Note on the Formation of the Skeleton in the Madreporaria.

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WITHIN the last few days there has been brought under my notice a short account by M. Armand Krempf[1] of the mode of origin of the calcareous skeleton in Madreporarian Corals.

M. Krempf, whose observations were made on a species of the genus "Seriatopora," writes as follows:

"It is easy to verify that the corallum ("polypier") of this animal, in conformity with the investigations of Heider, is formed by the imbrication of a multitude of small calcareous scales, themselves constituted by a small bundle of fibres of lime carbonate.

"I have been able, in addition, to demonstrate by means of a decalcification conducted with great caution, the substratum of organic matter in the midst of which the calcareous part of this scale has taken solid form.

"A very fine membrane limits each of these elements, tending thus to give it the physiognomy of a small cell. After suitable treatment of the fresh skeleton with decalcifying reagents, the whole of the delicate organic meshwork (trames agglomérées) forms a light translucent mass, similar to jelly and of extreme fragility.

[1] A. Krempf, "Sur la formation du squelette chez les Hexacoralliaires à polypier." Note by M. Armand Krempf, presented by M. Yves Delage ('Comptes Rendus,' 21st January, 1907).

"Thus there exists, contrary to the opinion of Gardiner (1900), who was not able to disclose it in his preparations, an organic substratum in the skeleton of the "Coralliaries."

"Contrary again to the opinion of Duerden (1904), who admits the existence of a fundamental substance, but who considers it as homogeneous, this substance has a histological constitution, well characterised, which realises all the appearances of a cellular structure.

"These facts much depreciate in value Koch's hypothesis of extracellular secretion. They seem to fully justify Heider, who considers the 'polypier' as formed by the accumulation of calcified cells.

"At the same time this is not so; the calcareous scales whose juxtaposition forms the corallum are not the skeletons of calicoblasts. They have not the value of cells."

Before proceeding further with M. Krempf's description a few remarks may be made regarding these preliminary statements.

The first statement that M. Krempf "finds it easy to verify that the skeletal parts are formed by the imbrication of a multitude of small calcareous scales" is a corroboration of observations which were unknown to zoologists previous to the publication of my work on the "Madreporaria."[1]

That paper for the first time gave a description and illustrative figures of the minute skeletal elements which everywhere compose the corallum. I described these elements as "calcareous scales," and showed the imbricated manner of their apposition with one another, and their various shapes and positions at different parts of the corallum (l. c., pp. 114, 115, 127; figs. 7 A—C; 8 A—C, etc.).

The references made by M. Krempf to von Heider's work are somewhat ambiguous, as they lead one to infer that von

[1] M. M. Ogilvie, "Microscopic and Systematic Study of Madreporarian Types of Corals," 'Phil. Trans. Roy. Soc.,' London, vol. 187 (1896), B, pp. 83—345. Also see my monograph on the "Stramberger Korallen" (Palæontographica, Stuttgart, 1897, Suppl. ii, No. 7, pp. 73—282, pls. vii—xviii).

Heider had deciphered this structure in 1881. Full references to the papers of von Heider and Koch are made in my work (l. c., pp. 91—97). Von Heider made a special study of the soft parts, and observed here and there certain cells in whose organic contents small groups of calcareous fibres were included, and the nuclei were either shrunken or vanished. To these cells he gave the name of "calicoblasts," and thought they occurred in the mesoderm, but must, in some way, accumulate to build the corallum. As I explained in my paper, Heider's surmise was that the individual skeletal parts in the Madreporaria were formed in a manner analogous with the skeleton of Alcyonarians, but that in the former the calicoblasts produced a solid structure at the outer limit of the mesoderm, whereas the analogous cells in the Alcyonarian polyp formed calcareous spicules, which remained isolated throughout the whole life of the polyp (l. c., p. 93, and cf. Heider, "Korallenstudien," 1886). Heider admitted he could not trace the connection between the groups of fibres as he observed them in cells of the embryonic skeletal disc, and the various complex structures of the mature skeleton.

Subsequent observers said that the cells referred to by von Heider were components of the ectodermal tissue, and that they never contained inorganic material as he depicted; that the calcareous material of the corallum was originally of the nature of a secretion thrown out by the cells of the ectoderm (ref. Ogilvie, 1896, l. c., pp. 101–2).

This was the position when my work was published by the Royal Society of London, and I there demonstrated that the whole corallum was composed of a series of calcareous lamellæ, each of which was primarily an organic tissue comprising innumerable minute cellular parts, in each of which lay a group of calcareous fibres. As these parts corresponded in appearance to the "calicoblast" described by von Heider, I applied this term and wrote: "Each lamina (average width ·003 to ·005 millim.) is a deposit of calicoblasts, the wavy outline corresponding to originally separate cells" (l. c., p. 123; pp. 114—117; etc.).

I demonstrated by descriptions and illustrations (p. 123, 124, 138; figs. 13, 14, 17, etc.) that several layers of calicoblasts were shed from the ectoderm of the polyp during each period of active growth, and that these adhered more closely with one another than with the previously or subsequently formed series of layers, yet that each layer was complete in itself; farther, that each individual calcifying part originally limited by organic walls (which I termed cell-walls), retained its individuality during its transformation into a "calcareous scale," and could be obtained apart from its neighbours as an individual entity.

It creates rather a confusion of ideas when M. Krempf implies that von Heider had held the view that the "calcareous scales" were the "skeletons of calicoblasts"—since von Heider was not aware that the "juxtaposition of calcareous scales formed the corallum," and he could not possibly have claimed for these skeletal elements, as I did, that they were transformed cell-products, and represented the "fibre-containing cells," which he had observed in the cellular tissue, and termed calicoblasts (cf. Ogilvie, l. c., p. 125).

The second part of M. Krempf's account in the 'Comptes Rendus' describes a series of observations which bear upon the relationship of the ectoderm to the layer of skeletal elements immediately external to it. Before quoting from M. Krempf, I shall indicate the direction followed in my investigations of this subject.

My sections of the soft parts corroborated the observations of Dr. Fowler and Dr. Bourne (cf. Ogilvie, l. c., pp. 101–2). Comparing my sections of the soft parts with my preparations from the corallum, I was able to observe farther that in these positions, such as the periphery of the calyx, which corresponded to the most closely nucleated and actively-dividing parts of the ectodermal tissue, the calcareous scales were most thickly piled in the corallum, and their organic remnants ("dark points") most closely grouped—sometimes in little rings, sometimes in rows.

"In all cases we have simply to do with centres and axes

of calcification, around which the calicoblasts are grouped in the living polyp, and from which, therefore, similarly oriented fibres ultimately radiate when complete calcification has taken place" (l. c., p. 128; refer to p. 133, fig. 18; p. 148, fig. 29, etc.).

The wider spacing or closer massing of the unit elements in the skeletal layer was thus shown to depend upon localisation of "centres of calcification" in the ectoderm, and the number produced in a single growth-period to be greatest where fissional activity was most marked in the ectodermal layer. Careful measurements conducted over many species farther showed that the size of the "calicoblast cells" in the ectoderm was the same as the size of the unit elements in the skeletal layer (p. 117, 136, etc.). Upon such grounds "I took the nuclear fission to be associated with the separation of the organic outer layer" containing the skeletal elements, and concluded that, in virtue of fissional processes in the cellular tissue of the ectoderm, calcifying calicoblasts were constantly being eliminated, and the vitality of the ectoderm itself renewed.

"The fibre-containing calicoblasts which lie next the skeleton are shed off, so to speak, from the polyp, new cells constantly taking their place in the ectoderm by cell-division" (Ogilvie, l. c., p. 102).

"At the beginning of any particular growth-period the calcification goes on only locally at certain points of the calicoblastic layer of the colony" (id., l. c., p. 131; cf. p. 143).

"The calicoblasts remain adherent to one another in dense groups or may be more uniformly distributed. And in this manner they are gradually left behind on the skeleton, and completely calcify, while active cell-division develops constantly new ectodermal cells. The calicoblasts adherent to the skeleton represent such as were already in course of losing living continuity with the polyp at the time when the polyp was removed from the skeleton" (id., l. c., p. 116).

"The scale-like arrangement on the surface presents irregularities—sometimes like thicker zones, sometimes thicker

patches. Those are doubtless due to irregular disposition of the calicoblasts, as they originally separate from the ectodermal polypal layer" (id., l. c., p. 116).

Mr. Duerden's work,[1] referred to by M. Krempf, brought the first confirmation of my description of the primarily organic nature of the layer external to the ectoderm in which the skeletal elements developed, but Mr. Duerden described it as homogeneous, and thought it took origin from the ectoderm probably by a process of secretion, and that the calcareous groups of fibres which made their appearance must be regarded as "ectoplastic" in origin. Against this I wrote as follows:

"On Mr. Duerden's interpretation, if I understand it aright, we are to believe that the exceedingly particular skeleton arises by a sort of crystallisation in an organic cuticular matrix produced by, but distinct from, the ectoderm. I still uphold my opinion, supported by remarkable correspondences of measurements, which cannot be mere coincidences, that the individual ectoderm cells or nuclear parts exert a determining individual influence on the origin of the lime-forming skeletal units (= "calicoblasts" in my work) in the cuticular product, which is, after all, a composite product from many ectodermal cells, and persists in retaining its originally particulate character." ('Quart. Journ. Micr. Sci.,' 1905.)

"Each individual lime-forming part or 'calicoblast' of the skeletal layer derived its origin from an ectoderm cell in virtue of divisional processes, part of the cell layer continuing as ectoderm, part being shed as the layer of calicoblasts" ('Quart. Journ. Micr. Sci.,' vol. 49, pt. 1, Oct., 1905, pp. 207, 208).

M. Krempf now recognises the distinct partitioning of the groups of calcareous fibres by organic strands, but says although these simulate cell-walls in their appearance, the contained

[1] J. E. Duerden, "The Coral Siderastraea radians and its Post-larval Development," Washington, U.S.A., publ. by Carnegie Institution, Dec., 1904.

portions have not morphologically the value of cells, as nuclei can only be shown to be present in some of them. The following is M. Krempf's description:

"In the ectoderm which carpets the skeleton, and which consists of a protoplasmic layer with scattered nuclei, in which it is somewhat difficult to define cellular limits, one sees the skeletal element appear in one place and another under the form of a small mass, readily stainable with nucleus dyes.

"It presents distinct fibrous structure. Its fibres, clearly individualised, are in general regularly parallel with one another and most often are disposed perpendicularly to the surface of the calicoblastic epithelium. Its shape varies according to the points of the skeleton where one observes it. Sometimes the shape is that of a small parallelepiped, fairly regular and flattened, sometimes it recalls that of a Lepidoptera scale, sometimes even that of a cup compressed parallel with its vertical axis and hollowed by a not very deep cavity."

The setting of the fibres in the layer external to the ectoderm and in all the skeletal lamellæ was shown in my illustrations and was very frequently described by me, as also the varieties of form displayed by the skeletal elements at different parts of the corallum (l. c., pp. 113, 121, 125, 128, 136, 137, 138, 144, etc.). To continue M. Krempf's observations:

"There is always a small nucleus, homogeneous and highly chromophil, placed at one of the sides of the mass.

"This element, arrived at its complete development, calcifies entirely. It then ceases to form part of the still living cell within which it is developed and adheres to the skeleton with which henceforth it is embodied. But the nucleus of the cell which formed it is not carried away with it. It withdraws on the contrary into the midst of the protoplasmic layer which remains living, and after a period of rest, the duration of which I cannot fix, it presides at the elaboration of a new element similar to the preceding.

"It is only after having assisted at the formation of a

certain number of these elements that it becomes embodied in the last-formed, finally removed from the living layer and incorporated in the skeleton where good preparations enable it to be recognised. It has then almost completely lost its sensitiveness to colour, but it has preserved almost without alteration its characteristic shape and its dimensions.

"In the preparations which I have examined and which up to the present only concern a single species, I have found an average of 150 scales unprovided with nuclei for one nucleated scale. If one is justified in supposing that none of the nuclei disseminated in the skeleton can escape observation, the necessary conclusion would be that one determinate calicoblast can, during its life, produce a total of about 150 calcareous scales."

M. Krempf, in the foregoing description, appears to reserve the term "calicoblast" for that evanescent stage in the production of a skeletal element which immediately precedes its actual separation from the ectoderm, in fact to limit it to the nucleated fibre-containing body in the ectoderm. It must, however, be remembered that von Heider gave the term to fibre-containing bodies in which, as a rule, the nucleus was shrunken or vanished. Thus so far as terminology is concerned, I was strictly accurate when in my work I applied the term to organic, fibre-containing bodies, whether nucleated or non-nucleated; calcareous scales are most certainly what I defined them to be—"calcified calicoblasts."

It is another question whether each of them may be looked upon as the morphological equivalent of a cell, or cellular part.

Until M. Krempf's evidence is given in full, it is impossible to form any opinion regarding his statement of the oft-repeated withdrawal of a nucleus into the ectoderm. Meantime, from the brief description he now puts before us, I see no reason to infer that the presence of a spent nuclear body in a skeletal element marks out that particular element as the morphological equivalent of a cell, whereas the other skeletal elements have not that morphological value. Each time that

there is a definite aggregation of protoplasmic material with reference to the nucleus, a living cell takes form, and each time that, by an act of fission, an organic, fibre-containing unit is added to the skeletal layer, that unit may be termed the structural equivalent of a cell, although it is not itself living. Some proportion of the nuclear vitality has been employed in the making of each fibre-containing unit. In a word, each calcareous scale represents the product of a nucleated body.

The most important morphological point in M. Krempf's description is his statement that the nucleated cell is finally transferred "from the living layer to the skeleton." This has been the real point of controversy. To quote from my work in 1896 :—"Fowler and Bourne have observed the specialised character and large size of the calicoblastic cells at the growing points of the skeleton in several corals, among others Galaxea. Both these authors regard the calicoblasts as ectodermal cells, which merely secrete calcareous substance without being themselves calcified." . . . "I find that the cells themselves become incorporated in the skeleton." . . .

On M. Krempf's own showing, this transferred nucleated cell becomes a calcareous scale, undistinguishable from its neighbours; in the farther processes of calcification there is no difference between nucleated and non-nucleated skeletal elements.[1]

M. Krempf has given his attention especially to the histological processes, and we may expect a valuable addition to our knowledge of these. The outstanding features in his

[1] It may be of interest to add that in my preparations I sometimes observed traces of nuclei with the organic remnants in calcareous scales; in some, the reaction to stains was quite marked; in others, very faint; and in still others, no nucleus could be discerned by means of stains. I felt I could not draw any secure conclusion as to the absence or presence of the nuclei, and knowing how irregularly they were distributed in the ectodermal tissue, I did not follow this line of observation, but in my published work limited myself to the statement that each "scale" contained organic remnants.

results are his recognition of the controlling agency of ectodermal nuclei, and of divisional processes in ectodermal tissue as the means of origin of the external organic layer in which are contained the primary groups of calcareous fibres. These, together with his observation of the marked individualisation of each calcareous group, confirm the interpretation I gave of the relationship between the ectoderm and the skeletal parts.