The Lime-forming Layer of the Madreporarian Polyp.

By

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Having just received Mr. Duerden's new and valuable work on 'The Coral Siderastrea Radians and its Post-larval Development,' I wish to draw attention to one or two of the points in which his work covers the same field of investigation as my work on 'Madreporarian Types of Corals,' published in 1896. My work in no sense professed to be a study of the histology of Madreporarian corals; it explicitly dealt with the coral skeleton, and it set forth, for the first time, the exquisitely fine lamellar structure of the skeletal parts. My microscopic observations of skeletal structures have been verified by many students since the work appeared, but zoologists generally have regarded my view that the crystalline deposit took origin within organic tissue as quite wrong. Mr. Duerden, who approaches this subject from the histological standpoint, arrives at results which, in this very important feature, corroborate my view.

Those familiar with the scientific literature of the Madre-


poraria know that, previous to my work, the ectoderm was said to consist of a single layer, and the calcareous skeleton to derive origin from this ectoderm by secretion. As Koch wrote, "The ectodermal cells actively separate out calcareous matter, and at the same time continue their own existence."

I found that in all variations of form, from the simple dissepiment to the highly decorative row of granulations on many septa, the calcareous skeleton had a quite particular relationship to the polypal wall, and that the skeletal lamellae were composed primarily of a number of minute, crystalline, calcareous groups, in size closely corresponding to that of the ectodermal cells, but that secondary mineralogical changes tended to obliterate, more and more, this first definite relationship (l.c. aut., p. 113, 115, etc.). Mr. Duerden entirely corroborates this result (Duerden, l.c. pp. 30, 34, 44, etc.).

I also found that the unit-groups of crystalline fibres composing the skeletal lamellae showed the presence of organic residue, usually as minute granules and specks, and that in transverse sections of thick septa, the organic residue was quite apparent in the series of skeletal lamellae at the margins next the ectoderm, even after the older lamellæ had undergone considerable calcification changes. In some of the criticisms of my work by zoologists I was told I had mistaken such appearances, and had seen only fragments of algal filaments penetrating the skeleton. I had foreseen this might be said and purposely given drawings of coral skeletal parts penetrated by filamentous algae to show that I was familiar with this quite different adventitious appearance. What I described was a persistent essential feature in every skeletal part of every species I examined, and now Mr. Duerden entirely corroborates this observation. But this is the observation which overturns the previous conception of the origin of the Madreporarian calcareous skeleton, for, as I pointed out, that skeleton is composed of layers primarily organic, secondarily inorganic, and separated successively from the polypal ectoderm during the growth-periods of the polyp.

So far, then, Mr. Duerden’s work confirms mine. But in
any comparative reference to Mr. Duerden's work and mine a difficulty arises from our different use of the term "calicoblast."

Von Heider, from his observations of the coral polyp, advanced the idea that the skeletal matter was laid down within certain cells, and he termed these cells "calicoblasts," or "lime-forming cells." Subsequent zoological writers insisted that the calcareous matter was secreted by the ectoderm, and laid down outside it, nevertheless they adopted von Heider's term "calicoblast," using it for the ectodermal cells in these parts of the polypal body-wall outside which the calcareous skeleton was deposited. This adoption of von Heider's term by zoologists who upheld the principal of deposition of the limy skeleton external to all organic tissues was, in my opinion, inappropriate, and has been very misleading in the literature.

When I succeeded in separating the skeletal unit with its minute group of calcareous crystals and its organic residue, and found its size corresponded on the one hand with that of an ectodermal cell, on the other with the breadth of a skeletal lamella, I considered it to be the true representative of von Heider's "calicoblast," and applied the term to it. I never applied von Heider's term to an ectodermal cell in the ectoderm, but strictly to the unit-component of the skeletal layers, saying that the unit-component was the product of an ectodermal cell, was at first entirely organic, but that afterwards a group of calcareous crystals developed within it, and the "outlines of the individual calicoblasts became vaguer as their calcification was more complete." I showed that "each skeletal lamina (average width .003 to .005 mm.) was originally a deposit of calicoblasts," the calicoblastic laminae in the septum being an exact replica in form of the ectoderm of the polyp (aut., l. c., pp. 115, 117, 124, 127, 137, etc.).

Thus I discriminated between:

(a) The ectodermal cell-layer from which a series of calicoblastic layers takes origin.
(b) The layer of "fibre-containing calicoblasts next the skeleton."

(c) Older layers of similar fibre-containing calicoblasts in more and more advanced stages of calcification.

At the same time, in my work, I took the broad position that the ectoderm might be regarded as a many-layered structure, the innermost layer being the persistently organic, cellular layer of the body-wall, the next layers being "calicoblastic," i.e., undergoing transformation from organic to inorganic condition, each farther layer being more and more crystalline. "We may look upon the superficial layers of the skeletal elements and of incompletely calcified calicoblasts as the outer layers of a many-layered ectoderm" (aut., l. c., p. 116).

Mr. Duerden's description of the relationship of the skeletal lamina to the ectoderm is the same as mine, but he uses a different terminology. He follows the precedent of Dr. Bourne and others in using the term "calicoblast" for the part of the polypal ectoderm adjacent to the skeletal tissues, constantly using the term "calicoblast ectoderm." He then applies a new term to the next layer of organic tissue in which the calcareous crystals are deposited (i.e., the outer layer which I called "calicoblastic"),—describing it as a "homogeneous, mesogloea-like matrix in which the minute calcareous crystals forming the skeleton are laid down" (Duerden, l. c., p. 34). Then he states that the "calicoblast ectoderm" does not lay down the skeleton, but that it probably secretes this matrix or membrane in which the skeleton is laid down.

Thus Mr. Duerden applies the term "calicoblast ectoderm" to that which I called simply "ectoderm," and describes as a homogeneous "matrix," "membrane," or "sheath" the next layer described by me as a layer composed of individual calicoblasts in which the crystalline groups made their appearance. The difference in the use of terms will be evident from the following quotation, where Mr. Duerden describes the appearance of the lime-forming layer after decalcification.
“When of sufficient thickness to have contained skeletal fibres, now dissolved away, this membrane appears fibrous, but immediately bordering the calicoblast layer” (by which he means the ectoderm) “it is homogeneous” (Duerden, l. c., p. 34).

Seeing that the term “calicoblast” means “lime-forming,” why not apply it to the membrane which, in Mr. Duerden’s own interpretation is a lime-forming layer? Why apply the term “calicoblast” to the persistent ectoderm, which is not directly lime-forming, as was erroneously supposed by those who made the precedent? Moreover, in common with me, Mr. Duerden considers this lime-forming layer to be separated time after time by the ectoderm, and to be originally organic, secondarily inorganic. Had he used the same terminology as I did, designating as “calicoblasts” the skeletal unit-elements (partially organic, partially fibrous) present in the layer, and the whole layer a “layer” or “lamella of calicoblasts,” the similarity of our results would have been self-evident, the important feature being that the ectoderm does not separate out calcareous matter, but organic matter, within which the crystals develop.

The point of difference between Mr. Duerden’s results and mine is one of histological detail. From the remarkable coincidence in size between the cells of the persistent ectoderm and the calicoblast unit-element in the apposed skeletal or lime-forming layer, I drew the conclusion (aut., pp. 115, 117, 124, 125, 217, etc.) that the change from the organic to the inorganic state went on in individual cellular parts of the lime-forming layer, and that each individual lime-forming part or “calicoblast” of the 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.

Mr. Duerden finds the lime-forming layer homogeneous in character, without cell limitations, and, as I made no further investigation of the subject, I willingly accept Mr. Duerden’s
observation of the primarily homogeneous nature of the lime-
forming layer. It is no less a layer of organic matter, and
Mr. Duerden compares it with the mesogloea between the
endoderm and ectoderm (l. c., pp. 22, 34). Mr. Duerden
finds the skeletal unit-elements laid down within this layer as
definite in size as I did, and the width of the successively
separated lime-forming layers about '0025 mm. (cf. Duerden,
l. c., pp. 44, 113). I determined the height of the calicoblast
or skeletal unit-element in Galaxea as '0025—'0035 mm.,
which corresponded to the width of the septal lamellae. Mr.
Duerden adopts a term I frequently used for these unit-
elements, viz. "calcareous scales," but the other term,
"calcified calicoblasts," which I also used, he discards,
because he confuses it with what he himself terms "calico-
blast," viz. a cell in the ectoderm. My use of the term was
for cellular parts separated from the ectoderm and incor-
porated in the lime-forming layer (Duerden, l. c., p. 113).

The absence of cell limitations in the organic tissues of the
coral polyp is not unusual, the middle layer or "mesogloea"
being generally homogeneous. Of Siderastrea radians
Mr. Duerden writes, "In sections the combined ectoderm and
endoderm vary from '015 to '003 mm. in thickness, both
layers being about equal. The endoderm is a syncytium
showing no signs of cellular divisions." . . . "The actual
calicoblast layer (= ectoderm), like the endoderm, is at first
very narrow, and in the growing areas of the skeleton shows
no evidence of cell limitations. . . . The nuclei are nearly
as numerous as in the endoderm, and are large and finely
granular" (Duerden, l. c., pp. 30, 31). He notes that at
the growing edges of the septa nuclei become more frequent
in the ectoderm, and tend to exhibit a definite network.
Active fission at these parts is well known to observers, and
I took the nuclear fission to be associated with the separation
of the organic outer layer. Mr. Duerden, however, thinks
the organic outer layer probably originates from the ectoderm
by a process of secretion, in some manner wholly external
to the polypal tissues. Accordingly, he says the calcareous
fibres which develop in the organic outer layer are "ecto-
plastic in origin (l. c., p. 113). But is this quite accurate
when they arise in an organic mesogloea-like membrane?

Whatever its mode of origin, whether by secretion or by
fission of cellular tissue, the lime-forming layer is at first
organic and continuous. And it appears to me it will not
cover the facts simply to say that the skeletal units arise in
an organic sheath or matrix, and are in their individuation
wholly unaffected by the ectoderm cells or nuclear parts.

On Mr. Duerden's interpretation, if I understand it aright,
we are to believe that the exceedingly particulate 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 deter-
mining 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.

I should like also to refer briefly to an excerpt which Mr.
Duerden makes from my work, and which, away from the
context, might easily convey to the reader a somewhat
erroneous impression. On p. 43 Mr. Duerden refers to my
explanation of the appearances of "dark points" and a "dark
line" in the median plane of the septum, and says "Miss
Ogilvie considers that the dark appearance of the centres
results from the presence of the carbonised residue of the
originally unchanged parts of the calicoblasts, within which
she considers the Madreporarian skeleton to be formed. It
must be stated, however, that the dark appearance is only
seen when sections are viewed by transmitted light. With
reflected light the middle region appears lighter than the
rest of the septum, and thus can scarcely be occupied by
black organic matter."
From the excerpt, it might be concluded that I supposed the middle region of the septum was always occupied by black organic matter. On the contrary, I examined my slides both by transmitted and reflected light, and knew very well that in some cases the middle region of the septum appeared lighter. But, as I wished to point out, there were cases where bright coaly specks were undoubtedly present, and would justify the term "dark points" met with so often in the literature of Madreporaria.

In my work I accepted Dr. Bourne's term "centres of calcification" for the "dark points" expressly because it assumed nothing with regard to the actual condition of any deposit that might originally, or by secondary changes, be present at the "centres" of calcification. My aim, in the passage to which Mr. Duerden made reference (aut., p. 127), was to demonstrate the frequent presence of organic matter at the septal axes or centres of calcification, and to identify it with the organic residue in the skeletal units or calcifying calicoblasts which composed the lime-forming skeletal layer, doubled at the septum.

I wrote, "The appearance of the 'dark line' with transmitted light, although generally opaque, is not always so. . . . The 'points' in a transverse section of Galaxea, for example, appear at one place homogeneous, and yellowish or dingy-brown in colour; in another place the 'point' seems a fairly large, circular area, filled with granular, powdery material, and then it is usually dark." Again, "In all cases we have simply to do with centres and axes (ideal) 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." In explaining lateral ornamentation of the septa, I wrote, "Small pits are present on the ectodermal, skeletal-producing surface. Subsequently the skeletal layer of the septum is an exact cast of the form of the ectodermal flap. . . . The component calcified calicoblasts of the layer have their fibres set at right angles to the sides of the pit, and the
eminence of the growth-lamella assumes a hemispherical, conical, or any other form, according to the shape of the ectodermal pit. . . . In all cases the fibres radiate around what was formerly the axis of the pit. By continuous deposition of lamellae a fascicle of fibres is determined, whose axis coincides with this axis" (aut., l. c., p. 137, cf. p. 139, etc.).

Mr. Duerden writes, "I conceive that the so-called centre of calcification is really the organic centre or axis around which the skeletal matter is deposited in a radiating or feather-like manner, and that at an early stage in the living, growing skeleton, the centre is occupied by the mesogloea-like matrix, within which it has been shown that the calcareous fibro-crystals are deposited" (Duerden, l. c., p. 43). This interpretation of the "dark points" and "dark lines" does not differ from mine in so far as relating them to organic residual fragments of an organic layer undergoing changes of calcification.

Further, my explanation (aut., l. c., p. 113) of the cause of the appearance of dark and light bands in the succession of growth-lamellae, viewed by transmitted light, is the same as given by Mr. Duerden on p. 42 of his work; the margins of "dark, finely-granular particles, similar to those at the centres of calcification," having been detected by me and their significance interpreted as all-important evidence in my demonstration of the separation of successive calicoblast or lime-forming layers, and the gradual transformation of each to build up a skeletal growth-lamella (cf. Duerden, p. 44; Ogilvie, pp. 111, 150, fig. 30a.)