An Outline of Phycology in Denmark

The Second International Phycological Congress · 1985

Cover illustration: The oldest picture of algae published in Denmark. From Ole Borch: 'Plantae in planis silicibus enatae' (in Thomas Bartholin: 'Acta medica et philosophica Hafniensia', vol. I, 1671/72, Kbn. 1673). *Quercus marina* is obviously *Fucus vesiculosus*. The *Furcellaria*-like species is most probably the remnant of a *Fucus*. According to Borch *Linum marinum* is Rokkesnore, an old Danish name of *Chorda filum*.

An Outline of Phycology in Denmark

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Copenhagen, 4-10 August 1985

Introduction

Although Denmark is a relatively small nation, it has made and continues to make, significant contributions to phycology. Lyngbye, Kolderup Rosenvinge and Børgesen were Danish phycologists who are still known to almost every algal taxonomist. The history of these people and their work is fascinating. Leafing through 'Tentamen Hydrophytologiae Danicae', which was the most important work of Lyngbye and which was published in 1819, one is impressed by his thoroughness and clarity. In studying his manuscripts in which the illustrations have been coloured by hand, his specimens in small envelopes, and the diaries of his travels, written in neat almost microscopic handwriting, one is able to follow his thoughts almost as if he were alive today. This shows us that outstanding observations do not need sophisticated instruments, but may equally be the product of a keen eye and an enquiring mind.

For details of his work, and that of other Danish phycologists, reference must be made to the bibliography. What follows is a short description of the more important Danish phycologists and their major contributions, placed in the context of the conditions under which they worked.

Area Studied

The Danish parliament today represents the territories of Denmark, the Faroes and Greenland. In the period covered here, Danish influence has also extended to Norway, Iceland, South Schleswig and Holstein (now part of the Federal Republic of Germany), three islands in the West Indies, a small territory on the Gold Coast etc. It is little wonder, then, that the publications of Danish naturalists relate to a wide geographical range. None-the-less, Denmark proper, between the North Sea and the Baltic, has been the region most studied by Danish phycologists.

The gradual transition in salinity from the waters of the North Sea (in Danish 'Vesterhavet') (30 to 35 ‰) to that of the Baltic Sea (Østersøen) (5 to 10 ‰) around the island of Bornholm, offers a region of special interest for phycologists. Some of the larger marine algae penetrate into the Baltic but become very reduced in size or occur in the deeper waters with increasing salinity. Other such algae have inner limits of distribution at Skagerrak, Kattegat or the Sound and the Belts (the waters which connect the North Sea with the Baltic). Sites for larger marine algae are limited by the absence of rocky shores except at Bornholm. Stone reefs, scattered boulders and man-made structures provide sites of attachment for more conspicuous forms. In contrast, sites for microscopic algae which do not require a firm substrate are numerous and varied. Greenland, the Faroes and some of the territories no longer forming part of the Danish kingdom, are richer in rocky shores. Their algal vegetation has been studied extensively by scientists from the University of Copenhagen.

The algal vegetation of freshwater Danish lakes and ponds is abundant and diverse. There is a distinct geographic boundary through Jutland which follows the front margin of the last glaciation (about 18 000 years ago). Many such waters now suffer from pollution and from the use of fertilisers on the surrounding land. Running waters are not only affected by pollution, but have often had their courses artificially straightened. A few water courses remain relatively undisturbed.

The pre-Linnean period

There was clearly some awareness of algae in northern Europe by the end of the Viking Age. The oldest familiar description of an alga can be found in an Icelandic saga: Egil Skallagrimson's 'Sønnetabet' (The loss of a son). This derives from the Edda legends which were originally passed on verbally, and were only written down at a later date. In this saga, Egil is determined to die of hunger in his sorrow over the death of his son. However, his daughter prevents this by persuading him to eat 'Søl' (*Palmaria palmata*). This made him so hungry and thirsty that he changed his mind. Pre-scientific knowledge of algae also existed in other Nordic countries, and algae are even mentioned in Eskimo legends which date from before the European discovery of Greenland.

The oldest medical manuscripts and printed herbals date from the 12th to the 16th centuries. A 'Fucus' is mentioned in these. The name used to be applied to many algae and a firm identification is not now possible. Since the Danish books were mostly translations of foreign (especially German) herbals, the name must have referred to a common, widespread and easily recognizable species, such as *Fucus vesiculosus*. The name *Alga marina* which is mentioned several times seems, from its context, to refer to *Zostera marina*.

During this period, and on into the 17th century, botanical publications in Denmark were dominated by those relating to the use of plants in medicine and cooking. The first evidence in Denmark of scientific reasoning relating to the algae may be ascribed to Ole Worm (1588-1654). He was Professor of Medicine etc. at the University of Copenhagen. As this was before the publication of scientific journals, Worm kept up a lively correspondence (amounting to 1793 letters). One letter written in 1648 by the Dutchman Jan de Laet, asks Worm's advice about *Plantae petreae*, algae which grow on rocks. Worm

Ole Worm

replied that 'It is amazing how something can grow from a hard and firm rock without the roots being attached inside it; merely with the aid of a widening of the stem and fibrils which penetrate into minute openings they cling with such stubbornness to the rocks that they cannot without considerable effort (even when dried) be torn off. And what is yet more remarkable is their ability to absorb so much nourishment from the firm and sapless rock that they are able to grow to a height where they can be seen. Neither can we say that they grow by absorption of solid particles. Thus their sap must be formed by the salinity of the ocean, its foaminess and stickiness, which is absorbed at the foot of the plant and is then gradually distributed through it all to be used as nutrition and for growth. However, as to the fact that they are usually observed as having a compressed shape, i.e. the branches do not grow in all directions as on terrestrial plants, but only in two, I do not know whether I should ascribe this to the movement which occurs with the advancing and receding motion of the waves. But these matters require further discussion and closer examination'. It never occurred to him that the algae might absorb nutrients through their entire surface.

Stimulated by the discovery of new continents, it became fashionable among the nobility and cognoscenti of Europe to collect natural and ethnographical objects. These included stones and various curiosities of natural or man-made origins. In Denmark, Ole Worms's collection was the largest and the first to become well known. The illustrated index of his collection was printed in 1655 as a folio called 'Museum Wormianum' and became known throughout Europe. It is for this reason that collections elsewhere became known as 'museums'. Some algae are mentioned in the 'Museum Wormianum' and these are the first Danish phycological exhibits. Unfortunately, they have not been preserved for posterity. They were fragile and, as with the rest of the collection, they were used, and worn out, during lessons at the University. Almost all of the objects, once held in the collection of the Natural History Department, have disappeared.

Worm was aware of the green balls formed by *Cladophora aegagropila* and which occurred in Lake Sorø in Sealand. He thought this 'Pila stagnalis' to be entangled moss and plant fibres.

Worm's contemporary, Joachim Burser (1583-1639) was German by birth but he was Professor of Medicine and Natural History at Sorø. He also collected *Cladophora aegagropila* from Lake Sorø and thought it to be a living plant. His material has been preserved and is depicted with a note of explanation in his Danish plant collection. The

collection and his 25 volume 'Hortus Siccus' is now kept in Uppsala (Sweden). The 'Hortus Siccus' has reference to *Laminaria saccharina, Fucus serratus, Chorda filum* and *Ulva lactuca* from Danish shores. The first two are also described in his friend Bauhin's 'Pinax', and these are the oldest taxonomic descriptions of Danish algae.

Other early samples of algae are to be found in Christopher Heerfordt's herbarium of Lolland-Falster which dates from about 1656. It includes the algae *Chara baltica* and *Chara aspera* as 'Aparine maritima'.

Ole Borch

Worm's speculations about the nutrition of algae were developed by Ole Borch (1626-1690) in 'Plantae in planis silicibus enatae' (plants which grow on stone surfaces). This appeared in the first volume of Denmark's first scientific periodical (Acta Medica & Philosophica Hafniensia), published in 1673. It is clear that he was aware that rock-plants on land, and algae in water, simply use the rock as a substrate for attachment. It is this to which the first 'shoots' attach themselves with 'the root' transforming into a disc which holds the plant securely. For examples, he mentions *Quercus marina* (*Fucus vesiculosus*) and *Linum marinum* (*Chorda filum*). He argues that algae must be able to absorb nutrients through their entire surface, by means of small pores which exclude sea-salt (because, when algae are burnt, sea-salt is not found in the lye formed from their ashes). In the same journal, Ole Borch mentions 'Alga Saccharifera' (*Palmaria palmata* (sic!)) from Iceland, and its excretion of sweet-tasting substance when it dries.

The economic period

In the subsequent century, progress in natural sciences came to a halt or even regressed as a result of war expenses and the lack of understanding of successive governments. It was not until the middle of the 18th century that trade, technical inventiveness etc. began to prosper. The outstanding example set by Linné from Sweden was one to be followed. Science was now to be promoted and employed for the benefit of society. The Age of Enlightenment had begun.

Peter Forsskål

Both King Christian IV (died 1648) and one of his successors, King Frederik V, invested in art and science. King Frederik V financed an ill-fated expedition to Arabia (1761-1767) during which all participants, with the exception of Niebuhr, perished. Among those who died was P. Forsskål, a Swedish-Finnish naturalist on service in Denmark. His abundant collections from the middle-East include the first marine algae from that region. The 36 species were later identified and named by Vahl, Mertens, Agardh, Zeller, Børgesen and modern specialists. Forsskål was very industrious. He even collected algae on his way along Øresund. He discovered that sea-water, strained through fine linen, could be made to emit light for several nights. Although he had brought a primitive microscope, he could not see the dinoflagellates which undoubtedly were the cause.

The German botanist, G.C. Oeder, was appointed the royal botanist in Denmark in 1753. He was the first full-time professor to be appointed at the court or at the university. He immediately began to plan a great 'Flora Danica', and this work extended to 17 volumes published between 1761 and 1883 and involved 11 editors. 290 algae are described with varying degrees of exactness, depending on the editor. Otto Friedrich Müller (1730-1784) described many of these including small algae. Those requiring

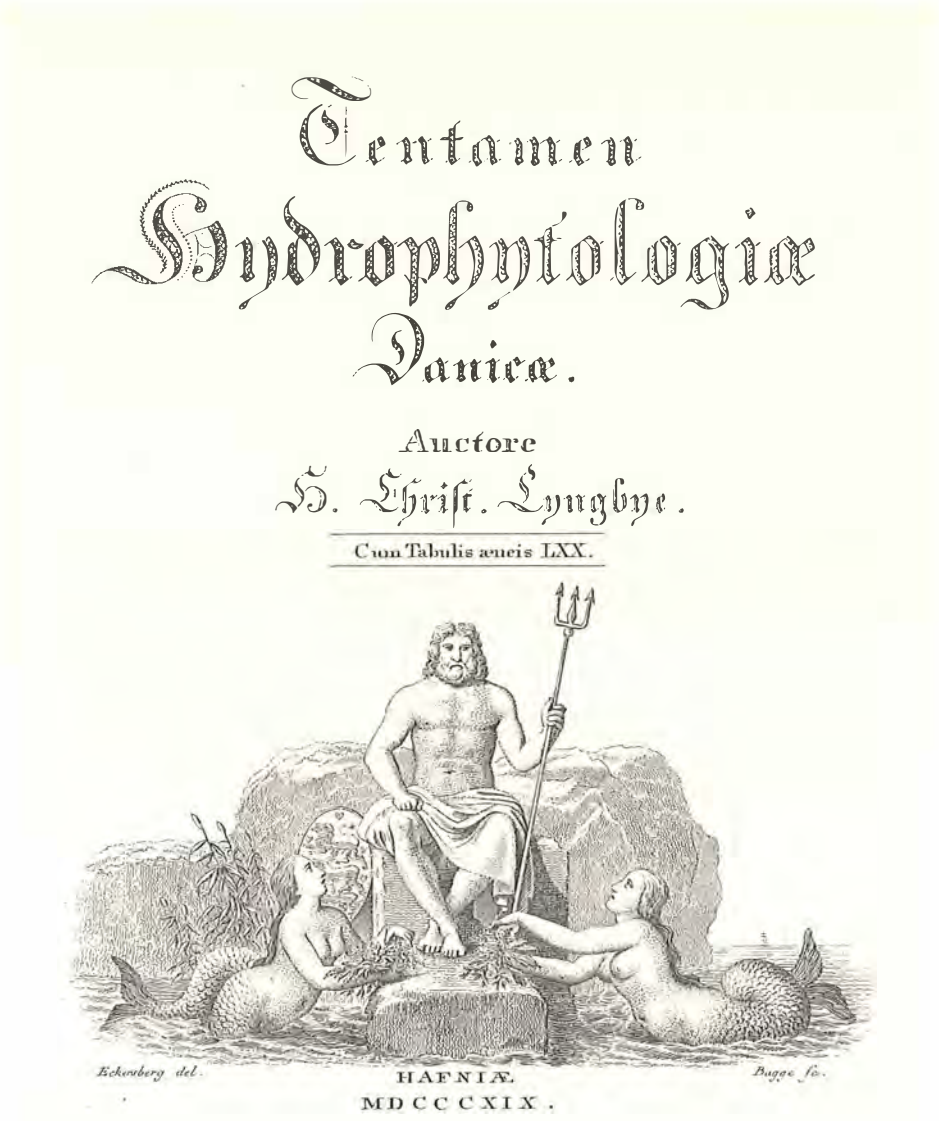
Otto Friedrich Müller

microscopical examination are ill-suited to this kind of publication which was not planned with them in mind. Neither the material nor the types are preserved. Apparently, he believed that God had created the species sufficiently distinct that one only had to go out and collect them again if it was necessary. Müller worked as a private tutor at Frederiksdal Castle, north of Copenhagen. Here, and in the financial comfort which followed his marriage, he could devote himself to the study of cryptogams and infusoria (bacteria, protozoa and smaller metazoa). The studies by Müller of aquatic organisms were particularly familiar to invertebrate zoologists. His investigations of microscopic algae and protozoa provided him with quite a new perspective, compared with his predecessors who studied museum and herbarium specimens. He used graphs and provided measurements long before anyone else. He was faced with the problem of deciding where to draw the boundary between the plants and the animals. He ended up placing the small motile algae in Linné's 'Vermes' but also realized that motility was not a good criterion. He described *Gonium pectorale* in his 'Vermium terrestrium et fluviatilium historia' in 1773, and this is depicted in his escutcheon. He described oogonia of *Vaucheria*, copulation in *Spirogyra, Nostoc* (he called this 'waterpie') amongst others. His posthumous 'Animalcula Infusoria', published in 1786 after being delayed by Linné, deals with, among other topics, *Volvox, Ceratium*, bacteria and the asexual reproduction of *Gonium pectorale*, also described in 1781.

In his carefully reasoned, yet curious, treatise from 1783 and entitled 'Om et besønderligt Væsen i Strandvandet' ('Concerning a peculiar creature living in beach sand'), Müller described a living colony of *Bacillaria paxillifera*. He compares its movements with the strategic operations of an army. He reflects on whether or not it should be regarded as a single organism, or as a colony of plants or animals. Despite the fact that he finally accepts it as being a single animal, one still gets the impression of a man struggling to develop an understanding of what is happening in nature.

P.K.A. Schousboe

P.K.A. Schousboe (1766-1832) was appointed as the Danish consul-general in Morocco where he studied higher plants and seaweeds. Whereas his manuscript on the vegetation of Morocco was printed, his manuscript on the seaweeds, with its 431 hand-coloured plates, was not. This work, and the algae, are kept in Paris. Parts of it were edited and published by Bornet in 1892. The University of Copenhagen was able to buy some duplicates from the Schousboe family.



Lyngbye and his period

With the death of Müller, the subject of phycology lay dormant in Denmark until the appearance in 1819 of the 'Tentamen Hydrophytologiae Danicae' by H. Chr. Lyngbye.

Lyngbye was a parson who developed a great interest in natural history. He was a short man, modest, kind and popular with his parishioners. He became the private tutor of a country squire, Hofman Bang, at Hofmansgave near Odense Fjord. It was he who introduced Lyngbye to the algae. The two made many collections in Denmark and Norway. Lyngbye studied these in great detail, and after collecting in the Faroe Islands, he was able to submit his Tentamen to the University for consideration as a prize essay.

The Tentamen is written in latin, and contains an account of all algae known at that date from Denmark, Holstein, the Faroes, Iceland, Greenland and Norway (which had a common government with Denmark until 1814).

Although Lyngbye was almost blind in one eye, he made 267 drawings – some of which were based on microscopical investigations. His drawings were made into 70 copper plates. 39 issues of these plates have been coloured by hand. In total, 321 specimens are described with diagnoses, synonymies and additional observations. The work of Lyngbye was important for three reasons. Firstly, because of the detail with which the species were described and because of the careful drawings. Secondly, his work greatly increased the knowledge of the geographic distribution of the flora of Denmark, the Faroes and Greenland. Finally, the book was valuable because it contained descriptions of many new genera and in it Lyngbye erected a new classification of the algae.

Lyngbye's work caused a great sensation, and was generally well received. However, the great Swedish phycologist C.A. Agardh, working in Lund, was critical of it. This conflict with the great Scandinavian authority of phycology led to long-lasting disagreements between Agardh and many other Danish scientists, although good relationships were eventually restored. It must be remembered that at this time classifications of algae were only just appearing. Lamouroux published the first classification since Linné in 1813. Shortly afterwards, Agardh published his work in which the structure of the thallus and the nature of the fruit were taken into consideration. Lyngbye thought that the fruits of the red algae, the tetrasporangia and the cystocarpia, were important. He studied these structures and provided descriptions of those he could find. He notes in his preface that the fruits were generally unknown or poorly understood, and that the sexual organs were quite unknown. In some cases, for example with *Odonthalia* and *Rhodomela subfusca*, the fruits look much the same despite the differences between the plants. Consequently, Lyngbye did not use these features in his classification, but confines mention of them to the generic diagnoses. The manuscript was duly completed and submitted to the University of Copenhagen just as Agardh's 'Synopsis Algarum Scandinaviae', with its new classification, was published in 1817. It is unlikely that Lyngbye could ever have developed a system like Agardh's because he was very occupied with his other matters. These not only included his duties as a clergyman but extended to interests in archaeological excavations, reading runic stones, philology, collecting folk ballads from the Faroes and marine invertebrates. These activities brought him further prizes and membership of various learned societies.

Lyngbye's descriptions of genera and his illustrations were extraordinarily careful. He also took great care with the synonymies. He described several new algae and made new observations on a variety of other species. The Danish algal flora was now one of the best studied in Scandinavia, and the knowledge of the flora of the Faroes was greatly extended. Most of Lyngbye's herbarium may be found in the Botanical Museum of Copenhagen, and his type material is still extensively consulted.

Lyngbye was invited by the University of Copenhagen to defend a thesis in 1836. To that end he prepared a treatise, the 'Rariora Codana' on marine botany and zoology, which was submitted and accepted. It contained many delicate illustrations. However, the document was lost by a local farmer who had been entrusted with returning it from the printer. It reappeared some time later, by which time Lyngbye announced that 'he was on the point of taking the doctor's degree in quite a different place'. He was, by now, a sick man and he died a few months later. A monument has been erected by his graveside at Søborg by Danish botanists. The botanical part of the Rariora Codana was not published until 1880. This shows Lyngbye trying, for the first time, to apply the plant biogeographical principles of the Danish professor, Schouw, to the algae. However, the first to publish on this topic were J.G. Agardh (Sweden) and A.S. Ørsted (Denmark). Lyngbye, in his Rariora, classifies the algae found by him in Kattegat in relation to different depth zones. His work also includes observations on algae from the Faroes as well as other Danish and Scandinavian algae.

Lyngbye's patron, Hofman Bang, observed that a filamentous alga, which he called *Conferva (Microcoleus) chthonoplastes* was the first plant to invade diked-in land. The mucilage which it produced helped to bind particles of soil and this led to a build-up of sediment, layer by layer. His paper, 'De usu Confervarum in oeconomia naturae', published in 1817 assured him of membership in the Society of Science. He took in Caroline Rosenberg (1810-1902) as a foster daughter. She too developed an interest in algae. Her

Caroline Rosenberg

only writings with information about algae are letters. She was a most industrious collector, and her neatly prepared algae may still be found in a variety of herbaria to which they were sent as exchange material.

A.S. Ørsted, who was destined to become a professor of botany, also visited Bang. He found that the sand-binding *Conferva* was also common on flat beaches exposed to tidal waters. He described, as a palmella stage of a saprophytic diatom, a common purple sulphur-bacterium, *Erythroconis littoralis*, which formed red layers on the sediment.

At this time, knowledge about the plants and animals from the oceans amounted to little more than a catalogue, with little reference to the nature of the habitat. Ørsted attempted to rectify this situation, and carried out a survey of the flora of Øresund. The result, 'De regionibus marinis', published in 1844, is the first description on the natural history of a single body of water in Denmark (excepting Lyngbye's manuscript). He proposed that the flora and fauna of the seas may be divided into groups of species characterising different depths. Although both Lyngbye and, later, Liebmann, were aware of the vertical distribution of marine algae, Ørsted used a Ball's scraper ('radula Ballii') to collect animals and plants. He was therefore able to make an exact record of the depth at which organisms grew. J.G. Agardh also published an account of the zones of Scandinavian coastal algae in 1836. Ørsted's ideas were overshadowed by the more popular theories of Forbes, an English worker. Ørsted did reach his conclusions independently, and also sought to clarify the causes of zonation. He identified three major zones. The first extended from 0 to 2-5 fathoms, and was characterised by green algae. The second from

A.S. Ørsted

3-5 to 7-8 fathoms and characterised by the 'algae olivaceae'. The third zone, from about 8 to 20 fathoms, was rich in 'algae purpureae'. He then subdivided his first two categories. Category 1 was subdivided into a region containing Oscillatoriineae and one with Ulvaceae, while Category 2 was subdivided into a region with Fucoideae and Zostera, and one with Laminarieae. Ørsted, of course, realised that some representatives of all classes could be found in all of the zones. He believed that the different distributions were due to the physical and chemical conditions of the water, the geological character of the bottom, and the differential penetration of the different wavelengths of light. Ørsted adopted the view of Newton who had said that the red rays penetrated farthest and the blue the least. Consequently, he came to conclude that the 'animals as well as plants of the sea have the colour of the light that is to be found in the region in which they live'. He states that he does not understand why that is so, and called for further study.

We now know that the wavelengths of light are differentially absorbed in exactly the opposite sequence, and that the problem of vertical distribution is much more complex. However, credit must be given to Ørsted for first implicating the different wavelengths of light. Subsequently, Ørsted worked mainly with vascular plants. However, in crossing the Atlantic to central America, he made one more important observation. He noticed that water taken from the ocean and placed in aquaria often looked cloudy from the microscopic algae that were present, whereas popular belief was that the oceans were devoid of plant life with the exception of the floating Sargasso algae. In the guts of various animals he found remnants of what was later to be called 'plankton'. In a small paper of 4 pages he established one of the major principles in ecology, that 'also in the sea all animal food derives from the vegetable kingdom'.

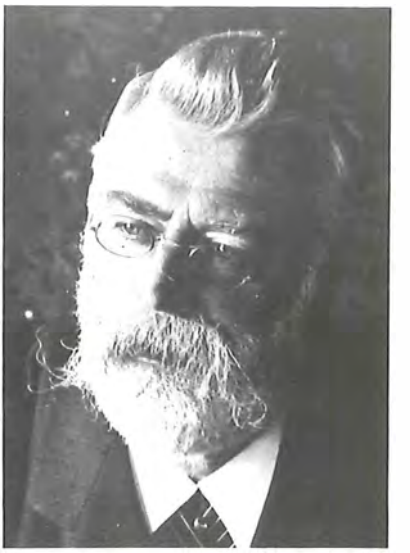
Around the time of Ørsted, information in the field of phycology had increased to a level that no single person could know everything. However, the amount of exact knowledge was rather limited and understanding was incomplete. These two pressures led to a shift towards specialisation. Some special fields of interest are considered below. The first field of phycology to become isolated as a special discipline in Denmark was diatomology.

Diatoms

The earliest Danish accounts of diatoms (e.g. *Bacillaria paxillifera*) were published by Müller and Lyngbye. None of Müller's material survives, and only two of his species are recognized today. Most of the remainder are regarded as species dubiae. Lyngbye's samples do survive, and more than half of the 28 species described in the 'Tentamen' are recognized today. Some of the others are mixed samples, and it is not possible to decide to which specimens Lyngbye's descriptions refer. One genus recognized today, *Fragilaria*, was named by Lyngbye.

By the time of P. Heiberg (1837-1875), regarded as the first Danish diatomologist, the quality of the microscopes and of the techniques for preservation had improved considerably. In 1863 Heiberg published 'Conspectus criticus Diatomacearum Danicarum'. This included records from 200 localities, as well as a survey of previous finds, such as those of Müller and Lyngbye. It is an excellent work, even by modern standards. It includes an introductory discussion of the morphology, of the terms used, of the principles of taxonomy and was beautifully illustrated by the author. Heiberg, like later workers, regarded the morphology of the frustules as forming the main basis of the taxonomy. He recognized that features such as the shape of colonies or the formation of gelatinous stalks were too variable to be reliable as generic characters, and that they even vary within a single species. Heiberg made most of his collections from freshwater. He included some fossil and sub-fossil forms, but his treatment of the marine diatoms was very incomplete. He published this work while still quite young and later he turned to other areas of botany. He died before reaching the age of 40, apparently embittered by financial problems and by conflicts with colleagues. His collections appear to have been lost.

The next Danish diatomologist, E. Østrup (1845-1917) began not much later than Heiberg. He published his major work almost half a century later in 1910. This opus, 'Danske Diatoméer' was based on 1400 samples, and increased the knowledge of the Danish diatom flora to such an extent that relatively few species have been added subsequently. His book contains descriptions and keys for the determination of diatoms, but very few illustrations. For these, the reader is referred to existing floras, such as that of van Heurck (1899). His surveys of the distribution of various species in Denmark, and of the relative frequencies with which they occur in a variety of habitats, are still very valuable. Shorter, more lavishly illustrated papers by Østrup deal with the diatoms of the Faroes, Greenland and of the Danish West Indies, as well as with fossil material.



Ernst Østrup

In the second half of the 19th century, diatoms were favoured objects for collection by people interested in natural history. Slides were produced with selected frustules arranged in beautiful patterns to be admired by amateurs and guests. Two Danes, P. Klavsen and Carl (Charles) Hansen, were masters of this special art. The latter lived in that part of Jutland which belonged to Germany from 1864 to 1920. Thousands of slides were prepared for serious botanical use, either for sale or for exchange.

J. Boye Petersen

More recent workers include J. Boye Petersen (1887-1961). He discussed the taxonomic separation of small species in the genus *Eunotia*, and argued that a restricted species concept was necessary for ecological and phytogeographical reasons. The same author tested the 'halobion' theory of Kolbe, using material from Denmark and Kamchatka. Petersen also studied soil algae including the aerophilous diatoms, and reviewed all that was known about them.

E.G. Jørgensen studied the distribution of diatoms in 71 lakes and ponds in relation to water chemistry (1948). Combining diatom physiology and ecology he linked the periodic occurrence of these algae to the availability of silicon (1957).

Odense, the capital of the island of Funen (Fyn), has long been a Mecca for diatomologists. Klavsen worked there all his life. He was succeeded by two outstanding specialists, Møller and Foged. All three, like Østrup, spent their spare time with diatoms, but earned their living by other means. M. Møller (1909-1974) was technically very skilled and a keen observer. He was able to detect errors in the descriptions of earlier authorities, such as Østrup. He only published a small number of papers, but was always ready to share his knowledge with others. He has made a lasting contribution to the subject by discussing diatom problems with his friend Foged over many years. N. Foged, now widely recognized as an authority on the group, published his first paper on Danish diatoms in 1946. In several of his early papers, he described diatom communities which can be found under differing physical and chemical conditions encountered in Denmark, Norway and arctic regions outside Scandinavia. Afterwards, he compared these communities with fossil samples from interglacial and postglacial periods, and was able to suggest the prevailing conditions at the time when the diatom material was deposited. Foged also exploited the composition of diatom samples to solve archaeological problems or to throw light on the feeding habits of animals. Many of his later papers deal with the composition of samples collected during his travels around the world. His collections are probably unmatched in respect of the number of taxa and regions represented.

Freshwater phytoplankton

More than a century elapsed after Müller's studies on the microscopic algae of lakes and ponds, before the subject was taken up again. This is not surprising in view of the insignificant size of these organisms. The man who redeveloped the field was a zoologist with wide interests, C. Wesenberg-Lund (1867-1955). His approach mirrored that adopted by a few scientists, mainly from Germany. His monumental 'Studier over de Danske Søers Plankton' (1904) (with an English continuation from 1908) gave an overall account of the species composition, biology and seasonal variation of freshwater zoo- and phytoplankton. The various plankton communities were illustrated by excellent photographs. Wesenberg-Lund was interested in the biology and habitats of freshwater organisms and was an early pioneer in the fight against pollution. He persuaded the authorities to establish a university laboratory for freshwater biology. His careful attention to detail was a style adopted by many of the successive generation.

Where Wesenberg-Lund simply registered the relative frequencies of algae, G. Nygaard, working with the zoologist K. Berg, included counts and weights. Their joint paper, 'Studies on the plankton in the lake of Frederiksborg Castle' appeared in 1929. In two subsequent publications, one limnological and one phycological, Nygaard compared the plankton of more habitats. The phycological part of 'Hydrobiological Studies on some Danish Ponds and Lakes' (1949) records more than 600 algal taxa from more than 200 localities. This contrasts with Wesenberg-Lund's descriptions of the more common species from only 9 lakes. The evident correlation between the degree of eutrophication and the representation of the various algal groups in the plankton, led Nygaard to introduce his 'compound quotient'. This developed an idea by Thunmark in an attempt to find a good numerical expression for the water quality based on the number of species recorded in each of the relevant groups. The compound quotient was his most successful attempt, and was obtained by dividing the number of desmid species *sensu* West (Desmidiaceae + Mesotaeniaceae) into the number of species of blue-green algae + centric diatoms + euglenoids + chlorococcalean green algae. The quotient has proved useful in demonstrating, for example, the progressive eutrophication of Lake Furesø which has occurred since the studies of Wesenberg-Lund at the beginning of this century. Nygaard also studied the plankton of other Danish lakes, and of lakes in arctic and tropical regions. Material from 17 lakes in South Greenland is described in a paper published in 1979. This also refers to the literature in which freshwater algae from Greenland are described. One of Nygaard's most popular achievements was his 'Dansk Planteplankton'. This was an illustrated flora of the most common and characteristic phytoplanktonic organisms. It appeared in two editions and is much appreciated at home and abroad. Several younger botanists have also undertaken quantitative studies on phytoplankton, often coupled with investigations of productivity. These include the works of J. Kristiansen and H. Mathiesen on Tystrup Sø (1964), K. Wøldike on the oligohaline Selsø (1973) and, in the same year, the study of K. Olrik on four lakes previously studied by Wesenberg-Lund and now considerably changed. All of these quantitative surveys were made with the use of Utermöhl's inverted microscope. As well as being scientifically instructive, these investigations and others not mentioned here, have been of great value in nature conservation. They help to identify those sites particularly deserving of protection and are indicators of increasing pollution or other unfavourable changes.

Danish phycologists have also studied fossil material, the taxonomy of specific algal groups, as well as ecological and physiological aspects of freshwater algae. Nygaard, Foged and Fjerdingstad studied deposits from bottoms of lakes. In so doing, they demonstrated that there have been changes in pH and in trophic conditions with the passage of time. Diatom frustules were the most valuable indicators, but Nygaard also included a careful study of the numerous chrysophycean cysts which he encountered. Nygaard initiated studies on primary productivity by phytoplankton. Initially he used the oxygen method, but in the 1950's the C^{14} technique developed by Steemann Nielsen was intro-

duced to freshwater habitats. With its application by H. Mathiesen (Aarhus), it rapidly became a powerful tool for monitoring eutrophication and cleaning effects in Danish lakes.

The freshwater Chrysophyceae have been particularly well covered in taxonomic studies. Petersen and Hansen studied species of *Synura*. This was followed by the works of B. Asmund (1904-1985) on the genus *Mallomonas*, and of J. Kristiansen on planktonic species in general. The latter worker investigated sexual reproduction of some species, and has extended the number of Chrysophyceae known in Denmark to 122. Many additional records of interesting freshwater algae were provided by the Czech investigator, H. Ettl (1980), after a stay in Denmark.

The relationships between the phytoplankton biomass and the life cycle of bottom-dwelling invertebrates have been studied by Nygaard and Kristiansen, in collaboration with P.M. Jónasson, a zoologist. The part played by the phytoplankton in the relationship between zooplankton and fish was studied by K. Olrik. Antagonism between different groups of algae, for example between green algae and diatoms, was demonstrated by Jørgensen. Steemann Nielsen reported that fish may be killed by poisonous blooms of *Prymnesium*, and J. Dahl recorded a similar effect caused by *Microcystis*.

The most important contributors to our physiological understanding of phytoplankton ecology were made by Steemann Nielsen and E.G. Jørgensen. These authors established, amongst other things, that adaptation to changing light conditions may occur in one of two ways. Some algae (*Chlorella*) are able to adjust the cellular levels of chlorophyll, while others (*Cyclotella*) escape from the harmful effects of strong light by changing the maximum rates of enzymatic processes.

Other freshwater algae

Of the benthic freshwater algae, the Charophyceae were collected and studied by P. Nielsen in the 19th century. He established an exsiccata which was distributed in 1869. A modern and comprehensive account of the same group, dealing with taxonomy, biology and ecology, was published in 1944 by S. Olsen. As a young botanist, but later to become known as a poet, J.P. Jacobsen produced a survey of Danish desmids in 1874. J. Schmidt published, in 1899, an account of the Danish blue-green algae. E. Hallas worked with *Oedogonium* and published her first results in 1905. However, much of her collections remained undescribed at the time of her death, but were studied and described in the literature by A. Andersen (1944). Species of *Vaucheria* from both freshwaters and brackish waters have been the subject of careful attention by T. Christensen. The first of his publications appeared in 1952. The Polish authority, J. Kadłubowska, studied Zygnemataceae collected by Christensen, and listed 70 species from Danish sites.

Einer Fjerdingstad worked on a wide variety of subjects relating to the benthic algae. His taxonomic preoccupation has been with species delimitation in blue-green algae. Some of his work was carried out in collaboration with his son, Erik. Einer Fjerdingstad is primarily a freshwater ecologist. In a series of papers he proposed the use of a modification of the classical saprobic system of Kolkwitz and Marsson. He suggested that one should not use individual species to indicate the various degrees of pollution, rather one should use communities of benthic algae or other attached micro-organisms.

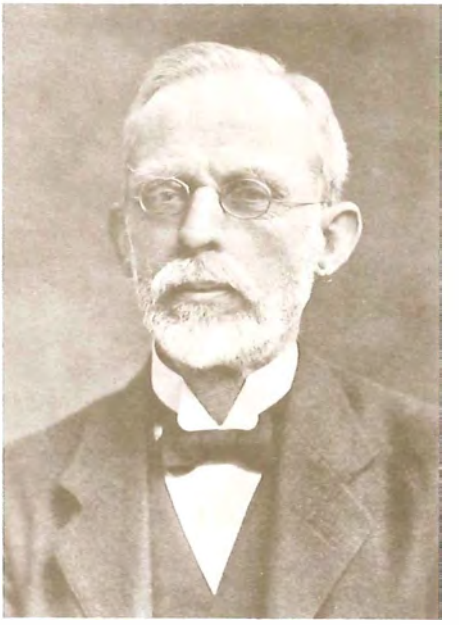
C. Hunding investigated the primary productivity of microscopic benthic algae in several lakes. He was able to show that benthic productivity (per unit surface area) may sometimes exceed that of the phytoplankton.

Soil algae have been the subject of several papers by Boye Petersen. These began to appear in 1915. As a pioneer in this field, he encountered many problems of identification. The green algae were a particular source of difficulties. He studied many in cultures, and described some as new. 25 species of diatoms living in Danish soils were found to be specifically aerophilous. All of these diatoms were small and motile, two features which

he regarded as being advantageous for organisms trying to survive in the interface between moist soil and dry air. Living algae were found deep in the soil. Even in samples from East Greenland where no farming has been carried out and where there are no earthworms, algae were found to a depth of 40 cm. His comprehensive survey, 'Studies on the biology and taxonomy of soil algae', was published in 1935.

Attached marine algae

Lyngbye's Tentamen provided the only synthesis in this field of phycology until after the turn of the century. The work which replaced it was 'The Marine Algae of Denmark, Contributions to their Natural History'. This was begun as an ambitious project by L. Kolderup Rosenvinge in 1909. It was destined to be incomplete. None-the-less, it remains



L. Kolderup Rosenvinge

one of the great Danish phycological works. Rosenvinge (1858-1939) was attracted by the beauty, diversity and reproductive complexity of the algae while still a student. He also worked on vascular plants. Shortly after receiving his Master's degree, he went abroad; first to work with Wittrock in Stockholm, then to Strasburger in Bonn and then to Pfeffer, a plant physiologist in Tübingen. While staying with Pfeffer in the summer of 1884, he carried out his first experiments to test the morphogenetic effects of environmental factors. This laid the foundation for his dissertation, published in 1888. After his stay in Germany, Rosenvinge went to France to study marine algae. He spent part of his time at the Atlantic coast and part at the Mediterranean coast. In Cherbourg he began investigations into the germination of fucacean zygotes. The results of this work, later continued on the west coast of Norway, were incorporated in his dissertation. He showed that the first cross-wall of the zygote is always formed perpendicular to the direction of incident light. It is this which causes the zygote to produce a lower daughter cell which is destined to grow into a rhizoid, and an upper cell from which the upright thallus develops. Before Rosenvinge completed his investigations on morphogenesis, he was given responsibility for an investigation of the terrestrial and marine vegetation of Western Greenland. He made one voyage with a boat from the Danish navy, and a second in an umiaq, a primitive, light rowing boat used by the local people.

While occupied with his collections from Greenland, Rosenvinge found time to publish two short papers, in French, on the morphology of *Polysiphonia*. The helical arrangement of the trichoblasts was discussed and on the basis of his observations he dismissed the morphogenetic theory of Schwendener that the regular arrangement of laterals was caused by pressure at an initial stage. After the second Greenland expedition, Rosenvinge obtained funds to allow him to collect material for 'The Marine Algae of Denmark'. He also began to lecture at the University, first only on algae, but later on cryptogamic botany in general. In 1913 he produced a comprehensive textbook on the subject, and this replaced that of 1867-1871 written by Ørsted. In 1916 Rosenvinge became the first Danish professor in this field of science.

As a result of his teaching activities at the University and the Polytechnic Academy, of his careful taxonomic studies (for example on the Acrochaetiaceae), the large flora progressed only slowly. The first part of the red algae appeared in 1909, the last in 1931 after Rosenvinge had retired. A few brown algae had been discussed in a short paper which appeared in 1935. The treatment of the blue-green algae was left to Schmidt. The green algae and most of the brown algae were not dealt with, even at the time of his death. Fortunately, the section on red algae was complete. It is based on 11 000 collections of his own and on older material brought together by Hornemann, Hofman Bang, Lyngbye and Rosenberg. This comprehensive work extends to 628 pages. It is mostly descriptive, but is highly valued because of the wealth of reliable information deriving from personal observations, and because of the author's own illustrations. An appendix which appeared in 1935 deals with the phytogeographic aspects. In this he demonstrates that, amongst other things, the 26 species which penetrate into the Baltic waters around Bornholm have a more northerly distribution outside Denmark than the remaining 132 species. He published observations on aberrant life cycles of *Phyllophora truncata* and of *Ahnfeltia*.

Rosenvinge is reputed not to have been very inspiring as a teacher, but he readily shared his wide knowledge with those who asked him. One of Rosenvinge's pupils, S. Lund (1905-1974), shared his interest in the larger marine algae. Lund assisted Rosenvinge in his work on the brown algae for the 'Marine Algae of Denmark'. After Rosenvinge's death, Lund published four parts of the intended brown algal volume between 1941 and 1950. Together these cover most Danish representatives of this group of algae.

Søren Lund

Like his teacher, Lund was very interested in the invasion into Danish waters by algae from abroad. He published on *Codium fragile* (first recorded by Rosenvinge), *Dictyota dichotoma* and *Colpomenia peregrina*. These species established themselves in Limfjorden – the sound that cuts through North Jutland from the North Sea to Kattegat, and is slightly warmer than the North Sea. He also recorded *Fucus distichus* subsp. *edentatus*, which has a northerly distribution, but which spread along the Swedish coastline to Copenhagen harbour. Lund eventually took up a position as librarian at the Institute of Fisheries and Marine Research. Although this did not offer significant laboratory facilities, it did allow him to work on the marine algae of East Greenland. This work was based on collections

Henning E. Petersen

that he had made during an expedition more than 10 years earlier. One of the tasks at the Fisheries Institute was to advise and survey the new Danish phycocolloid industry, based on *Furcellaria*. Lund was the first to provide a general account of the Danish marine vegetation. This appeared in a large handbook on fishery. His last contribution was the discovery of a *Ralfsia*-like stage in the life cycle of *Scytosiphon*. This was independently established by Nakamura in Japan. More recently, Aa. Kristiansen has followed in Lund's footsteps by writing a widely distributed account of the marine vegetation for the series 'Danmarks Natur' and by further studying the life cycle of *Scytosiphon* in conjunction with P.M. Pedersen.

Rosenvinge's university teaching was taken over by H.E. Petersen (1877-1946). Petersen was particularly well known for his work on phycomycete fungi, including those which parasitized algae. He also worked with vascular plants, the vegetation of bogs, plant anatomy and intraspecific variation. His phycological interests lay in the genera *Ceramium* and *Enteromorpha*. Both of these exhibited a puzzling degree of variability and he collected thousands of specimens to document this variation. He produced 9 publications about *Ceramium*, including the appropriate chapter of 'The Marine Algae of Denmark'. His work on *Enteromorpha* was planned for that same work. He realised the necessity to work on cultured material, the type of work which was carried out later by Bliding in Sweden and by J. Larsen in Denmark.

A number of further additions to the marine flora have been published recently, mostly by T. Christensen. R. Nielsen has greatly extended our knowledge of smaller green algae, such as those living on other algae or within shells. By experimenting with cultures, she was able to revise several genera. A very large number of brown algae have also been established in culture, and their life histories and taxonomy studied by P.M. Pedersen.

A number of waters have now been studied in quite considerable detail, as far as their algal flora is concerned. In this century, Lund extended Ørsted's early account of Øresund

to include the almost enclosed bay of Stege Nor on the island of Møen. The ecological surveys of Isefjorden (Sealand) by Steemann Nielsen contain a good deal of information about the algae. Part of this was contributed by Lund. Aa. Kristiansen has studied the algae of Øresund, including the harbour of Tuborg and the island of Saltholm. Her work contains accounts of seasonal variation. The algal flora of the bay of Ebeltoft Vig (East Jutland) was studied by J. Andersen, and that of a large part of Kattegat between Jutland and Samsø by L. Mathiesen. Much information is also to be found in reports to county agencies for environmental supervision. Many of these were prepared by Mathiesen.

The Danish Wadden-sea, S.W. Jutland has been analyzed as regards physical conditions, psammobious dinoflagellates and blue-green algae 1985 by H. Kaas, C. Koch and J. Larsen.

Marine plankton

Ørsted's paper of 1851 was the first Danish paper in this area, and served to demonstrate the ubiquity of marine plankton. The only previous work in Danish had been a translation of an account of the colour of the Red Sea initially written by Ehrenberg. Almost half a century elapsed before the topic was taken up again, this time by C. Hansen-Ostenfeld (1873-1931). Ostenfeld was a professor of Botany, first at the Agricultural High School, and later at the University of Copenhagen. He was primarily concerned with vascular plants, publishing extensively on them. Meantime, he maintained an interest in plankton, and accepted a post as head of a Plankton Laboratory, newly established by the Danish Institute for Fisheries and Marine Research. He had an excellent memory, and was able to register precisely what he saw. Beginning in his student days, he took part in several oceanographic expeditions, returning with plankton samples for subsequent study. His first paper on freshwater phytoplankton was published in 1895. This was followed by a

C. Hansen Ostenfeld

series of papers describing the phytoplankton communities along the shipping routes from Copenhagen to Iceland and Greenland. Between 1901 and 1916 he published on the taxonomy of the phytoplankton of the Caspian Sea, the Red Sea, the North Atlantic, the Indian Ocean near Thailand and various Scandinavian lakes. He also published on the genus *Phaeocystis*, on freshwater plankton from Kossogol in Mongolia, the Benguela Stream west of Africa, Lake Victoria, Lake Nyanza and the Aral Sea. In 1909 he published an account of *Biddulphia sinensis,* recently encountered in European waters and probably introduced by shipping into the Elbe. A larger, monographic, treatment of all plankton of Danish waters was published in 2 parts, the phytoplankton part appearing in 1916. This surveys all available information and opinions. As had previously been established with the brown algae, it was shown that the distribution of the planktonic algae reflected the salinity gradient between the North Sea and the Baltic.

Ove Paulsen

The scientific career of Ove Paulsen (1874-1947) had much in common with that of Ostenfeld. After being head of the Botanical Museum of Copenhagen for several years, he became professor of botany at the Pharmaceutical High School. He worked mainly with vascular plants, studying them on several expeditions but he also carried out simultaneous studies on phytoplankton. He was involved in several marine expeditions, sometimes with Ostenfeld and Johannes Schmidt. His first papers on plankton related to the North Atlantic and later, in 1907, he produced 'The Peridiniales of the Danish Waters'. He developed an international reputation because of this. He covered the same group for the large series 'Nordisches Plankton'. In 1912 he published 'Peridiniales ceterae', which dealt with the taxonomy, distribution and seasonal variation of various small or poorly known species. Two later papers focussed on the Mediterranean phytoplankton. His 'Observations on Dinoflagellates' (1949), with advice for the next generation of workers, was published after his death by Grøntved.

The next Danish botanist to concern himself with marine plankton was Steemann Nielsen. He worked for several years at the Plankton Laboratory, like Ostenfeld and Paulsen, and succeeded Paulsen as professor of botany at the Pharmaceutical High School. Eventually, he moved to the University of Copenhagen, as professor of freshwater biology. As a senior student he participated in the circumnavigation of the globe by 'Dana' from 1928 to 1930. His first publications from this were on the taxonomy of some plankton species and on planktonic productivity. They appeared shortly after the voyage.

After a substantial treatise on the Ceratia of the South Pacific, published in 1934, the study of planktonic photosynthesis became his main preoccupation, and remained so for the rest of his active life. As an employee of the plankton laboratory, he joined several cruises in northern waters. These provided material for his researches. Initially he measured photosynthesis by oxygen production in light and dark bottles. However, with the introduction of radioactive tracers about 1950, he applied a C^{14} method on the Galathea world cruise (1950-1952). He developed a method which could be used on a ship at speed. Consequently, he was able to develop a comprehensive insight into productivity in relation to many environmental conditions.

Jul. Grøntved

J. Grøntved (1899-1967) replaced Steemann Nielsen at the plankton laboratory. He had been introduced to the study of plankton by G. Seidenfaden on an expedition to West Greenland waters in 1928. Seidenfaden later entered the diplomatic services and became an ambassador in Thailand. Together, these men described their plankton samples in a substantial treatise. Although Grøntved had little prior knowledge on the subject, the work is regarded as an authoritative foundation for the subject. Grøntved was soon offered an opportunity to investigate the plankton of tidal flats as part of a more extensive programme on this habitat in Denmark. He edited a long series of taxonomic works. Later he was involved in studies of the planktonic photosynthesis, and of macroscopic and microscopical benthic vegetation. Inspired by the C^{14} technique of Steemann Nielsen, he applied it to these new habitats. The plankton laboratory was abolished after his death.

The electron-microscope was applied to the study of marine plankton of Denmark, the Red Sea, Western Greenland and the Indian Ocean by H. A. Thomsen. Much of this work relates to *Paraphysomonas*, to collar-flagellates, Prymnesiophyceae and heliozoa, and was used to resolve taxonomic, cytological and biogeographical problems. His work extends to the internal Danish seas, and has allowed the works of Ostenfeld to be updated.

F. Børgesen and the exotic algae

F. Børgesen was a contemporary of Rosenvinge and succeeded him as librarian and assistant at the Botanical Museum. He devoted himself to the study of algae. While quite young, he wrote several papers on the Desmidiaceae of Brazil and the Danish island of Bornholm, the freshwater algae from eastern Greenland, Jan Mayen, Iceland and the Faroes. He soon turned to tropical algae and northern algae outside Greenland (Rosenvinge was at this time occupied with the algae of Denmark and Greenland). Børgesen travelled to the Danish West Indies on three occasions, 6 times to the Faroes, to the Mediterranean, the west coast of Norway, the west coast of Ireland, the Canary Islands, India

F. Børgesen

and Ceylon. He sometimes travelled on ships belonging to the Danish Ministry of Marine, and sometimes he paid his own way. He brought home a wide variety of algae from many habitats and described them in numerous accounts amounting to several volumes. He obtained many additional species of algae by mutual exchange. His collections contain a large amount of type material and it forms the core of the collections from abroad at the Botanical Museum. Similarly, Rosenvinge's collections dominate the Danish herbarium. Occasionally, especially later in his life, he dealt with collections besides his own. Examples were collections from the Danish expedition to the Iranian Gulf and an extensive collection of algae from Mauritius.

Børgesen maintained a wide array of interests. He published an account of the peculiar vegetation of the Canary Islands. With O. Paulsen he produced a phytogeographical account of what was then the Danish West Indies. He also maintained a large garden at Hellebæk which he stocked with a wide variety of plants, some of which had not been seen previously in Europe. His interests extended to photography, and some of his work illustrating algae from the Faroes may be seen in Karsten and Schenk's 'Vegetationsbilder' published in 1906. Despite his interests, he was a reserved man.

Børgesen produced 119 publications, mostly on phycological matters and including four substantial accounts relating to the Faroes, the Danish West Indies, the Canary Islands and Mauritius. Others relate to algae of southern India, Ceylon and the Iranian Gulf.

His journeys to the Danish West Indies led to the publication of an account of the marine algae of this region (1913-1920). This extends to more than 700 pages and contains 600 drawings. Van Bosse, Lemoine and H.E. Petersen also contributed to this. In 1938 Frémy added accounts of the Cyanophyceae and freshwater algae. This was the first thorough treatment of algae from a tropical region, previous accounts amounting to little more than annotated catalogues. In this he employed morphological, anatomical and cytological characters as the basis for taxonomy. Many of his drawings were later exploited by Oltmanns and Fritsch in their classic text-books. Among his works are several on the anatomy and abundance of varieties of Chlorophyceae, about which there had previously only been fragmentary knowledge. He and Winge clashed over their interpretations of the algae of the Sargasso Sea.

The last tropic possessions of Denmark were the Danish West Indies. With the sale of these to the USA in 1917, Børgesen and the zoologist Th. Mortensen tried unsuccessfully to establish a tropical marine biological station there.

Børgesen later turned his attentions to the Canary Islands. Again, he broke new ground with his 'Marine Algae from the Canary Islands' (1925-1930) as previous knowledge had only been patchy. He studied the collections of Picconis, Vickers and his friend Sauvageau as well as his own. Lemoine, H.E. Petersen and Frémy also contributed to this work. In addition to his careful descriptions of 373 species (including 47 blue-green algae), he showed that 78% of the species were common to Europe and Africa and 50% of the Atlantic seaboard of America.

Børgesen's third great work deals with the marine algae of Mauritius and was published between 1940 and 1957. Its simple title belies a mammouth work of 15 parts with 4 additional papers. He never actually visited Mauritius, but was inspired to work on material from dredged collections made by Mortensen. He also worked with collections made by Vaughan, Gadin and Marin, and the collections at Kew. This was the last great work of Børgesen, who at the age of 90 was suffering from failing eyesight after 67 years of phycological researches. He asked T. Christensen to assist in the preparation of the last volume, which was published in the year following his death.

Towards the end he likened his life's work to a grain of sand in a pyramid.

The algae of the Faroes, Iceland and Greenland

The oldest source of useful information about algae of the Faroes is to be found in Landt's 'An essay to a description of the Faroes', published in Copenhagen in 1800. Of the 5 freshwater algae and 30 marine algae mentioned there, only some can be identified with certainty. The rest are uncertain, and two do not grow in the Faroes at all. Lyngbye's account is more reliable as the algae from his 1817 journey have been preserved. In 'The Flora of the Faroes' by Rostrup, Nordstedt (a Swede) more than doubled the number of freshwater algae described by Lyngbye with accounts of 70 species. The Norwegian phycologist Wille, using samples sent by a friend living on the Faroes, increased the number to 350. This large number is remarkable because of the small size of the islands and their relative isolation. Børgesen and Ostenfeld only encountered phytoplankton in the largest lake. Some benthic algae (e.g. *Chara globularis, Nitella opaca* and *Cladophora*) may form great masses of vegetation along the edge of the water. Similarly, *Ulothrix* and *Microspora* may sometimes form green margins along the edges of lakes and rivers. Favoured by the moist climate, *Prasiola crispa, Mesotaenium* and *Pleurococcus* may be found in abundance near human habitation. Børgesen concluded that the freshwater flora of the Faroes was European, and particularly like that of England. The northern islands have a component of arctic flora, with arctic/alpine phanerogams being well represented. Østrup examined the diatoms and thought many were typical of northern Europe.

Lyngbye has also extended the knowledge of the marine algae. In his Tentamen he included about 100 species, including several new genera. Børgesen, using material from his and others' collections, published in 'The Botany of the Faroes II: The Marine Algae' (1903) with about 200 pages. In 1905 follows in vol. III: 'The Algal Vegetation of the Faroese Coasts with Remarks on the Phytogeography', both with Danish forerunners. In this he concludes that the marine algae mostly resemble the flora of the nearest parts of the British Isles, then with northern Scandinavia and southern Iceland. The last work led to some agitated disputes between Børgesen and other workers as to the mechanisms of colonisation of species (carried by birds, water currents or across a postglacial land bridge?). This question is still open. In 1979, Jóhs. Jóhansen issued a popular illustrated account of the marine algae. Østrup described the epiphytic marine diatoms, and Ostenfeld, the marine plankton around the islands.

Børgesen wrote in 1898 in 'Some freshwater Algae from Iceland' that the knowledge of freshwater algae of Iceland and Greenland was very poor. Børgesen never visited Iceland, but he worked on small collections made by others. His species list for Iceland amounted to less than 90 species. The first attempts to study the ecology of Icelandic lakes was made

by Ostenfeld and Wesenberg-Lund in 1906. They collected fortnightly samples from Thingvallavatn and Myvatn, and described the phytoplankton which they encountered. The lakes have subsequently been studied more intensively by Icelandic workers. Boye Petersen travelled across Iceland on horse-back in 1914 in order to collect freshwater algae. He published on the Cyanophyceae in 1923 and in 1928 on the aerophilic algae in 'Botany of Iceland', a counterpart to the study of the Faroes. In 1935, he described the algae of Grimsey, a small island off the north coast of Iceland which lies on the polar circle. Østrup described diatoms from collections by H. Jónsson, Ostenfeld and Boye Petersen. He and others found that the freshwater and coastal algae are closely related to the western European flora.

Helgi Jónsson, mentioned above, produced a classic 'The Marine Algae of Iceland' from 1901 to 1903. This and 'The Marine Algal Vegetation' from 1910, both published as parts of 'Botany of Iceland' followed the style of Børgesen's works on the Faroes and Greenland. Jónsson carefully discusses the observations made by Strömfelt on the remarkable floristic differences between northern and eastern Iceland on one hand, and of the south and west on the other. Ostenfeld and Paulsen found similar differences with the marine plankton. Jónsson was born in Iceland, studied botany in Copenhagen and returned home to become a teacher. Under difficult conditions, he developed an unparalleled knowledge of the terrestrial and marine flora of his country. He made an interesting observation on *Rhodochorton islandicum*, 150 m above sea level on Vestmannaeyjar. He believed this to be a relict from an earlier time when the area was covered by sea.

Greenland is the largest island in the world, but has a climate which makes continuous studies difficult or impossible. Exploration of this island is based primarily on expeditions, and much remains to be established. The first collector of algae from Greenland was Wormskjold (1783-1845) who, in 1812 to 1814, travelled to the west coast. His observations may be found in his journal, later (1889) edited by Warming. Shortly afterwards he was provided with the opportunity to join the long Russian expedition to the Bering Straits and Kamchatka. All of his collections from this expedition were lost by fire.

Rosenvinge, in 1886 and 1888, explored the terrestrial and marine vegetation of the coasts of western Greenland. He published model works on both. The marine algae of Greenland appeared in 1893, later coming out in French. The second part was published only in French in 1898. The taxonomic works illustrate the clear and exact approach from which he has gained his international reputation. He published a further account of the marine vegetation of Greenland in 1898.

From 1898 to 1899, C. Kruse collected extensively in eastern Greenland. The collections were carefully analysed and described by H. Jónsson in 1904. In 1910, Rosenvinge presented an account of Lundager's collections. The freshwater algae were described by Børgesen in 1894 and 1910, by E. Larsen in 1904 and 1907 and by Østrup (marine and freshwater diatoms) from 1895 to 1910. There was then a break in studies until S. Lund joined an expedition to north-east Greenland and his account was published as 'The Marine Algae of East Greenland' in 1959. This was in two parts, a taxonomic part and a second part on geographical distribution. The flora of eastern Greenland still remains largely unknown because of the inaccessibility and length of the coastline.

After the death of Lund, T. Christensen published an account of some new marine algae from Greenland and P.M. Pedersen embarked on a series of papers on small brown algae. The southernmost part of Greenland is, despite its 60° latitude, lashed by storms and had escaped careful study. The first survey of the marine algae of this region of Greenland was issued in 1976 by P.M. Pedersen. Further studies on freshwater algae of Greenland have been made by the Swiss phycologist, H. Bachmann. In the 1970's phytoplankton studies employing electron-microscopy were conducted by G. Nygaard.

The erection of an arctic biological station on the island of Disko in western Greenland in 1906, later taken over by the University of Copenhagen, now offers laboratory facilities, a library and accommodation for those interested in continuing arctic studies.

Submicroscopical Studies

In 1912, J. Boye Petersen applied Löffler's method for staining bacterial flagella to non-motile algae such as *Pediastrum* and *Scenedesmus*. He showed that the structures previously referred to as pseudoflagella were in fact tufts of bristles. This inspired him to look more closely at *Synura* and other species. He discovered that in addition to the whiplash flagellum, there was a second kind of flagellum: the 'Flimmer flagellum'. He discovered that *Synura* was covered with minute scales and that the hyaline collar of *Codonosiga* was composed of fine soft tentacles. These studies were extended by a younger collaborator, J.B. Hansen, who had learnt electron-microscopical techniques in America. In a series of papers, he and Petersen were able to confirm and extend the earlier light-microscopical observations. This approach was continued and extended by J. Kristiansen who used it to investigate several other microscopic algae and by H.A. Thomsen in studying marine microplankton.

The approach has been expanded to include investigations of thin sections, as exemplified by the work of Ø. Moestrup, who learnt his skills at the feet of Irene Manton in Leeds from 1968 to 1969. He has investigated a wide variety of algae with respect to the structure of the flagella, flagellar roots and other cytological structures. He has published extensively on the fine structure of prasinophytes, and has reviewed the subject of algal flagellar structures in 1982. Such studies, together with those of other workers around the world, are being used to develop an improved understanding of the systematics and evolution of all algae.

The present situation

There are now about 15 active phycologists in Denmark, and the following notes simply indicate their major areas of interest. Most of them work at the University of Copenhagen. Most senior is Tyge Christensen who has published on nomenclature, systematics and taxonomy of *Vaucheria*, as well as publishing 'Algae: a taxonomic Survey' which reviews recent data and discusses ideas about evolutionary relationships among algae. Jørgen Kristiansen employs light- and electron-microscopical techniques to his studies of freshwater phytoplankton. He maintains a special interest in the Chrysophyceae, while Helle Nielsen works on benthic freshwater algae. Aase Kristiansen is an authority on the ecology of marine benthic algae. Poul Møller Pedersen also has interests in marine benthic algae, but in particular exploits culture techniques to investigate the life cycles of arctic brown algae. Ruth Nielsen uses a similar approach to study the Chaetophorales. Helge A. Thomsen has carried out numerous studies on the algal and heterotrophic flagellates of marine plankton. He investigates and records them with a combination of light- and electron-microscopical and video techniques. Øjvind Moestrup also maintains an interest in the marine flagellates, including toxic species, as part as a broader perspective on algal fine structure. Finally, J. Benth Hansen, who introduced electron-microscopy to phycology at the University of Copenhagen, is now curator of the Botanical Museum.

At the University of Aarhus, Lisbeth Mathiesen works on the ecology of Danish marine algae.

Niels Foged, Gunnar Nygård and E. Fjerdingstad have retired, but continue their work on algae in Odense, Hillerød and Copenhagen respectively.

Kirsten Olrik, Humlebæk, is a consultant on plankton algae, while Jytte Heslop Christensen, Århus, takes an active interest in the relationship between pollution and marine plankton algae.

In addition, several other people use algae in their research.

The teaching of phycology takes place in the Institut for Sporeplanter at the University of Copenhagen and at the newer University of Aarhus. Field courses are arranged at the marine laboratory at Frederikshavn, at the Limfjord and at the freshwater laboratory in Silkeborg.

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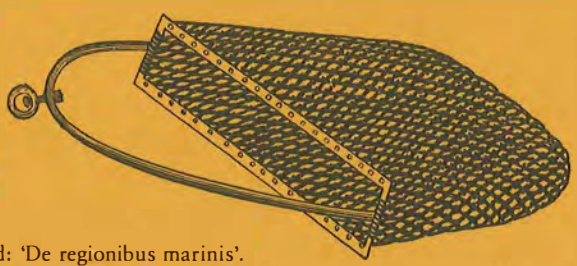

'Radula Ballii'. Figure from A.S. Ørsted: 'De regionibus marinis'.

Supported by the Danish Natural Science Research Council

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