

## The Significance of the Relationship between Corals and Zooxanthellæ.

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BOTH by the publication of his book, "Coral Reefs and Atolls", and by a recent contribution to NATURE,<sup>1</sup> Prof. J. Stanley Gardiner has materially added to the debt which all interested in problems of corals and of coral reefs already owe him. As a result, however, of work on the physiology of corals carried out during the course of the Great Barrier Reef Expedition, I am unable entirely to agree with Prof. Gardiner's conclusions in one important matter. He suggests that corals obtain supplies of carbohydrate from their contained zooxanthellæ, and also that the oxygen produced by the latter as a result of photosynthetic activity is of vital importance to the animals. My own conclusions as to the significance of the relationship between corals and zooxanthellæ are somewhat different, and, since this work—the result of the combined labours of Mrs. Yonge, Mr. A. G. Nicholls, and myself—is now largely completed, I am able to put them forward with confidence and no longer tentatively as in previous contributions to NATURE.<sup>2, 3, 4</sup> Moreover, it has proved necessary to publish this work in a series of six large reports,<sup>5, 6, 7, 8, 9, 10</sup> and a short summary of the results obtained is, therefore, not without some justification.

The zooxanthellæ of the Madreporaria are yellowish brown spherical bodies varying in diameter from  $6\mu$  to  $14\mu$ . Each contains a granular nucleus, one, and occasionally two, pyrenoids around which an amyloid assimilation product accumulates, and vacuolated cytoplasm which contains many oil droplets. The whole is bounded by a stout cellulose wall. They increase rapidly by division into two, but there is no evidence of the formation of spores, nor were they ever found in centrifuged water samples, while all attempts at culturing them outside the body of the animal failed. Unlike the green *Chlamydomonas* present in *Convoluta roscoffensis*, which, as shown by Keeble and Gamble,<sup>11</sup> occur free in the sea and form spores, the zooxanthellæ can live only within the tissues of the coral and are transmitted direct from parent to offspring by way of the planula. They are thus definitely degenerate. Within the tissues they occur only in the endoderm, most plentifully in the superficial regions. They are invariably contained within tissue cells, very frequently in wandering cells which convey them from place to place, and their absence from the ectoderm and mesogloea may be due to the mechanical difficulties of transporting such relatively large objects through the dense material of the mesogloea.

Although zooxanthellæ never occur in the ectodermal glandular margin of the mesenterial filaments, they may, especially under certain conditions, be very numerous in the 'absorptive' region which lies at the base of this. Degenerating zooxanthellæ are always most abundant in this region, although they may occur anywhere in the endoderm, but always in small numbers in a healthy coral. Boschma<sup>12, 13, 14</sup> has based his views, that zooxanthellæ are digested by corals, on the presence of these degenerating algæ in the 'absorptive' zone, but clear evidence was obtained that this region, as well as being the sole absorptive area, is also the only site of excretion. It is thus the only region of the coral where interchange between the interior of the tissues and the exterior takes place. Degenerating zooxanthellæ present are in process of excretion and not digestion.

The pyrenoid of the zooxanthellæ contains chlorophyll which, in the presence of light, forms the amyloid assimilation product (not apparently true starch),

utilising carbon dioxide and producing oxygen. Experiments with corals in sealed jars showed that the hydrogen-ion concentration of the water rises appreciably after nine hours in darkness, owing to the accumulation of carbon dioxide, whereas in the light the hydrogen-ion concentration remains constant, because the carbon dioxide is utilised by the zooxanthellæ. In *Dendrophyllia*, a deep-water coral which has extended its vertical range and is not uncommon on the surface of reefs, there is a similar rise in hydrogen-ion concentration in both light and darkness. In common with all deep and cold water corals, *Dendrophyllia* possesses no zooxanthellæ. The carbohydrate formed as a result of photosynthesis is in part converted into oil and stored in that form, as in diatoms and other algæ. Protein synthesis, which involves the utilisation of nitrogen and also of phosphorus and sulphur, was followed by estimations of the phosphorus exchange between corals and the surrounding water. Whereas *Dendrophyllia* excretes large quantities of phosphorus in the same way as any other animal, the reef-building corals which contain zooxanthellæ do not. On the contrary, they frequently remove phosphorus from the surrounding water, even when this has been greatly increased by the addition of phosphate. The zooxanthellæ are thus capable of utilising much more phosphorus than is normally produced by the katabolic processes of the corals in which they live. The same is probably true of nitrogen and possibly of sulphur.

The abundance of zooxanthellæ is thus dependent upon two factors, light and the presence of nutrient substances, carbon dioxide, nitrogen, phosphorus, and sulphur, the latter in turn depending on the metabolic state of the coral. It proved possible to demonstrate experimentally the effect of these limiting factors. In the case of light, comparison between reef-building corals from the surface of the reef and from depths of 7 or 9 fathoms revealed that the former had approximately double the population of zooxanthellæ, while individual colonies from the reef surface which had grown on the under-side of boulders in the absence of light were found practically devoid of zooxanthellæ. The results of an experiment whereby corals were kept in a light-tight box in the sea for 152 days showed that the animals could survive this treatment without obvious harm, but that practically all the zooxanthellæ had died and been extruded at the end of this period. In all cases they were ejected by way of the 'absorptive' zone. Reef-building corals deprived of zooxanthellæ in this way excreted large quantities of phosphate of about the same order of magnitude as *Dendrophyllia*. Sections of such corals revealed that, in place of the zooxanthellæ, there were great numbers of wandering cells with granular contents, and it would therefore appear that these cells normally contain zooxanthellæ, but in the absence of these they resume their original function of excretion. Such wandering cells are a constant and conspicuous feature in the histology of corals, such as *Dendrophyllia* and *Balanophyllia*, which never contain zooxanthellæ.

The metabolic activities of corals were lowered in three ways: by starvation, by heating, and by deprivation of oxygen. In the case of starvation, a series of experiments were set up in which corals were starved (in filtered sea water) and fed (with freshly caught zooplankton) under parallel conditions. In all cases it was found that starved Madreporaria quickly show a great reduction in the bulk of their tissues, and

that this is shown equally whether zooxanthellæ are present or not. Almost immediately after starvation begins, zooxanthellæ are expelled in large numbers—some, but by no means all, dead, and practically all intact—and this continues until almost all are extruded. There is no evidence whatever of any digestion of the zooxanthellæ by the corals, or of any transference of material, such as the fat which Keeble and Gamble showed was passed from the *Chlamydomonas* to the *Convoluta*, from the plants to the animal. *Chlamydomonas*, however, possesses no cellulose wall. It was conclusively proved that *Madreporaria* obtain no nourishment whatever from their contained zooxanthellæ, and also that the latter are not even necessary for the initial development and early growth of the newly settled larvæ.

Precisely the same results, so far as the zooxanthellæ are concerned, were obtained when corals were heated to 36° C. for two hours or placed for some days in water almost devoid of oxygen. As in the starved animals, the zooxanthellæ were ejected in great numbers by way of the 'absorptive' zone of the mesenterial filaments, and then passed out through the mouth in mucus strings. The same process was observed in Nature during the summer months when corals on the reef surface were subjected to temperatures of above 35° C. over low-water in the day time, and as a result were almost completely denuded of zooxanthellæ, which gradually multiplied again until, at the end of about three months, the usual content of zooxanthellæ was regained. Here again the extruded zooxanthellæ were intact and apparently alive and healthy when extruded.

In every case, as a result of starvation, heating, or deprivation of oxygen, the metabolic activities of the coral were reduced, and, as a result, the amount of nitrogen, phosphorus, sulphur, and carbon dioxide produced by them was greatly reduced. This lack of the necessary inorganic food materials of the zooxanthellæ is clearly the cause of their expulsion, which is effected by the wandering cells which convey them to the 'absorptive' zone where they are expelled. It is difficult to explain what impels the wandering cells to do this, but it may possibly be the abnormal raising of the hydrogen-ion concentration in the tissues. There is certainly, however, a mechanism here whereby the population of zooxanthellæ is maintained at the level which the metabolic state of the coral, that is the amount of available food, permits. When the population falls below this level, it quickly reaches the maximum possible, owing to the very rapid multiplication of the zooxanthellæ.

Unlike the zooxanthellæ, which are apparently unable to live apart from the animals and are definitely degenerate in so far as they have lost the power to form spores, the reef-building corals can, and, where light is absent, invariably do, live without zooxanthellæ, like all deep and cold water corals. To an individual coral colony the association with zooxanthellæ is *not* essential. Nevertheless, the vast majority of reef-building corals and practically all the Cœlenterata on the reefs possess them, and there can be no doubt that they play an important, probably a vital, rôle in the economy of marine life on a coral reef. This work on the physiology of corals has indicated what the significance of the association may be.

Before proceeding to this, however, the question of oxygen production by the zooxanthellæ must first be discussed. In the presence of light, the zooxanthellæ, as a result of photosynthetic activity, produce oxygen. Exact determinations showed that whereas the oxygen content of enclosed volumes of sea-water in which corals were kept for nine hours in the light might be doubled or even trebled, in the dark it fell to one half, or much less, during a similar period. Corals could be

kept in an enclosed volume of water for several weeks without suffering from lack of oxygen, owing to the presence of this closed system. A series of experiments, carried out over twenty-seven hours continuously, showed that only over the middle of the day, between the hours of 10 A.M. and 3 P.M. approximately, does oxygen production by the zooxanthellæ exceed oxygen consumption by the coral and the zooxanthellæ. Over twenty-four hours there was always a drop in oxygen content, showing that the production of oxygen by the zooxanthellæ cannot completely supply the wants of the coral. Mr. A. P. Orr found that the oxygen tension in pools on the reef surface at low tide at night fell as low as 17.8 per cent saturation, whereas under similar conditions by day it might rise as high as 230.4 per cent. As soon as the sea covered the reef, however, normal conditions again prevailed.

In spite of these facts, the benefit derived by the corals from this supply of oxygen is almost certainly more apparent than real. It was found that corals can survive exposure to water of less than 10 per cent oxygen saturation for several days, and that they can respire equally well in water less than 50 per cent saturated as in water fully saturated with oxygen. Under normal conditions, except in sheltered lagoons and other regions where coral growth is slight, they would never be exposed to such conditions; for water movements around the exposed areas of reefs where coral growth is invariably most prolific are always great, and the constant mixing of the water ensures a continuous supply of oxygen. Finally, were the zooxanthellæ absent, the great quantities of nutrient salts excreted by the corals and other Cœlenterata which contain zooxanthellæ would permit of a much greater growth of phytoplankton, with a consequent increase of oxygen in the water. The zooxanthellæ are really imprisoned phytoplankton which produce oxygen within the corals instead of in the sea-water. There is no satisfactory experimental evidence indicating that the oxygen produced by the zooxanthellæ within the corals is essential to these animals or that they would not flourish equally well in its absence.

An examination of the feeding mechanisms of more than forty genera of *Madreporaria* revealed that corals are carnivores with highly specialised feeding mechanisms for dealing with zooplankton of all sizes. This was abundantly confirmed by a study of their digestive enzymes. Protein alone can be digested extracellularly in the cœlenteron, but only to polypeptides, digestion being completed intracellularly where amino-acids are formed. Fat also can be digested intracellularly, but very slowly; while the only carbohydrate which can be digested, and that very slowly, is that found in animal tissues, namely, glycogen. Extracts of the mesenterial filaments showed no digestive action on zooxanthellæ or on any carbohydrate of plant origin. The *Madreporaria* are thus amongst the most highly specialised carnivores in the animal kingdom, being capable only of digesting animal matter with its constituent proteins, fats, and glycogen.

It is improbable that the small quantities of glycogen and fat which can be digested suffice for the energy requirements of the corals, in spite of their relatively low needs. It will be necessary, therefore, to break down proteins by deamination, with a consequent accumulation in the tissues of the nitrogen, phosphorus, and sulphur split off from the protein molecules in this process. This need for the formation of carbohydrate from protein would explain the remarkably dense population of zooxanthellæ in all healthy reef-builders. If the animal is to function with maximum efficiency it must rid itself of these end products of metabolic activity. The excretory

system consists of wandering cells, and though these rid the body of excrement quickly enough for the needs of an individual coral colony, it may well be quite otherwise in the case of a large population.

Coral reefs only maintain themselves owing to their remarkable powers of growth in the face of innumerable adverse factors, of which the power of the sea and the action of diverse boring organisms are the most potent. It is essential, therefore, that they should function with the utmost efficiency, and their powers of growth could not but be impaired were excretory products to accumulate in the tissues. But they possess in the zooxanthellæ the means whereby all excrement is automatically removed practically the moment it is formed (unlike photosynthesis, protein synthesis in plants proceeds in darkness as well as in light), and which increases as the tissues grow and the excretion of nitrogen, phosphorus, and sulphur increases. Coral reefs as a whole are largely a closed system, obtaining their food certainly from the zooplankton in the sea, but adding to the dissolved nutrient substances only when they die or expel surplus zooxanthellæ. It appears by no means improbable that the Madreporaria have attained their present great importance in the economy of marine life in tropical waters owing to the aid given to them

by their contained zooxanthellæ. In their absence the corals would have been unable to overcome the disadvantages inherent in the simplicity of their structure and of their metabolic processes.

The association between corals and zooxanthellæ is, therefore, essential to the plants, certainly not to individual coral colonies, but probably an indispensable factor in the necessarily exceptional powers of growth and repair possessed by the marine communities known as coral reefs.

- <sup>1</sup> Gardiner, *NATURE*, 127, 857; 1931.
- <sup>2</sup> Yonge, *NATURE*, 123, 89; 1929.
- <sup>3</sup> Yonge, *NATURE*, 123, 765; 1929.
- <sup>4</sup> Yonge, *NATURE*, 124, 694; 1929.
- <sup>5</sup> Yonge, "Studies in the Physiology of Corals", I. Feeding Mechanisms and Food. *Sci. Repts.*, G. Barrier Reef Expedition, Brit. Mus., 1, 13; 1930.
- <sup>6</sup> Yonge and Nicholls, II. "Digestive Enzymes". *Ibid.*, 1, 59; 1930.
- <sup>7</sup> Yonge, III. "Assimilation and Excretion". *Ibid.*, 1, 83; 1931.
- <sup>8</sup> Yonge and Nicholls, IV. "The Structure, Distribution and Physiology of the Zooxanthellæ". *Ibid.*, 1, 135; 1931.
- <sup>9</sup> Yonge and Nicholls, V. "The Effect of Starvation in Light and in Darkness on the Relationship between Corals and Zooxanthellæ". *Ibid.*, 1, 177; 1931.
- <sup>10</sup> Yonge, Yonge and Nicholls, VI. "The Relation between Respiration and the Production of Oxygen by Zooxanthellæ". *Ibid.*, 1 (in preparation).
- <sup>11</sup> Keeble and Gamble, *Quart. Jour. Micr. Sci.*, 51, 167; 1907.
- <sup>12</sup> Boschma, *Proc. Akad. Wet. Amst.*, 27, 13; 1924.
- <sup>13</sup> Boschma, *Biol. Bull.*, 49, 407; 1925.
- <sup>14</sup> Boschma, *Proc. Akad. Wet. Amst.*, 29, 993; 1926.

## New Physics Building at the National Physical Laboratory.

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BUSHY House at Teddington, which was erected about 1715 by the first Earl of Halifax, a president of the Royal Society and a pupil of Newton, played a not inconsiderable part in the life of the Royal Family of Great Britain. It was, however, destined to fill, after two centuries, an even larger rôle in the life of the nation. In 1900, after many preliminaries, Bushy House was selected as the future home of the National Physical Laboratory, and in 1902 the Laboratory was formally opened by the present King (then Prince of Wales).

Since that date, under the directorship first of Sir Richard Glazebrook and now of Sir Joseph Petavel, a great part of the extensive grounds of Bushy house has been gradually covered by a large collection of buildings devoted to the requirements of the various departments of the Laboratory. During the last few years, these buildings have overflowed on to land acquired for the purpose in the proximity of Bushy Park. But for more than a quarter of a century, physics, the most comprehensive department of the Laboratory, which indeed gives its name to the whole, continued to be inadequately accommodated partly in Bushy House and partly in a number of converted dwelling-houses on the outskirts of the grounds.

Plans for a new physics building were first got out

in 1924, and a design prepared by Mr. F. A. Llewellyn, of H.M. Office of Works, was exhibited at the Royal Academy in 1927. The proposed building had a frontage of 295 feet with wings 135 feet in length, forming three sides of a rectangle. The construction



FIG. 1.

of the central portion of the building was begun in January 1929, and the formal opening by Sir F. Gowland Hopkins, president of the Royal Society and chairman of the General Board of the Laboratory, took place on June 23 last.

The site of the building, which abuts on Bushy Park on two sides, enjoys immunity from traffic noises and vibrations. The structure is mainly of