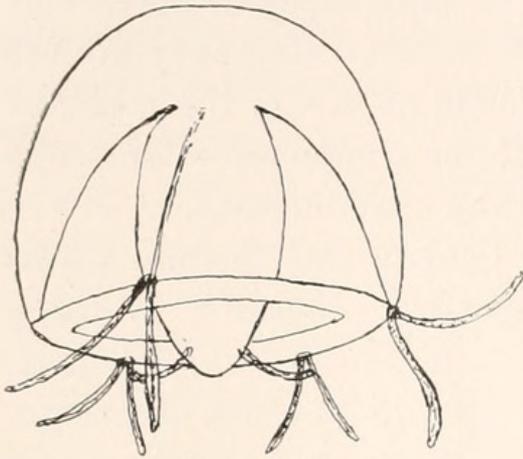


FIG. 5.

In Fig. 5 is shown a specimen with monstrously developed manubrium, protruding beyond the velum, and provided with but two tentacles. In several specimens similar enlargements were noted, though not so pronounced as in this, except in certain cases, apparently pathological, in which the entire bell was evaginated and greatly shrunken, with the manubrium greatly enlarged. No account was taken of such specimens, for they were evidently due to conditions other than those of health. It may be noted in this connection that several specimens were found exhibiting similar vesicular or pustular enlargement to those observed in connection with accounts of *Pennaria*. Here is further evidence, if such were necessary, that these enlargements, resembling distortions, could not have been produced by the enlarged gonads, for in the species under consideration the sexual organs were as yet undeveloped.

In Fig. 6 is shown in diagram an aboral view of a condition found in several specimens, in which there seem to be secondary, peripherally directed radial canals, extending nearly half-way over the bell. As this medusa has normally but four such canals this is a well-marked case of variation in the direction of a condition quite common in *Rhegmatodes* and many trachomedusae. I regret that none of the specimens to which I have had access are of approximate maturity so that such incipient variations might be traced forward to their perfection, in order to ascertain

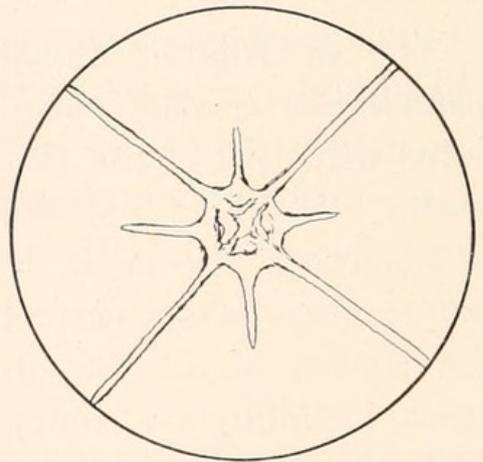


FIG. 6.

whether additional sets of tentacles, etc., would be found correlated therewith.

The origin and symmetrical interpolation of such secondary canals is very different, it seems to me, from that arising from the bifurcation seen in *Eucope* and *Gonionemus*, though their function in the economy of the organism may be the same.

Only one phenomenon more will be discussed in this connection, namely, that of double or twin medusae, which is shown in Fig. 7. Only one specimen of this character was found in the entire lot. In every respect — size, general form, organic relations, etc., the double feature alone excepted — the specimen seemed fairly normal, having this one further feature, that one was a trimerous specimen and that one set of tentacles contained three as against the

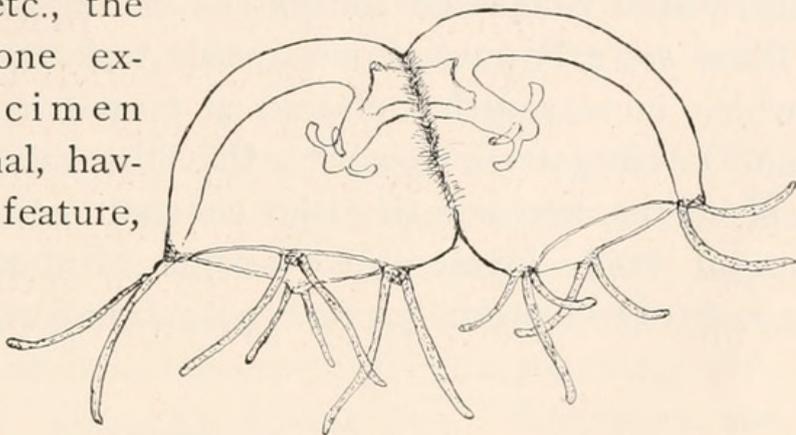


FIG. 7.

two each of the other sets. The furrow-like depression along the line of union presents the aspects of late coalescence similar to that involved in artificial grafting (*cf. Biological Bulletin*, Vol. I, p. 41).

But a more critical examination shows that the union is much more profound, involving the gastric cavity and therefore the whole chymiferous system.

The specimen was not seen alive, and hence nothing can be said as to coördination of physiological activities, mode of progression, etc. But from what has been proved from experimentation on these points (*cf. op. cit.*) it may safely be inferred that similar coördination at least prevailed in such a case as that under consideration.

Podocoryne.

Of medusae of this genus I have had at my command only a few more than one hundred specimens, a number too small

to warrant any formal deductions, but taken in connection with others it will not be amiss as showing the facts of variation pertaining to this genus.

Like Margelis this medusa is quite small when liberated, indeed never attains a size of more than 1 mm. in diameter, so far as I am aware. In general, it is similar in organization to Margelis, has four radial canals and four primary tentacles, between which a second series of the same number soon arises. Like Margelis there is apparently a fair degree of constancy in meristic features. Three trimerous specimens occurred in the lot, which comprised the extent of variations along this line. There were, however, considerable variations of size, form, etc., which increased the total to at least five per cent. It must not be forgotten, however, that the extreme minuteness of specimens, necessitating the constant use of the microscope, might easily involve an oversight of specimens in sufficient numbers to materially raise this ratio of variation.

Gonionemus.

It is among the members of this genus that I have been able to work out the most numerous and detailed series of variations. The total number of specimens of *Gonionemus* examined during the progress of the work was more than two thousand. (Of the first series studied no record was kept.) While smaller than the number of *Eucope*, to which reference has been made, the number is yet sufficiently large to insure against an unusual per cent which might be due to local or other incidental influences. Moreover, the collections were made during three summers, and by several collectors, so that the results obtained may be considered as closely approximating the actual state of variation now under way. It is a pleasure to acknowledge in this connection courtesies from Messrs. Coe, Parker, Perkins, Gray, and others for permission to examine collections of these medusae made by them, which has facilitated my work.

In these studies attention has been directed chiefly to the following structures: 1, radial canals; 2, gonads; 3, manubrium;

4, tentacles; 5, otocysts. Other features of subsidiary nature will have mention in their appropriate places.

It ought to be stated in passing to details and tabulation of results that only in the matter of radial canals and gonads have the entire two thousand specimens been examined, and not all of those with equal detail in each case. In number and variation of tentacles, spurs, anastomosing of canals, etc., the tabulations were limited to one thousand; and in the case of otocysts to less than one hundred, a reason for which will be given in the appropriate place. I may also state that owing to the insignificant sexual differences, usually requiring microscopic examination to certainly decide, no effort has been made to determine the relation of variation to sex.

Gonionemus is a rather well-defined trachomedusa, first definitely described from the Atlantic coast by Murbach ('95). It is characterized by the typical four radial canals, which have the folded gonads suspended along their under surfaces, cruciform manubrium, as seen in transverse section, normally with four oral lobes and sinuously folded lips. Tentacles are numerous and similar, each characterized by a suctorial bulb near the tip, beyond which it often makes a sharp bend.

These medusae abound from June to October in a small pond near the Marine Laboratory, known as the "eel pond," which communicates with the open harbor by a narrow inlet. Lately they have been taken in the outer harbor, though in small numbers. I may mention this fact of the localized habitat, since it may well be a question whether its peculiarity may not be an important factor in the physiological aspects of the variations to be considered.

Taking up now the consideration of the several points in the order given, attention will first be directed to the

Radial Canals.

On this point an estimation of the ratio of numerical variation based upon fifteen hundred specimens gave nearly five per cent (4.82). On the matter of their form or disposition, *i.e.*, whether in their course to the marginal canal the bells

were divided into symmetrical segments, the results showed no less than thirty per cent of variation. On the variations shown in their aboral confluence, or union with the gastric pouch, the calculations gave 14.4 per cent.

Of the entire number examined only a single specimen was found having but two radial canals and two gonads. These were at an angle of 180 degrees, *i.e.*, dividing the bell into two symmetrical halves, as shown in Fig. 8, excepting along the rela-

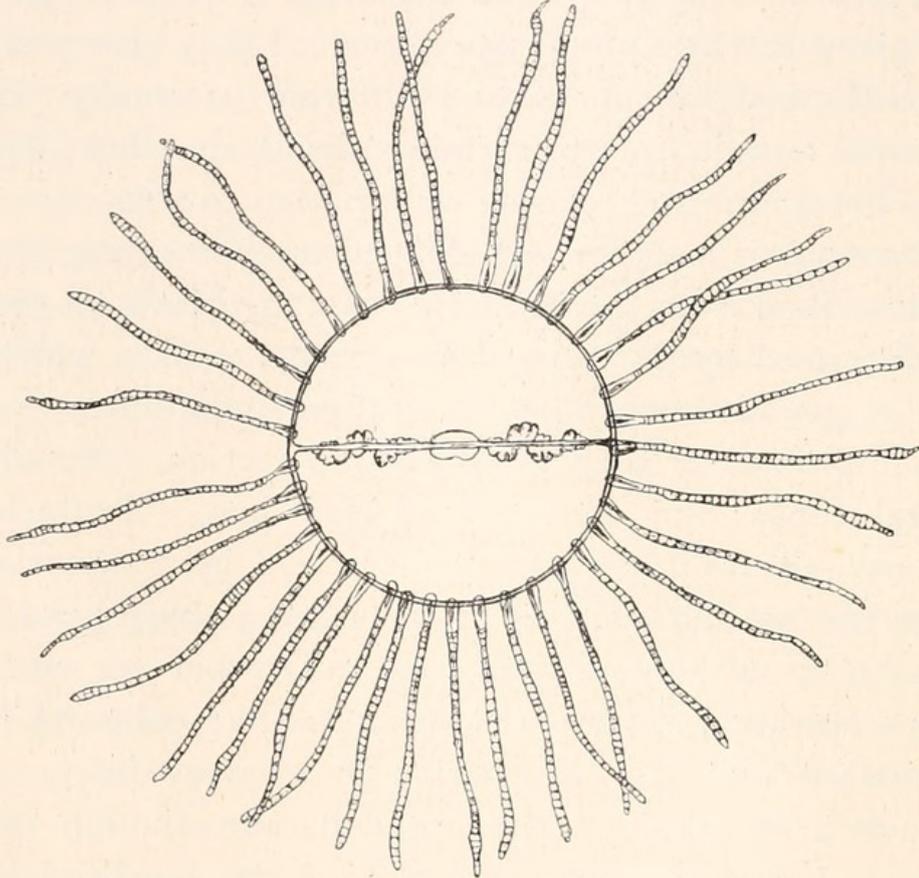


FIG. 8.

tive number of tentacles upon each half. One other specimen, however, was found having only two canals, similarly disposed and with a similar number and disposition of gonads; but in it there was a rather evident rudiment of a third springing from the peripheral end of one of the canals, thus destroying the bilateralism characteristic of the first.

The largest number of canals found was six. This, while much more common than those with two, was much less so than specimens with three and five. Seven specimens in all were found having this number, and in one of these the sixth was due to the evident forking of one of the five apparently

primary canals, which divided the bell into approximately pentamerous segments, as shown in Pl. III, Fig. 12. In another there was a very evident forking of two of the four primary canals, as shown in Pl. III, Fig. 9; for while the bell was divided into hexamerous segments, the manubrium was symmetrically tetramerous. In every one of the other five hexamerous specimens the canals converged at the aboral pole in a perfectly symmetrical way, though the hexamerism extended to the manubrium in only two specimens, and in these only

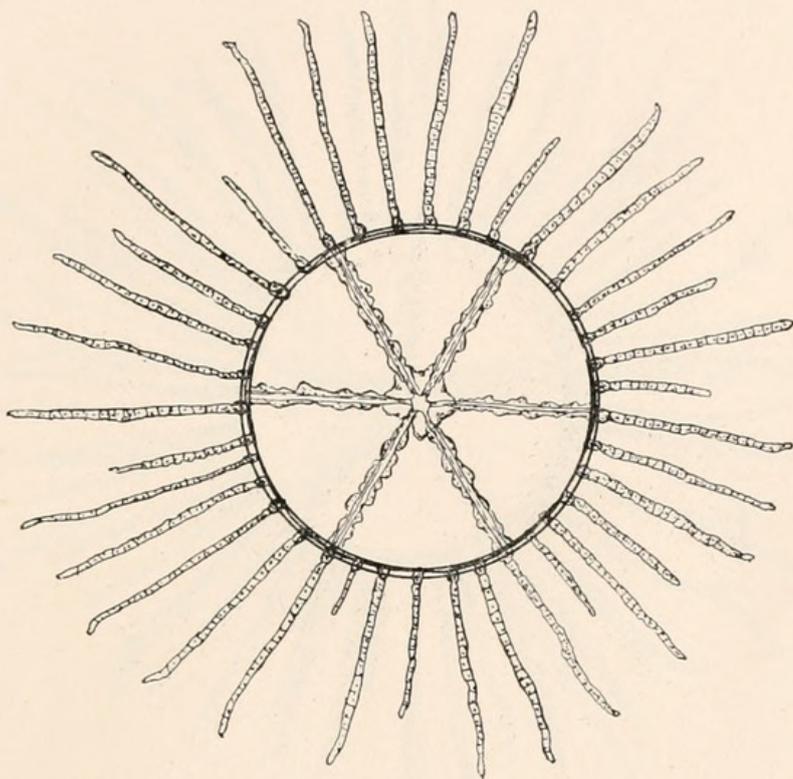


FIG. 9. — Hexamerous specimen showing pentamerous stomach and varying size and distribution of tentacles.

the basal portion or gastric pouch was strictly hexamerous. In at least two other of these hexamerous specimens the oral lobes of the manubrium were four (*cf.* Fig. 9).

Of specimens having three and five canals there were by far the larger number, with the preponderance slightly in favor of the trimerous variety, but not sufficiently so to warrant any conclusions as to the question whether the course of variation was toward a trimerous rather than a pentamerous condition. Of those with three canals there were twenty-one specimens, while of those with five there were eighteen specimens. Of those making up the total of seventy-two specimens there were

twenty-five specimens from distinctly tetramerous forms, having short forks less than one-third the length of the entire canal, or of such other variable aspects as to warrant their inclusion under this head. Pl. II, Figs. 6-9, and Pl. III, Figs. 1-5, will best illustrate this point.

It now remains to consider somewhat more in detail the individual variations exhibited by these several types. Directing attention first to those illustrated by the figures just cited, it may be seen that the variation here seems to be in several

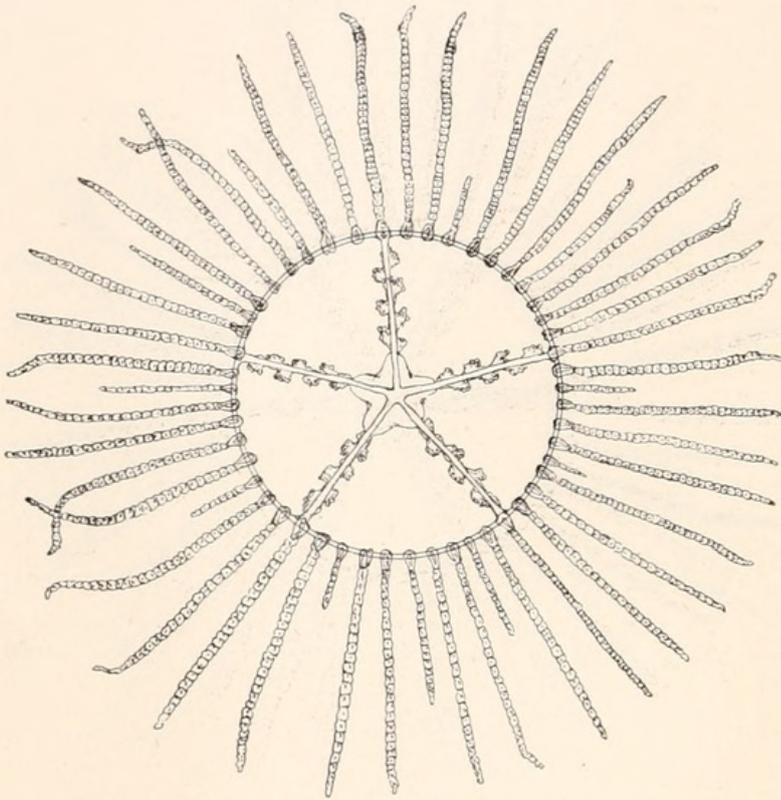


FIG. 10. — Symmetrically pentamerous specimen, but with the several series of tentacles appearing at irregular intervals.

directions. (1) Atrophy, as shown in Pl. II, Figs. 4, 6, 8, and 9. In all these the evidences of degeneration are quite clear. First, in Figs. 6 and 9 there is the atrophy of the connection of one of the canals with the gastric pouch and the correlated reduction of the fourth gastric pouch and the further failure of the obsolescent canal to develop its usual gonad, the merest rudiments of which are apparent. Furthermore, in the same figure there is shown a still further atrophy of a second canal, which extends only about halfway to the margin, and correlated with that fact is the associated imperfect development of its gonad. A still further illustration of this degenerative

tendency is shown in Pl. III, Fig. 6, where only the vestige of the fourth canal is shown, the reduction in extent of two others, with the further correlation of the evidently bilobed condition of the gastric pouch.

(2) Asymmetry. This is more or less consequent upon the atrophy already noted, as will be seen from a comparison of the figures just cited, and involves to a certain degree the entire organism, gastric and oral symmetry, no less than that of the

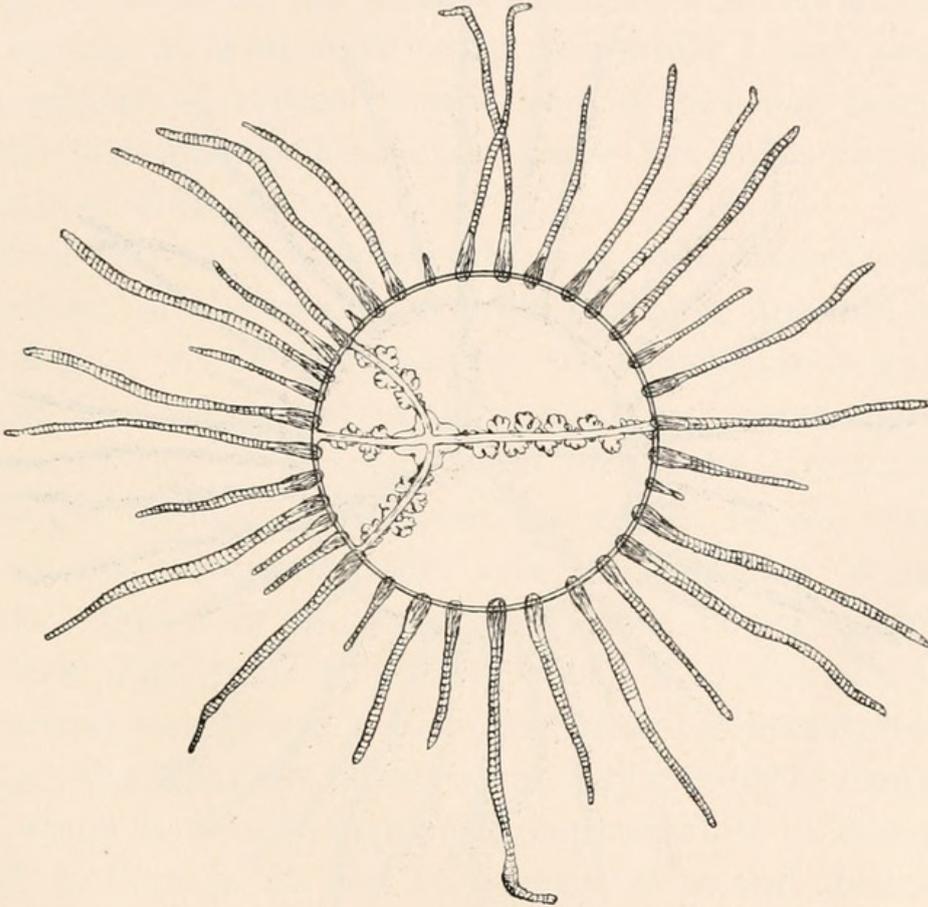


FIG. 11. — Tetramerous specimen of very unsymmetrical type.

bell and tentacles. Some further reflections on these lines will more naturally come up in connection with later discussions.

Another type of variation is shown in Pl. III, Figs. 1-5. In these specimens, while the tetramerous type is more or less evident from the number of canals, gonads, or gastric pouches, still there is a rather definite tendency toward a trimerous aspect of the medusa as a whole, so far as the segmentation of the body is concerned. In Fig. 1, while there is a clearly tetramerous condition exhibited which extends to the several organs involved, there is yet such an approximation of those

marked *a* and *b* as to leave the bell and number of tentacles in a closely trimerous symmetry. In Figs. 3–5 this evolution of trimerism is so evident that it would seem to point toward a preponderance of variation in this direction. As, however, will be seen later, facts of a very different kind seem to point as clearly in the opposite direction. It may as well be pointed out in this connection that the loopings of canals shown in the figures under consideration are variously simulated by

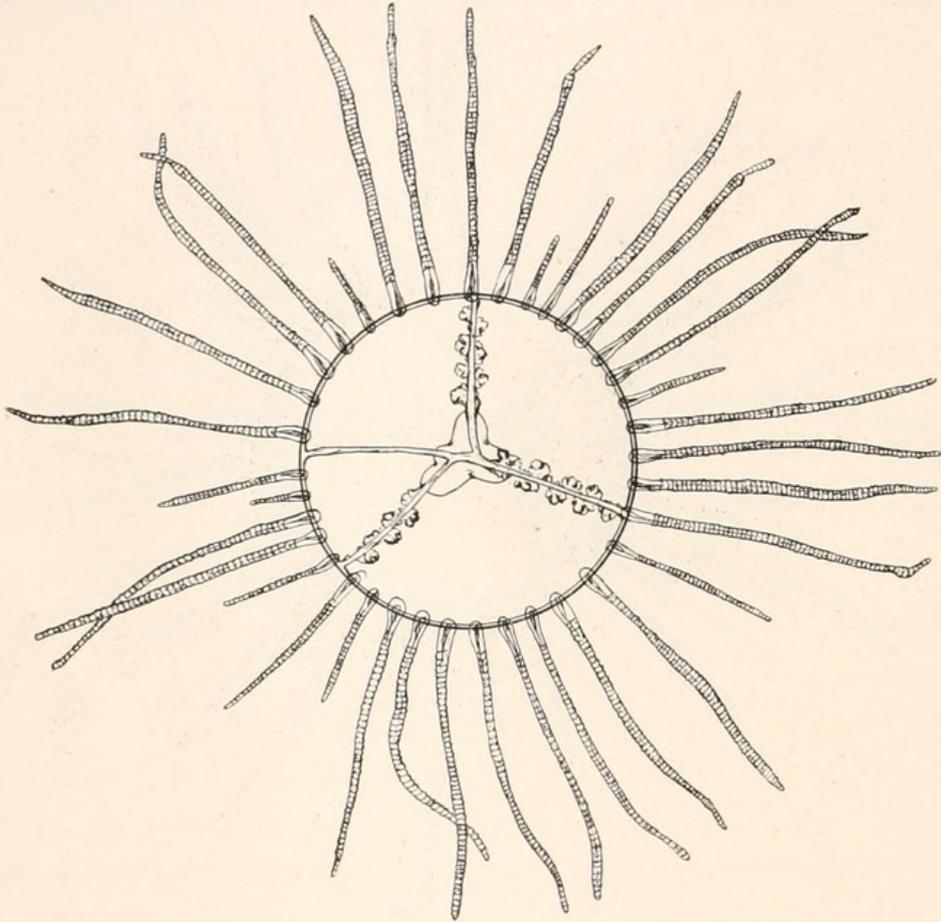


FIG. 12. — Specimen of very unsymmetrical character.

structures shown in Pl. II, Figs. 1–4, and 10. A critical comparison however, while showing many unusual features in these latter structures, will probably demonstrate their fundamental likeness; but this will be considered later.

We may next consider a type of variation fairly illustrated by Pl. III, Figs. 9 and 11. As will be seen from a glance, there is here exhibited a clearly defined tendency toward an increase in the number of canals, hardly less marked than that of decrease just considered. Indeed, specimens with bifurcated canals of this character were rather more common than those

of the last type, a fact, when taken in connection with the closely similar number of distinctly pentamerous forms, of great importance as showing that in neither case are we warranted in concluding that the course of variation is in one direction rather than in another. In order to reach anything approximating conclusiveness on this point a larger number of specimens studied through a successive series of years would be necessary. As I have already intimated, the collections forming the basis of the present discussion of this genus were made during at least four years, and while I have not made this a matter of critical comparison, it has not been at all apparent that during this period there has been any appreciable ratio of difference.

Passing now to the consideration of other aspects of variation evident in the canals, attention is next directed to their morphology. As is well known, the chymiferous canals in medusae are tubular structures of fairly constant size in members of the same species and of similar sizes, and their courses are usually direct from the center to the margin in most of the Hydromedusae. As Agassiz and Woodworth ('96) have shown in the case of *Eucope*, however, there are not a few departures from this rule. The same is true of *Gonionemus*, as a glance at Pls. I and II will demonstrate. Not only does the diameter of the canal vary greatly in many specimens, which is of only incidental concern, but in many cases, as in Pl. I, Figs. 9, 11, and 12, various loops and diverticula in the form of spurs are formed at various points and at various angles along their course. These are of varying sizes, lengths, etc., and were found on between one and two per cent of all the specimens examined. In the paper just cited the authors suggest in these facts a possible simulation of a condition "characteristic of the Discophores" (p. 122). Whether there is in these structures anything more than simulation or parallelism as compared with the Scyphomedusae, I shall not at present discuss.¹ As compared with the typical canal, however,

¹ It may not be amiss, however, to state in this connection that in Rhematodes there is a much more evident correspondence or resemblance in this matter than in either *Gonionemus* or *Eucope*. While possessing a large number of

there seems to me to be little doubt that they are fundamentally of similar origin and function. While in many cases there are extremely small serrations of the canal walls, in other cases (Pl. I, Figs. 1 and 2 ; Pl. III, Figs. 4 and 5) they are more prominent, even occasionally forming anastomosing connections between adjacent canals. Similarly the loops already referred to are probably in most cases anastomosed spurs.

An examination of the several figures of Pls. I-III will bring to the attention some interesting and rather anomalous illustrations of another phase of the structures under consideration. As will be seen, there is here almost every degree of intergradation between the perfectly symmetrical cruciform aboral junction of the chymiferous canals and the perfectly circular canal about the base of the gastric pouch into which the radials connect before their connection with the gastric cavity. By careful injections through the radial canals I have clearly demonstrated a direct continuity of the chymiferous system throughout these several channels. Little doubt can therefore remain concerning the fundamentally similar character of these various structures. Nor is it more doubtful that in function they are fundamentally similar; and while concerning the question of their significance in relation to the affinities of the Hydro- and Scyphomedusae there may be room for wide difference of view, that they serve similar functions in both is highly probable, if not quite certain.

In passing to the consideration of a specimen of unusual form, it should be noted that in the origin of spurs, extra canals, etc., they were with very slight exceptions, which seem to me easily explained, centrifugal, *i.e.*, from the central toward the peripheral portions of the body. The apparent exceptions are shown in Pl. II, Figs. 4 and 7, where portions of canals extend from the margin toward the center. As will be noted, however, there are in both cases spurs from the central region in the line of the peripheral branches which would strongly

radial canals, many of them show bifurcations toward the margin, and in not a few cases are there found centripetally developing canals similar to those of *Carolina*. This medusa likewise shows many other phases of variation, spurs, anastomoses, etc., of canals, but no details will be undertaken in this connection.

suggest that there had been complete unions of these partial canals at an earlier stage and that the present condition was the result of atrophy such as is shown in Figs. 6 and 9. It would seem therefore quite just to conclude that these several structures, spurs, partial canals, loops, etc., have had their development usually from the central pouches or canals and not from the peripheral or marginal canal.

The unusual specimen, to which reference is made in this connection, is shown in Fig. 13 of the text. It would appear to partake somewhat of the nature of a monstrosity and in some respects of the nature of a marginal bud, suggestive of a secondary medusa. Aside from the general form there is little to confirm this possibility; there is no sign of manubrium; and the canals and tentacles are quite continuous with those of the primary medusa. As will be noted, there are vestiges of gonads upon the peripheral termination of the median canal, while the branches are wholly devoid of any signs of such structures. Only a single specimen of this character was found and it exhibits another aspect of erratic variation.

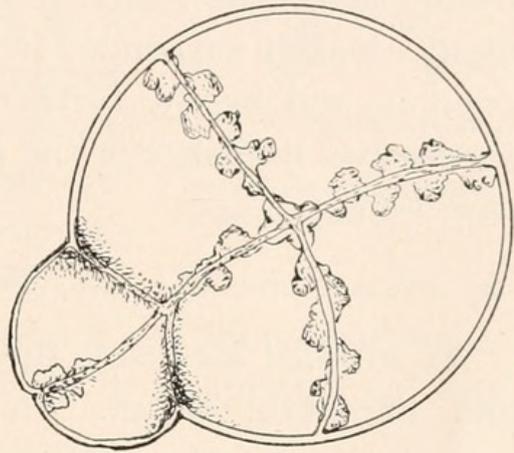


FIG. 13.

Gonads.

In the comparisons of gonads only specimens apparently sexually mature were taken (as noted before, no distinction was made between sexes). In the cases wholly devoid of gonads the size and other organic conditions were considered as sufficient to warrant the conclusion that they were probably of such age and general development as are usually correlated with perfect sexual maturity. In the whole number of specimens examined 3.6 per cent showed numerical variation of the gonads; of specimens with less than the normal number, two per cent; of those with more than the normal, 1.2 per cent; of specimens without trace of gonads, .4 per cent. As will be

seen in comparing these ratios with those concerning the radial canals, there is here again a slight tendency toward the smaller or trimerous forms, though not specially marked, especially when account is taken of the fact that only on specimens with more than the normal canals would additional gonads be found, while it was not rare to find in tetramerous forms specimens with only three gonads, or even less, one tetramerous specimen having a single gonad. Concerning variations of the several gonads of individual specimens no account was taken, owing to the difficulty of determining relative differences in organs loosely suspended in sinuous folds, as are these in *Goni-nemus*, and by the further fact of the continued growth and successive discharge of the sexual products, as seems to be the case here.

Manubrium.

As in most medusae, the manubrium is a rather prominent and important organ. In correlation with the tetramerous organization of the medusa, the manubrium, including in this general term the basal gastric pouch and oral opening and lobes, is of similar form and adjustment. As will be noted, however, by a comparison of the several tables, there are many exceptions, or, in other words, considerable variation. In most cases, however, as comparison will show, there is in the variation an obvious correlation with other variations, notably with that involving the radial canals. But here again the exceptions are sufficiently numerous to warrant the conclusion that there is in this organ itself individual variation, apparently devoid of any adaptive end or relation.

Aside from the facts of meristic nature above noted, there are features of variation which would seem to be of a purely substantive character. For example, in several specimens the manubrium was greatly extended lengthwise, reaching in some cases quite beyond the velum, occasionally as much as one-fourth its total length. While of course this organ is very extensile, yet in many hundreds of specimens examined alive, in many cases while the animal was engaged in engulfing food, I have never seen the manubrium extended beyond the velum.

While no emphasis is placed on this feature of variation, it is yet worthy of note in comparison with such medusae as *Coryne*, *Dipurena*, etc., in which the greatly elongated manubrium feature is rather distinctive.

In Fig. 14 is shown an interesting and anomalous feature which is more or less monstrous, namely, a spike-like growth from one side of the basal portion of the manubrium. While in some respects it might be comparable with an oral tentacle of *Margelis* or *Nemopsis*, still only in a somewhat remote way. It was rather rigid, yet devoid of any chitinous or other rigid support. As will be seen, it has the form of an elongate, attenuate process, about twice the length of the manubrium. It would seem, as suggested above, to be a wholly unique if not anomalous structure, without evident correlation with, or adaptation to, any other organ or function.

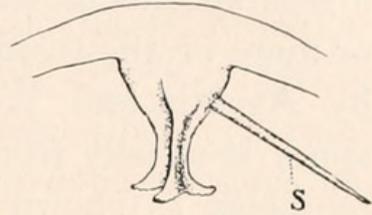


FIG. 14. — Semidiagrammatic sketch of manubrium of medusa showing anomalous projecting spur, *S*.

Tentacles.

As compared with *Eucope*, *Obelia*, *Podocoryne*, and many other genera, there seems to be a very different order and relationship among the tentacles of *Gonionemus*. In the smallest specimen measured the diameter was but 2 mm., and the number of tentacles twenty-nine. The largest specimen found measured 19 mm., and the number of tentacles was sixty-eight. That mere size is not, however, determinant of numbers will be seen when it is stated that a specimen measuring 4 mm. had thirty-nine tentacles, while one measuring 6 mm. had but thirty. While, as stated above, the largest measured specimen had sixty-eight tentacles, two others measuring 15 and 16 mm., respectively, had each seventy-two tentacles, and a specimen measuring 14 mm. had seventy-one tentacles. While it should be stated that these observations were made upon specimens preserved in formaldehyde, which may have thereby suffered some shrinkage, still since the preservative was in all cases the same medium and of the same, or very nearly the same, per cent, they would presumably be similarly affected.

However, the matter is not in any wise dependent upon data of this character. Even a glance at Figs. 9–12 will show, though diagrammatically, the relative number and distribution of the tentacles about the margin, while an inspection of the tables will show how very variable is this matter.

Bifurcation of tentacles, tentacular spurs, etc. — In all some fifteen specimens were found having variations involving one or more of the features indicated under this head. As noted by Agassiz and Woodworth ('96) in *Eucope*, the origin of spurs is usually from the base, as is also the doubling of the tentacles, as shown in Pl. IV, Figs. 2, 7, and 10. In several specimens there was an evident bifurcation of the terminal portion, as shown in Pl. IV, Figs. 5, 6, 8, and 9. In the specimens shown in Pl. IV, Fig. 6, this had occurred in close conjunction with the peculiar suctorial bulbs or pads so characteristic of this genus, while in Fig. 8 it is shown as having occurred somewhat proximal to these structures. A single specimen was found having three of these organs on a given tentacle at considerable intervals. In several specimens the tentacular pads or bulbs associated with the bases of the tentacles exhibited peculiar cordate lobings, sometimes on the outer border, more frequently on the inner edge, or from both, as if about to divide, though in no case was division found to be complete in a given bulb. However, this feature will acquire some significance in relation to the double and triple tentacles shown in Fig. 2, where the pads are correspondingly double and triple.

As compared with the specimens of Figs. 7 and 10, however, there will be seen no such correlation,—a fact which would suggest a measure of caution concerning the possible relation of the apparent division of the basal pads and the doubling of tentacles. This caution is further emphasized by the fact that in their origin new tentacles appear wholly apart from these pads, which only after some time are gradually developed on their ventral bases.

I am unable to agree with Agassiz and Woodworth (*op cit.*, p. 139) that these double and triple tentacles are due to coalescence of the bases. Whatever may be the case with *Eucope*,

TABLE I. — TETRAMEROUS SPECIMENS.

RADIAL CANALS.	GONADS.	GASTRIC LOBES.	ORAL LOBES.	TENTACLES.
4	4	4	4	12, 12, 12, 12.
4	4	4	4	12, 12, 15, 16.
4	4	4	4	17, 15, 14, 5.
4	4	4	4	15, 14, 14, 14.
4	4	4	4	12, 11, 13, 13.
4	3	3	3	20, 18, 10, 13.
4	4	4	4	10, 10, 11, 8.
4	4	4	4	16, 15, 17, 17.
4	4	4	4	14, 12, 12, 11.
4	4	4	4	16, 16, 16, 16.
4	4	4	4	14, 14, 14, 14.
4	4	4	4	15, 15, 15, 15.
4	4	4	4	14, 14, 14, 14.
4	4	4	4	12, 12, 12, 8.
4	4	4	4	17, 17, 21, 14.
4	4	4	4	17, 17, 19, 17.
4	4	4	4	16, 16, 16, 16.
4	4	4	4	11, 11, 11, 11.
4	4	4	3	15, 15, 16, 16.
4	4	4	4	12, 11, 12, 10.
4	4	4	4	13, 12, 12, 11.
4	4	4	4	16, 13, 15, 14.
4	4	4	4	15, 15, 15, 15.
4	3	4	4	13, 13, 10, 9.
4	4	4	4	13, 11, 12, 12.
4	4	4	4	11, 11, 11, 11.
4	4	4	4	12, 10, 11, 11.
4	4	4	4	13, 14, 14, 13.
4	4	4	4	17, 17, 17, 15.
4	4	4	4	14, 14, 14, 14.
4	4	4	4	15, 16, 14, 15.
4	4	4	4	16, 15, 16, 14.
4	3	3	3	12, 11, 8, 4.
4	4	3	3	11, 12, 11, 11.
4	4	4	4	12, 12, 13, 13.
4	4	5	5	21, 13, 13, 14.
4	4	4	4	11, 14, 11, 7.
4	4	4	4	14, 14, 13, 17.
4	3	4	4	14, 15, 14, 9.

TABLE II.

RADIAL CANALS.	GONADS.	GASTRIC LOBES.	ORAL LOBES.	TENTACLES.
3	3	3	3	14, 20, 22.
3	3	3	3	14, 19, 19.
3	3	3	3	20, 21, 21.
3	3	3	3	16, 20, 22.
3	3	3	3	14, 18, 24.
3	3	3	3	15, 15, 17.
3	3	2	2	13, 17, 24.
3	3	3	3	12, 15, 18.
3	3	3	3	13, 15, 18.
3	3	3	3	12, 12, 21.
3	3	4	4	13, 14, 18.
3	3	3	3	15, 15, 16.
3	3	3	5	15, 17, 23.
*4	4	4	4	9, 13, 16.
*4	4	4	4	15, 15, 17.
5	5	4	4	11, 12, 14, 17, 18.
5	4	4	4	8, 12, 14, 15, 16.
5	5	5	5	7, 8, 9, 10, 11.
5	5	4	4	11, 9, 9, 11, 8.
5	5	3	3	4, 9, 11, 9, 15.
5	5	4	4	12, 10, 7, 8, 13.
5	5	5	5	12, 11, 11, 7, 11.
5	5	4	4	12, 10, 10, 11, 11.
5	5	4	4	11, 7, 9, 9, 11.
5	5	5	5	8, 9, 7, 9, 8.
5	5	4	4	6, 10, 14, 12, 10.
5	5	5	5	11, 13, 9, 10, 11.
5	5	5	5	8, 9, 15, 17, 16.
5	5	4	4	11, 10, 13, 13, 13.
6	6	5	5	6, 5, 6, 6, 6, 6.
6	6	4	4	7, 9, 8, 12, 18, 9.
6	6	6	5	7, 9, 8, 6, 4, 8.
6	6	6	5	7, 11, 7, 8, 9, 5.
6	6	5	5	11, 4, 9, 7, 7, 12.

* While in these specimens four canals were present, two in each were so closely approximated as to divide the bell into trimerous sectors.

with *Gonionemus* all the facts would seem to point to their independent origin, in many cases the tentacles being of conspicuously different sizes, and in others exhibiting all phases of intermediate conditions between the simple bifurcation of the terminal portion through the budding of a smaller tentacle from the side of the larger, on to the symmetrical double tentacles as shown in Figs. 3, 4, and 10.

In only one case was a trifid tentacle found. This is shown in Pl. IV, Fig. 9. However, while a trifid structure there seems to be a degeneration of the median lobe, which was in all probability the terminal portion of what was originally a normal tentacle, from which later were budded the two lateral shoots, each in turn becoming more prominent than the median tip and developing in the appropriate places the characteristic suctorial pads. The degenerating middle tip would very naturally suggest the probability that an injury might have been the predisposing cause of the secondary tips; on the other hand, it must not be overlooked that in each of the other specimens with double tips no such cause seems at all evident. I am inclined to consider the cases as simply the expression of the intrinsic capabilities of variation, more or less evident in the several classes of organs already considered.

As yet no reference has been made to the order in which second, third, and subsequent series of tentacles arise. *Gonionemus*, unlike *Eucope*, seems to have no such association of tentacle and sensory bulb as serves to locate in part the primary set of tentacles and the order of appearance of the subsequent series. While usually there is a single primary tentacle at the terminus of each radial canal, this is not invariably the case. An inspection of Figs. 9-12 will show that there may be a very wide range of variation in this respect. The following data, taken at random from many observations, will further illustrate the same general fact.

TABLE III.

Showing the number and order of succession of tentacles of three series, counted from a primary set at some arbitrary point, as a radial canal. The large figure gives the number of any given series occurring together, while the small exponent figure indicates the series concerned, *viz.*, primary, secondary, or tertiary.

- A. 2¹, 1², 1¹, 1³, 1¹, 1², 3¹, 1³, 4¹, 2³, 2¹, 1³, 1¹, 1³, 4¹, 1², 6¹, 1², 1¹, 1², 2¹, 1², 4¹, 1³, 4¹.
- B. 2¹, 1³, 1², 4¹, 1³, 4¹, 1², 8¹, 1³, 1², 1³, 2¹, 1³, 1², 4¹, 1³, 2¹.
- C. 1¹, 1², 1³, 2¹, 1², 1¹, 1², 1¹, 2², 1³, 1¹, 2³, 1¹, 1², 2¹, 1², 1¹, 1², 1¹, 1³, 1¹, 1², 1³, 2¹, 1², 3¹, 1², 1¹.
- D. 3¹, 1², 1¹, 1³, 3¹, 1², 1¹, 1³, 5¹, 1², 3¹, 1², 1¹, 1³, 5¹, 1², 3¹, 1², 1¹, 1³.
- E. 4¹, 1³, 1¹, 1², 1³, 1¹, 1², 3¹, 1², 3¹, 1³, 3¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1³, 3¹, 1³, 2¹, 1², 1¹, 1², 1¹, 1³, 1¹, 1².
- F. 1¹, 1², 1¹, 1², 1¹, 1³, 1¹, 1², 1¹, 1³, 1¹, 1², 1¹, 1³, 1², 1¹, 1³, 1¹, 1³, 2¹, 1³, 1¹, 1³, 5¹, 1³, 1¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1², 1¹, 1³, 1¹, 1², 1¹, 1³.
- G. 1¹, 1², 1¹, 1², 1¹, 1³, 1², 1¹, 1³, 1¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1³, 1¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1³, 1¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1³, 1¹, 1², 2¹, 1³, 2¹, 1³.
- H. 1¹, 1³, 2¹, 1², 2¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 1¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1³, 1¹, 1², 1¹, 1³, 3¹, 1², 1¹, 1³, 1¹, 1², 1¹, 1², 1¹, 1³, 2¹, 1², 2¹, 1³, 1¹, 1³, 2¹, 1², 1¹, 1³.
- I. 3¹, 1², 2¹, 1³, 1¹, 1³, 2¹, 1², 1¹, 1³, 2¹, 1², 1¹, 1², 2¹, 1³, 1¹, 1³, 1¹, 1³, 1¹, 1³, 1¹, 1³, 4¹, 1³, 3¹, 1², 1¹, 1³, 1¹, 1², 2¹, 1³, 6¹, 1³, 2¹, 1², 1¹, 1³, 1¹, 1³.

SUMMARY.

	PRIMARY.	SECONDARY.	TERTIARY.	TOTAL.
A.	35	6	7	48
B.	26	4	6	36
C.	18	11	6	35
D.	26	6	4	36
E.	29	8	8	45
F.	25	9	11	45
G.	29	9	12	50
H.	36	13	13	62
I.	39	7	14	60

As will be seen from these series of tabulated relations in the appearance of tentacles, there is apparently no order whatsoever. Compared with the Figs., *op cit.*, where is shown similar relation (not to say absence of relation), there can hardly be discerned any such thing as definite series or sets of tentacles arising in definite succession. On the contrary, new tentacles seem to arise wherever and whenever in the growth of

the bell the adequate marginal space becomes available. And the fact that this seems so variable would appear to warrant the inference that growth occurs at irregular intervals and areas over the body of the medusa. Might not this fact throw some light upon the marked unsymmetry of such forms as those shown in Figs. 10 and 11? This suggestion would seem to find some further support in the fact that very young specimens appear to be more constant in their symmetry than those more mature.

Otocysts.

In formalin specimens there is a degree of opacity induced, especially about the marginal area of the bell, which often renders difficult any satisfactory examination of these sensory bodies. Hence only a limited number of critical determinations on this point were made, but these were sufficient to show a degree of variation both in their number and arrangement quite as marked as in that of other organs.

Normally they should occur in somewhat symmetrical order between the bases of the tentacles. This, however, is rarely the case. There seems about the same variation in their occurrence and relations as in the case of the tentacles, though I was not able to discover that the latter had any determining influence upon them. In only a few cases have I been able to demonstrate the presence of more than a single otolith in a given cyst, and in no case more than two. On this point, however, the opacity above referred to, and the abundant pigment about the bases of the tentacular bulbs were material obstructions to such determinations, and suggest tentative conclusions. In matter of shape and size these organs present likewise considerable variation. Pl. IV, Fig. 1, presents the average aspect of form at *a*, while at *b* are shown forms not unusual but variant.

Summary and Review.

1. Variation among Hydromedusae is of wider extent than had been supposed.
2. Variation is much greater in some genera than in others.

3. Variation among Hydromedusae appears to be much less symmetrical and less definitely correlated than among Scyphomedusae.

4. Many phases of variation seem to be wholly devoid of any adaptive features or tendencies.

5. The ratio of variation is higher among the tentacles than among other organs, and in many species higher than in all other organs combined, — a feature which is perhaps the most conspicuous case of adaptation apparent in the entire series.

Among the earliest references to variation in Coelenterates is that of Ehrenberg ('37) relative to variation in Aurelia. Later, Romanes ('74-'76) took up the subject with much more detail, giving an extended account of the nature and extent of variation, particularly in Aurelia, in which he figures and describes many "monstrous forms of medusae" and points out interesting correlations of radial canals, gonads, tentacles, etc.

Within recent times these observations have been much extended, notably by Brown ('94), who distinguished more than two per cent.

Sorby ('94), Herdman ('94), and Unthank ('94) have each recorded many interesting facts of variation in this medusa.

In 1895 Brown still further extended his observations upon Aurelia, and in connection therewith undertook a comparison of a large number of the Ephyrae. He was able to distinguish no less than 22.6 per cent of numerical variation in tentaculocysts, a ratio very close to that earlier determined for adult Aurelia. The observations seemed to show upon the whole a tendency toward an increase in meristic characters.

Ballowitz ('98) records extended observations upon Aurelia, specially with reference to the gonads. While in general there was more or less correlation in the numerical variation of these organs with the actinal lobes, it was apparently less constant than had been claimed by earlier observers. The highest number noted was seven, while three was the minimal number. One specimen in particular, which he names *Ephyra abnormitat*, seems to be an unusual monstrosity, having a very large balloon-shaped body with a correspondingly large manubrium.

He explains it as probably due to an enormous expansion of the top of the Ephyra, thus forming the balloon-like body.

It may not be amiss in this connection to record observations of a similar character as to numerical variations upon the Aurelias of Woods Holl which quite confirm those cited.

Observations upon the Hydromedusae seem to have been heretofore quite limited. Those of Forbes ('48), Agassiz ('49), Hincks ('68), Romanes ('74-'76), Agassiz and Woodworth ('96), include all the more important observations which have come to my knowledge. The latter would seem to be about the only series made upon a large number of specimens with the purpose of ascertaining the extent and character of variation in a single genus.

SYRACUSE UNIVERSITY, September 1, 1900.

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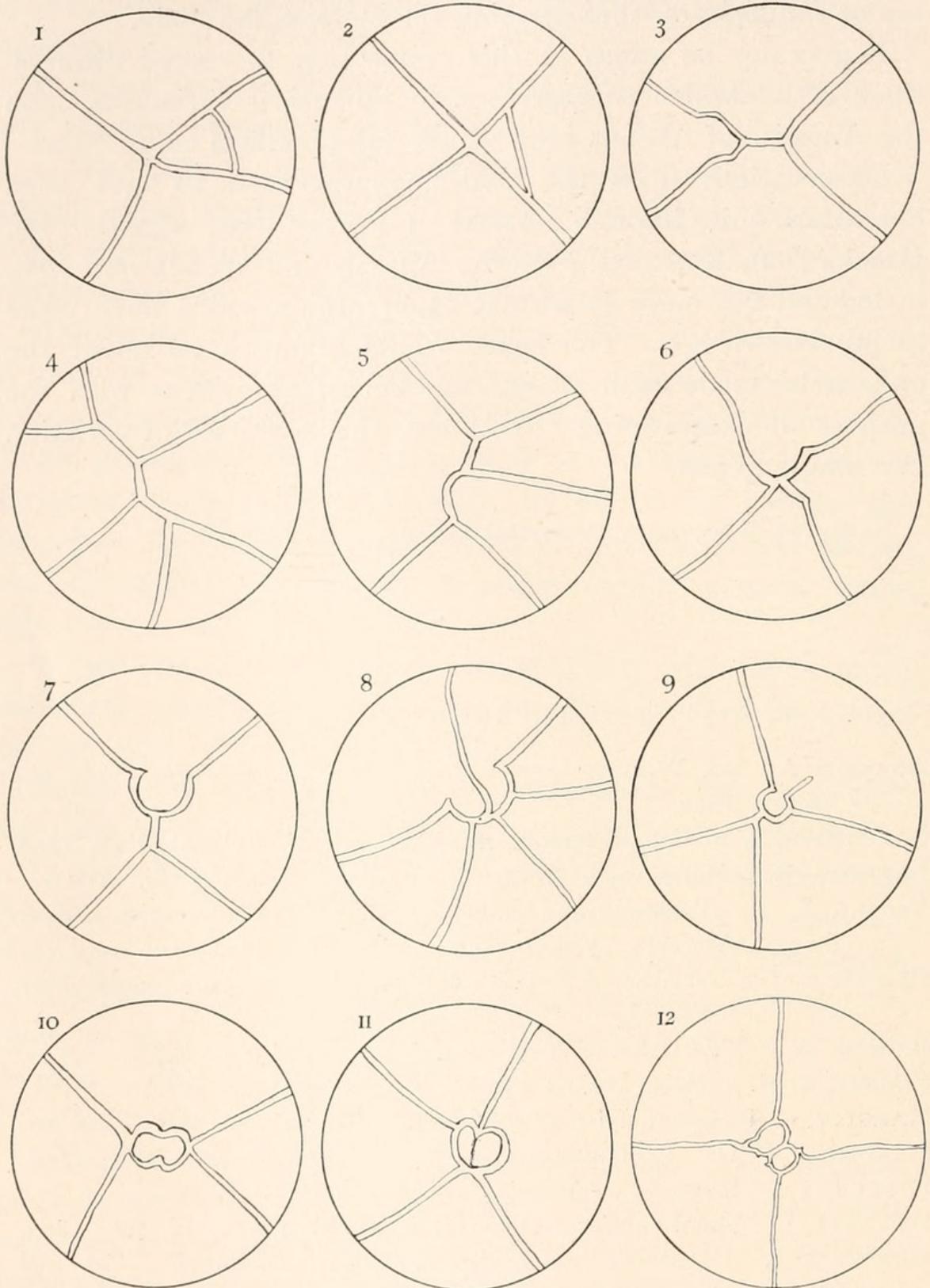


PLATE I. — Diagrammatic figures, illustrating variation in form, number, and arrangement of the radial canals.

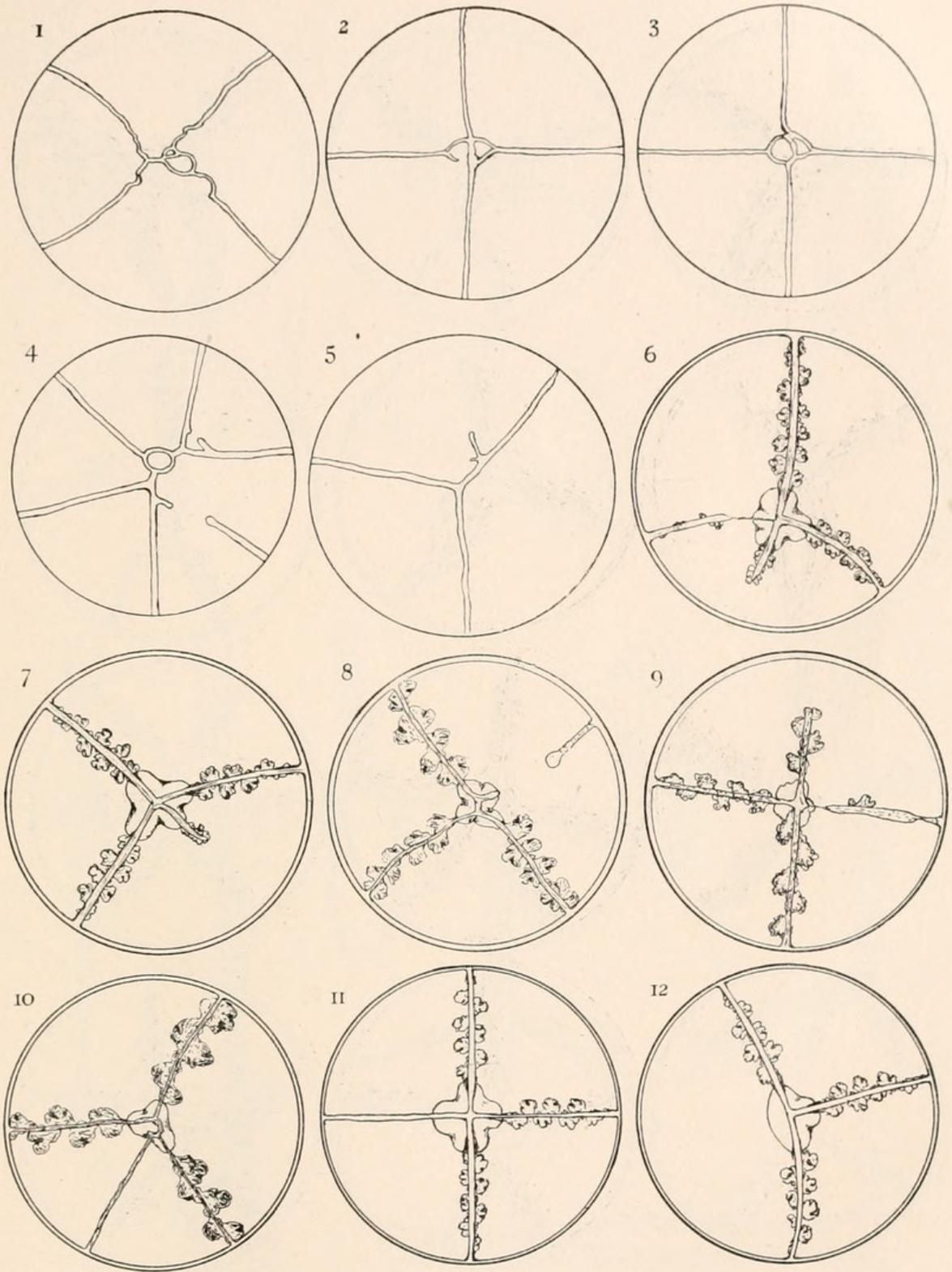


PLATE II. — Showing various phases of atrophy, spur-like branches, etc. of radial canals.

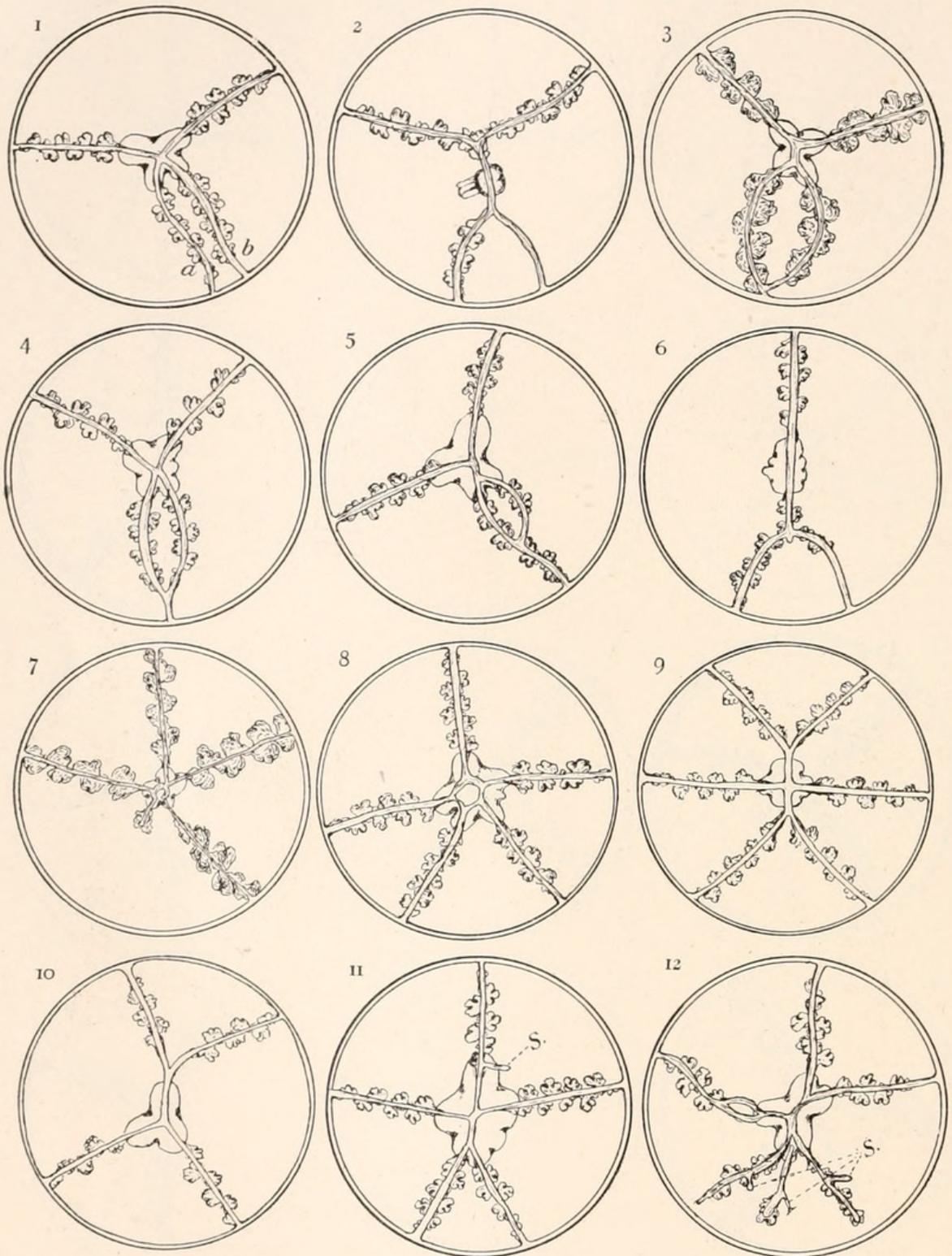


PLATE III. — Figs. 1-6 show varying phases in the evolution of trimerism. Figs. 11 and 12 show at *S* the development of spurs.

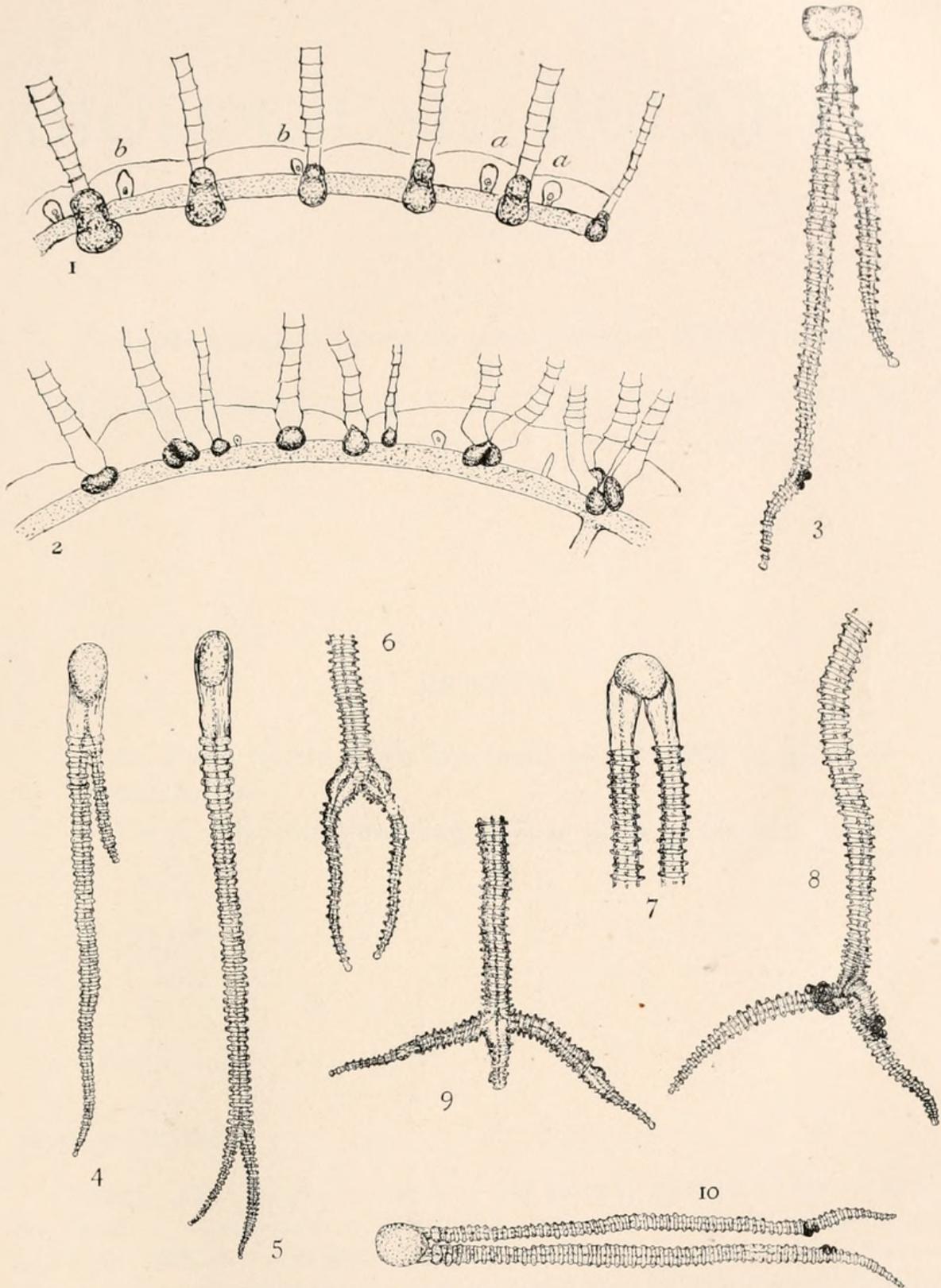


PLATE IV. — Fig. 1, *a, a*, normal: *b, b*, variable forms of otocysts. Fig. 2 showing variation in tentacles. Figs. 3-10 show various phases in forking or budding of tentacles.



Hargitt, Charles W. 1901. "VARIATION AMONG HYDROMEDUSAE." *The Biological bulletin* 2, 221–255. <https://doi.org/10.2307/1535717>.

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