ELECTRON MICROSCOPY AND ALGOLOGY*

By T. V. Desikachary, F.A.Sc.‡

(*University of Saugar, Sagar, M.P.*)

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In 1936 the first alga, a diatom, was photographed with the electron microscope, by Krause. Since then more and more algæ from the Chlorophyceæ, Chrysophyceæ, Bacillariophyceæ, Cyanophyceæ and Phæophyceæ have been studied using this powerful tool. Among the specific aspects under intensive study may be mentioned wall structure, flagellar structure and the structure of the chloroplasts, chromatophores and pyrenoids. These investigations with the aid of the electron microscope (hereafter cited as EM) have already contributed a great deal on the micromorphology of algæ. In many cases they have supplemented observations with the optical microscope while in a few cases they have supplanted the latter. Some of the important contributions in this new and fascinating field of research are reviewed here with a view to understand the full import of these investigations into the micromorphology of algæ.

Wall Structure

Bacillariophyceæ.—Kolbe and Gölz (1943), Gerloff and Gölz (1944), Hustedt (1945, 1952), Kolbe (1948, 1951, 1954), Helmcke and Krieger (1951 *a*, 1951 *b*, 1951 *c*, 1951 *d*, 1952 *a*, 1952 *b*, 1952 *c*, 1952 *d*, 1953, 1954 *a*, 1954 *b*), Okuno (1944 *a*, 1944 *b*, 1947, 1948 *a*, 1948 *b*, 1949 *a*, 1949 *b*, 1950 *a*, 1950 *b*, 1951, 1952 *a*, 1952 *b*, 1952 *c*, 1953 *a*, 1953 *b*, 1953 *c*, 1953 *d*, 1954 *a*, 1954 *b*, 1954 *c*, 1954 *d*, 1954 *e*, 1954 *f*, 1955 *a*, 1955 *b*), Desikachary (1952, 1954 *a*, 1954 *b*, 1954 *c*, 1956), Desikachary and Aleem (1955), and Desikachary and Kanwar Bahadur (1954 *a*, 1954 *b*, 1954 *c*) have studied a large number of diatoms for the structure of the areolæ, striæ, spines, etc. Hustedt (1945, 1955), Kolbe (1948), Okuno (1953 *c*) and Desikachary (1954 *c*) have summarised the results of these different studies and their bearing on the classification of the areolæ. Kolbe (1951), Helmcke and Krieger (1952 *b*, 1953, 1954 *a*) and, Fott and Rozsival (1950) have described the canal raphe of Nitzschiaceæ and Surirellaceæ. A full review of these investigations has been published by the present writer (1956).

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‡ Now at the University Botany Laboratory, Madras-5.

Chrysophyceæ.—The structure of the scales in Chrysophyceæ (Manton, 1955; Parke, Manton and Clarke, 1954, 1956; Asmund, 1955; Houwink, 1951, Petersen and Hansen, 1956) and in particular of the coccoliths (Braarud, 1954 *a* and 1954 *b*; Braarud and Nordli, 1952; Braarud, Gaarder, Markali and Nordli, 1952; Gaarder, Markali & Ramsfjell, 1954; Gaarder & Markali, 1955 *a*; Halldal and Markali, 1954 *a*, 1954 *b*; Deflandre and Fert, 1952; Downie and Honeycomb, 1956) have been, probably for the first time, described in very great detail with the help of the EM. Based on these EM studies Braarud, Deflandre, Halldal and Kamptner (1955) give a new classification of the coccoliths. They distinguish three main types of coccoliths: I. Holococcoliths, *e.g.*, crystalloliths from *Crystallolithus hyalinus*, calyptroliths from *Sphærocalyptra papillifera* and zygoliths from *Homozygosphæra triarch*, II. Heterococcoliths, *e.g.*, cricoliths from *Hymenomonas carteræ*, cyrtoliths from *Anthosphæra* and *Discosphæra tubifer*, caneoliths from *Syracosphæra mediterranea*, placoliths from *Coccolithus huxleyi* and scapholiths from *Anoplosolenis brasiliensis*, and III. Pentaliths, *e.g.*, *Braarudosphæra bigelowi*. The same classification was further enlarged by Halldal and Markali (1955) who also give a full list of coccoliths studied so far. These two authors recognise in addition to the above two more types of coccoliths, *viz.*, Lepidoliths from *Thorosphæra flabellata* and Cribriliths from *Pontosphæra discopora*.

Chlorophyceæ.—The fibrillar structure of the wall, their lamellation and their relation to the inner protoplasmic contents as well as their chemical composition were studied by Preston and Nicolai and their collaborators (Preston and Kuyper, 1951; Preston *et al.*, 1953, 1948; see also Preston, 1954 especially, pp. 91–112) in a number of green algæ belong to the cœnocytic orders. These investigators have observed evidences which have some taxonomic significance. In *Pediastrum* spp. Moner (1955) has observed the cell-wall to be made up of two layers, a continuous internal membrane and a hexagonally reticulate layer on the outside.

Cyanophyceæ.—The structure of the sheath in the blue-green algæ has been studied by Bringmann (1951), Frey-Wyssling (1954) and Singh (1954). According to Singh the sheath in *Scytonema pseudoguayanense* consists of a two directional arrangement of cellulose fibrils in a menstrum of proteinaceous material.

A dinoflagellate, *Exuviella baltica*, was studied recently by Braarud, Markali and Nordli (1955; see Braarud, 1955) and they have observed the presence of small spines on the wall.

FLAGELLAR STRUCTURE

The studies of Manton and her collaborators (Manton, 1952, 1953, 1955; Manton and Clarke, 1951 *a* and *b*; Manton *et al.*, 1952) on the structure of the flagella in some flagellates and also in the reproductive bodies of certain algæ are classical examples illustrating the limits of the optical microscope and the potentialities of the EM in the ultramicroscopic studies of algæ. The structure of the flagellum as described by them (see Manton, Clarke and Greenwood, 1953, Text-Figs. 1–3) with 9 peripheral fibrils and two axial fibrils, probably, is the basic pattern of the structure of the flagellum in all the flagellates with variations (see Manton *et al.*, 1953, p. 328). The structure of the flagellum in *Synura* was studied by Manton (1955) and in six species of *Chrysochromulina* by Parke, Manton and Clarke (1954, 1956). The latter authors have also described the structure of what was for a long time known as the third flagellum, 'Haptonema', and have shown clearly how far the observations made with the optical microscope had gone wrong. Lewin and Meinhart (1953) have described in great detail the role of the flagella in mating in *Chlamydomonas mœwusii* and the formation of a protoplasmic bridge between copulants during mating. Petersen and Hansen (1954) have described the collar in *Codonosigia botrytis* as a ring of very fine protoplasmic tentacles or threads. Among the many other studies on flagella may be mentioned also those of Chen (1949), Houwink (1951), Brown (1951) and Astbury and Saha (1953).

CHLOROPLASTS AND PYRENOIDS

Chloroplasts or chromatophores and pyrenoids have been studied in a few algæ such as *Spirogyra*, *Euglena*, *Enteromorpha intestinalis*, *Cladophora glomerata*, *Mougeotia* sp., *Closterium acerosum* and *C. lunula* (Steinmann, 1951; Wolken and Palade, 1952, 1953; Leyon, 1954). According to Leyon the pyrenoids occur in chloroplasts which do not have the well-known 'grana'. The pyrenoids themselves, are lamellated, the lamellæ being three to four times as thick as and continuous with the lamellæ of the chloroplast. The arrangement of the lamellæ in the pyrenoids is varying in different algæ. The work of Leyon has to be followed up by investigations on diverse other algæ, especially the chloroplasts of such related algæ as *Ulothrix* and *Microspora* with or without pyrenoids, and if proved to be true of many others too, a change in the concept of the structure of the pyrenoids, etc., as is now known from the work on light microscope (see Fritsch, 1935, 65) would seem necessary.

Electron Microscopy and Taxonomy

The impact of these investigations on the microstructure of algæ has been pointed above. There is however one point which is being much debated at present, *i.e.*, the utilization of the microstructure as observed with the EM in taxonomy, and indeed taxonomists have expressed divergent opinions on the subject as is apparent from selected literature referred to below.

Kolbe (1948, 1951) and Helmcke and Krieger (1954 *a*) have effected taxonomic changes based on evidences from EM studies. Desikachary (1952 and 1956) envisages their utilization in taxonomy and suggests that identification be based on gross or major characters assessed by the light microscope and confirmed by studies of the minute characters with EM. However, Hustedt (1952, 1955) doubts their taxonomic value. It seems hardly necessary to emphasize that a right understanding of the details of the areolar structure will lead to a correct and precise concept of genera and species and in any event be a check on the creation of new and doubtful taxa on meagre evidences. The real identity of *Nitzschia closterium* f. *minutissimum* (see Hendey, 1954) is a revelation made possible only by the EM. A large amount of our present knowledge of the physiology of the diatom is based on this organism and is in need of revision.

The taxonomy of coccolithophorids is based on the structure of the coccoliths. On account of their very minute size it has not been possible to have a satisfactory and complete picture of their structure, even with the most advance optical equipment. This handicap has been cause for a great amount of confusion in their classification. Braarud and Nordli (1952) have shown by EM studies of the coccoliths that *Pontosphæra huxleyii* includes three distinct species one of *Gephyrocapsa* and two of *Coccolithus* and none of *Pontosphæra* itself. In other cases too the coccoliths have been found to be different from that known from studies with the light microscope. For example, *Syracosphæra carteræ* Braarud et Fagerland has been known to have discoliths (Schiller, 1930) but has been shown to have tremaliths type of coccolith by EM studies. Braarud (1954) based on a study of *Hymenomonas* found a similarity in structure of the coccoliths of *Hymenomonas roseola* and *Syracosphæra cartaræ* and transferred the latter to the former genus as *H. carteræ*. Braarud *et al.* (1952) are of the view that further studies in the EM of other coccolithophorids may reveal many details of the coccolith morphology that a new coccolith classification may be necessary and possibly also a reclassification of the Coccolithophoridaceæ (see also Deflandre and Fert, 1952 and Braarud *et al.*, 1955). Braarud (1954 *a*) feels that many other taxonomic questions within the group may have to be reconsidered when further studies have given a more satisfactory basis for evaluating the various characters for a taxonomic distinction between the species and genera of coccolithophorids. Halldal and Markali (1954 *b*) have recognised the importance of these studies. " During the short period electron microscopy has been used in the investigation of coccolithophorids it has become apparent that the taxonomy of the group needs to be reviewed on several points. However, far more observations are needed to obtain satisfactory rearrangement of the species." It has seemed to these authors (1954 *a*) especially worthwhile to study in the EM coccoliths of cells which are first examined in the light microscope and identified according to present-day monographs.

Halldal and Markali (1955, p. 20) write that the inclusion of Electron micrographs of coccoliths in the classification appear to them to be mandatory.

Parke *et al.*, (1954, 1956) in their studies with *Chrysochromulina* spp., observed certain characters which introduced some doubt in the specific identification by the light microscope. But they refrain from establishing genera and species on characters which cannot be seen with the light microscope.

Petersen and Hansen (1956), in their studies on *Synura* spp., say that in future it will be necessary to make use of electron micrographs of scales in order to determine the species with adequate precision.

Braarud (1955) in a recent paper has ably summarised the probable use of these studies in the taxonomy of marine plankton.

Thus it may be seen from the above that opinions of taxonomists in the matter of utilization of the results of EM studies in micromorphology in different groups of algæ vary from scepticism to one of extreme enthusiasm for the new structural knowledge gathered by using this powerful tool. There are still workers who would like to use these evidences with reservations. The present need is probably to first collect complete and extensive data based on studies with the EM of species and genera determined earlier with the help of light microscope. Only then we would be in a position to evaluate them to yield a reasonably workable synthesis of characters derived both by light and electron microscopic studies as may serve in taxonomy.

SUMMARY

Since 1936, when the first alga was investigated with the help of the Electron Microscope more and more algæ have been studied. These studies have greatly contributed to our knowledge of the submicroscopic morpho-

logy of algæ. A review of the most important aspects of these investigations is given in this paper.

The utilization of the results of these Electron Microscopic investigations in taxonomy is discussed.

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