obviously closely connected with the rate at which the organisms are able to assist in the migration of chemical elements in the biosphere. This rate, or the geochemical energy of living matter, depends on several specific properties of the organisms, namely, the average weight, the volume and surface of the individual, the rate of reproduction and the rate of dispersal over the earth's surface (Vernadsky[14]). Special methods have been elaborated by the Laboratory for the determination of these constants (Vernadsky[15]; Cholodovskij[3,4]).

Since the fundamental idea behind all the studies which have been directed by Prof. Vernadsky is to understand in a quantitative way the whole immensely complex series of processes connected with dynamic biogeochemistry, it is only natural that some of his publications represent attempts at building up comprehensive theories. Here belongs, first of all, his profoundly philosophical treatment of the whole problem of the biosphere[1], which one would like to see republished, since in the last few years a great number of new facts has been accumulated, and many hypotheses can be either substantiated, or modified. Another remarkable work is the history of natural waters[16], where 485 'species' of water occurring in Nature are distinguished and classified according to their genesis and properties. A general discussion on the geochemical problems in oceanography[17] represents another brilliant summary of a very difficult subject.

Scientific workers who prefer definitely ascertained facts to far-reaching hypotheses may argue that the time is not yet ripe for an all-embracing treatment of living matter as a factor in the history of our planet. No one, however, after acquainting himself with Prof. Vernadsky's work, will be able to doubt that such a treatment is not only thoroughly scientific, but also is already yielding important results bearing a promise of establishing surprising interrelations between the so-called inorganic and organic worlds. It is a matter of deep regret that most of the publications by Prof. Vernadsky and his school are in a language which prevents his views from becoming more widely known amongst biologists, chemists and geologists, for all of whom they open new and promising fields of study.

B. P. UVAROV.

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Origin and Nature of the Association between Invertebrates and Unicellular Algæ

By PROF. C. M. YONGE, University of Bristol

THE widespread occurrence of zoochlorellæ or zooxanthellæ within the tissues of invertebrates is now universally recognised, the extent of knowledge on this subject up to 1930 being well summarised by Buchner[1]. Nevertheless the actual nature of this association, or rather of the many forms which this may take and the connexion between these, is greatly in need of clarification. It is unfortunate that of the many workers in this field none, save Brandt, one of the earliest, has studied conditions in more than one or two groups. My own work on the comparative physiology of digestion and on symbiosis between zooxanthellæ and Anthozoa and Mollusca, together with a critical examination of recent, largely experimental, work on this type of symbiosis, has enabled me to throw some light on the origin and nature of this association.

Association with unicellular algæ is almost certainly confined to animals which digest intracellularly. This has been suspected by many workers, but confirmation has had to await the full elucidation of the conditions of digestion throughout the invertebrates (see Yonge[2] for a summary of the present state of knowledge). Unicellular algæ occur in Protozoa, Porifera, Cœlenterata, Ctenophora, Turbellaria, Rotifera, Gastropoda and Lamellibranchia, all of which digest intracellularly. The conditions both of symbiosis and of digestion in Polyzoa and Echinodermata require further investigation. Zooxanthellæ do occur in compound Ascidians from tropical seas as recorded, for example, by Hastings[3] in a number of species collected by the Great Barrier Reef Expedition, but Mr. H. G. Smith, to whom I recently gave these for examination, finds that the algæ are confined to the common test and never occur in the actual tissues. Berkeley[4] has recently definitely established that a green flagellate occurs in the Chætopteridæ which, like all Annelida, digest extracellularly. The work of Wilson[5], who found indications of intracellular digestion during the metamorphosis of *Owenia*, affords a possible explanation of the origin of this association.

A survey of the animals which contain algæ reveals that some of these are carnivores, notably the Cœlenterata, the Turbellaria and those Gastropoda which harbour algæ, while the others are omnivorous or definitely herbivorous, such as the Protozoa, Porifera and Lamellibranchia. The association with algæ would appear to have arisen in different ways in these two groups.

In the carnivores (Cœlenterates, in particular, are such specialised carnivores that they will neither accept nor ingest plant matter) the association was originally probably one of parasitism by the plant. This is strongly indicated by the very beautiful work of Gœtsch[6] on the association of algæ (Chlorellæ) with the Hydrida. *Pelmatohydra* and *Hydra circumcincta* never contain algæ. Spontaneous infection by algæ has been observed in *Hydra vulgaris*, and Gœtsch was able to bring about artificial infection and maintain this so long as conditions remained suitable for the algæ, which were, however, confined to certain parts of the body. In *Hydra attenuata*, artificial infection was easier, and the algæ spread more extensively throughout the tissues, becoming increasingly difficult to dislodge as time passed. Finally, according to Gœtsch, they so affect the tissues of the host animal as to form a new race, *Hydra viridescens*, where the association may be regarded as a true symbiosis. In both *H. vulgaris* and *H. attenuata*, infection is preceded by an enfeeblement of the animals and is accompanied by pathological symptoms indicating a definite parasitism by the plant. In *Chlorohydra viridissima*, there is a permanent and normal association with algæ, which are extremely difficult to remove experimentally from the tissues, the colourless animals so obtained being very easy to reinfect and actually taking in other algæ (*Oocystis*) if Chlorellæ are not available. In *Chlorohydra* alone are the algæ transmitted from generation to generation by way of the egg.

Gœtsch's work probably gives the key to the final establishment of symbiosis between carnivorous animals and algæ. An initial stage of parasitism by the plant is followed by the establishment of tolerance by the animal and later, as in *Chlorohydra*, the algæ are normally always present. Nevertheless, as Gœtsch and Van Haffner[7] have shown, *Chlorohydra* can, under appropriate conditions, flourish when deprived of the algæ. Van Haffner has shown that very similar conditions prevail in the freshwater Turbellarian, *Dalyellia viridis*. Further examination of conditions in the Cœlenterata and the Turbellaria reveals that one of two things may happen. The animal may become dependent on the plant, which still remains capable of an independent existence, or the plant becomes dependent on the animal, being specialised exclusively for life within its tissues, while the animal continues to feed normally.

The first of these alternatives is exemplified in the well-known case of *Convoluta roscoffensis* (Keeble and Gamble[8]) where the animal finally ceases to collect food and preys on the contained algæ which, though they become modified within the tissues of the animal, are members of the free-living genus *Carteria*. *Convoluta paradoxa* (Keeble[9]) occupies an intermediate position between *Dalyellia* and *C. roscoffensis*. The second alternative is exemplified by conditions in the reef-building corals (Yonge and Nicholls[10,11]) where the zooxanthellæ are never found free in the sea, have apparently lost the capacity for sexual reproduction, and have acquired a very thick cellulose wall. The animals are not only capable of feeding normally, but actually display all manner of adaptations for this. They certainly *never* digest the zooxanthellæ. Similar conditions probably prevail throughout the Anthozoa (and possibly the Scyphozoa), the opposite conclusions of Brandt[12] for anemones being open to question (his results are being reinvestigated).

Turning to the origin and establishment of symbiosis in herbivorous animals, the best indication of the preliminary stages appears to be furnished by the work of Van Trigt[13] on the Spongillidæ. Here the algæ (*Pleurococcus*) are taken in by the collar cells and passed into amœbocytes. Under favourable conditions they maintain themselves for a time but, should other food fail, they are quickly digested. The algæ are apparently capable of no more than prolonging existence for some time under conditions in which other algæ are immediately killed and digested. An increased resistance to the digestive activities of the animal may well have led to the establishment of conditions such as those recorded by Pringsheim[14] and Parker[15] in *Paramecium bursaria*. Here a very well-balanced condition has been established, the infected animals being capable of existing in the light autotrophically for a long period, so long as the necessary nutrient salts and calcium are present. Only in extreme cases are the algæ digested by the animal, which is, however, capable of living without them, feeding on algæ, bacteria and especially yeasts.

Symbiosis may also be established by the transference of an alga, already specialised for such an existence, from one type of animal to another. Naville[16] has recorded the interesting case of the Nudibranch, *Æolidiella alderi*, which feeds exclusively on the Actinian, *Heliactis bellis*, which contains zooxanthellæ. Not only are the nematocysts in the cerata of the mollusc identical with those of the anemone but also the same zooxanthellæ flourish in the ingesting cells of the 'hepatopancreas'. The zooxanthellæ in the test of compound Ascidians (which appear to be identical with those of corals and other reef-dwelling Anthozoa) may well be derived in the first place from those contained in planulæ, being in some manner incorporated in the common test during the growth of this. In the Tridacnidæ, where is found one of the most striking cases of dependence by animals on contained algæ, the animal literally 'farming' the plants in the thickened mantle edges (Yonge[17]), the zooxanthellæ may also in past time have been acquired from planulæ.

A study of the nature of the association as it exists in different animals at the present day reveals, as the foregoing account has already indicated, many gradations. This can most conveniently be reviewed by discussing first the possible advantages gained by the algæ and then those gained by the animals.

The algæ obtain protection once they have succeeded in establishing themselves. They obtain ample supplies of carbon dioxide, which would probably always be available, but, more important, also of nitrogen and phosphorus. Many of the early workers in this field emphasised the significance of 'nitrogen hunger' in the sea, but this is no more important, as we now know, than 'phosphorus hunger'. In the reef-building corals, not only is all the phosphorus liberated by the animals immediately utilised by the zooxanthellæ, but phosphorus is also taken from the surrounding water even though the content has been artificially increased to a very high figure (Yonge and Nicholls[10]). The algæ in *Convoluta* can utilise uric acid or urates, but these algæ when living free in the sea may normally feed saprophytically.

In other cases also the algæ appear capable of existing to some extent saprophytically within the bodies of the animals. Thus Pringsheim has found that the Chlorellæ in *Paramecium bursaria* not only survive but also may actually increase in darkness, provided that the animals are well fed. Since the algæ cannot photosynthesise under these conditions, it is clear that they must obtain organic matter from their hosts. Van Haffner has come to similar conclusions in his work on the Chlorellæ contained in *Chlorohydra viridissima*. He states that they may increase in darkness and that they are always especially numerous and increase most rapidly in those regions of the animals where carbohydrate is most abundant. In correlation with this tendency to saprophytic nutrition he finds that the Chlorellæ within the animals have smaller pyrenoids than those which are free-living. The conditions here, therefore, are somewhat akin to those in *Convoluta roscoffensis*.

The advantage which the association brings to the animals also varies very greatly in different cases. In the presence of light, oxygen is continually being formed by the algæ. In corals and other Anthozoa this may, during the middle of the day, be greatly in excess of the amount used by the animals and plants in respiration (see Yonge, Yonge and Nicholls[18]). But it is noteworthy that few workers, though all have mentioned the production of oxygen, lay much stress upon it. Though it has been proved in many instances that, under experimental conditions, 'green' animals will survive for longer periods in deoxygenated water in the light than will 'colourless' animals of the same species, yet it is almost universally admitted that such conditions would seldom, if ever, be encountered by the animal in Nature.

There is also universal agreement that the plants make use of the end-products of animal metabolism, notably carbon dioxide, nitrogen and phosphorus, and that this automatic removal of excrement may be of great advantage to the animal. There can, as already stated, be no doubt that this occurs, though its actual significance in the life of the animals is more difficult to assess. In *Convoluta roscoffensis* and *C. paradoxa* its great significance is placed beyond question by the absence in these animals of organs of excretion. In Protozoa, Porifera and Cœlenterata organs of excretion do not occur, so that this test cannot be applied. I have previously summarised in NATURE (Yonge[19]) my reasons for thinking that, though individual corals can live well without contained zooxanthellæ, yet, because of the help they give by automatically removing the end-products of metabolism, the zooxanthellæ are "probably an indispensable factor in the necessarily exceptional powers of growth and repair possessed by the marine communities known as coral reefs".

The most disputed point of all is the extent to which the algæ provide food to their hosts. The animal may obtain food from them in one of three ways. In the first place, organic matter (notably fats and carbohydrates) may pass from the living algæ to the tissues of the animal. Pringsheim has shown that this must be the explanation for the autotrophic mode of life possible to green *Paramecium bursaria*. Brandt[20] came to similar conclusions in his work on colonial Radiolarians, stating that starch passes from the living zooxanthellæ into the protoplasm of *Sphærozoum*, *Acanthometra* and *Siphonosphæra*. Famintzin (quoted by Buchner), on the other hand, thought that this starch was derived from degenerating algæ. This matter requires, as Buchner has observed, further investigation. In *Chlorohydra* Gœtsch has shown that green individuals will survive starvation in the light for about four months, whereas colourless individuals live for only half this time. He inclines to the view that organic matter, in particular fat, is passed from the algæ to the animal under such conditions, but Van Haffner comes to the opposite conclusion both for *Chlorohydra* and *Dalyellia*. He does think, however, that degenerating algæ may be used as food by the animal. In *Convoluta roscoffensis* and *C. paradoxa* there is an undoubted passage of fat from the algæ to the tissues of the animals, during the early stages of the association. Keeble and Gamble have figured the process and I have myself prepared sections of *Convoluta roscoffensis* which confirm their statements.

The second alternative is that the animals digest the algæ after these have, for some reason or other, probably starvation, died in the tissues. Van Haffner is the only author who has laid great stress on this, but it may be of considerable significance. It does not, however, follow that a degeneration of the algæ necessarily means that they are digested; for in corals, degenerating algæ are continually being ejected from the body of the animal by way of the mesenterial filaments (and the process can be very greatly increased by subjecting the corals to excessive heat, lack of oxygen or starvation) but these are *never* digested. A starved coral will live no longer in light than in darkness (Yonge and Nicholls[11]).

Finally there remains the possibility that living algæ are killed and digested by their hosts. In extreme cases this occurs, according to Pringsheim, in *Paramecium bursaria*. In the Spongillidæ it continually occurs, as Van Trigt has shown, while I have found that it is an equally normal process (and a more essential one) in the Tridacnidæ. But all of these animals are naturally herbivorous and the powers of resistance to digestion by the algæ are limited, particularly in the Spongillidæ. In *Convoluta roscoffensis* and *C. paradoxa* the algæ are certainly digested, the former species finally losing the power of feeding altogether, and becoming completely parasitic on its contained algæ. This appears to be the only case of an animal which becomes completely dependent on the algæ for nutrition.

Several points of interest emerge from this discussion on the possible food value to the animals of the algæ. One is that in herbivorous animals the power to resist digestion by the animal entails specialisation on the part of the algæ (for example, in *Paramecium bursaria*); another is that the ability to feed on the algæ represents a specialisation on the part of the carnivorous animals such as *Convoluta*, though in this case the absence of a cellulose wall around the algæ is possibly of significance. The presence, on the other hand, of an exceptionally stout cellulose wall around the zooxanthellæ of corals and other Anthozoa possibly explains the inability of such animals to obtain nutriment from these even after they have died in the tissues. In *Tridacna*, where the zooxanthellæ are otherwise very like those of the corals, I have been unable to find so thick a cellulose wall. The passage of organic matter from the algæ to the host, as in *Paramecium* and *Convoluta*, probably involves specialisation by the plants, but it also indicates that these are in a position to produce more food than they need themselves for maintenance and multiplication. In the corals the endoderm is invariably packed with zooxanthellæ (as many as 25,000 may occur in a single planula of *Pocillopora*) and these increase as the coral grows. There is never likely to be any superfluity of food under these conditions; indeed, as already stated, the zooxanthellæ will extract phosphorus from the surrounding water.

This summary will have indicated, if nothing else, that the nature of the association between animals and unicellular algæ varies greatly in different cases. If by symbiosis is meant only a relationship which is mutually advantageous to both parties, then the only adequately investigated cases which meet this requirement are *Paramecium bursaria*, *Chlorohydra* and the reef-building corals (and probably all Anthozoa). In every other instance, one party in the association is exploited in some measure by the other.

In conclusion, I wish to record my thanks to the Royal Society of London for a grant which has assisted the investigations from which many of these conclusions have been drawn, and also to Mr. H. G. Smith for kindly permitting me to mention the results of certain unpublished work.

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Obituary

PROF. A. P. CHATTOCK, F.R.S.

PROF. ARTHUR PRINCE CHATTOCK, emeritus professor of physics in the University of Bristol, died at his home in Clifton, Bristol, on July 1 at the age of seventy-three years. Educated at University College School, University College, London, under Carey-Foster, and at Stuttgart, he started his career as an electrical engineer in the firm of Siemens. In 1885, however, he was appointed as the first lecturer in physics in University College, Bristol. He spent the following year in Liverpool under Sir Oliver Lodge and then returned to Bristol to take up the duties of a newly created chair in this subject.

From 1887 until 1910 Prof. Chattock was known to a generation of students of physics at Bristol as an inspiring and self-sacrificing teacher, and to his contemporaries as an experimenter who, despite meagre facilities, carried out pioneer work of the first rank. Among these researches may be mentioned that on the mobility of gaseous ions, and the Chattock-Fry pressure gauge originally designed for the work of Stanton on the wind pressure on structures, and later incorporated in wind tunnel measurements. An ingenious magnetic potentiometer devised by him deserves notice, as also an attempt, though negative in result, to verify Weber's theory of electromagnetism.

The foundation of the University of Bristol in 1909 brought additional responsibilities to his office. Modest and retiring almost to a fault, Prof. Chattock felt that he could not face them, and to the great regret of his colleagues, both lay and academic, he retired from his post to live in the country. There he stayed for ten years, engaged in poultry farming and on work for the Ministry of Agriculture on the physics of incubation.

In 1920, however, Prof. Chattock was induced to return to the University laboratories for a few years under the terms of his emeritus professorship, with facilities for continuing his researches in physics. In this later period, he carried out with L. F. Bates a classical determination of the gyromagnetic effect in iron. This, coupled with later work by Bates and Sucksmith, and more recently on paramagnetic substances by Sucksmith in the