GERM CELLS OF COELENTERATES

V. EUDENDRIUM RAMOSUM

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NINETEEN FIGURES

1. INTRODUCTION

In this series of studies forms have been considered which showed some differences in origin, growth, and ripening of the germ cells, or which were taken as types of certain taxonomic groups. It has been found that the different types of coelenterates do not necessarily show distinctions with respect to their germ cells, but may, on the contrary, be essentially alike. The study of Eudendrium was undertaken, not as a type of some morphological group, but because of certain obvious, though more or less superficial, peculiarities in the history of its germ cells, and in particular with the egg cells.

Whatever may have been found to be the ultimate method and place of origin of the egg cells in most of the forms studied, a cursory examination would usually show the egg cells to be first observable in the reproductive bodies, whether they were gonophores or medusae. In Eudendrium this is not the case. No doubt most zoologists who have examined this hydroid, or have made use of it for class work, have noted the presence of egg cells in the stem or branches, even when there were no reproductive bodies in that neighborhood. Such a condition is a common and rather striking feature of Eudendrium and might indicate some peculiarity of the germ-cell history. It is also true that the history of the egg cells in Eudendrium has been discussed rather widely and certain phylogenetic implications made which have considerable theoretical importance. These considerations have led to a new study of the germ cells of this form, with a brief review of the work previously done.

Eudendrium is a common Tubularian hydroid of our Atlantic coast; it is also widely distributed in other parts of the world. The reproductive cells are developed within simple, more or less sac-like, gonophores which in the mature animals seem to have few, if any, of the characteristic structural features of polyps or of medusae. However, such gonophores (often called sporosacs) are commonly referred to in discussions and in text-books as degenerate medusae or medusoid buds, and it is this assumption of the degenerate medusoid character of the gonophores which is mainly responsible for certain interpretations of the germ-cell history of Eudendrium which I believe are erroneous. It is only necessary to point out that the female gonophores, at least, arise from, and by the modification of, a hydranth or polyp which, in the beginning, resembles in structure other polyps of the colony. Since this may easily be demonstrated by a study of the developing reproductive bodies, it is manifestly quite incorrect to speak of the female gonophores of Eudendrium as medusoids, and any discussion, phylogenetic or otherwise, which proceeds upon such a basis is, of course, quite futile and meaningless. While I have not given the same attention to the method of formation of the male gonophores, it may be doubted whether these have any more of the medusoid character than do the female gonophores.

Ciamician ('78), studying *Eudendrium ramosum*, decided the egg cells arose from the ectoderm of the gonophore itself. His figures clearly show that he distinguished the egg cells only after they had become of some size, and his conclusions do not, therefore, touch the question of the real place and method of origin. Kleinenberg ('81) came to the conclusion that the egg cells arose in the ectoderm, passed into the entoderm, and migrated into the gonophore, where they again entered the ectoderm and completed their growth and development. Weismann ('83), in his study of *E. racemosum*, found egg cells in the ectoderm and entoderm, but, since those in the ectoderm were always smaller, concluded this layer was the place of origin. The region of the colony concerned in the formation of the eggs was the stem just below the terminal hydranths. He accounted for

this as the germinal zone, chiefly on account of the abundant food supply in a region so close to the polyps, thus calling attention to the essential relation between germ-cell formation and abundant nourishment. This region is also near the growing zone and the germ cells were believed to arise only from young cells. However, these young cells were regular ectoderm cells and not a special kind of cell, for he says:

One can say positively, that the same small egg cells] are visibly distinguishable in no way from other young ectoderm cells, for one can always recognize the place at which later a germ zone will form and can demonstrate that in that place are no cells which could be so designated [as germ cells]. The germ cells are therefore not in this case definitely contained in the colony from the beginning and differentiated only at the time of sexual maturity, but they arise only at this time out of a growing mass of young cells.

This essential relation between the origin of germ cells and an abundant food supply so positively stated by Weismann and since then abundantly confirmed by other authors, he did not maintain in later publications. In like manner, his own observations and demonstrations upon the origin of the germ cells from the ordinary cells of the hydroid body, both of ectoderm and of entoderm, he later discarded in favor of a theoretical view that they came from a peculiar and self-perpetuating tissue or substance, the germ substance. Weismann studied other species of *Eudendrium*, notably *E. capillare*, in which he found egg cells only in the entoderm. Their origin and growth, he says, must therefore be from and in the entoderm alone, "since it is inconceivable, that otherwise one should never find egg cells in the ectoderm."

C. W. Hargitt ('04) studied several species of *Eudendrium*. He found the egg cells of *E. racemosum* both in ectoderm and entoderm, but believed the entoderm to be the place of origin, since it contained the smaller cells. The same was true for *E. dispar* and *E. ramosum*. Weismann's account for *E. capillare* was entirely confirmed, viz., that egg cells were found always and only in the entoderm, and a similar condition existed in *E. tenue*. This author finds that "the ova arise in hydroids by

differentiation of cells of either one or both the entoderm and ectoderm." Growth takes place in the position where they are formed through the nutritive activities of surrounding cells, and a migration toward the gonophore region is also characteristic. It is suggested that the presence of germ cells in a certain region may act as a stimulus to the production of gonophores. Goette ('07), studying *E. rameum* and *E. racemosum*, found the smallest germ cells in the ectoderm, and he looks upon this as the seat of formation of germ cells in *Eudendrium*. From his work on various hydroids he is convinced that the place of origin of germ cells in these organisms is a varied one in different species or even in the same species; i.e., the germ cells may sometimes arise in the ectoderm and sometimes from the entoderm, even in the same species.

In regard to the formation of male germ cells, Ciamician ('78) believes the sperm mother cells arise by transformation of entoderm cells within the gonophore. It may be doubted whether his conclusions can be considered really to touch the matter of ultimate origin; his figures do not give this impression. Weismann ('83) is of the opinion that they arise not in the gonophore, but in the stalk of the hydroid and later migrate into the gonophore. He confirms Ciamician on their entodermal origin. Goette ('07) sees the ectoderm as the point from which the sperm cells as well as the egg cells come.

These are the chief papers dealing with the facts of germ-cell formation in *Eudendrium*. Other papers are found which discuss the facts without adding any observations or new facts. Weismann ('04) discusses *Eudendrium* and its germ cells along with other hydroids and here takes the positive ground, contrary to his own earlier brilliant observations, that the germ cells of *Eudendrium* and of all *Hydromedusae* arise in the ectoderm. This is apparently a necessary assumption for him, since his thesis of the distinctness and self-perpetuation of the germinal substance requires more constancy of germ-cell position than the observed facts present. The same hypothesis also involves germ-cell formation early in the development of the hydroid and an unbroken line of such cells up to the time of the

formation of the reproductive bodies. This part of the theory is established by making certain ontogenetic and phylogenetic implications concerning the degeneracy of the gonophores and the origin of germ cells in the stem and not in the gonophore. These implications are not firmly grounded upon fact.

This later theoretical position of Weismann is the one which has been generally accepted and is the position almost universally taken in text- and reference books and in general papers not dealing specifically with the subject of germ cells of coelenterates.

2. OBSERVATIONS UPON EGG CELLS

Study of entire stems. Examination of a stained and cleared portion of a female colony, such as is shown in figure 1, usually shows a number of deeply staining cells, some large and others small, scattered through the stem. The large cells appear as growing eggs and the small ones seem to be like them except in size. The impression gained from the study of such a preparation is that of a considerable number of egg cells scattered through the colony and widely distributed along the stems of the hydroid.

A detailed and careful study of these cells was made and their distribution plotted. About sixty slides, made by staining and mounting entire portions of different colonies made up of stems, branches, polyps, and gonophores, were examined. These observations demonstrated that the deeply staining cells were not universally distributed, but were more or less localized in certain regions, especially in the branches which come from the main stem of the hydroids. Figure 1 is a camera outline of a part of a colony in which the dots mark the position and relative size of the deeply staining cells. In all such preparations the hydrorhiza and main central stem of the hydroid showed no deeply staining cells, the bases of the branches arising from the main stem were likewise devoid of such cells, but further distalwards they were present, sometimes in considerable numbers. The pedicels of young lateral hydranths and of gonophores, as well as the distal and younger parts of the lateral branches even where hydranths and gonophores were absent, were the regions

in which these cells were most abundant. The cells, of varying sizes, were usually in groups, the largest cells always opposite the point of emergence of a branch which bore small hydranths or gonophores, while in the stem both distalwards and proximalwards the cells become smaller. The base of each hydranth or gonophore pedicel seems to be the center of a group of these cells, a condition suggesting their local origin. Where no gonophores are present these deeply staining cells may still be grouped at different places, but the larger cells in the center of such groups may be demonstrated to be at about the place where gonophores develop as the colony grows. In most groups of this character the cells are quite small, no large growing eggs appearing till the gonophore begins its development. On the other hand, where gonophores are forming or have formed, the adjacent group of deeply staining cells show numerous large cells and few small ones. The size and location of the deeply staining cells lead one to look upon them as egg cells, but it is essential to secure positive evidence on this point. If these are egg cells it must be further determined whether they arise in these positions or have reached them by a migration from a more or less distant point of origin.

Figure 2 is an outline of an optical section of the part of the stem shown at *A* in figure 1. While the difference in size of the deeply staining cells may not be especially significant, their difference in position is material. Those cells which extend from the supporting layer to the enteric cavity are gland cells, the deeper cells which do not reach the enteric cavity are egg cells. Figure 3 represents *B* of figure 1 and shows a number of egg cells all in the process of growth. Figure 4 is a similar drawing of region *C* of figure 1. Here most of the deeply staining cells do not touch the enteric cavity; the larger ones show all the characteristics of egg cells without any question, most of the smaller ones are also egg cells. Figure 5 is an optical section of a distal portion of a stem of the colony in a region devoid of gonophores or lateral branches and hydranths. So far as the staining is concerned, they are quite like the cells shown in figures 2 to 4, but most of them extend the full distance from

the supporting layer to the enteric cavity. In some (*gl*) the cytoplasm bordering the cavity stains differently than the deeper part of the cell; these are gland cells. Other cells do not extend to the cavity, and still others, while they extend to the enteric cavity, do not show such a differential staining capacity. Some of these are gland cells, while the interpretation of the others is uncertain.

The study of entire stems in optical section is necessary and very helpful in determining the number, size, shape, and distribution of the egg cells, but lack of sharpness in such preparations, especially with high powers, makes it impracticable to secure positive evidence concerning the finer details of structure of the smaller cells. Such evidence must be gained from the study of sections; this will be described very shortly.

A second problem possible of elucidation by the study of entire stems concerns the migration of germ cells. Weismann ('83, '04) claims the egg cells arise only at the distal end of the main stem and at the distal ends of the chief branches, from which points there are extended migrations into the gonophores. I do not understand this to mean that after a colony has become mature the germ cells begin to form from the young cells at the distal ends of branches and migrate throughout the colony to the gonophores, which are especially abundant toward the base of the colony. Such a migration does not occur, for the main stem and the basal ends of the larger branches are always devoid of egg cells, which could hardly be the case if egg cells moved from the distal ends of branches to the lower branches. Weismann states in his earlier works that egg cells may only migrate distally, never proximally, though the contrary is implied in the figures and descriptions of his later discussions (Weismann, '04, vol. 1, p. 414). I take it, rather, that he means the germ cells arise in the young parts of the colony, migrate toward the regions where gonophores are to be produced and upon their appearance the egg cells take their position in the gonophores.

The migration just outlined would not be very great in extent, and it is probable that some such movement takes place. The egg cells on the right of figure 4 are elongated as though

killed in the midst of an amoeba-like action. The mode of formation of the gonophore, however, suggests more of a passive transportation of the egg cells due to the growth of the stem and gonophore; this would be sufficient to account for a part of the translocation of these cells. Goette ('07) has pointed out the probability of this as a factor in the location of germ cells within the gonophores of other hydroids, and it seems to be significant here. Figure 6, an optical section of a very young gonophore rudiment, shows the point clearly. The hydranth which becomes entirely transformed into several gonophores is almost sessile as it first arises, but ultimately it has a long stem or pedicel. The growing point is in the stem below the hydranth, and any germ cells which might have been in the young rudiment would be pushed far away from the main stem in the growth of the hydranth stalk. At *A* in figure 1 and in the hydranth between *A* and *B* we have the region of formation of future gonophores. Germ cells are already present here in the stem, and when the tissues of the stem begin to evaginate to form the gonophores, the germ cells present would be carried outward during growth. This would account in part, but probably not entirely, for the presence of germ cells in the gonophores.

Some indirect evidence also bears on this same question of migration. It is very common to find the conditions shown in figure 4, where a stem contains large and small germ cells side by side. If there be a definite germ region and a definite path of migration, a section of any portion of the stem should contain germ cells of about the same size; the presence of large and small egg cells in the same region, therefore, may be taken as evidence of the formation of the small cells in that position. If the evidence is accepted, the large cells may be considered to have arisen in that same location and their shape is not indicative of migration. Other evidence is at hand which seems to suggest the formation of egg cells at various places, a growth in those positions and little or no migration. Figure 1 shows groups of cells all along the branches, some large and others small, each group centering about a lateral hydranth or gonophore. Such a condition is more consistent with the origin of

each such group of egg cells in that place than with a single germinal zone at some distance and later migration of eggs into the places of ripening and development.

One other point of general interest comes from this study of entire stems or parts of colonies. At *A* in figure 1 there is a group of egg cells in the stem, the same is true in region *B*, and between the two is a hydranth whose stalk contains eggs. Gonophores are not present here, but these are regions where gonophores would have developed in the living colony. The evidence for this is easily obtained by a study of gonophore formation in different colonies. Probably the simplest explanation for such an arrangement is the suggestion of C. W. Hargitt ('04) that the presence of a group of egg cells may be the stimulus for the formation of the gonophore. So far as I have observed in *Eudendrium ramosum*, groups of germ cells are always present before a gonophore begins its development.

Study of sections. The study of stained and cleared portions of the colony gave a clear understanding of the relative position of egg cells in stems, hydranths, and gonophores, and of the numbers and sizes of egg cells, but did not permit a positive determination of the place and method of origin of such cells. It was also impossible to distinguish small egg cells and gland cells, since all deeply staining cells had much the same appearance. These difficulties should not obtain in sections, hence various parts of the colony were sectioned and studied.

A longitudinal section through the stem, just proximal to a terminal hydranth, is shown in figure 7, one-half the width of the section being represented. In the entoderm a typical egg cell which has undergone some growth is shown at *ov*, lying deep in the entoderm against the supporting layer and separated from the enteric cavity by entoderm cells. Its cytoplasm is composed of uniformly distributed granules, large and deeply stained; the nucleus is large, with a distinct nucleolus, and contains a relatively larger amount of chromatin than the regular entoderm cells. The chromatin is distributed chiefly about the nuclear membrane with a small amount forming a network in the nuclear sap. These characteristics are more or less applicable

to all egg cells until they become very large; the position of egg cells, deep in the tissues against the supporting layer, is also characteristic. Another egg cell, *ov*, quite similar, but staining less deeply, is present in the ectoderm. At *a* in the ectoderm are cells which differ in certain respects from other ectoderm cells, especially in a slightly more compact and deeper staining cytoplasm and in having a nucleus somewhat larger than nuclei of other ectoderm cells. If we may speak of these as primordial egg cells just arising from the interstitial cells of the ectoderm, it would suggest an ectodermal origin of egg cells in Eudendrium.

Figure 8—a continuation of the same stem shown in figure 7—shows at *ov* two small egg cells in the entoderm and none in the ectoderm. These show all the characteristics enumerated for the larger eggs just described. At various other places in the sections of the same stem similar cells are found, both in ectoderm and in entoderm. In the entoderm gland cells (fig. 7, *gl.*) might be mistaken for egg cells, but their shape and position differentiate them, even though the staining capacity is somewhat like that of egg cells. Many other cells from a similar portion of colonies, as well as from regions adjacent to hydranths and gonophores, showed these egg cells. The very large eggs were always in the entoderm, but as there were also small cells in the entoderm and some undoubted egg cells in the ectoderm which were larger than some in the entoderm, it is not possible merely on the basis of size to determine which layer is the seat of origin of the eggs.

Figure 9 is from a transverse section of a portion of a stem at the place of junction with the stalk of a hydranth and developing gonophores. In the entoderm is a very large growing egg and at *ov* in the ectoderm (lower right side of figure) is a small cell which has much the appearance of an oöcyte at the very beginning of its growth period. The deeply staining cytoplasm, the large, richly chromatic nucleus, the spireme or loop-like character of the chromatin, have every appearance of cells found in other coelenterates which were interpreted as some phase of synizesis or synapsis. This cell can hardly be an ectoderm cell in an ordinary division, since it is the only cell

in this region, either in ectoderm or entoderm, which has such an appearance; also it has certain obvious differences from all the adjacent ectoderm cells, and just as obvious resemblances to a young oöcyte. This cell is the only one found which presented such an appearance; neither in ectoderm nor entoderm of any of the material could a similar cell be discovered. One cell is not sufficient to warrant any conclusions with respect to the interpretation of this appearance, but in view of its similarity to such stages in *Campanularia*, *Clava*, *Aglantha*, and other coelenterates, it may possibly be of the same nature. A considerable amount of material was used, secured at slightly different times, and many sections made; just why the early stages so clearly demonstrated in other forms were so rare (or absent) in *Eudendrium* is not known. The material used showed in every case the beginning of gonophore formation, and it is possible this is too late to show the origin of egg cells, but from every colony younger portions devoid of gonophores were examined and one would expect the germ cells to be in an immature condition if they were present.

The place of origin of egg cells in this form cannot be positively determined from the material at hand, though I incline to the opinion that it is the ectoderm and that the small cell *ov* of figure 9 marks the earliest differentiation of such a cell. In this respect my observations confirm the belief of some workers and are opposed to those of others; but the place of origin is not, in my opinion, a matter of especial significance, and I agree with C. W. Hargitt ('04) and Goette ('07) that there may be variation in the place of formation of the germ cells in hydroids, perhaps even in the same species. The place of origin not having been demonstrated, the method of origin is likewise uncertain. In *Campanularia* and *Clava* the derivation of germ cells from the tissue cells was clear; the position of the smaller egg cells in *Eudendrium* resembles that of these other forms. Again one may have the suspicion that *Eudendrium* agrees in a general way with the method of germ-cell formation of those forms, but no more may be said on the evidence obtained from this study.

Growth of egg cells. Whatever may be the origin of the egg, it lies for the entire early period of its growth within the entoderm. An explanation for this is obvious, in such a position the egg is very close to the enteric canal with its circulating fluid from which the nutrient material is obtained for growth and for elaboration of reserve stuffs. Figures 3, 4, and 6 to 9, show the relation of growing eggs to the entoderm and enteric canal. Since the egg does not come into contact directly with the enteric cavity—entoderm cells always being interposed—it seems probable that these entoderm cells aid in nourishing the egg. After the oöcyte or young egg is formed and before it has begun to grow to any marked extent, it has the structure already described, viz., compact, granular, deeply staining cytoplasm with a large nucleus and nucleolus (figs. 7 and 8).

In the egg which has started its growth or in which a period of rapid growth is just initiated certain changes become noticeable; these are illustrated in figures 9 to 13, which represent a series of eggs of different stages of growth, all from the same general region of one colony. The eggs represented in figures 9 and 10 are from the stem of the hydroid close to a lateral branch which bears gonophores; they are just entering upon the period of rapid growth. The chromatin of their nuclei is in a more obvious network, the nucleolus more or less vacuolated, but sometimes homogeneous and without vacuoles (fig. 10), the cytoplasm not so dense as formerly, but still not alveolar, without yolk, but containing a scattered lot of prominent and intensely staining bodies. These bodies are of nuclear origin and are similar to the granules found in the cytoplasm of *Clava*, *Campanularia*, and *Aglantha*, which were derived from the chromatin of the nucleus.

While the egg is small these bodies are more or less scattered through the entire mass of the cytoplasm. When growth is well under way and proceeding rapidly, this extranuclear chromatin is massed close to the nucleus (fig. 11) and does not extend far into the cell body. This may indicate a rapid absorption of the material by the cytoplasm. The cytoplasm at such a period is more loosely arranged and shows a beginning of an

alveolar structure; the nucleus contains a more marked reticulum of chromatin, and the nucleolus is much vacuolated. Such an egg as that shown in figure 11 would be found in the pedicel or in the base of the hydranth which is producing gonophores. Figure 12 is an egg which has just reached the young developing gonophore, i.e., it is in almost its final position where it ripens and develops. The cytoplasm is noticeably alveolar, not deeply staining because of so loose a texture, and with a ring of chromatic granules close to the nucleus which is abundant enough to indicate considerable movement of nuclear substance into the cytoplasm. The nucleus does not differ from the earlier condition save for an increase in size and an increase in the amount of chromatin which results in a more marked reticulum.

The egg shown in figure 13 is located in the gonophore and is well started upon its growth, though not yet more than one-fifth of the final volume of a ripe egg. It differs from a mature egg mainly in size, the structure being quite similar. Large yolk spheres occupy most of the cytoplasm, the granular cytoplasm not being very abundant, while chromatin material is still passing from the nucleus in somewhat less abundance than formerly. The nuclear reticulum shows regions of concentration of chromatin at the nodes of the network, and a large vacuolated nucleolus similar to that of earlier stages is present, but not represented in figure 13. In later growth the changes from the above description are not great, yolk is produced to an enormous extent and the egg is loaded down with it. The nucleus probably does not change greatly, though it was not studied in the later growth phases. After the egg reaches the young gonophore the latter elongates, carrying the egg away from the hydranth and at the same time finger-like extensions of the stem surround the egg and supply nourishment to it during its later growth. The growth is completed, and maturation, fertilization, and development all take place within the gonophore, an embryo in the form of a planula finally escaping.

3. OBSERVATIONS UPON SPERM CELLS

Male gonophores are produced upon different colonies than the female gonophores and differ from them in appearance and somewhat in structure. So far as my observations go, I can confirm the conclusions of Weismann ('83) that the sperm cells of *Eudendrium* arise in the stem or stalk of the hydroid from entoderm cells and migrate into the gonophore. The growth of the gonophore also aids by passively carrying these cells into position.

A brief account of the formation of the gonophore is necessary in order clearly to understand the significance of germ-cell formation. The growing point of the hydroid is in the stem, immediately below the terminal hydranths where the cells are richly protoplasmic and the ectoderm and entoderm not differentiated into gland cells, nettling cells, and the like. The narrow, growing zone is followed proximally by the usual coenosarc tissue with its differentiated cells of various sorts, both in ectoderm and entoderm. Newly formed lateral hydranths and gonophores develop at a point some distance proximal to this growing zone and their origin may be recognized, before there is any actual new growth, by the change in the character of the cells. This recognizable change is the production of a new growing zone in the coenosarc at that point, and this involves a regressive change of the differentiated ectoderm and entoderm into the same small, richly protoplasmic cells which are found in the growing point of the main stem. After this change has occurred the perisarc opposite this group of cells is dissolved, an evagination of the coenosarc occurs and gradually a new structure is differentiated from this bud.

Thus in the production of gonophores as well as of hydranths, differentiated cells undergo a regressive change and after further growth once more becomes differentiated. There is no difficulty in demonstrating this typical method of growth in female as well as in male colonies. This is very significant, when it is also found that the male germ cells arise in the stem adjacent to the gonophore, apparently from regular entoderm cells. If active, growing, undifferentiated cells may, by differentiation,

become typically functional ectoderm and entoderm cells, then later undergo a regressive change and become typical growing cells which results in the formation of a new polyp after a later second differentiation, there is nothing strange in thinking of similar regressive changes of entoderm resulting in the formation of germ cells.

The earliest indication of cells clearly distinguishable as sperm mother-cells was found in the entoderm of the stem of the hydroid not far distant from the base of the pedicel of a developing gonophore. Figure 14 shows these cells in the entoderm, with rather deeply staining cytoplasm and large nuclei which contained a good deal of chromatin concentrated close along the nuclear membrane. A large nucleolus was present. These sperm mother-cells arise in relatively small groups deep in the entoderm, but whether by modification of entoderm cells or by division of entoderm cells could not be determined. Such cells divide rapidly to produce larger masses of spermatogonia (fig. 15) which may be so numerous as to extend in unbroken lines from the stem along the pedicel and into the developing gonophore. As the growth of the gonophore continues, most of these spermatogonia are found in the gonophore itself and fewer in the pedicels and stems. Mitotic divisions are abundant in all such groups of spermatogonia, whether in the stem, pedicel, or developing gonophore, but most abundantly in the cells within the gonophore.

As the gonophore first forms, the spermatogonia are in continuous rows of groups, as shown in figure 17, but as growth continues and the gonophore becomes more definitely formed, these cells are more distinctly massed (fig. 18), and there is an ultimate localization into distinct testis-like groups (fig. 19). The character of the spermatogonial cells of young developing gonophores is shown in figure 16. Divisions are taking place, some growth is evident, but all are of the stage of spermatogonia. At about this period the cells undergo a synzesis-like change and rapidly thereafter transform into spermatozoa.

4. SUMMARY

In female colonies of *Eudendrium* egg cells appear to be widely distributed, but careful examination demonstrates their presence only in the smaller branches. They are always in groups located near the gonophores or in regions where gonophores would have formed in the living colonies. The egg cells originate in such positions, probably by modification of ectoderm cells, but they pass into the entoderm, where early growth takes place. The location of the eggs in the gonophores is due in part, probably, to an active migration and in part to a passive translocation caused by the growth of the tissues which go to form the gonophore. An escape of nuclear material, probably of chromatic nature, into the cytoplasm is coincident with the onset of the growth period in the egg. In the male colonies sperm cells arise in the deeper portion of the stems adjacent to, or in the region of later formation of, gonophores.

The germ cells of *Eudendrium* have commonly been discussed as arising very early in the history of the hydroid from a distinct germinal tissue, and much later, at the time of maturity, migrating into the reproductive bodies which are conceived as degenerate medusoid buds. Observations do not substantiate any of these interpretations, since the germ cells arise from ectoderm or entoderm cells just previous to the development of the gonophores, and the gonophores are not degenerate medusae, but, in female colonies at least, develop by a modification of ordinary polyps. There is no apparent phylogenetic significance in the manner, place, or time of formation of the germ cells of *Eudendrium*.

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ABBREVIATIONS

a, possible egg cells
ec., ectoderm
gl., gland cells

ov., egg cells
pr., perisarc of the hydroid stem
sp., male germ cells

PLATE 1

EXPLANATION OF FIGURES

1 Portion of female colony showing method of branching, position of hydranths and of gonophores. The dots in the stems represent the position of egg cells. *A*, *B*, *C*, are the portions of the stem shown in figs. 2, 3, 4, respectively. $\times 11$.

2 Optical section of region *A*, fig. 1. The deeply staining cells in the entoderm include some egg cells and some gland cells. $\times 255$.

3 Optical section from region *B*, fig. 1. The deeply staining cells in the entoderm are egg cells. $\times 255$.

4 Optical section of stem from region *C*, fig. 1. Most of the shaded cells are egg cells. The presence of large and small eggs in the same region suggests their origin in this place; the shape of some eggs suggests a possible migration. $\times 255$.

5 Optical section through a stem near the distal end of a colony, a region devoid of gonophores. It is difficult to say which of the deeply staining cells are gland cells and which eggs. $\times 473$.

6 Optical section of stem and polyp, the latter becoming a gonophore. Egg cells present. $\times 150$.

PLATE 2

EXPLANATION OF FIGURES

7 Longitudinal section of stem just below a terminal hydranth. Growing egg cells, *ov.*, are present both in ectoderm and in entoderm. The cells in the ectoderm marked *a* may possibly be primitive egg cells. $\times 1010$.

8 Longitudinal section of the same stem as previous figure, showing two egg cells in the entoderm. Other similar cells are found both in ectoderm and in entoderm. $\times 1010$.

9 Transverse section of stem at junction with the pedicel of a gonophore, showing a large growing egg in the entoderm and a cell, *ov.*, in the ectoderm which is suggestive of the early formation of a primordial germ cell. $\times 1010$.

10 Growing egg cells from entoderm of stem. Nuclear material is passing into the cytoplasm. $\times 1765$.

11 Growing egg from the same colony as previous figure. Egg located in the entoderm at the base of the hydranth which bears the gonophores. Prominent collection of nuclear material in the cytoplasm near the nucleus; the cytoplasm is becoming slightly vacuolated. $\times 1765$.

PLATE 3

EXPLANATION OF FIGURES

12 Growing egg from a gonophore of the same colony as those of figures 10 and 11. Cytoplasm rather loose and somewhat alveolar with nuclear substance in the cytoplasm. $\times 1765$.

13 Larger egg from another gonophore of the same region as that of figure 12. The cytoplasm is filled with large yolk spheres, and the nuclear substance is still passing into the cytoplasm, though less abundantly than previously. A nucleolus is present in this egg, but was not shown in this section. $\times 1765$.

14 Male colony. Longitudinal section of stem below the pedicel of a gonophore, with a small group of germ cells in the entoderm. $\times 1010$.

15 Male. Longitudinal section of a stem just below the terminal hydranth and above a lateral branch which is forming gonophores. The entoderm contains a mass of cells, the deeper ones of which are primitive sperm cells. $\times 1010$.

16 Longitudinal section through a developing male gonophore showing a group of spermatogonia in the entoderm. $\times 1010$.

17 to 19 Longitudinal sections through developing male gonophores. The germ cells are shown in the pedicels and in the bodies, more or less scattered in figure 17, but becoming definitely localized in figure 19. $\times 255$.