Article XXV.—BORING ALGÆ AS AGENTS IN THE DISINTEGRATION OF CORALS.

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Plate XXXII.

J. Queckett in his 'Lectures on Histology' (London, 1854) first drew attention to the fact that corals are frequently penetrated in all directions by tubules, which are now known to result from the growth of filamentous plants within the calcareous skeleton. A few years later Prof. A. Kölliker (Proc. Roy. Soc., Vol. X, p. 95, 1859) described similar tubes in the horny fibres of sponges, the tests of Foraminifera, and many molluscan and brachiopod shells, as well as in numerous corals. Kölliker considered them all as parasitic unicellular fungi. Prof. Moseley in 1875 (Proc. Roy. Soc., Vol. XXIV, p. 64) found the coralla of both *Millepora* and *Pocillopora* to be permeated by fine ramified canals, formed by parasitic vegetable organisms. These were green in color, in abundant fructification, and were regarded by Moseley as fungi.

The late Prof. P. M. Duncan in 1877 (Proc. Roy. Soc., Vol. XXV, p. 288) published the results of a thorough investigation into the subject of Thallophytes boring into recent Madreporaria. Six different species of corals were examined, of which apparently *Balanophyllia verrucaria* Pallas was the only available fresh material. Duncan found no chlorophyll in the filaments liberated on decalcification, and came to the conclusion that the principal parasite was a fungus allied to the Saprolegniæ; this he named *Achyla penetrans*. The fungoid character of the boring organism has been accepted by recent writers on coral morphology, such as Bourne and Ogilvie. In an Appendix to his communication Prof. Duncan refers to thread-like, dark green organisms of a vegetable nature which ramify on the surface of certain deep-sea corals (363 fathoms) and penetrate within it.

MM. Bornet and Flahault in 1889 (Bull. Soc. Bot. de France, Tom. XXXVI) published an important contribution upon the plants living within the calcareous shell of molluscs.

They summarize the results of previous observers and recognize in all ten different genera of shell-boring plants: four, of which *Gomontia* is the principal, belong to the green algæ (Chlorophyceæ), four to the blue-green algæ (Cyanophyceæ), and two are probably fungi. Representatives from the red algæ (Rhodophyceæ) have since been added by later workers. The life history of most of the forms is yet imperfectly known. Bornet and Flahault point out the very important rôle which boring plants play in the corrosion and ultimate disintegration of molluscan shells, especially in quiet bays where the shells are not mechanically broken up by the incessant action ot the waves.

The papers above mentioned contain references to other accounts of boring algæ and fungi, all of which seem to indicate that Thallophytes infest and assist in the disintegration of nearly every form of calcareous matter. Their filaments have been met with in Foraminifera, corals (recent and fossil), the calcareous tubes of annelids and cirripedes, molluscan shells (empty and living), fish scales, and calcareous pebbles. Apparently the endodermal skeleton of echinoderms is free from their attacks.

On macerating freshly collected Jamaica corals I have often found specimens which exhibited irregular green patches over a greater or less area of the newly exposed skeletal surface, the coloration varying much in intensity. Occasionally colonies were obtained in which the color was a delicate red. The old, partly corroded, under-surface of freshly gathered corals is also frequently green. The fresh surface of the corallum gives no indication as to the cause of the green or red color, so that evidently it is within the skeleton itself. Fracturing the coral serves to establish that the coloration penetrates only a short distance below the surface, and in the interstices minute green filaments can be seen ramifying over the surface of the dead corallum and frequently extending across the dissepimental chambers. On exposure to the tropical sun for several days or weeks the corals usually become bleached, but after a period of two or three years certain specimens stored in cases still retain a faint green or pink tinge.

Again, in the course of a morphological study of West Indian coral polyps, I have decalcified numerous preserved colonies or fragments of such belonging to about thirty different species, all obtained from shallow water. In almost every instance the space from which the calcareous skeleton was removed was found to be occupied by a colorless, green, or red mass of fluffy texture, which on examination under the microscope proves to be made up of filamentous algæ, sometimes mixed with fine particles representing the organic matrix of the skeleton. The filaments obtained from near the surface of the corallum are colored, due either to the presence of chlorophyll or to a red cell fluid; while those more internal are colorless and contain but little protoplasm, suggesting a non-active condition. There can be no doubt that the coloration seen on freshly macerated coralla is due to the occurrence of these perforating green and red algæ in great abundance. Where present in less numbers the filaments do not sensibly affect the usual white appearance of a coral skeleton.

The filaments to which special attention has been given were obtained in every case from the living region of the colony, that is, from the more superficial part of the corallum which is covered by the polypal tissues. Of the green algæ only two species occur: one with transverse walls, probably belonging to the genus *Gomontia* (Fig. 3), and another with continuous tubes, belonging to the group of the Siphoneæ, probably an *Ostreobium*[1] (Fig. 1). Both are extremely variable as regards the size and form of the filaments, and are often closely intermingled in the same specimen of coral. Sometimes a filament will extend for a great distance without branching. At other times the unicellular form will branch frequently in a somewhat dichotomous manner and assume a root-like appearance; or, again, its filaments may pass uninterruptedly into spheroidal, club-shaped, or irregular enlargements filled with spore-like bodies (Fig. 2, *a–c*). The red alga is constituted of simple, closely intermingled filaments, and occurs much less fre-

[1] The botanical issues of the subject will be fully dealt with by Dr. G. T. Moore, Algologist of the United States Department of Agriculture, who is at present engaged upon a study of the boring algæ infesting West Indian molluscan shells.

quently than the green (Fig. 4). The red and green forms may occur together in the same coral. No fungus has been met with.

The non-septate green alga bears the closest resemblance, in the varying form of the filaments and also in its spheroidal club-shaped, or irregular sporangia, to the figures of *Achyla penetrans*, as given by Duncan and by Bourne (Trans. Roy. Dubl. Soc., Ser. II, Vol. V, 1893, pl. xxv), and no doubt they will prove to be the same. Duncan has shown that the fossil corals of Silurian age were also affected by closely allied, if not specifically identical, forms.

The universal presence of boring algæ in West Indian corals suggested an examination of corals from other regions. By permission of Prof. Alexander Agassiz, and through the courtesy of the officials of the Smithsonian Institution, I have been enabled to examine the collections of recent corals made by Prof. Agassiz during his explorations of the coral-reef areas of the Pacific in 1899–'00, and now deposited for report in Washington. The surface of many of the specimens, even where covered by the polypal tissues when alive, is yet strongly green in color; and the decalcification of fragments from some dozen species selected at random reveals in every case the presence of filamentous algæ. The filaments seem to differ in no respect from those remaining after the decalcification of West Indian corals, the non-septate form occurring in greatest quantity. The skeleton of the alcyonarian coral *Tubipora* was likewise infested with non-septate filaments, along with a filamentous blue-green alga.

The actual chemical and physical processes involved in the penetrative activity of the algal filaments is not yet definitely understood. The corroding action is probably similar to that observed when the roots of living plants come into contact with a slab of marble. Duncan (*l. c.*, p. 254) considered that the growth of the parasitic organisms within the hard calcareous structures was due to "the combined results of the formation of a soluble bicarbonate of lime by the action of the carbonic acid gas evolved from the growing end of the tubular filament, of the pressure incident to growth, and of the movements of the cytioplasm and cell-wall." He regarded the cell-wall as being in close contact with the sclerenchyma of its canal, so that solution took place only at the growing apex, and the soluble product could pass outward only through the filaments themselves. Kölliker had expressed practically the same conclusion. Recently Karl Lind, in a paper entitled 'Ueber das Eindringen von Pilzen in Kalkgestein und Knochen' (Inaugural-Dissertation, Leipzig, 1898), has discussed very fully the different views as to the perforating action of fungal hyphæ. Experiments showed that the entrance of the hyphæ into plates of limestone, bones, etc., was dependent upon the presence of nutritive matter within the hard substance. Lind also concludes that carbonic acid produced by the organism is the chief agent in the solution of the calcareous matter, and that the soluble bicarbonate passes to the exterior not through the filament itself, but in a narrow interval existing between the hyphal wall and the calcareous boundary.

Apparently the corrosive action of perforating algæ has never received any attention in the numerous discussions which have taken place upon the possible factors in the destruction and disappearance of corals. Bourne (Trans. Roy. Dubl. Soc., Ser. II, Vol. V, 1893, p. 225) attributed to it considerable importance in the separation of the discoid *Fungia* form (Anthocyathus) from the pedicle to which it is primarily attached (Anthocaulus). The fragile nature of the dead part of the stems of *Mussa corymbosa* Bourne also considers to be due to their being bored by *Achyla* and by the boring sponge *Clione*. From my own observations in the neighborhood of coral reefs, extending over several years, I am disposed to accord the process of algal corrosion an important, if not the most important, part in the disintegration of coral masses. The results presented above give good reason for assuming that in general all corals are infested with boring algæ, even to their most superficial regions of growth. Among the thirty different species of West Indian corals examined the only places where filaments have not been found are at the growing apices of branching corals like *Madrepora* and *Oculina*. Here the calcareous deposition apparently takes place a little in advance of the upward growth of the algal filaments, for the latter are always to be found in the older parts of the corallum.

Decalcification of the dead stems and under parts of colonies usually discloses a still greater abundance of filaments of the true boring types, while from the actual surface is obtained an immense variety of other vegetable growths. On the shores of the quieter bays and lagoons the fragments of dead corals picked up are frequently green in color, and exhibit all stages in the process of corrosion.

The decalcification of so-called 'rotten' coral is also found to leave behind large quantities of a fluffy material, nearly the whole of which is algal matter in a living, active condition. But in addition to the two species of algæ usually occurring in the living regions of a colony many other forms are found, crowded in such a manner that it is difficult to say which actually penetrate the skeleton and which are only superficial. Two different representatives of the blue-green algæ are often present, and frequently a *Leptothrix*-like bacterium. Boring sponges sometimes occur, but in my experience are not very common in corals. 'Rottenness' in corals would thus appear to be largely due to the corrosive action of algæ, supplemented by the boring animal organisms referred to below.

In addition to the possible solution of calcareous corals by the carbonic acid in sea-water the principal factors which have hitherto been considered as leading to their destruction are the various animal forms infesting the skeleton. Most writers have pointed out the influence in this direction of the numerous boring molluscs, sponges, echiurids, and echinoids, and the cirripedes and annelids frequently included within the corallum. All these undoubtedly weaken the skeleton greatly and must facilitate its fragmentation when rolled about by the waves. Mere fragmentation, however, will result only in the formation of coral sand or mud, as contrasted with actual solution. The direct influence of the infesting animal organisms in bringing about the solution of the calcareous skeleton seems much less than that of the ever-present and ever-active, though less obvious, corroding algæ. Once a coral is attacked by these, the growth of the ramifying filaments apparently never ceases so long as the necessary conditions of plant life remain; even when the dead coral is broken up into fragments the growing filaments still continue their corroding action on the separate particles, and by the production of soluble bicarbonates lead to their ultimate disappearance.

In the sand found around the small coral islands outside Kingston Harbor, Jamaica, and also on the coral flats, I have often observed the comparative scarceness of fragments or particles which can be referred to actual corals. It appears to be composed largely of fragments of shells of molluscs, spines and plates of echinoids, and nullipores. The greater porosity of corals, along with the attacks of the boring algæ, are probably the causes leading to their more rapid disappearance by solution. On dissolving small quantities of coral sand in acid the whole of the inorganic matter disappears and organic débris only remains. Among this the filaments of the coral-boring algæ, still bearing chlorophyll, are sometimes found, so that evidently the parasites may continue their corroding activity when the host is reduced to coarse particles. Prof. Sollas (Nat. Science, Vol. XIV, p. 27, 1899) found the coral sand taken from the shores of the lagoon of the atoll Funafuti to contain scarcely any coral, but to be composed almost entirely of the shells of Foraminifera. He also observes that from specimens collected on other atolls by the late Prof. Moseley it would appear that the sand of Funafuti is by no means singular in this respect.

The explanation of the origin of coral atolls associated with the name of Sir John Murray rests upon the fact that there has been a constant progress outwards of the actively growing margin of the reef, followed by solution of the internal coral left behind, the disappearance of the coral leading to the formation and the deepening of the lagoon. Murray (Proc. Roy. Soc. Edin., Vol. XVII, p. 79, 1890) has supported his theory of the solution of coral by the carbonic acid in sea-water by laboratory experiments, and most writers on the subject are prepared to accept a slight solubility of coral by this means. So far as the production of lagoons is concerned

Bourne (Proc. Roy. Soc., Vol. XLIII, 1888) doubts if this solubility of coral in sea-water is more than sufficient to counterbalance the effect of the redeposition of lime and the additions from the actual colonies still living within the lagoon.

It is just in such quiet spots as lagoons that the various boring algæ would be expected to grow most favorably, and by their incessant ramifications lead to the ultimate disintegration of any block of coral, following it even when reduced to fragments. The formation of an atoll is without doubt a very complex matter, and many and varied agencies are therein concerned, the destructive forces at one time predominating and the accumulative at another. All that is here contended for is that coral-boring algæ are important factors which must be taken into account in considering the causes of the destruction and disappearance of the older corals as the newer growth progresses outwardly.

As a result of the elaborate investigations carried on by Prof. Alexander Agassiz for the past fifteen years, embracing all the principal coral-reef areas of the world, it is becoming manifest that coral formations are but comparatively superficial in character; apparently they never assume the great thicknesses which have frequently been ascribed to them on imperfect data. Only under special circumstances, as where accumulations of sediment are taking place, do coral masses become permanently preserved; under ordinary conditions they are disintegrated and returned to the sea in a soluble form, or redeposited elsewhere either interstitially or as a cementing material. Here, again, there is no doubt that the corrosive action of boring algæ constitutes one of the most important factors in the resolution of the calcareous skeletons.

The above results having been brought to the notice of Prof. A. Agassiz, he has very kindly sent me his observations on the same subject and permitted their publication in the present connection:

"At the time Duncan published his paper I took up the subject with Mr. Pourtalès enough to satisfy ourselves that boring algæ played a prominent part in the disintegrating effect of corals, and I have not failed to notice the existence of these parasitic vegetable organisms in the coral reefs I have visited, but without making closer examinations of them. I have frequently noticed their presence in the so-called broken corals (which are, rather, rotten fragments) dredged up from below the depths at which corals live, and have taken it for granted that both rotten corals and so-called broken shells are reduced to that state by the action of parasitic boring algæ.

"The absence of fragments of corals on the lagoon beaches of atolls is due not wholly to solution but to the absence of corals in lagoons as compared to their presence on beaches on the sea-faces; and the absence of corals in lagoons is not wholly due to solution but to the adverse conditions for their excessive growth existing in the lagoons of atolls. This absence of fragments of corals is perhaps best seen at the Bermudas and Bahamas, where the sands of the lagoon beaches are almost wholly made up of broken shells, Foraminifera, etc. The same is the case with many of the atolls of the Pacific."

EXPLANATION OF PLATE XXXII.

Fig. 1. Isolated filaments of the non-septate green alga from the corallum of *Colpophyllia gyrosa* Edw. & Haime. The filaments are full of chlorophyll granules, and the small portion to the right is in an actively growing condition with distinct pyrenoids.

Fig. 2. Different forms of reproductive bodies (Sporangia?) occurring on the non-septate green alga.

a. From *Porites antræoides* Lamarck.

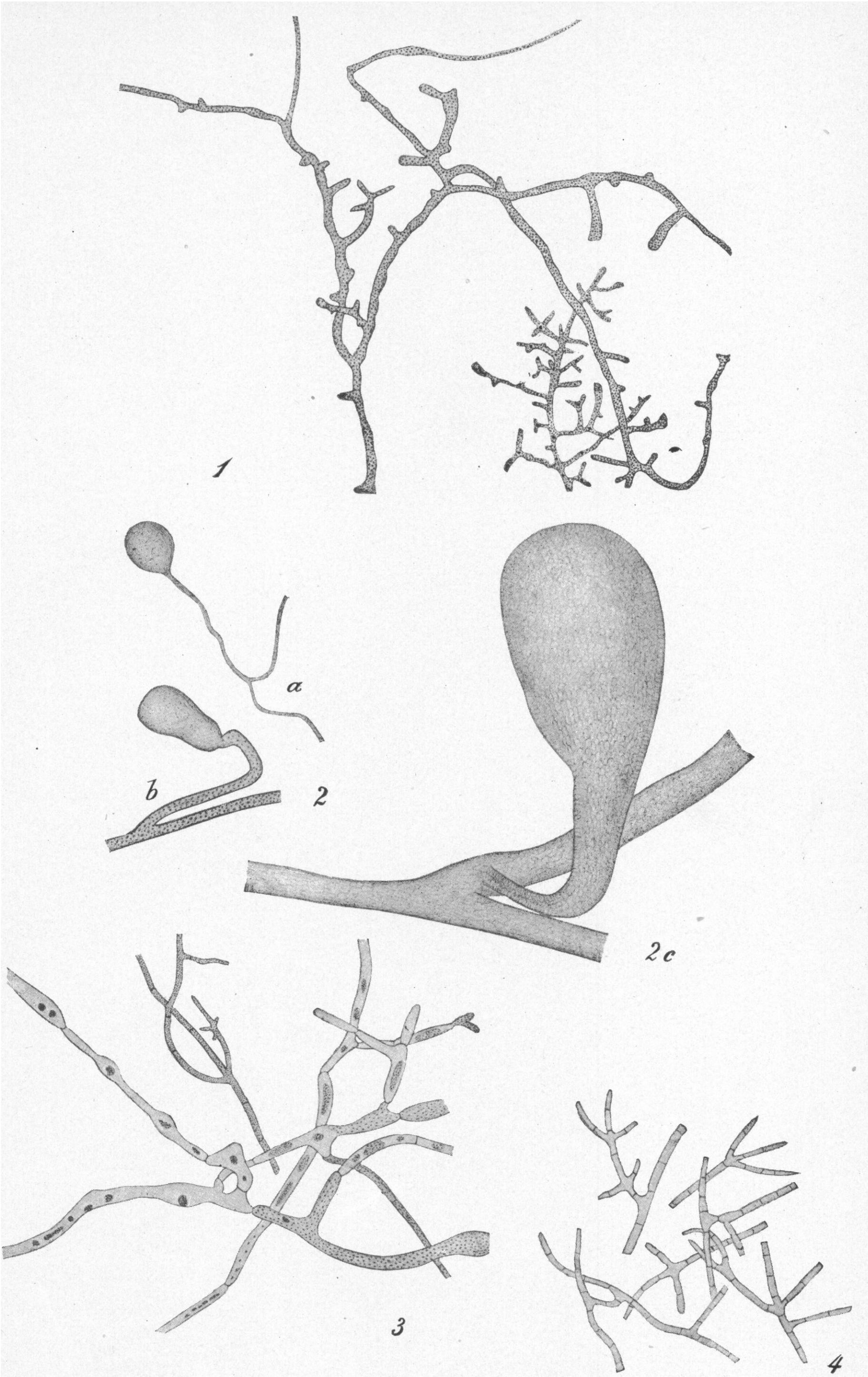
b. From *Colpophyllia gyrosa* Edw. & Haime.

c. From *Stephanocœnia intersepta* (Esper).

The spores are not yet evident in *a* and *b*, but in *c*, which is enormously larger than the others, they are fully ripe and ready to separate. Oval-shaped bodies, apparently differing in no respect from those in the sporangia, occur in the enlarged filaments in *c*, so that no sharp line of distinction between the reproductive capsule and the filament from which it arises can be established.

Fig. 3. Isolated filaments of the septate green alga from the corallum of *Manicina areolata* Linn. The chlorophyll granules occupy the whole surface of the filaments in some places, while in others they are shrunk into isolated aggregations.

Fig. 4. Isolated portions of filaments of a red alga from the corallum of *Porites astræoides* Lamarck.



CORAL BORING ALGÆ.

Photograph by C. E. Taylor. La Soufrière, St. Vincent, from Richmond Estate. *Frontispiece.*

EXPLANATION OF PLATE XXXIII. (Frontispiece.)

La Soufrière, St. Vincent, from the southwest, showing the steep bluffs on the coast due to landslides, and the coating of dust over the surface. The bay in the foreground is the mouth of the Wallibou River, and the bluff on the farther side of it shows the old deltal plain, surmounted by the light-colored deposit due to the present eruption. The surface of this, for a depth of 8 or 10 inches, is darker than the lower part, because it is wet. The remains of Wallibou factory are in the middle of this view. A nearer view of these ruins is shown in Plate XXXVII. See page 340.