1: INTRODUCTION

Recent years have witnessed a renewed enthusiasm for diatom taxonomy, which has been reflected in the publication of numerous articles (e.g. Reimann & Lewin 1964; Hasle 1964, 1965a, b, 1968a, b, 1971 etc.; Round 1970a, b, 1972a, b etc.; Ross & Sims 1970, 1971 etc.), in the holding of several symposia on Recent & Fossil Marine Diatoms and in the founding of a new journal, 'Bacillaria', (first issue 1978). The impetus for this upsurge of interest came largely from the introduction of electron microscopical techniques, but while the technology employed in taxonomic studies has changed, the philosophy underlying diatom taxonomy has not and, indeed, has hardly altered since the end of the last century.

Diatoms were discovered late in the eighteenth century, two of the first recognised being '*Vorticella pyraria*' and '*Vibrio paxillifer*' (now *Didymosphenia geminata* and *Bacillaria paxillifer* respectively), which were described by O.F.Müller (1786). Over the next sixty years many more taxa were described and illustrated, although observations were limited by the quality of the microscope lenses then available. During this period the affinities of the group were debated extensively (e.g. see Kützing's 1844 discussion 'Sind die Diatomeen Pflanzen oder Thiere'); some, notably Ehrenberg, believed the diatoms to be animals, while others, e.g. Lyngbye (1819), asserted that they were plants. As a consequence of this controversy careful attention was given both to the structure of the cell wall and to that of the cell interior.

By the middle of the nineteenth century, most authors accepted that the diatoms should be classified in the plant kingdom and the main thrust of diatom studies shifted elsewhere. This was the age of the amateur microscopist, a time of competition when each man strove to resolve finer detail than had hitherto bee[illegible]sible. The [illegible] valve with its intricate markings provided an excellent test object for microscope lenses. Moreover, the durability and beauty of their frustules make diatoms attractive as items to be collected just as one might collect coins, stamps or birds' eggs. As the collectors and microscopists pursued their hobbies, they also classified the organisms they observed and so it was that diatom taxonomy came to be dependent almost solely on the morphology of the siliceous elements of the cell wall. At the same time taxonomy became separated from other diatom studies (except ecology), a situation which remains largely unaltered today and which is much to be regretted.

At first, however, the separation was less marked and diatom taxonomy was partly dependent upon features other than those of the frustule. Thus, the system of classification developed by Petit (1877) employed chromatophore arrangement and structure as characters in addition to frustule morphology. Cleve (e.g. in his 'Synopsis of the Naviculoid Diatoms' 1894-5) was also fairly catholic in his approach, while Mereschkowsky (1901, 1903a, b) and Karsten (1899, 1905-7) placed great emphasis on the structure of the 'endochrome'.

Nevertheless, such 'freethinkers' were rare and soon the study of chromatophores was neglected and works such as those by Mereschkowsky were consulted only occasionally and then not in connection with taxonomy. Petit's system was supercededby Schütt's (1896), which employed frustule symmetry and valve structure,but not chromatophore arrangement, as primary taxonomic criteria. Practitioners of the 'endochrome classification' were regarded increasingly as eccentrics, (see Simonsen's 1974 remarks about Karsten).

In the twentieth century, one man came to dominate diatom taxonomy and it has largely been his attitudes, right or wrong, which have determined taxonomic practice. Friedrich Hustedt, who published articles on the ecology and taxonomy of diatoms for about sixty years until his death in 1968, was a firm believer in the uselessness of cytological characters: there are scarcely any works among his immense output which contain original information about chromatophores, nuclear structure and division, etc. The greatest of his taxonomic works is probably the contribution to the Rabenhorst Kryptogamen-Flora (1927-66), although unfortunately this remained uncompleted at the time of his death. A smaller work (1930) remains the most useful text for the identification of freshwater diatoms, in spite of various errors and omissions. Hustedt described many hundreds of species and his influence on diatom taxonomy was immeasurable; (see, for example, Table 25, which summarises the changes in the taxonomy of the genus Nitzschia).

During Hustedt's 'reign' few others contributed appreciably to diatom systematics. Two exceptions are worth note: A.Cleve-Euler produced a monograph of the diatoms of Sweden and Finland (in several parts, e.g. 1952), while B.J.Cholnoky (in the period 1950-70) described new species at an amazing speed, most of them from South Africa. Neither of these authors, however, departed from Hustedt's practice of discounting all but frustule morphology as of value in taxonomy.

In the late 1940's and early 1950's there came the first major studies of diatoms made using the transmission electron microscope, or TEM, (e.g. Helmcke & Krieger 1953- ; Hendey, review article 1959). Initially, workers seemed little concerned with the application of electron microscopy to the elucidation of taxonomic problems (indeed, the Helmcke & Krieger Atlas has been continued in this vein), but soon this became the primary aim of most EM investigations. Later, the scanning electron microscope, or SEM, was developed and has been widely used.

But the practice of diatom taxonomy has not changed even though the tools used by the taxonomist have. There is no fundamental difference between the approach employed by, for example, Hasle (1964, 1965a, b etc.), Dawson (1973a, b, 1974), Cox (1975a, b), Ross et al (1977), etc., and that of Hustedt. Is this satisfactory?

While Hustedt and others trod the path described above, other workers began to examine other aspects of diatom biology which are relevant to diatom taxonomy, but which have not been considered adequately by the taxonomist. Thus, Geitler's (1932, etc.) studies have thrown considerable light on sexual reproduction and the variation of cell size, shape and structure during the life cycle in pennate diatoms, while von Stosch (e.g. 1951, 1956, 1958; von Stosch & Drebes 1964 etc.) has made similar studies of centric diatoms. Our knowledge of the details of diatom cytology has been advanced through recent studies of thin sections (see the review by Duke & Reimann 1977), although little more is known about the variation within the Bacillariophyta in the general organisation of the cell - viz., the positions and numbers of the pyrenoids; chromatophore arrangement; position and structure of the nucleus etc. - than was known to Karsten and Mereschkowsky.

In this dissertation, various aspects of the biology of one family, the Nitzschiaceae, are discussed, mainly in relation to the taxonomy of the group. On the basis of observations made using both light and electron microscopy, an attempt is made to evaluate the usefulness to taxonomy of different characters, both those of the silica frustule, and those of other components of the diatom cell. Representatives of as many as possible of the larger groupings previously recognised within the Nitzschiaceae have been studied and the pattern of variation encountered related to the currently accepted classification. Three species of Hantzschia have been examined in some depth in order to investigate the extent of infraspecific variation.

Some comments are necessary concerning the arrangement of the dissertation. After a few preliminary chapters describing methodology and terminology, and some fairly general sections on cell division, colonial organisation, etc., the work centres upon the taxonomy of the various genera belonging to the Nitzschiaceae. Points are discussed as they arise: thus, for instance, part of the discussion concerning the nature of the diatom species is to be found closing the sections on Hantzschia marina, H. virgata and H. amphioxys, species in which infraspecific variation has been monitored more closely. The final discussion represents an attempt to synthesize what has gone before.