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The species concept in diatoms

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Diatoms are the most species-rich group of algae. They are ecologically widespread and have global significance in the carbon and silicon cycles, and are used increasingly in ecological monitoring, paleoecological reconstruction, and stratigraphic correlation. Despite this, the species taxonomy of diatoms is messy and lacks a satisfactory practical or conceptual basis, hindering further advances in all aspects of diatom biology. Several model systems have provided valuable insights into the nature of diatom species. A consilience of evidence (the 'Waltonian species concept') from morphology, genetic data, mating systems, physiology, ecology, and crossing behavior suggests that species boundaries have traditionally been drawn too broadly; many species probably contain several reproductively isolated entities that are worth taxonomic recognition at species level. Phenotypic plasticity, although present, is not a serious problem for diatom taxonomy. However, although good data are now available for demes living in sympatry, we have barely begun to extend studies to take into account variation between allopatric demes, which is necessary if a global taxonomy is to be built. Endemism has been seriously underestimated among diatoms, but biogeographical and stratigraphic patterns are difficult to discern, because of a lack of trustworthy data and because the taxonomic concepts of many authors are undocumented. Morphological diversity may often be a largely accidental consequence of physiological differentiation, as a result of the peculiarities of diatom cell division and the life cycle.

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[T]he determination of species in the Diatomaceae is at all times a task of difficulty, . . . much enhanced when the observer does not enjoy the opportunity of examining these organisms in their living state, or has only prepared or fossil specimens, within reach of his observations (Smith 1855)

Diatoms! you might as well collect and attempt to classify wall-papers (unattributed remark in Comber 1897)

Scis quod dicunt: uno diatomate viso, omnia visa sunt (adapted from Beard 1990)

I. INTRODUCTION

At least two dangers face anyone who tries to review the species concept with reference to a particular group of organisms, such as the diatoms. One is that the review focuses so strongly on the practicalities of species recognition in the group that it becomes little more than a list of useful characters, of no general interest. The other is that the review becomes an essay on species concepts in general, peppered with examples and illustrations from the group in question, chosen not because of their intrinsic worth, but because they are the only ones available that fall within the remit of the review. I have tried to follow a middle course, with the extra danger that I will please no one. I believe the attempt is justified for three reasons. First, diatoms are remarkably abundant, playing a very important part in global cycling of many elements, but particularly C and Si. Recent estimates of global net primary production suggest an overall total of 105 Pg (105×10^{15} g) of carbon fixed per year, of which 46% is oceanic and 54% is terrestrial (Field *et al.* 1998). Of the oceanic component, approximately one-quarter takes place in oligotrophic regions where diatoms account for no more than 25–30% of primary production (Nelson *et al.* 1995); but in highly productive areas, diatoms predominate. Overall, therefore, it might not be unreasonable to estimate that diatoms could account for between 40 and 45% of oceanic production, producing perhaps 20 Pg of carbon per year, making them more productive than all the world's tropical rainforests (Field *et al.* 1998). Diatoms play a particularly important part in sustaining fisheries, as the major producers of 'new' phytoplankton biomass, sustained by fluxes of nutrients from deeper waters as opposed to nutrients recycled via the 'microbial loop' (Falkowski *et al.* 1998). Diatoms are also the major sources of biogenic silica, transforming dissolved orthosilicic acid into the hydrated amorphous silica of their frustules; their contribution to the global biogeochemical cycle of silicon greatly outweighs that of silicoflagellates and radiolaria (data of Lisitzin: Tréguer *et al.* 1995). Thus, understanding diatoms and their species diversity can scarcely be irrelevant ecologically, especially in the context of enhanced atmospheric CO_2 levels (Smetaček 1999). Second, diatoms are found in almost all aquatic and many subaerial habitats, and exist in a huge variety of shapes and sizes; even on conservative estimates, they contain tens of thousands of species (e.g. Gordon & Drum 1994), yet the group has apparently existed only since the early Mesozoic (Medlin *et al.* 1997). Their explosive diversification demands an explanation, which must include how diatoms speciate. Third, diatoms are increasingly used in paleoecological reconstruction and ecological monitoring (Stoermer & Smol 1999), in which accurate identification of species and knowledge of geographical distributions are essential. Here, the current state of diatom taxonomy at the species level is a serious impediment to further progress. A recent paper by Spamer & Theriot (1997) illustrates how messy diatom taxonomy has become, by reference to a group of small-celled *Stephanodiscus* Ehrenberg species. Here, misidentification, nomenclatural errors, changes in the circumscription of taxa, and a failure to document research properly have created an impressive body of information about a cosmopolitan diatom that does not exist! Without greater attention to the species concept in diatoms, such problems will recur and get worse (see, for instance, section II d).

The species concept is one of the most widely debated themes in biology and no single review can now do justice to the literature. The controversies that still surround the subject could suggest that we are attempting to define the undefinable, or that we have not grasped some essential point about the evolution of diversity; thus, having asked the wrong questions, we are inevitably dissatisfied with the answers. Or, the fuss may be justified and the nature of species and speciation may be *the* central issue in evolutionary biology, so that Mayr (1963) could write "species are the real units of evolution, as the temporary incarnation of harmonious, well-integrated gene complexes . . . [without] speciation, the production of new gene complexes capable of ecological shifts, . . . there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution". Or, perhaps species have no reality, so that defining them is arbitrary, although they may nevertheless be useful for communication. One advocate of this nominalist standpoint suggested that: "species have no actual existence in nature. They are mental concepts and nothing more . . . conceived in order to save ourselves the labor of thinking in terms of individuals, and they must be so framed that they do save us labor" (Bessey 1908). The continuing uncertainty about species certainly contradicts the assurance of a recent dictionary, which reports modern usage of 'species' for "a taxonomic grouping ranking next below genus and subgenus, which contains organisms that are uniquely distinguished from others by certain shared characteristics and usually by an inability to interbreed with members of other such groupings" (Brown 1993; actually, I think this is rather good!). Similar definitions are found in many basic biology texts (e.g. Roberts 1976; Villee *et al.* 1989; Avila 1995), although in others the approach is more circumspect (e.g. Campbell 1987).

The principal focus of discussion during the last 60 years has been the 'biological species concept' (BSC) and it is the assimilation of this concept into common parlance that is reflected by the dictionary definition given above, which differs from earlier definitions in similar dictionaries (e.g. Craigie 1919: a species is "a group or class of animals or plants . . . having certain common and permanent characteristics which clearly distinguish it from other groups"). Various definitions of 'biological species' have been offered in the scientific literature. One of the most recent is "A species is a group of interbreeding natural populations that is reproductively isolated from other such groups" (Mayr & Ashlock 1991). A well-known older version (Mayr 1942) stated that the interbreeding could be actual or potential, but this was later deleted because "it is irrelevant for species status whether or not they [the isolating mechanisms] are challenged at a given moment" (Mayr 1982). Sometimes, ecological criteria have also been included, reflecting the idea that each species has its own niche (see, for example, Hutchinson 1978): "A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature" (Mayr 1982). Van Valen (1976) went further, suggesting that a species is "a lineage (or closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range".

According to Mayr (e.g. 1982), the key part of the BSC is reproductive isolation. Speciation occurs through the evolution of intrinsic isolating mechanisms, which prevent gene exchange between populations that formerly interbred. Criticisms of this idea come from several sources. Some say that it is operationally flawed, because it is impossible in practice to avoid dependence on phenetic comparisons, and that it is no less arbitrary than other concepts because all degrees of reproductive isolation occur, from complete intersterility to panmixis (Sokal & Crovello 1970). In any case, the critics say, who ever sees sex, except in humans, domestic animals, a few laboratory superstars (such as *Drosophila*), and garden birds? And how many species can ever be studied experimentally or genetically [e.g. through the use of isozymes or random amplified polymorphic DNA (RAPD) analyses], to detect whether gene flow occurs? Others have concentrated their criticisms of the BSC on the mismatch between reproductive isolation and the pattern of variation, giving examples of reproductive isolation between entities that, it is implied, no one would wish to recognize as distinct taxonomically, and examples where the members of readily distinguishable kinds of plants or animals are interfertile. Whether gene flow is effective in integrating members of a species together into a single cohesive entity has been questioned (Ehrlich & Raven 1969; Endler 1977; Raven 1986). Recent data suggest that rates of gene flow have often been seriously underestimated (Linhart & Grant 1996), but discontinuous variation can certainly be found between populations that potentially or actually interbreed, and such populations can exhibit unique derived characteristics (synapomorphies). In other words, phylogenetic structure can exist despite the absence of intrinsic isolation mechanisms (e.g. Bremer & Wanntorp 1979). To deal with this and provide a species concept that can be used as a basis for cladistic analysis of relationships, a number of phylogenetic species concepts have been put forward, such as "a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983). Meanwhile, there has been philosophical discussion of whether species are individuals or classes (Ghiselin 1997; Ruse 1998) or neither (Stamos 1998).

In order to avoid having to give a detailed evaluation of the many other species concepts that have been suggested (e.g. Stuessy 1990; Ereshefsky 1992; Mayden 1997; see also Mann & Kociolek 1990), it is probably best to step back and consider why any 'species concept' has been formulated and what a 'species concept' is. It is unclear to me that many of the formulations in the literature (examples of which are given above) are concepts at all (see also Mayr 1996). Instead they are definitions. A concept is "a product of the faculty of conception; an idea of a class of objects, a general notion; a theme, a design"; definition, on the other hand, is "a precise statement of the nature, properties, scope or essential qualities of a thing; an explanation of a concept . . . " (Brown 1993). Definitions are attempts to convey precisely what a concept entails and are important because without them concepts are untestable. However, rejection of a particular definition does not make it necessary to reject the underlying concept that prompted its formulation. Thus, even if we reject any or all of the definitions of the BSC provided by Mayr and others, that does not mean that gene flow and reproductive isolation are irrelevant to an understanding of what species are, how they evolved, and how they are delimited. Indeed, what critics often object to in the BSC is not the idea of reproductive isolation being an important aspect of speciation, but the emphasis in some BSC definitions on isolation through *intrinsic* barriers to interbreeding.

The more that I examine the plethora of species concepts and definitions that are available, the more I come to the conclusion that there is substantial agreement between many of them; they are often more compatible than their authors suggest. The exceptions are definitions that represent an extreme nominalist or essentialist position (Mayr 1982, pp. 255–265). The agreement comes, I suggest, because species are real—they do exist, at least among most eukaryotes—and hence can be discovered. And they exist because of the uncontroversial existence of sexual reproduction and meiosis.

The notion of species has its origin in the observation that variation among living organisms is discontinuous and nonrandom. The distributions of characteristics are often correlated to different degrees in an organized pattern, so that variation is hierarchical. Hence, we can recognize nested sets. However, in the majority of eukaryotes, the hierarchy breaks down among very similar individuals and here we observe variation that is almost continuous or reticulate. It is the boundary between hierarchical and nonhierarchical variation that underlies the concept of species: variation is essentially hierarchical among species and nonhierarchical within them (see also Davis 1999). No other taxonomic category corresponds to a boundary of this kind, between qualitatively different patterns of variation. Admittedly, the boundary is sometimes fuzzy, but it exists (the exception concerns asexual organisms: see below), and it exists independent of whether we can find an explanation for it, making it possible (although not necessarily desirable) to classify without understanding the evolutionary processes that have produced and maintain the boundary. Historically, when human beings have been confronted on a day-to-day basis with the variation pattern among organisms, they have often distinguished entities at this minimal level that correspond to modern 'species' (for Europeans and European vertebrates, I take this as self-evident; for folk taxonomy in other areas, see Diamond 1966; Mayr 1969; Berlin 1973). This was done long before anyone had developed an adequate genetical theory of evolution. But it is unsatisfying to observe a pattern and have no explanation or understanding of it, because there is always the possibility that the pattern is in fact trivial and meaningless. Two-dimensional random arrays of dots may form patterns that one finds difficult to believe arose by chance. As Leonardo da Vinci noted, "when you look at a wall spotted with stains or with a mixture of stones . . . you will be able to see in it a resemblance to various landscapes . . . or again you may see battles and figures in action; or strange faces and costumes and an infinite number of things which you can then reduce into separate and well-drawn forms . . . " (Richter 1952).

Despite the arguments between those who advocate species definitions that make overt reference to reproductive processes (whether this is the BSC of Mayr 1942, 1982; the specific mate recognition concept of Paterson 1985; or the cohesion concept of Templeton 1989, which defined species as "the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability") and those who do not (e.g. proponents of the various phylogenetic species concepts: for references, see Ereshefsky 1992; Davis 1997, 1999), almost everyone does seem to agree that the hierarchy of variation has a limit, below which variation is reticulate, and that this is almost wholly because of gene transfer and recombination during sexual reproduction (breakdown in hierarchical variation through endosymbiosis is a special case that need not concern us here). If sexual reproduction is absent, then the primary mechanism of genetic transfer between lineages is also absent and essentially all variation is hierarchical; here, the ranking of a particular group as a 'species' is a matter of convention and utility. Hence, gene flow is indeed at the heart of the matter, as the architects of the 'Modern Synthesis' said it was (Mayr & Provine 1980; Mayr 1982). It does not follow that gene flow will always prevent divergence and the development of hierarchical structure in interfertile populations, nor that detectable divergence will automatically accompany reproductive isolation (although given time this is inevitable: e.g. Maynard Smith 1989); but the only mechanism that integrates populations and leads to the formation of a boundary between hierarchical and nonhierarchical variation is gene flow, brought about principally by sexual reproduction, in conjunction with dispersal and migration. Thus, it can never be irrelevant for taxonomists to know about the mating system, phenology, and spatial dynamics of the organisms they study, and it is always going to be an impediment to paleontologists that they have no direct access to this type of information. The systematics of fossil organisms will always be deficient (see also Cox 1993).

If the whole idea of 'species' is based on observation and is the concomitant of uncontroversial properties of most eukaryotes (meiosis, sexual reproduction, and dispersal), why is it so difficult for taxonomists to agree upon a definition of the species category, or about the boundaries of particular species taxa? One reason is that gene flow is not all or nothing. Its effectiveness in integrating populations varies in time and space, and with respect to which genes are being considered. Gene flow is sometimes insufficient to oppose selection, allowing the formation of locally adapted populations and sometimes producing clear discontinuities in the distributions of adaptive characters. However, with respect to other genes in the same populations, gene flow can be a powerful integrating force, despite the strong selection operating on adaptive characters, even when there is nearly complete reproductive isolation. For neutral alleles, levels of hybridization that are for all practical purposes undetectable by direct observation can homogenize populations of two species, given enough time. For example, if the proportion of successful hybrid matings is only 1 in 100,000, the difference in allele frequencies between two large populations will decline to 13.5% of its starting value in 100,000 generations (Clarke *et al.* 1996). As a result of such slow 'molecular leakage', phylogenetic trees based on neutral or slightly advantageous genetic differences can be seriously misleading, as apparently they were in the Polynesian land snails studied by Clarke *et al.* (1996).

Another reason for disagreements about the limits of species is simple ignorance. In many cases, our knowledge of the variation pattern is poor and based on only a few preserved specimens, which may well be unrepresentative of the populations from which they were derived. The agreement between folk taxonomies and modern classifications of birds and other higher animals, to which I have already alluded (Diamond 1966; Mayr 1969; Berlin 1973), is a useful demonstration of the nonarbitrary nature of species, but it would almost certainly not have come about if both taxonomies had not developed over many years and had not been informed by observations (both casual and planned) of huge numbers of individuals. The boundary between hierarchical and nonhierarchical variation cannot be detected without extensive sampling and analysis. Poor sampling can easily lead to the impression of discontinuities where in fact there are none. On the other hand, poor analysis can lead to the impression of continuous variation where more careful study would reveal subtle structure.

Faced, then, with unavoidable difficulties arising from the evolutionary process itself and from operational difficulties resulting from only too limited material and time, how is the taxonomist to proceed? Good advice comes from Ruse (1987, 1998), who suggests, after Whewell, that we use as many different independent sources of data as we can and look for agreement (consilience, congruence) between them: "make a virtue of pluralism. If you try to find a sole method of characterizing species and separating one group from another, if you privilege one set of activities and pretend that they alone are truly 'biological' . . . you are going to run into problems when you try to show why your method uniquely leads to a natural classification: to species which are real. Rather, we should see that species are real or natural precisely because they do separate out organisms on ground of breeding *and* of physical features *and* (probably) much more, like ecological or molecular characteristics" (Ruse 1998). This total evidence approach is what we have called the Waltonian species concept (Mann *et al.* 1997: 'compleat taxonomy', in imitation of Walton's *Compleat Angler*—Bevan 1993). The Waltonian concept asserts that species are real and discoverable, but that they may not be amenable to simple definition. They are, in a sense, whatever a competent systematist says they are, as Regan said (1926: "a species is a community, or a number of communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name. Groups of higher or lower rank than species can be defined in a similar way"), but this is not an excuse for cynicism about the whole enterprise of taxonomy. Instead, we should recognize that the Waltonian species concept requires a rigorous, multidisciplinary approach and that Regan's 'competence' means the inclination to search for, and the ability to find, a consilience of evidence concerning the real boundary between hierarchical and nonthey frequently disagreed about the limits and status of particular taxa. Cleve (1894–95) discussed the value of various characters in diatom taxonomy and seems to have believed that each character is valuable at a particular level in the taxonomic hierarchy, but there was no suggestion there or in most other major taxonomic works of the late nineteenth or early twentieth centuries that species are in any way a 'special' taxonomic category.

The most interesting essay on diatom species from the nineteenth century is by Comber (1897); it may be relevant that he did very little taxonomy himself. Comber tentatively challenged the view among most of his contemporaries, following Darwin, that species were arbitrarily defined, like varieties and genera. Species, he suggested, are real and clearly differ from varieties. The distinction between them "lies in the degree of differentiation of the sexual elements", which leads to reproductive isolation. This "cuts up the originally continuous chain of related forms into separate sections, incapable of completely fertile crossing. Such sections are what appear to me to be natural species". What we would now call gene flow provides cohesion: "the characters of the entire group may be gradually changed by the action of natural selection, but through continual crossing they are changed together . . . When, however, through isolation, geographical or otherwise, and from part of the group being exposed to different conditions of life, a differentiation in the sexual elements of the individuals composing that part is brought about, so that they can no longer produce fully fertile offspring when crossed with the others, the more or less sterile hybrids no longer hold their own . . . a new 'species,' as I understand the term, comes into existence". Comber's essay is a good early statement of allopatric speciation and the biological species concept, later developed by Mayr, Dobhzhansky, and others (see Mayr 1982). Unfortunately, as Comber was the first to admit, no one knew much about sexuality and reproductive isolation in diatoms. For practical purposes, therefore, he fell back on what he perceived as the consequence of reproductive isolation, viz. a discontinuity in the pattern of morphological variation: ". . . we may adopt, as the practical criterion of specific distinction, the existence, or non-existence, of an unbroken series of intermediates". He then gave some examples from Cleve (1894–95) where his procedures would lead to changes in current taxonomy, and also some examples where previous authors had united diverse forms under one species because of continuous variation, for example, Grunow's (1879) treatment of *Nitzschia sigma* (Kützing) W. Smith: "*N. sigma* embraces a great number of forms, the extremes of which would not with certainty be relegated to one species were it not that so many intermediate forms exist between them" (Comber 1897). This particular example needs reinvestigation, but the procedure described––of using morphological variation as a surrogate for reproductive isolation, while still advocating reproductive isolation as the primary basis for separating species—is the same as has been advocated more recently, for sexual organisms in general, by Mayr (e.g. Mayr & Ashlock 1991, pp. 29–30), and for diatoms by Lange-Bertalot (1990; see below).

The principal diatom taxonomists of the twentieth century, like their forebears, have rarely discussed their underlying species concept. Species concepts are not discussed by Cleve-Euler (1951), although she did make suggestions about the treatment of infraspecific categories. Nor are they treated in the many floristic papers by Hustedt (for bibliography, see Simonsen 1987), nor in either of the two major floras he wrote (Hustedt 1927–66, 1930). However, Hustedt did discuss systematic concepts in two papers published in 1937. He regarded genetic differentiation as necessary for varietal rank, whereas variation resulting from a phenotypic response to ecological conditions could be recognized through the use of *formae* (1937a, 1937b, 1956). Following Darwin, he apparently saw no qualitative distinction between varieties and species. Varieties "sind kleine Einheiten, die sich von den Arten, zu deren Formenkreis sie gehören, nur durch ein oder wenige, nach unseren Begriffen geringfügige, aber erblich bedingte Merkmale unterscheiden" (Hustedt 1937a). But varieties had to be distinct to be valid: continuous series of transitional forms linking different morphologies demonstrated that 'true' varieties were not present (Hustedt 1937a). In this, therefore, Hustedt's philosophy ran counter to Comber's theory and to nineteenth century practice, and Hustedt accordingly rejected or downgraded many varieties, even those he had described himself (e.g. his treatment of *Sellaphora* [*Navicula*] *pupula* (Kützing) Mereschkowsky in Hustedt 1927–66). As for species, Hustedt (1937b) gave some rules for taxonomists to follow. If closely related but different forms often occur together in the same ecological conditions without intergradation, then they are probably separate species. Different forms, separated from each other geographically, are probably also different species, although at some stages in their life cycles they may be indistinguishable, as a result of ontogenetic convergence—diagnostic characters can be lost during size reduction. As a result, the affinities of intermediate forms and small cells ('Kümmerformen') can be determined with certainty only if the whole life cycle is known or if the taxonomist has a deep knowledge of biogeography and ecology.

Few diatom taxonomists dared to question Hustedt's taxonomy, or the philosophy behind it, during his lifetime (*floreat* 1908–1967: Simonsen 1987). Those that did risked a vigorous response (e.g. Hustedt 1937a; Mayer 1940). Petersen (1950) was an exception. He noted that Hustedt regarded many species as cosmopolitan but suggested that Hustedt's species concept was too broad; as a result, the taxa Hustedt described were "useless in ecology as well as plant-geography". "One would not expect at the outset to find the same species in a tropical and a northern flora or in northern Europe and northern America, even under approximately identical climatic conditions". Petersen realized, however, that it was impossible at that time to test his idea, because literature records were generally ambiguous. He therefore recommended that all records should in the future be backed by voucher specimens. Unfortunately, this is rarely done even now.

Berg (1944) also criticized Hustedt's approach to species taxonomy, but it is unclear exactly what he proposed to put in its place. Berg considered that most species of pennate diatom intergrade, so that species distinctions are often arbitrary. He suggested that taxonomy would improve if a wider range of characters was employed and there was a greater emphasis on experimental studies of variation (and preferably also hybridization). Alas, more than 50 years later, this advice too is still pertinent.

Elmore (1896, 1921) rejected the use of varieties altogether, leaving species internally undifferentiated, partly because he hierarchical variation. The fruits of this difficult and lengthy search are species: "the minimal groupings among which descent relationships are hierarchic" (Davis 1997).

II. HISTORICAL REVIEW

Pre-Darwinian concepts of species in diatoms

It is difficult to review the species concepts used by diatom taxonomists, because few of them have ever explained their thinking; sometimes too, there has been a marked discrepancy between theory and practice. Diatom species began to be described well before the Darwinian revolution (e.g. Agardh 1830–32; Ehrenberg 1838; Kützing 1834, 1844; Rabenhorst 1853; Smith 1853, 1856). At that time, most people regarded species as separate and immutable (Mayr 1982) and it is perhaps not surprising that early classifications of diatoms contained almost no discussion of species concepts, or that they contained very few descriptions of infraspecific taxa (because variation within species was held to be 'accidental'—a kind of imperfection). Thus, Kützing (1834) listed varieties for only three of the c. 120 species he catalogued and he made it quite clear that he regarded the difference between them as trifling ("nur höchst unbedeutend"). In one of the few pre-Darwinian comments on the nature of diatom species, Smith (1856) revealed the underlying essentialism of the period: "The determination of genera being mainly an artificial mode of aiding research, or conveniently grouping together forms possessing in common important and obvious characteristics ... must, to a great extent, be influenced by the theoretic views, and be left to the ... judgement of the individual enquirer; but it is far otherwise with the determination of species. We here seek to discover the distinctions which have been impressed by nature upon every individual derived by reproduction or by self-division from the original product of the creative act". Likewise, Gregory (1857) revealed his essentialistic philosophy when he commented, in relation to the description of his new variety *N. fusca* of *Navicula smithii* de Brébisson *ex* W. Smith [now *Diploneis smithii* (de Brébisson *ex* Smith] Cleve): "It may be that the present form *N. fusca,* is the typical one, and the other [*N. smithii*] a variety of it; but in my experience I have only seen *N. fusca* in the gatherings above named [from West Scotland], while I observe *N. smithii* in every marine gathering". [As it turns out, both *Diploneis smithii* and *D. fusca* (Gregory) Cleve are probably heterogeneous, containing several species: see below and Droop 1994, 1995.]

In Smith's taxonomy (1853, 1855, 1856), varieties were phenotypic variants, arising through the peculiar method of cell division found in diatoms: "while a typical outline of its frustule is the general characteristic of a species, this outline may be modified by the accidental circumstances which surround the embryo during its growth ... The process of self-division now intervening, and necessarily stereotyping the shape with which it commences, multitudes of frustules slightly deviating from the normal form are ... produced, so that the observer, judging from a single gathering, may be led to fix upon a variety as representing the typical form and size of the species" (Smith 1856). One consequence of such views was the search for reliable specific characters, which would give unambiguous guidance about species boundaries. For example, Smith (1856) considered that the arrangement and density of the rows of pores in the valve (the striae) "are features which may safely be regarded as of specific importance", although Gregory (1855) and Greville (1859) doubted whether any characters were foolproof: "scarcely any one character taken by itself is to be relied on ... even a combination of characters which may be sufficient for the determination of species in one genus, may be unsatisfactory in another" (Greville 1859).

Post-Darwinian concepts of species in diatoms

Darwin considered that his account of the gradual evolution of species from varieties had solved the species problem. For him, there was no essential difference between varieties and species. [There is] "no infallible criterion by which to distinguish species and well-marked varieties ... I look at the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again in comparison with mere individual differences, is also applied arbitrarily, for convenience' sake"; "a well-marked variety may ... be called an incipient species" (Darwin 1878). And because the distinction between species and varieties was arbitrary, systematists would no longer "be incessantly haunted by the shadowy doubt whether this or that form be a true species ... The endless disputes whether or not some fifty species of British brambles [*Rubus* spp.] are good species will cease. Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and if definable, whether the differences be sufficiently important to deserve a specific name". Darwin's optimism was misplaced. People still argue about brambles and the history of diatom systematics shows that the use of 'species' and 'variety' became even more contentious after 1859, not less.

Even before *The Origin of Species* was published, diatomists' use of 'species' and 'variety' began to change. Gregory (1857) sometimes described varieties "to avoid unnecessary multiplication of species", even when he thought two entities were probably distinct. However, after 1859 further changes were made, beginning with Grunow (1860, 1862a, 1862b). No explanation was given at the time, but it is not unlikely that Darwin's opinions were influential, because Grunow seems to have regarded species and varieties as differing in degree, not kind. In publications such as those listed above and in Cleve & Grunow (1880), Grunow used variety for what he interpreted as minor variants, or for local races, or to break up a continuum of variation within a particularly variable species into more or less arbitrary units (for example, see his 1860 treatment of *Navicula radiosa* Kützing), and he often changed the status of his own taxa, from species to variety or vice versa. In one extreme example [*Berkeleya rutilans* (Trentepohl *ex* Roth) Grunow], he distinguished 30 varieties to describe infraspecific variation (Grunow 1880).

From 1880 onward, huge numbers of species and varieties were described (e.g. see VanLandingham 1967–79) and most authors apparently viewed these categories in the same way as Grunow (e.g. Cleve 1894–95; Van Heurck 1896), although considered that scarcely any species had been studied in enough detail to justify such distinctions and partly because "the term variety can scarcely be applied to diatoms. The species of diatoms present the same varieties now that they did in Tertiary times; so if these varieties are thus fixed, they are not varieties, but species" (Elmore 1921). Hendey (1937) also rejected the use of varieties and forms: "no one is yet in a position to say . . . how or in what respects a variety differs from a form or what relation either has to the species." Hendey conceived species as "an orbital system of disparate units expressing itself in time and space, somewhat analogous to a solar system". Superficially, this appears to resemble Hutchinson's concept of species as clusters in a taxonomic or niche hyperspace (Hutchinson 1968), but although Hendey's was certainly a phenetic concept, like Hutchinson's, it is difficult to comprehend exactly what Hendey meant, especially in view of comments such as "under normal conditions the units are concentrated into genic clusters and scatter centrifugally as conditions become adverse. The whole system is analogous to a complex kinetic system, in which the units act and are acted upon at random." Elsewhere, Hendey (1937) indicated that different stages of the life cycle and phenotypic variants should not be given taxonomic status, and that, if two forms are linked by a continuous series of intermediates, neither should be recognized taxonomically. Later, although still recognizing very few varieties, Hendey (1964) seems to have adopted a Darwinian approach to species, in which varieties are incipient species: "for a variety to have a reality worth recognising it should not only differ from the type but should occupy a different living space, or the same living space at a different season. If the difference between them is one of kind as well as of degree, the variants should be given specific rank". But, as in 1937, intergradation was considered decisive for rejecting varietal status and in this respect Hendey's taxonomy strongly resembles Hustedt's.

In the last 20 years there has been more widespread discussion than hitherto of the species concept in diatoms (e.g. Cox 1997; Krammer & Lange-Bertalot 1986; Mann 1989a; Mann & Kociolek 1990; Rines 1994; Mann & Droop 1996; Round 1996b, 1998). Most of the points that have been made are dealt with below, in the context of recent data. Rines (1994) apparently advocates the view that species are minimal monophyletic units, following Mishler, Donoghue, and others. Arguments against the 'monophyletic species concept' are given by Davis (1997, 1999, who gives references) and seem compelling.

Fantasies

In the literature on diatom species there are some claims and ideas that are intriguing, and may be true, but as yet have no basis in fact. One such is Mayer's description of hybrids in *Pinnularia* Ehrenberg (Mayer 1940, 1946). Mating has been recorded between morphologically dissimilar diatoms (section IV a), but even if it had not, it would be almost inconceivable that hybrids such as those found in higher plants are never formed. However, for claims of hybridity to be believable and interesting, one must first demonstrate that the two parents are significantly different (hybridization within a well-defined sexual species such as *Homo sapiens* is rarely remarkable, except to the participants and their families), and then document formation of hybrids, either through direct observation (e.g. Geitler 1958a, 1969) or indirectly, using genetic markers. Mayer did neither and his claims of hybrids are therefore dismissed (e.g. Krammer 1992a).

Another fantasy is the interpretation of diatom variation put forward by Bonik (1982). In the late 1970s, Lange-Bertalot and Simonsen published a revision of *Nitzschia* Hassall sect. *Lanceolatae* Grunow (Lange-Bertalot 1976, 1980; Lange-Bertalot & Simonsen 1978). The outcome of the revision was that many previously described species were reduced to synonymy (section II d). The remaining species formed two groups, one containing extremely variable cosmopolitan species, such as *N. intermedia* Hantzsch *ex* Cleve & Grunow, *N. frustulum* (Kützing) Grunow *in* Cleve & Grunow, or *N. gandersheimiensis* Krasske (later made a synonym of an even larger species complex, *N. tubicola* Grunow *in* Cleve & Grunow: see Krammer & Lange-Bertalot 1988), the other containing much less variable species with a restricted geographical or ecological range, such as *N. pumila* Hustedt, *N. graciliformis* Lange-Bertalot et Simonsen, or *N. alpina* Hustedt (Lange-Bertalot & Simonsen 1978; Krammer & Lange-Bertalot 1988). From this and on the basis of a previous discussion of gene flow among species of *Nitzschia* sect. *Lanceolatae* by Bonik & Lange-Bertalot (1978), Bonik constructed an elaborate model to explain the variation pattern. This involved the idea that gene flow could potentially occur, directly or indirectly, between any of the sect. *Lanceolatae,* so that together they would form a 'syngameon' or 'comparium' (Grant 1981; Bonik 1982), isolated reproductively from other groups of diatoms but able to exchange genes internally, although at different rates. Where the rate of gene flow was high and the habitats occupied were widespread and 'mesic' (i.e. not extreme), the result would be the evolution of very variable, generalist species. On the other hand, most matings within a local population would be intraclonal and this, together with restricted gene flow between populations, would allow the formation of local, ecologically specialized species, especially in extreme but stable habitats: "Die Syngameon-Interpretation mit ökologisch spezialisierten Teilpopulationen setzt voraus, daß der Genfluß innerhalb der lanceolaten Nitzschien zwar praktisch global erfolgt, im wesentlichen jedoch auf lokale Populationen beschränkt bleibt . . . Auf diese Weise können und müssen sich ökologisch different angepaßte Lokalpopulationen ausbilden, die natürlich auch morphologisch voneinander unterscheidbar sein können. Diese Ökotypenbildung mit begrenzter genetischer Grundlage schreitet umso besser voran, je stabiler die Umweltbedingungen sind und je stärker der Genfluß unter diesen Bedingungen eingeschränkt ist" (Bonik 1982).

Bonik's idea is attractive and the syngameon concept has been quoted with approval by Lange-Bertalot (1990; Krammer & Lange-Bertalot 1986). However, there are two problems with Bonik's hypothesis that reduce it to 'fantasy' and make further discussion unprofitable. First, the idea was based on a taxonomic analysis that was always questionable (e.g. see Mann 1982) and has increasingly been abandoned, even by its principal architect, Lange-Bertalot (section II d). It is by no means clear that variation is truly continuous in species such as *N. tubicola* or *N. intermedia,* and the relationship that was claimed to exist between morphological variation, geography, and ecology needs reexamination. Second, there is very little information about the reproductive biology of *Nitzschia,* and none about gene flow among its species. What little we do know about reproductive behavior in the sect. *Lanceolatae* (Geitler 1932, 1973b, 1985) does not rule out the possibility that the taxonomic difficulties with this group might reflect auto- or apomixis (cf. *Rubus, Hieracium,* or *Taraxacum* among higher plants: Grant 1981) and certainly provides no support for Bonik's hypothesis. This seems now to be the opinion also of Lange-Bertalot (1990).

Currents and countercurrents: the last 25 years

The last 25 years have seen radical and sometimes unpopular changes to generic classifications of diatoms, as a result of new information from scanning electron microscopy (SEM) and protoplast characters (a summary of change up to 1988 is given by Round *et al.* 1990); these do not concern us here. In parallel, however, there have been extensive changes in species-level taxonomy, most of them carried out by the 'Frankfurt school', a highly productive group of diatomists associated with Professor Horst Lange-Bertalot. In numerous papers and books, including the four parts of the *Süsswasserflora von Mitteleuropa* (Krammer & Lange-Bertalot 1986, 1988, 1991a, 1991b), together with associated volumes (e.g. Krammer & Lange-Bertalot 1985; Lange-Bertalot & Krammer 1987) and addenda (Lange-Bertalot 1993a,b), 'monographs' (e.g. Krammer 1992a, 1992b, 1997a, 1997b; Lange-Bertalot & Moser 1994), floras and inventories (e.g. Lange-Bertalot & Metzeltin 1996a; Metzeltin & Witkowski 1996; Metzeltin & Lange-Bertalot 1998; Moser *et al.* 1998; Lange-Bertalot & Genkal 1999a, 1999b), and shorter papers (e.g. Lange-Bertalot 1995, 1996, 1999a, 1999b, 1999c, 1999d, 1999e; Lange-Bertalot & Metzeltin 1996b; Lange-Bertalot *et al.* 1996; Metzeltin 1996; Witkowski *et al.* 1997), this school has described hundreds of new species and revised many more, mostly in books and series not subject to peer review. The rate of output is astonishing (whether expressed in pages or taxa), and the effects on taxonomy, and consequently on those who study the ecology, paleoecology, and biogeography of diatoms, are extensive and profound. Hence, no review of diatom taxonomy would be worthwhile if it did not examine in detail the species concept that Lange-Bertalot *et al.* have adopted.

Lange-Bertalot and Krammer have sometimes called their approach 'typological' (Lange-Bertalot & Ruppel 1980; Krammer & Lange-Bertalot 1986; Lange-Bertalot 1990), but this should not be taken at face value because they clearly do not accept the four postulates of the typological species concept listed by Mayr & Ashlock (1991) and nowhere advocate the essentialistic philosophy that underpins typology (Mayr 1982; Mayr & Ashlock 1991). Recently they have stopped referring to their concept as typological (Lange-Bertalot 1997, 1998: these two papers are almost identical). Their species concept is outlined in several publications (Lange-Bertalot & Simonsen 1978; Krammer & Lange-Bertalot 1986; Lange-Bertalot 1990), but must also be deduced from actual practice, particularly in relation to the genus *Nitzschia.* It seems that they are attempting to use morphological evidence to infer the limits of biological species *sensu* Mayr, as recommended by Comber (1897).

Lange-Bertalot's revisions of *Nitzschia* were prompted by practical considerations. While searching for bio-indicators of water quality, he found that some of the most important diatoms in polluted waters were members of *Nitzschia* sect. *Lanceolatae* (Lange-Bertalot 1976, 1979), but that these were useless for environmental monitoring because they could not be separated into species or identified reliably using existing floras. He therefore began a taxonomic revision of sect. *Lanceolatae.* In his first major paper on *Nitzschia,* Lange-Bertalot (1976) did not explicitly discuss his species concept but individual accounts of species show that taxa were combined if there seemed to be continuous intergradation between them, or if the differences between them were considered minor. For example, nine species and varieties described by Hustedt were considered to intergrade and thus were made synonyms of *N. intermedia,* while *N. holsatica* Hustedt was rejected on the basis that the primary diagnostic character—the formation of stellate colonies—is a growth form, produced in response to optimal growth conditions [Lange-Bertalot (1980) treated colony formation as warranting form status only].

Fuller discussion followed in later papers. According to Lange-Bertalot & Simonsen (1978), 'real' species are separated by reproductive barriers: "sexual incompatibility exclusively can be decisive for the separation of real, i.e. biological species". The BSC was also quoted with approval by Krammer & Lange-Bertalot (1986) and Lange-Bertalot (1990), and reaffirmed most recently by Lange-Bertalot (1997, 1998). It seems, therefore, that the BSC is ultimately the guiding principle behind the changes introduced by Lange-Bertalot and his coworkers, although Lange-Bertalot (1980) discussed some of the classic difficulties with the BSC, such as its application to apomictic organisms. In a perceptive review of diatom taxonomy, Ettl (1993) also supported the BSC: "Für die moderne Systematik sind zwei Definitionen von Arten bedeutend, die eine als biologische, die andere als strukturelle. Die erste ist für theoretische Erwägungen die allein relevante". However, while advocating the BSC in theory, Lange-Bertalot and Ettl seem to have believed that in practice a biological species definition is impossible for diatoms. Lange-Bertalot therefore sought to establish a surrogate basis for species definition, according to the idea that "on the basis of a number and specificity of morphological differences, one should be able to find an 'indicator' of reproductive isolation . . . features which allow the deduction of such to be traced" (Lange-Bertalot 1990; this was based on the ideas of Mayr, which are summarized by Mayr & Ashlock 1991). This effectively meant emphasizing presence/absence characters. Hence, for example, the revisions of *Nitzschia* sect. *Lanceolatae* relied heavily on whether the raphe is interrupted by a central nodule or runs unbroken from pole to pole. As to quantitative characters such as valve shape and the linear densities of the structural elements of the valve (striae, areolae, fibulae, and so on), "it seems more likely that they must be regarded as smaller differences due to various ecologic influences which may be manifested genetically ('local races') rather than to sexual incompatibility" (Lange-Bertalot & Simonsen 1978). However, no information was presented about reproductive isolation or phenotypic plasticity and no morphometric analyses were made, and independent estimates of relationships, using molecular genetic data, were not yet possible during the earlier phases of Lange-Bertalot's work on *Nitzschia.*

According to Lange-Bertalot (1990), attempts to distinguish 'real' species should be based on extensive studies of many cells from many populations, as argued earlier by Hustedt (1937b; see above). The chances of success in taxonomic revision would be high "if many individuals of all developmental stages of their peculiar cycle and many populations from different localities are the basis of a taxon", which will then be a "well founded hypothetical species, which might be confirmed or rejected". The probability of success would be low "if a taxon is based on very few specimens or even tends to zero if only one specimen is the random sample in discussion" (Lange-Bertalot 1990). There is, then, very little difference between what Comber recommended should be the basis for distinguishing species and what Lange-Bertalot and his colleagues claim to have done.

Clear differentiation from other species has also been stressed by Lange-Bertalot as essential for species definition. "We propose . . . to introduce new species only when criteria for a clear differentiation from the earlier taxa are definable . . . in the past species delimitations have often been set arbitrarily into a continuous range of morphologic characters" (Lange-Bertalot & Simonsen 1978). "Each author should clearly present the features on which a new taxon differs from already established ones. It is essential that each diagnosis contains a differential diagnosis"; the taxonomist "will have to substantiate and to justify his decisions. His procedures will only be correct in terms of scientific theory, if his hypotheses are formulated in such a manner that they can be falsified . . . by new findings . . . we assume diatomists have put much too many taxonomical species into circulation, and they continue to do so".

This, then, is supposedly the basis for the species taxonomy of Lange-Bertalot and his colleagues. Thorough study of many populations will lead to the distinction of entities that correspond, by and large, to 'real' biological species, leading to a stable taxonomy. To aid identification, descriptions of new taxa should make it quite clear what the diagnostic characters are, so that taxa are, in some sense, testable hypotheses.

Although one cannot help but admire and envy the energy and enthusiasm of Lange-Bertalot, Krammer, and their coworkers, critical analysis of their output leads me to the conclusion that, whatever the merits of their approach in theory, their practice is flawed. Their species concept is unclear and has apparently changed without explanation; their delimitation of particular species is inconsistent; and their revisions, descriptions, and diagnoses often fail to provide "clear differentiation" between taxa [I have found it particularly difficult to use the latest revisions of *Cymbella sensu lato* (Krammer 1997a, 1997b)]. To demonstrate some of the problems that have arisen, I have examined in some detail Lange-Bertalot's work on *Nitzschia,* having had a long-term interest in this genus myself (Mann 1978). Lange-Bertalot (Lange-Bertalot 1976, 1980; Lange-Bertalot & Simonsen 1978) made extensive revisions of species limits in *Nitzschia,* particularly in the sects *Lanceolatae* and *Lineares* Grunow, leading to the abandonment of many previously recognized taxa, especially those described by Hustedt. Since 1980 there have been further revisions, continuing to the present.

The documentation of type material in these papers is useful and will remain so for as long as the type method is used, although I have detected some errors in the figure captions [in a few cases the same diatom valves are illustrated, with different captions (Lange-Bertalot 1976; Lange-Bertalot & Simonsen 1978; Krammer & Lange-Bertalot 1988; Lange-Bertalot 1990], which give cause for concern. Such errors show that, when type material is documented, it is important to follow Simonsen's (1987) superb example by photographing type specimens and tying each photograph to a located specimen, not merely to a whole slide preparation or source locality (Mann 1998); only then is typification exact and the associated research repeatable.

More important than any lapses of editorial control [and I am not guiltless: cf. my inclusion of a picture of *Diploneis* Ehrenberg *ex* Cleve under *Pinnularia* in the first printing of Round *et al.* (1990, p. 557, fig. g), and one of *Campylodiscus* Ehrenberg under *Surirella* Turpin (*ibid.*, p. 645, fig. g), which I did not detect until it was pointed out by Lange-Bertalot & Metzeltin (1996b)] are the changes Lange-Bertalot has made in his own classification since 1980, because he has now reversed many of the taxonomic changes made in *Nitzschia* by Lange-Bertalot (1976, 1980) and Lange-Bertalot & Simonsen (1978). For example:

1. *Nitzschia recta* var. *robusta* Hustedt was combined with the type by Lange-Bertalot & Simonsen (1978), then separated as an independent reproductive community ('Sippe': see below for an explanation of this term, and also Lange-Bertalot 1997) within *N. recta* Hantzsch *ex* Rabenhorst by Krammer & Lange-Bertalot (1988), and most recently made a separate species, *N. rectirobusta,* by Lange-Bertalot & Metzeltin (1996a). Species status is justified by Lange-Bertalot & Metzeltin (1996a) on the basis of differences in striation density and silicification, and the fact that *N. recta* and *N. rectirobusta* often occur in association without intergradation. Why was this possibility not examined before these taxa were combined in 1978? It seems in fact, that Lange-Bertalot & Simonsen (1978) only examined one specimen of *N. recta* var. *robusta* (Lange-Bertalot & Simonsen 1978, p. 47).
2. *Nitzschia gessneri* Hustedt was considered conspecific with *N. impressa* Hustedt by Lange-Bertalot & Simonsen (1978), who also suggested that both species might be conspecific with *N. tenuis* Grunow ("it is very probable that *N. impressa* is only a forma of *N. tenuis*"). Krammer & Lange-Bertalot (1988), however, treated *N. gessneri* as an independent species, whereas *impressa* and *tenuis* were included as varieties of *N. linearis* W. Smith. They gave essentially the same description and morphometric data for *N. gessneri* in 1988 as in 1978, and no explanation was given for the change in taxonomic treatment. Lange-Bertalot & Metzeltin (1996a) list both *N. tenuis* and *N. gessneri* as independent species, but give no discussion whatsoever of either; how, then, was the earlier taxonomic hypothesis falsified?
3. Lange-Bertalot & Simonsen (1978) suggested for *N. bryophila* Hustedt that its "morphology (except striation density) and ecology is in accordance with *N. pseudofonticola* . . . Thus a conspecificity with this latter species can be suspected". In 1988, Krammer & Lange-Bertalot stated that a link between these species could no longer be entertained "nach erweiterter Kenntnis ihres Variabilitätsspektrums". But the descriptions and morphometric data are almost identical in the two publications, giving no hint

as to what the new knowledge might be that caused the change of mind.

4. *Nitzschia regula* Hustedt was treated as a synonym of *N. intermedia* even by Hustedt himself (1949) and this policy was continued by Lange-Bertalot (1976) and Krammer & Lange-Bertalot (1988). Lange-Bertalot (1993a) decided, however, that the species could be separated ecologically and so reinstated *N. regula* (see also Lange-Bertalot & Metzeltin 1996a); he also suggested that the species differ in the shape of the valve poles. However, given the great diversity of *N. intermedia,* as circumscribed by Lange-Bertalot (1976, pls. 4–6) and Krammer & Lange-Bertalot (1988, pl. 61), the morphological diagnosis offered is virtually meaningless, and to separate the species on the basis of ecology begs the question.
5. *Nitzschia philippinarum* Hustedt and *N. woltereckii* Hustedt were made synonyms of *N. intermedia* by Lange-Bertalot (1976). Krammer & Lange-Bertalot (1988) also suggested conspecificity, although they admitted some doubt about this ("teils stärker, teils schwächer ist der Verdacht"). Moser *et al.* (1995, 1998) restored *N. philippinarum* and *N. woltereckii* as separate species, alongside *N. intermedia.* No reasons were given.
6. *Nitzschia bulnheimiana* (Rabenhorst) H.L. Smith and *N. frustulum* were considered synonymous by Lange-Bertalot (1976), following examination of type material. *Nitzschia inconspicua* Grunow, on the other hand, was separated from *N. frustulum,* contradicting the long-established practice of Hustedt (1930), who said they were conspecific. Two years later, however, Lange-Bertalot & Simonsen (1978) concluded that *N. inconspicua* and *N. frustulum* intergrade; they therefore readopted Hustedt's treatment, with both *N. inconspicua* and *N. bulnheimiana* as synonyms of *N. frustulum.* In their discussion, they emphasized that careful studies had been made of the type material of all three species, using light and electron microscopy, as well as of other material (in the text they said they illustrated type material of *N. frustulum* by transmission electron microscopy, whereas the caption indicates that the figure in question, fig. 292, is of *N. bulnheimiana*). Despite the claims made in these earlier studies and the confidence of the 1978 paper ("as was earlier shown for *N. intermedia, N. frustulum* is a typical taxon to demonstrate the extreme variability in size, outline and structure density"), further changes were to follow. Krammer & Lange-Bertalot (1988) returned *N. inconspicua* to full species status and resurrected *bulnheimiana* as a variety of *N. frustulum.* No explanation was given for the reappearance of *bulnheimiana,* while the new view about *inconspicua* was said to reflect studies of many *N. frustulum* 'Sippen' from every continent. Denys & Lange-Bertalot (1998) recently reinstated *N. bulnheimiana* as a separate species. They indicated differences between *N. bulnheimiana* and *N. frustulum* "in life form (tube-forming versus free-living) and quantitative morphological features (mainly fibulae and striae density), but also in ultrastructural details", and they concluded that "it is therefore clearly more appropriate to reinstate a distinction at the species level". For corroboration they noted that where these diatoms occur sympatrically, "a clear morphological separation remains". At the very least, the example of these three species suggests that Lange-Bertalot's first analysis (1976) was premature, and was based on insufficient data.
7. Other species that have received varying treatment include *N. acicularioides* Hustedt, *N. adamata* Hustedt, *N. agnita* Hustedt, *N. bacata* Hustedt, N. *bavarica* Hustedt, *N. calcicola* Aleem et Hustedt, *N. capitellata* Hustedt, *N. diversa* Hustedt, *N. fonticola* Grunow *in* Van Heurck, *N. gandersheimiensis, N. garrensis* Hustedt, *N. hollerupensis* Foged, *N. kuetzingioides* Hustedt, *N. laevis* Hustedt, *N. paleaeformis* Hustedt, *N. pseudocommunis* Hustedt, *N. radicula* Hustedt, *N. rectiformis* Hustedt, *N. romana* Grunow *in* Van Heurck, and *N. suchlandtii* Hustedt.

There has been more consistency in the taxonomic treatment of species in other genera, although they have not been studied by Lange-Bertalot for as long as *Nitzschia.* Nevertheless, the same kinds of change are evident, for example, in *Achnanthes petersenii* Hustedt, *A. septentrionalis* Østrup, *Cymbella compacta* Østrup, *Eunotia suecica* A. Cleve, *Fragilaria intermedia* var. *littoralis* Germain, *Frustulia rhomboides* var. *crassinervia* (de Brébisson) Ross, *Frustulia saxonica* Rabenhorst, *Gomphonema lagenula* Kützing, *G. sphaerophorum* Ehrenberg, *G. turris* Ehrenberg, *Navicula acceptata* Hustedt, *N. dismutica* Hustedt, *N. exilis* Kützing, *N. monita* Hustedt, *N. mollicula* Hustedt, *N. opportuna* Hustedt, *N. paludosa* Hustedt, *N. rostellata* Kützing, *N. symmetrica* Patrick, *N. thingvallae* Østrup, *Neidium amphirhynchus* Ehrenberg, *N. amphigomphus* Ehrenberg, *Stauroneis fonticola* Hustedt, and *S. gracilis* Ehrenberg (Lange-Bertalot & Ruppel 1980; Krammer & Lange-Bertalot 1986, 1991b; Lange-Bertalot & Metzeltin 1996; Metzeltin & Witkowski 1996; Metzeltin & Lange-Bertalot 1998; Lange-Bertalot & Genkal 1999a, 1999b). All of these have had their status changed (some have also been transferred to other genera, but this is a separate issue that I am not addressing here), with minimal explanation; it is not a complete list. In addition, since 1990 many new species have been described that would undoubtedly have been included in existing taxa using the descriptions and concepts of the *Süsswasserflora von Mitteleuropa* (Krammer & Lange-Bertalot 1986, 1988, 1991a, 1991b).

Because the conclusions Lange-Bertalot has drawn at different times contradict each other and cannot be reconciled, some or all of them must be wrong. Lange-Bertalot & Simonsen (1978) summarized their findings about *Nitzschia* thus: "only comparatively few taxa published during this century proved to be well defined, distinct species after our examinations . . . the more we become acquainted with different populations of taxa, the more we become convinced that there are wide, continuous variability ranges in criteria like outline, size, striation and fibula densities. Differences which have formerly been regarded as sufficient for species differentiation become successively smaller and finally disappear as criteria suitable for identification. Any taxonomic limitation on the species level must become arbitrary in such a continuous range of forms". As a result, they abandoned many of the species described by Hustedt. Lange-Bertalot has now reversed many of these changes. Is this because of new data, or because of second thoughts about interpretation?

In several examples (see above), the data given in the later papers are no different from those given earlier, and so here there must have been a change in interpretation—a change in

Lange-Bertalot's working definition of species. This in turn suggests that there has been a change in what is considered a satisfactory surrogate for reproductive isolation, because Lange-Bertalot apparently still considers reproductive isolation as central to the concept of species (Lange-Bertalot & Metzeltin 1996a, pp. 11, 17). However, I can find no explanation of any such change in any of Lange-Bertalot's many works since 1990. Without an explanation and without full documentation of the material used in each study, it is difficult to see how Lange-Bertalot's work can be repeated and it is difficult to estimate which of his taxonomies is most likely to be correct—is it the latest, fine-grained taxonomy, with its many species, morphotypes, and 'Sippen', or the slightly older, more conservative treatment contained in the *Süsswasserflora von Mitteleuropa* (Krammer & Lange-Bertalot 1986, 1988, 1991a, 1991b) or, for *Nitzschia,* the revisions of the late 1970s? Or perhaps we should return to the taxonomy of Hustedt (1927–66, 1937–39, and so on), after correcting the nomenclatural errors Lange-Bertalot has exposed? To assume that the latest taxonomy (whether by Lange-Bertalot or anyone else) is the best, superceding all previous classifications, is only reasonable if one relies on authority rather than logic to decide between different options (cf. Williams & Round 1994). Hence, much of the work done in the last 20 years will have to be done again. New studies of the variation pattern are needed, properly documented, together with an understanding of how this pattern has arisen and how it is maintained. Meanwhile, we may echo the comment that "immature, new classifications with the resulting regular revisions and additional name combinations discredit our field of research" (Lange-Bertalot 1993a).

A stable new species-level taxonomy cannot be achieved quickly, and while it is being developed we have to have some way to refer to taxa or populations whose taxonomic status is unclear. Lange-Bertalot and his colleagues have themselves addressed this problem. In the last 10 years, they have described many new species and infraspecific taxa, and they have also made many new combinations, having reluctantly embraced most of the new genera proposed by Round *et al.* (1990) ["we have held back for a long time before finally working with the *forced* production of genera" (Lange-Bertalot 1997, my emphasis)]. But in the new series, *Iconographia Diatomologica,* and elsewhere, as well as introducing new species and varieties, Lange-Bertalot *et al.* have made extensive use of informal categories, including 'morphotypes' and 'ecotypes', and they also refer to 'Sippen'. Krammer also describes many 'morphotypes', sometimes within species and sometimes within varieties. Concerning 'Sippen', Lange-Bertalot (1997) states "In many cases we do not exactly know the genotypic reality that lies behind the phenotypic group (in German = 'Sippe' = reproductive community). 'Sippe' + rank = taxon". [Does this mean that phenotypic groups are always reproductive communities (biological species *sensu* Mayr?) but yet might not have genotypic reality?] Krammer (1992b, p. 27) first indicates that a 'Sippe' will be genotypically uniform ("Vermehrungsgemeinschaften, bei denen ein einheitlicher Genotyp vermutet werden kann, werden als Sippen bezeichnet") and then suggests that 'Sippen' generally contain a number of 'Kleinsippen' that are difficult to tell apart morphologically and can be referred to as 'morphotypes'. Morphotypes in turn include "Formen, Formengruppen und Formenschwärme" that cannot be categorized fully because of inadequate knowledge. Krammer cannot really mean that 'Sippen' are strictly uniform genotypically (i.e. clonal), because otherwise morphotypes would by definition be the result of phenotypic plasticity. Lange-Bertalot (1997), on the other hand, states that "morph ('Morphotyp') . . . [means] a group without an assigned taxonomic rank, due to lack of knowledge over its biology . . . It can later be described as a valid species or infraspecific taxon". This use of 'morphotype' is the same as that of Droop (1994, 1995). There seems, therefore, to be a degree of confusion about what 'Sippen' and 'morphotypes' are. Earlier, Geitler used 'Sippe', 'Kleinsippe', and 'Rasse' almost interchangeably (e.g. Geitler 1975), for populations within a species sharing some peculiarity of shape and size, striation density, sexual reproduction, cell attachment, and so on (section III e and Mann 1989a). Geitler's 'Sippen', then, are simply genotypically differentiated populations. When Geitler recognized such populations taxonomically, he gave them varietal status (e.g. Geitler 1975, 1982).

It was to avoid implications about the genetic, reproductive, or taxonomic status of populations that we decided to use deme terminology in several previous publications (Mann 1984a, 1989a; Mann & Droop 1996). A deme is "any assemblage of taxonomically closely related individuals" (Gilmour & Gregor 1939) or "any group of individuals of a specified taxon" (Gilmour & Heslop-Harrison 1954). Gilmour & Heslop-Harrison (1954) stressed that 'deme' should always be used in conjunction with a prefix indicating the basis for grouping. Thus, a 'phenodeme' is a deme differing from others phenotypically, a 'genodeme' is a deme differing from others genotypically, a 'gamodeme' is a deme composed of individuals that can interbreed, a 'phenoecodeme' is a deme occurring in a specified kind of habitat that differs from other ecodemes phenotypically, and so on. However, Gilmour & Gregor's 1939 publication did not make this demand and as a result 'deme' is often used without a prefix; zoologists frequently use 'deme' where 'gamodeme' is meant (e.g. Mayr & Ashlock 1991). For the remainder of this review, I will use deme terminology.

III. EVIDENCE CONCERNING THE NATURE OF DIATOM SPECIES

Although a wide variety of approaches has been used to study species and infraspecific variation in diatoms, there have been very few concerted attempts to understand a particular species or species complex, using more than two or three different methodologies. For this reason, it is difficult to present the same kind of integrated, detailed picture of species and speciation that can be provided for, for example, *Pandorina morum* (O.F. Müller) Bory (Coleman 1959, 1977; Coleman *et al.* 1994) or *Closterium ehrenbergii* Meneghini (Ichimura 1981, 1996; Ichimura & Kasai 1990). I will therefore review the different kinds of evidence that can be brought to bear on the species question in diatoms before discussing what we know about particular species complexes in sympatry and in allopatry.

Detailed studies of morphology and morphometrics

Until 1970, knowledge of the variation pattern was largely restricted to light microscopic observations of the morphology of diatom valves. Basic morphometric data (length, width, striation density) have been gathered for almost as long as diatoms have been studied, while shape, striation pattern, and other features visible under light microscopy (LM) have been assessed visually and described verbally. The first consilience we could look for is agreement between this traditional documentation of the variation pattern and more rigorous studies involving statistical treatment of morphological data and image analysis. As yet, there have been relatively few such morphometric studies. Notable examples include the series of papers on *Stephanodiscus* by Theriot (Theriot & Stoermer 1981, 1984a, 1984b, 1984c, 1986; Theriot 1987, 1992a; Theriot, Håkansson & Stoermer 1988; Theriot, QQi, *et al.* 1988; Julius *et al.* 1997), studies of various pennate diatoms, using novel shape descriptors (Stoermer & Ladewski 1982; Stoermer, Ladewski & Kociolek 1986; Stoermer, Qi & Ladewski 1986; Theriot & Ladewski 1986; Goldman *et al.* 1990; Mou & Stoermer 1992), and recent work on the *Diploneis smithii-fusca* complex (Droop 1994, 1995; Droop, unpublished observations). The overall conclusion that can be drawn from most of these studies is that traditional visual assessment considerably underestimates the complexity of the variation pattern.

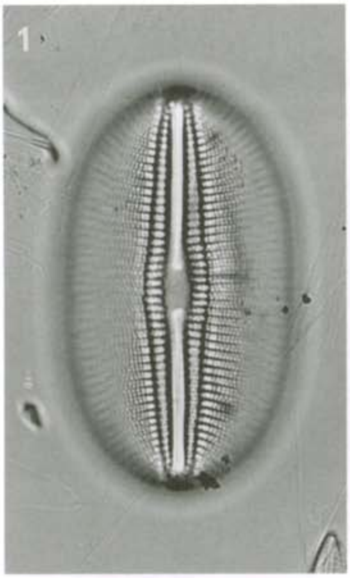
Within the *Stephanodiscus niagarae* Ehrenberg complex, widespread in the freshwater plankton of North America, Theriot has been able to distinguish several subtly different entities that were previously undetected. Some of these are sympatric or parapatric and yet remain separate (see below), and clones retain their characteristics when grown in the same medium in the laboratory (Theriot 1992a). They have been recognized as new species. Other morphometric studies have not as yet been used to support specific taxonomic changes. The studies of *Didymosphenia* M. Schmidt *in* A. Schmidt and *Gomphoneis* Cleve show heterogeneity among allopatric or allochronic populations (populations growing in different places or at different times; Stoermer & Ladewski 1982; Stoermer, Ladewski & Kociolek 1986; Stoermer, Qi & Ladewski 1986), but for the most part this is not easily interpreted, because no information is available about phenotypic plasticity in these haptobenthic freshwater diatoms. It is possible that the differences between populations reflect growth in different environments. In *Tabellaria* Ehrenberg *ex* Kützing, *Diploneis,* and Lake Baikal *Didymosphenia,* on the other hand, heterogeneity has been demonstrated within samples, suggesting that separate genodemes coexist in sympatry (Knudson 1953a, 1953b; Stoermer, Qi & Ladewski 1986; Theriot & Ladewski 1986; Mou & Stoermer 1992; Droop 1994). In the case of *Diploneis smithii* and *D. fusca,* two very similar diatoms sometimes regarded as intergrading forms of the same species (Hustedt 1927–66, vol. 2, pp. 660–661), at least 11 phenodemes were found coexisting in marine sands from Ganavan Beach, near Oban, West Scotland (Droop 1994; Figs 1, 2, 8, 11). A subsequent investigation of two of the Ganavan demes (Figs 10, 11: demes 3 and 4) suggested that they also occur elsewhere, although allopatric populations are not quite identical (Droop 1995). Recently, new morphometric studies (Droop, in preparation) have shown that many of the Ganavan demes occur more than 80 km away, on the Isle of Cumbrae (Figs 3–7, 9, 10), and that they have been there for at least 140 years (Figs 13–18). Figure 19 shows the results of a principal components analysis (PCA) of populations collected from Cumbrae in 1997 (by S.J.M. Droop) and 1858 (by Mr R. Hennedy; Hennedy supplied material to Prof G. Walker Arnott in Glasgow, whose material passed to several other diatomists, including H. Van Heurck). Representatives of demes 1–4 and 6–8 (the numbering corresponds to the numbering of the equivalent Ganavan demes) are present in both old and new material (Figs 13–18) and cluster tightly together (Fig. 19). This suggests strongly that the demes are genotypically distinct entities that have retained their identity through several reproductive cycles. Demes resembling Ganavan demes 10 and 11 are present in the older Cumbrae material (e.g. Fig. 18), but do not appear in the PCA because of their rarity. Cumbrae samples also contain some demes ('x' and 'y' in Fig. 19, and see Fig. 12) that have never been found at Ganavan.

Sympatric demes such as those of *Diploneis* and *Tabellaria* differ in size and shape and, in *Diploneis,* also in various aspects of valve structure and stria pattern visible with the

→

Figs 1–12. *Diploneis.* Examples of demes belonging to the *D. smithii–D. fusca* complex, from West Scotland. Deme numbering corresponds to that used by Droop (1994) for material collected from Ganavan. The demes differ in size (even after allowance is made for changes occurring during the life cycle), striation density, stria structure (uniseriate vs biseriate), and the shape and extent of the longitudinal canals near the raphe. Although all have a simple linear–elliptical outline, shape varies subtly, with some demes being simply elliptical (e.g. Figs 3, 8), but others tending toward being rectangular (e.g. Figs 1, 7, 9). Light microscopy, bright-field optics (here and elsewhere, slide coordinates for most specimens photographed are recorded at E). Scale bar (in Fig. 12) = 20 μm.

Fig. 1. Deme 5, Ganavan, near Oban, E 1014/1. 1 March 1991.
Fig. 2. Deme 6, Ganavan, near Oban, E 1016/1. 1 March 1991.
Fig. 3. Deme 8, Bell Bay, Isle of Cumbrae, E 2673.2/1. 3 May 1997.
Fig. 4. Deme 7, Bell Bay, Isle of Cumbrae, E 2673.2/1. 3 May 1997.
Fig. 5. Deme 2, Fintry Bay, Isle of Cumbrae, E 2679.2/1. 3 May 1997.
Fig. 6. Deme 11, Bell Bay, Isle of Cumbrae, E 2673.2/1. 3 May 1997.
Fig. 7. Deme 10, Kames Bay, Isle of Cumbrae, E 2682.2/1. 3 May 1997.
Fig. 8. Deme 9, Ganavan, near Oban, E 1016/1. 1 March 1991.
Fig. 9. Deme 1, Bell Bay, Isle of Cumbrae, E 2673.2/1. 3 May 1997.
Fig. 10. Deme 3, Fintry Bay, Isle of Cumbrae, E 2679.2/1. 3 May 1997.
Fig. 11. Deme 4, Ganavan, near Oban, E 1014/1. 1 March 1991.
Fig. 12. Unnumbered deme ('x' in Fig. 19), Isle of Cumbrae, BM slide, Van Heurck Types du Synopsis des Diatomées de Belgique 104. 2 August 1858.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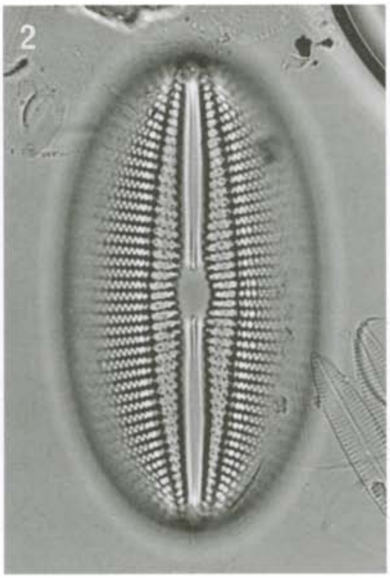
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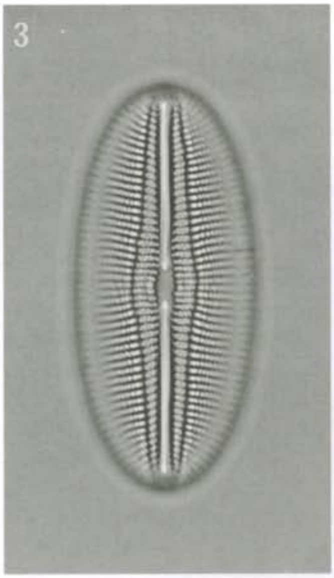
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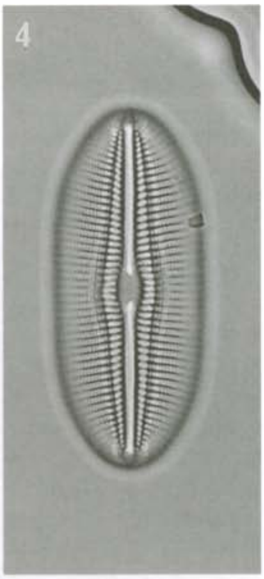
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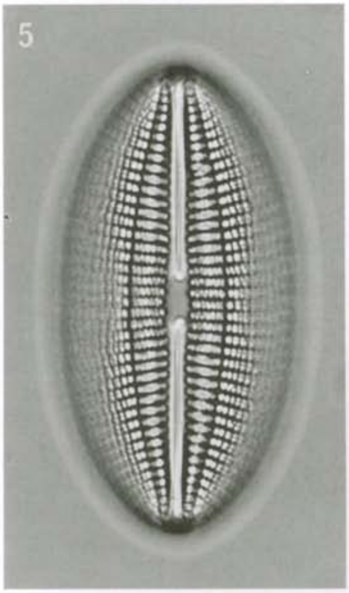
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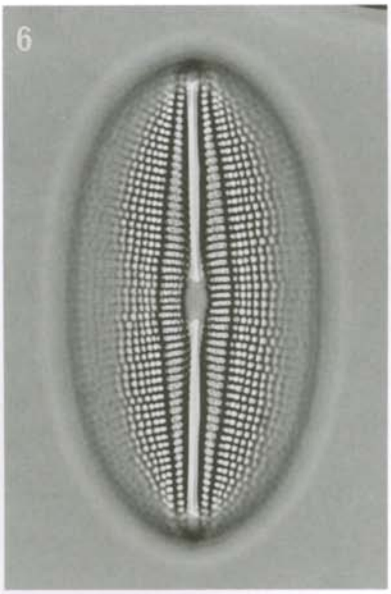
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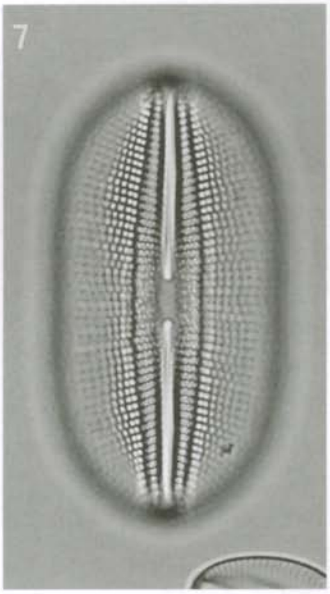
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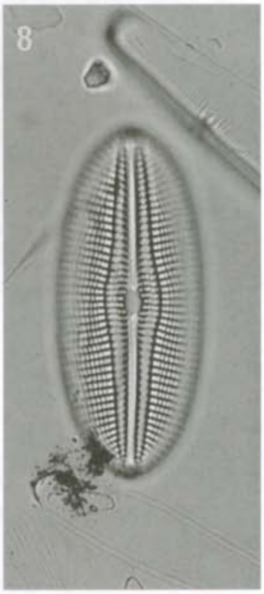
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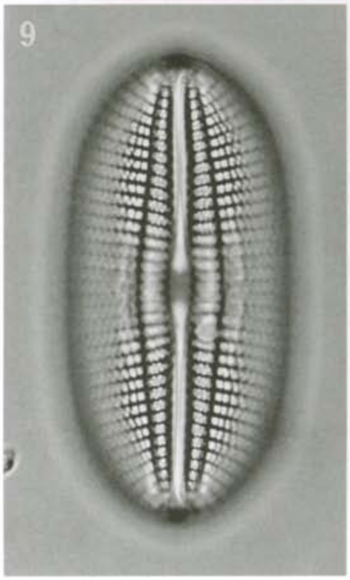
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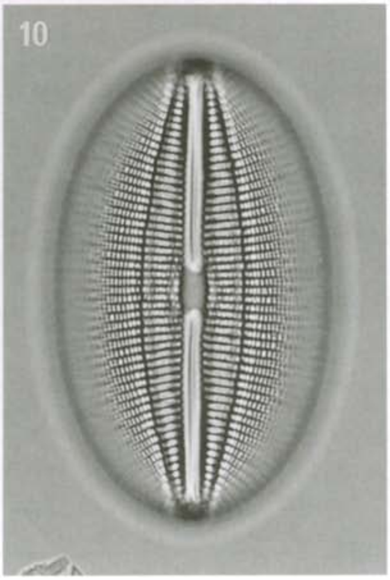
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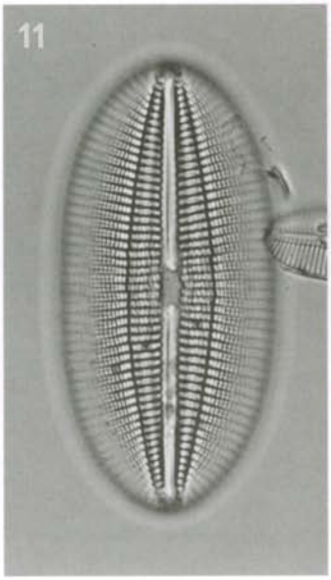
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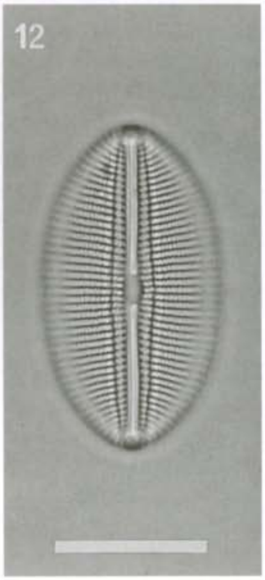
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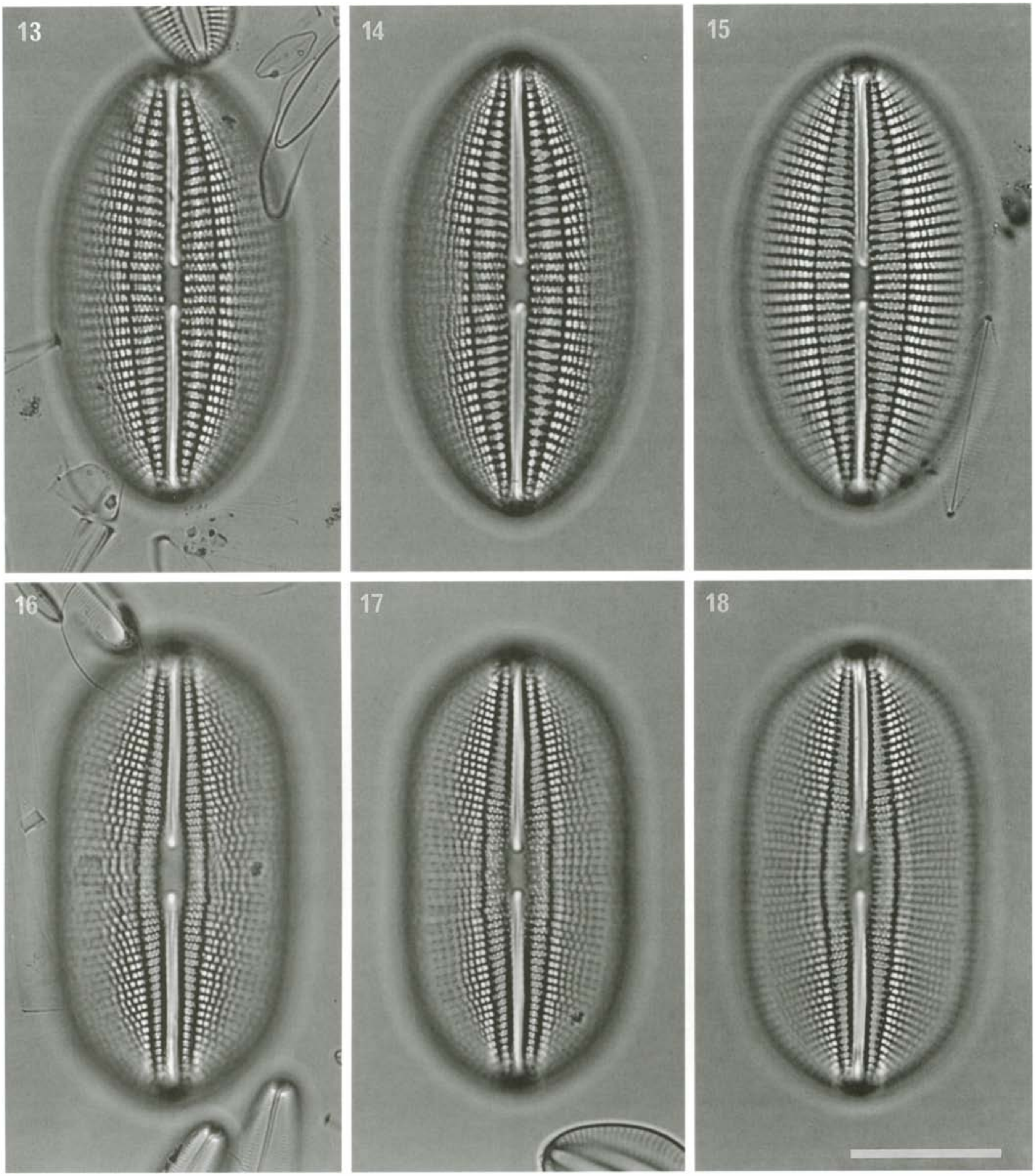


Figs 13–18. *Diploneis smithii-fusca* complex. Examples of two demes, from allopatric and allochronic populations from West Scotland, collected in 1858, 1991, and 1997. Valves of a single deme collected at different times and different places are virtually identical with respect to the characters listed in the caption to Figs 1–12. Deme numbering corresponds to that used by Droop (1994) for material collected from Ganavan. Light microscopy, bright field optics. Scale bar (in Fig. 18) = 20 μm.

Fig. 13. Deme 2, Ganavan, near Oban, E 1014/1. 1 March 1991.

Fig. 14. Deme 2, Fintry Bay, Isle of Cumbrae, E 2679.2/1. 3 May 1997 (see also Fig. 5).

Fig. 15. Deme 2, Isle of Cumbrae, BM slide, Van Heurck Types du Synopsis des Diatomées de Belgique 104. 2 August 1858.

Fig. 16. Deme 10, Ganavan, near Oban, E 1014/1. 1 March 1991.

Fig. 17. Deme 10, Kames Bay, Isle of Cumbrae, E 2682.2/1. 3 May 1997 (see also Fig. 7).

Fig. 18. Deme 10, Isle of Cumbrae, BM slide, Van Heurck Types du Synopsis des Diatomées de Belgique 104. 2 August 1858.

light microscope. Extensive, detailed studies of single species using SEM are rare, but those that have been undertaken tend to support the impression from LM-based morphometric studies: the pattern of variation is much more complex and subtle than was evident hitherto. The *Diploneis smithii-fusca* demes (Figs 1–18) differ in details of valve ultrastructure, such as the presence or absence of pores externally at the ends of the striae, or the course of the central and polar external raphe endings (Droop 1994; Droop, in preparation). Within *Hantzschia* Grunow species too, one can demonstrate extensive variation in valve ultrastructure within a single species or among closely related species (Mann 1978, 1981a). Sympatric demes of *H. marina* (Donkin) Grunow can differ in size, striation density, areola shape, the presence or absence of cribra in addition to hymenes occluding the areolae, the shape of the central external raphe endings and terminal fissures, and girdle band ornamentation (Mann 1978, 1981b; Mann & Droop 1996; Mann, unpublished data). Studies of allopatric demes show further variation. Even more extensive variation occurs within the *H. virgata* (Roper) Grunow complex, where there can also be differences in the internal central raphe endings, the course of the raphe system, fibula spacing and morphology, the structure of the girdle, and chloroplast morphology (Mann 1978, 1981a; Mann & Droop 1996). The diversity of chloroplast morphology exhibited in this species complex (Figs 20–23) is unusual for a group of closely related species or infraspecific taxa, because most genera are remarkably uniform in chloroplast number and arrangement [an exception is *Lyrella* (Mann & Stickle 1993)]. *Hantzschia virgata* has traditionally been subdivided into a number of varieties, but even these show evidence of heterogeneity, at least in allopatry. The *H. amphioxys* (Ehrenberg) Grunow cluster has recently been separated into several independent species by Lange-Bertalot (1993a), which must nevertheless be regarded as close relatives. Sympatric populations within this complex can differ markedly with respect to valve, raphe, and girdle structure. For example, some have a prominent marginal ridge at the junction of valve face and distal mantle (Fig. 25), whereas others do not (Fig. 24). The girdle is sometimes composed largely of closed bands (complete hoops of silica; Figs 26, 27), whereas elsewhere most of the girdle bands are split rings (Figs 28, 29) (see also Mann 1978).

Lee & Round (1987, 1988, 1989) have illustrated some very subtle variation within *Amphora ovalis* (Kützing) Kützing, *A. copulata* (Kützing) Schoeman et Archibald, and *A. pediculus* (Kützing) Grunow *ex* A. Schmidt, visible for the most part only with SEM and concerning details of areola and raphe structure. The same demes can be found in several lakes or rivers, and two or more demes sometimes occur together in the same catchment, if not the same sample.

Mention should also be made of a series of papers on freshwater diatoms by Japanese workers, especially H. Fukushima, T. Ko-Bayashi, and their colleagues. Sophisticated statistical methods are not employed in these papers, which have been published principally in *Diatom* and the *Japanese Journal of Water Treatment Biology* (e.g. Ko-Bayashi *et al.* 1986; Fukushima *et al.* 1988, 1997), but the photographic documentation of diatom populations is so extensive that these papers constitute a valuable resource for anyone studying variation, biogeography, and speciation in diatoms.

Complications of polymorphism and phenotypic plasticity

The significance of variation in valve morphology, or indeed of any character, needs to be tested through extensive study of natural populations and experimental analysis of phenotypic plasticity. Most diatomists probably would assume that features such as raphe endings, areola structure, and girdle structure are genetically fixed, because there is often considerable uniformity in them within higher taxonomic units. For instance, most *Neidium* Pfitzer species have forked terminal raphe fissures and external central raphe endings that turn in opposite directions (Round *et al.* 1990), while the Naviculaceae (*sensu* Round *et al.* 1990) almost always have apically elongate areolae. However, the assumption that areola or raphe structure, or other structural features, are constant within populations or clones has rarely been tested and the degree of phenotypic plasticity is unknown in most cases. Ideally, phenotypic plasticity should be assessed from studies of clones in culture, but if this cannot be done, plasticity must be estimated from observations of natural populations.

Some genera are constitutively heterovalvar, with each cell bearing thecae with differing morphologies. Examples include *Corethron* Castracane, *Gephyria* Arnott, *Peronia* de Brébisson et Arnott *ex* Kitton, *Cocconeis* Ehrenberg, *Achnanthes* Bory, *Rhoicosphenia* Grunow, and many others (Round *et al.* 1990; Crawford & Hinz 1995; Crawford *et al.* 1998). Sometimes heterovalvy is very subtle, such as in the positioning of the rimoportulae in *Licmophora* C.A. Agardh, where both valves of a frustule have a rimoportule at the broad end (the valves are wedge-shaped), but only one has a rimoportule at the narrow end (Wahrer *et al.* 1985). These genera generally pose no problem for taxonomists and need no further discussion, because it is usually easy to detect which thecae belong with which, even in cleaned samples containing few complete frustules. Elsewhere, it has been shown that polymorphism can arise through random or programmed changes in the orientation of the morphogenetic apparatus between one cell division and the next. Thus, for example, some *Nitzschia* species produce cells with two types of symmetry (nitzschioid and hantzschioid), while as a result of the asymmetrical development of their valves, raphid diatoms can have two types of frustule (*cis* and *trans*), according to whether the two valves have the same or opposite polarity (Mann 1980; Mann & Stickle 1988; Pickett-Heaps *et al.* 1990). However, the interconversions between these symmetries are simple and again should cause no difficulties during species delimitation.

As with desmids, polymorphism and phenotypic plasticity can often be detected readily in natural populations of diatoms, because the two halves of the cell wall are formed at different times and, quite possibly therefore, under different environmental conditions. Hence, although diatomists tend on the whole to study isolated valves, enough frustules are present in many samples for it to be possible to check, through the occurrence of 'Janus cells' (named after the two-faced doorkeeper of Roman heaven), whether grossly different morphologies can be produced by a particular cell lineage. A subtle example of a Janus cell is shown in Figs 26 and 27: the polar raphe endings are extremely similar within each valve, but differ between valves. However, the Janus cell approach will work only if significant environmental change takes place sufficiently frequently within the average life span (half-life)

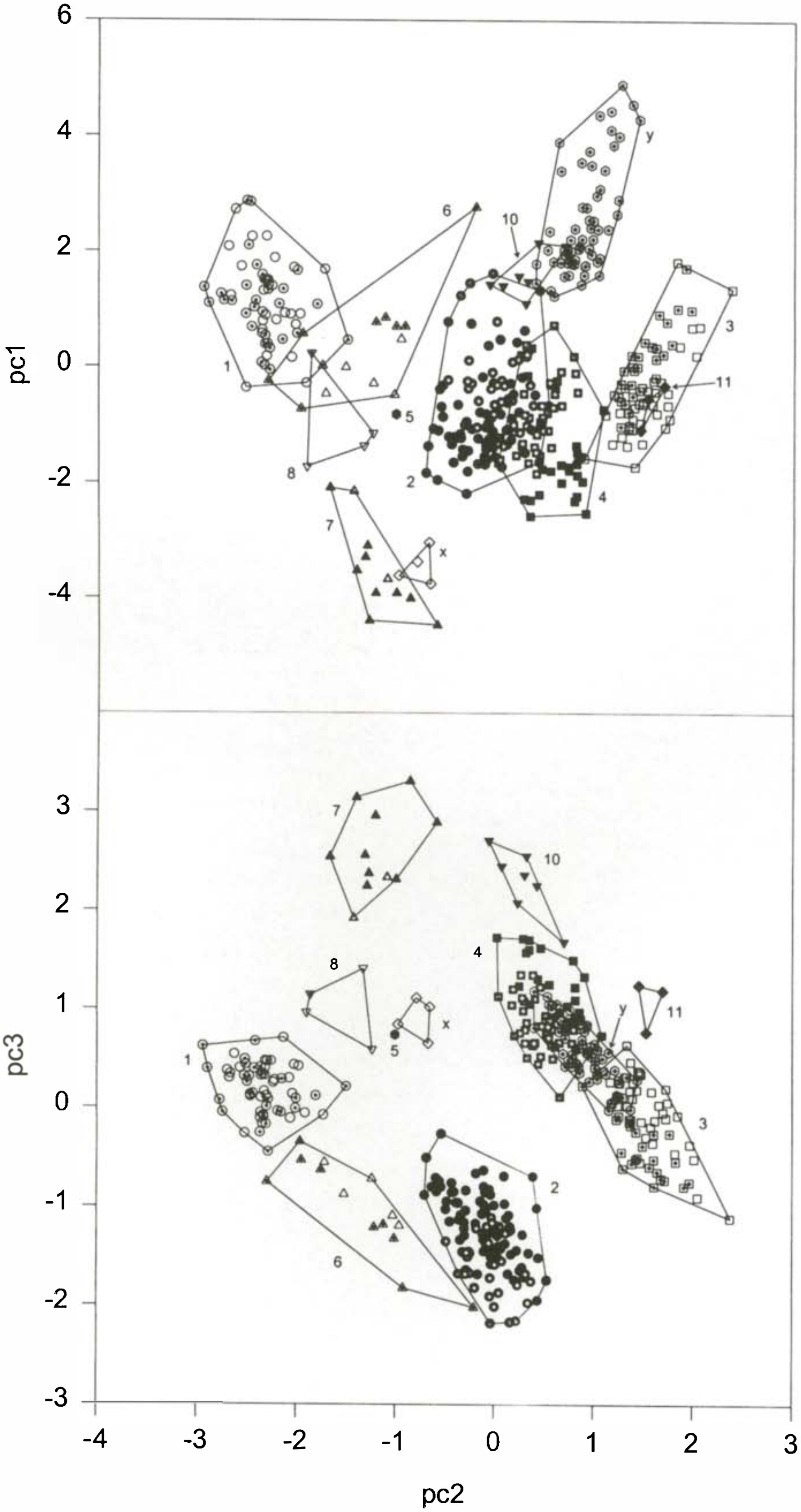
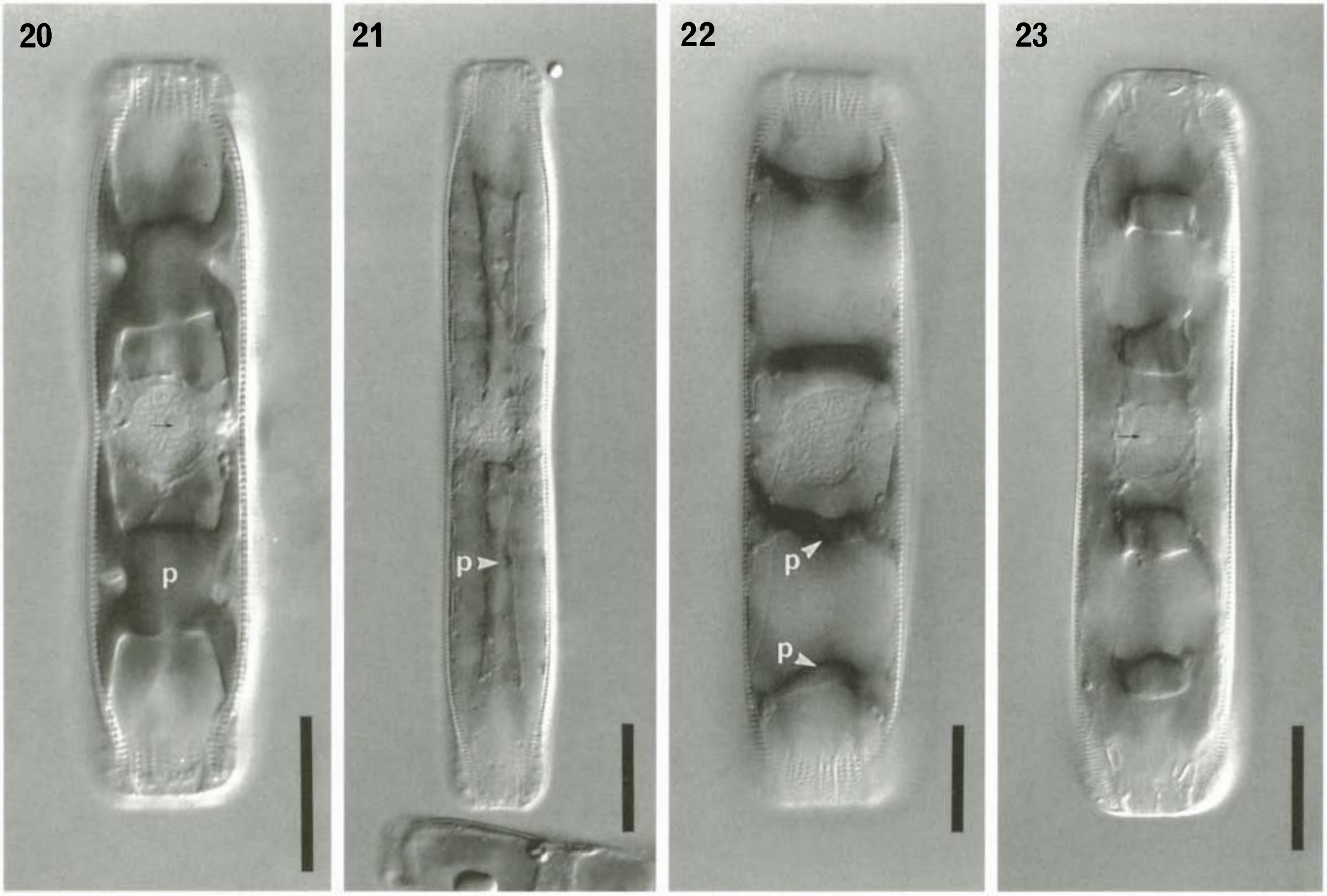


Fig. 19. Principal components analysis (PCA) of *Diploneis smithii-fusca* complex. Plots of PC1 against PC2 and PC3 against PC2 from analysis of 400 valves drawn from two allochronic populations collected from the Isle of Cumbrae, West Scotland, in 1858 and 1997 (Droop, in preparation). Two hundred valves were measured at random for length, width, rectangularity, striation density measured near the raphe, shape of central raphe endings, and stria structure (see Droop 1994 for explanation). Polygons and symbols delimit each deme (identified on the PCA



Figs 20–23. *Hantzschia virgata,* living cells (from marine epipelon) in girdle view, each containing two plastids, one either side of the central nucleus (a prominent nucleolus is visible within the nucleus in Figs 20 and 23, arrows). Light microscopy, differential interference contrast optics. Scale bars = 20 μm.

Fig. 20. *Hantzschia virgata* cf. var. *leptocephala* Ostrup. Each plastid apparently stellate, with a single almost isodiametric pyrenoid (p). Portobello, Edinburgh.

Fig. 21. *Hantzschia virgata* var. *gracilis* Hustedt. Pyrenoid elongate, axile (p). Tyninghame, East Lothian, Scotland.

Fig. 22. *Hantzschia virgata* cf. var. *virgata.* Plastids subdivided into two halves linked by a narrow isthmus (not shown), each containing its own elongate pyrenoid (p). Tyninghame, East Lothian, Scotland.

Fig. 23. *Hantzschia virgata* cf. var. *wittii* (Grunow) Grunow *in* Cleve et Grunow. Plastids as in Fig. 22, but with globular pyrenoids. Tyninghame, East Lothian, Scotland.

of a theca [thecae, and hence the cells that bear them, are not immortal (Mann 1988a; Jewson 1992a, 1992b)]. And care must be taken that the two valves do actually belong to the same cell (which is not always so easy to determine as it might seem) and that the valves are fully formed and have been released. Wood's (1959) claims to have found a cell bearing a *Coscinodiscus* Ehrenberg valve on one side and an *Asteromphalus* Ehrenberg valve on the other, and to have found another combining *Coscinodiscus* and *Actinocyclus* Ehrenberg (Wood 1963) have never been repeated (even in the extensive survey by van der Spoel *et al.* 1973) and must be viewed with extreme scepticism, if not discounted altogether. In other cases, although no one doubts the accuracy of the observations, their interpretation is unclear. An example is the suggestion by Braarud (1935) that *Chaetoceros borealis* and *C. concaviformis* are conspecific, based on the discovery in natural populations of chains of cells and Janus cells that seemed to contain morphologies characteristic of both species; current floras nevertheless continue to maintain them as separate (Hasle & Syvertsen 1996).

In spite of the potential of the Janus cell approach, there certainly need to be many more experimental studies of polymorphism and phenotypic plasticity, using clonal cultures. It is astonishing that there have been so few attempts by diatom taxonomists to determine the extent to which the characters they have relied upon for generations, such as shape, striation

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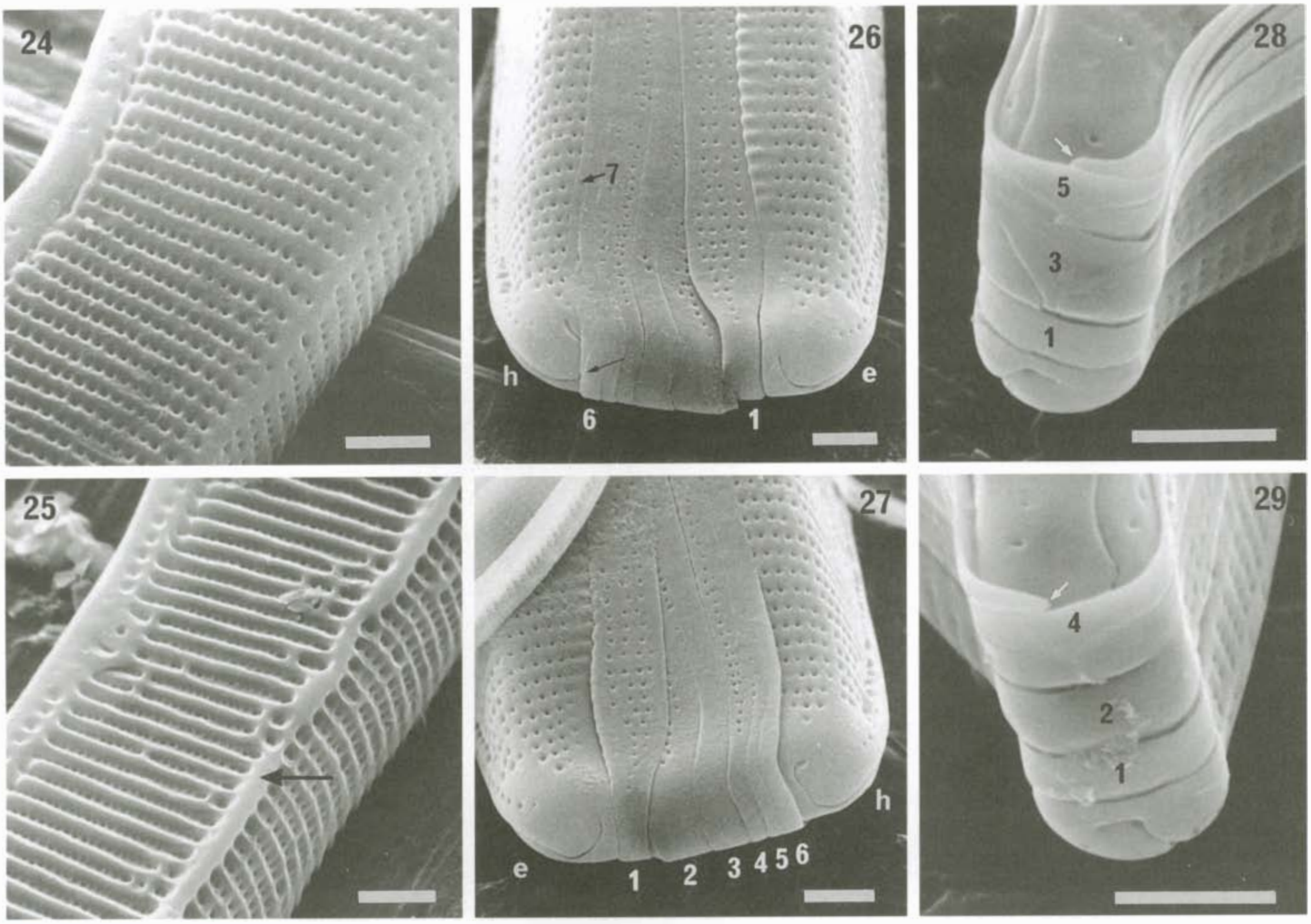
plots), and within each polygon the 1858 valves are shown as open symbols; the 1997 valves are shown by the same shape of symbol but containing a cross. Deme numbering corresponds to that used by Droop (1994) for the equivalent demes collected from Ganavan, near Oban, West Scotland, except that two demes were not present at Ganavan; these are labelled 'x' and 'y'. All demes are completely separated by a combination of PC1–PC3 and agreement is good between old and new populations.



Figs 24–29. *Hantzschia amphioxys* sensu lato, cleaned frustules, scanning electron microscopy. Scale bars = 2 μm.

Fig. 24. Center of valve, dorsal side, showing simple striae and absence of marginal ridge. Sea Mills, Bristol, West England.

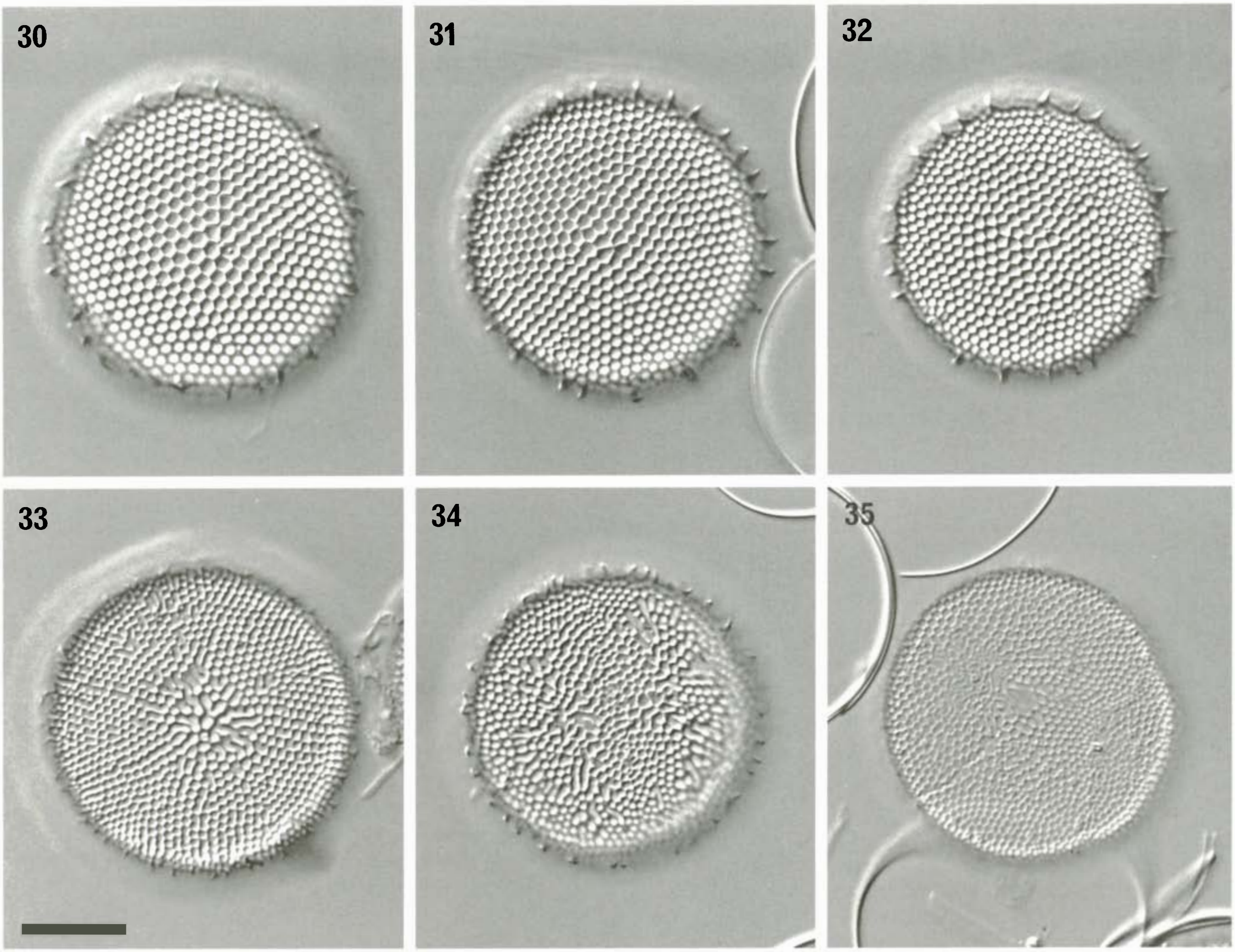
Fig. 25. Center of valve, dorsal side; note the prominent marginal ridge (arrow) and thickenings of the transapical ribs. Culvert at Bigsweir, Gloucestershire, West England.

Figs 26, 27. Both poles of a single frustule, girdle view. Bands 1–6 (numbered, Fig. 27) are closed at both poles; band 7 is open (Fig. 26, arrow). Note also that this is a Janus cell, with dissimilar terminal raphe fissures on the two valves, with the epivalve (e) having simply deflected raphe endings, whereas the hypovalve (h) has J-shaped fissures. Sea Mills, Bristol, West England.

Figs 28, 29. Both poles of a single frustule, from a different deme to Figs 26, 27, though sympatric with it. Band 1 is closed at both poles, but bands 2–6 are split rings, with open ends alternating with closed ends at each pole. Figure 28 shows the open ends of bands 2, 4, and 6 (arrow); Fig. 29 shows the open ends of bands 3 and 5 (arrow). Sea Mills, Bristol, West England.

density, and valve dimensions, can be altered by subjecting clones to different nutrient regimes, salinities, and temperatures. The necessary experiments are not difficult to design (although care is needed to ensure that any change is not the result of mutation and selection within clones) but few have been done. Exceptions include studies of *Phaeodactylum* Bohlin (see below; but *Phaeodactylum,* with its organic theca, is perhaps the least typical of all diatoms) and experiments by Cox (1995), Fryxell (1988), Fryxell & Hasle (1972), Geissler (1970a, 1970b, 1982, 1986), Hasle (1983b), Hasle & Evensen (1976), Hasle *et al.* (1971), Jahn (1986), Lewis *et al.* (1997), Li & Chiang (1979), Lundholm *et al.* (1997), McMillan & Johansen (1988), Mizuno (1987), Paasche *et al.* (1975), Schmid (1979, 1984, 1990, 1997), Schultz & Trainor (1970), Schultz (1971), Steinman & Sheath (1984), Syvertsen (1977), Villareal & Fryxell (1983), von Stosch (1980, 1985), and Wendker & Geissler (1988). Planktonic centric diatoms have received more attention than any other group.

Viewed from a taxonomic standpoint, the results of experiments with clones and analyses of Janus cells are generally reassuring. The visible phenotype *is* plastic, but usually only within narrow limits. Furthermore, graduated changes in environmental variables generally produce graduated, rather than abrupt changes in morphology. Thus, in *Skeletonema subsalsum* (Cleve-Euler) Bethge, valves become progressively more rounded and the marginal linking processes become progressively longer as salinity is increased from 3 to 10 psu, although change is greatest between 3 and 5 psu (Paasche *et al.* 1975). Similar changes occur in *Pleurosira* (Meneghini) Trevisan (Li & Chiang 1979, as *Proteucylindrus*). Slight, gradual decreases in valve width or diameter can occur with elevated (Geissler 1982; Jahn 1986) or lowered salinity (Cox 1995), and salinity can also bring about slight changes in striation density (Geissler 1986). In clones of *Thalassiosira* Cleve species studied by Syvertsen (1977), low temperatures (3°C) induced a valve morphology usually considered characteristic of *T. gravida,* with radial rows of distinct pores, whereas high temperatures (17°C) induced *T. rotula* morphology, with radial



Figs 30–35. *Thalassiosira eccentrica,* cleaned valves from a culture isolated in March 1999 from North Berwick, East Lothian (Scotland, UK), showing plasticity of the phenotype. The most strongly silicified valves (Figs 30, 31) show a typical 'eccentrica' pattern, with curved tangential lines of areolae; they also have prominent marginal spines. More lightly silicified valves show a progressive tendency towards fasciculation (Figs 32, 33), with areolae arranged in radial sectors. More delicate valves also occur with a disorderly pattern (Fig. 34); these sometimes have multiple pattern centers and no or reduced marginal spines (Fig. 35) (cf. Fryxell & Hasle 1972; Schmid 1984). Scale bar = 10 μm.

ribs but no discrete pores except near the margin; at intermediate temperatures (10°C) transitional morphologies were found. A graduated response was also noted in girdle band morphology, although in this case the response was related not only to temperature but also to levels of N and P. Graduated changes in areola arrangement can be induced by temperature and salinity in *Thalassiosira tumida* (Janisch) Hasle *in* Hasle *et al.* (Fryxell 1988) and by salinity in *T. decipiens* (Grunow) Jorgensen (McMillan & Johansen 1988), and von Stosch (1980, 1985) found that light intensity affects silicification and the numbers of a peculiar type of pore (the endochiastic areola) in the cell walls of *Coscinodiscus alboranii* Pavillard. Figures 30–35 show something of the range of valve morphology that can be produced by a clone of *Thalassiosira eccentrica* (Ehrenberg) Cleve. In some cases, orchestrated changes in morphology can be detected in natural populations and correlated with seasonal events, for example, in the summer and winter phases of various antarctic diatoms (Fryxell 1994).

The most extreme case of polymorphism is in *Phaeodactylum,* which exists principally as three interconvertible morphotypes (oval, fusiform, and triradiate) that differ not only in shape but also in wall structure, the degree of silicification, and ability to form chains in culture (Lewin 1958; Lewin *et al.* 1958; Borowitzka *et al.* 1977; Borowitzka & Volcani 1978; Gutenbrunner *et al.* 1994). Other well-documented instances of stepped polymorphism (where a clone can produce two or more quite different valve morphologies, without intermediates) include *Mastogloia* Thwaites and *Aulacoseira* Thwaites. Stoermer (1967) showed that valves corresponding to two taxa, *M. grevillei* W. Smith *ex* Gregory and *M. elliptica* (C.A. Agardh) Cleve *ex* A. Schmidt var. *dansei* (Thwaites) Cleve, could occur on opposite sides of the same frustule, although how often the interconversion takes place and whether it can occur in both directions is not known. Here the polymorphism is manifest in a difference in stria density and structure: *grevillei* valves have widely spaced biseriate striae (striae containing two rows of pores), whereas *dansei* valves have finer uniseriate striae. Stoermer's observations seem to have been ignored by subsequent authors, such as Krammer & Lange-Bertalot (1986; Stoermer's paper is listed but its implications are not discussed on pp. 432–435), Hartley (1986), and Hartley *et al.* (1996). A change from uniseriate to biseriate striae has been noted too by Schmid (1997) in '*Centronella reicheltii*' (see below). Hendey (1986) reported dissimilar thecae in a cell of a *Grammatophora* Ehrenberg species. One theca had a strongly undulate septum like that in *G. angulosa* Ehrenberg, whereas the other had the almost flat septum of *G. oceanica* Ehrenberg. Typical cells of *G. oceanica* and *G. angulosa* were present in the same sample. Hendey's own interpretation of this Janus cell, that it represents the initial cell of a hybrid F_1, is at best a nonparsimonious explanation of the data; the simplest explanation is that it reflects phenotypic plasticity.

The significance of polymorphism in *Mastogloia, Phaeodactylum,* and *Grammatophora* is unknown. In *Aulacoseira,* on the other hand, polymorphism can be shown to be related in part to regulation of colony length, with special valves being formed at intervals to allow the chains to break (Müller 1903; Hustedt 1927–66; Davey & Crawford 1986). Polymorphism in *Aulacoseira* can also involve resting spore formation (e.g. Skabichevskij 1953; von Stosch 1967). Morphologically distinct resting spores and internal valves occur in many other diatoms (von Stosch 1967; Round *et al.* 1990; Hasle & Syvertsen 1996; McQuoid & Hobson 1996) and have sometimes caused difficulties for species differentiation. For example, resting spores of the raphid diatom *Craticula cuspidata* (Kützing) D.G. Mann possess special types of valve that were previously recognized as separate varieties or even separate genera! (Schmid 1979; Mann & Stickle 1991). Such examples may be more common in pennate diatoms than has been thought: Edlund & Stoermer (1997) illustrate an unnamed *Pinnularia* species, in which the resting spore valves have c. two thirds of the striation density present in normal valves. In fossil deposits, it may be difficult or impossible to link resting spores with the vegetative cells that produced them, undermining taxonomy and phylogenetic reconstruction at all levels (Hargraves 1986).

Stepped (switching) responses to environmental change also seem to occur in some *Cyclotella* (Kützing) de Brébisson species. In the *C. meneghiniana–cryptica* complex, Schultz (1971) showed that, in some clones, marginal chambering (*meneghiniana* morphology) is lost at high salinity and replaced by a more delicate radial striation (*cryptica* morphology). However, Schultz found that some clones, originally isolated and identified as *C. meneghiniana* Kützing, will produce only *meneghiniana* morphologies, regardless of culture conditions, suggesting that *C. cryptica* Reimann, Lewin et Guillard and *C. meneghiniana* may be separate species. Meyer & Håkansson (1996), using the Janus cell approach, have shown switching between different types of central area pattern in *Cyclotella polymorpha* Meyer et Håkansson, but the causes of this are unknown. Although Meyer & Håkansson noted that the different patterns produced by *C. polymorpha* are similar to other taxa described within *Cyclotella* (*C. comensis* Grunow, *C. ocellata* Pantocsek, *C. kuetzingiana* Thwaites vars *radiosa* Fricke and *planetophora* Fricke), they did not synonymize any of these with *C. polymorpha,* implying that they believed that similar morphologies can be produced by a variety of related but different species. Bailey-Watts (1988a, 1988b) documented the production of three different morphologies in natural populations of a small *Stephanodiscus* species; the proportions of the three changed during the spring diatom bloom in Loch Leven, Scotland. Later, Kling (1992) found, using clonal cultures, that valve morphology alters with growth phase and size reduction. One of the three morphologies previously had been thought to be so different from normal *Stephanodiscus* that it justified the erection of a new genus, *Pseudostephanodiscus* Sieminska (1988).

Villareal & Fryxell (1983) suggested that *Thalassiosira antarctica* Comber and *Porosira glacialis* (Grunow) Jørgensen exhibit a switching response to temperature between −1.5°C and 4°C, involving changes in the external morphology of the areolae, fultoportules, and occluded processes, but because cultures were apparently not grown at intermediate temperatures, a continuum of variation cannot be ruled out. *Eucampia antarctica* (Castracane) Mangin produces heavily silicified frustules during the winter, but more lightly silicified frustules during the period of maximum growth (von Stosch 1967; Fryxell 1989; Fryxell & Prasad 1990). Switching between bipolar and tripolar or multipolar organization occurs during auxosporulation or vegetative enlargement in some centric and pennate diatoms, for example, *Biddulphiopsis titiana* (Grunow) von Stosch et Simonsen (Franz & Schmid 1994), *Bellerochea malleus* Brightwell (von Stosch 1982), *Neostreptotheca torta* von Stosch (von Stosch 1986), and *Achnanthes longipes* C.A. Agardh (Pickett-Heaps *et al.* 1990; Chepurnov & Roshchin 1995). If vegetative cells were all that had been available in these cases, it might have been difficult to prove that cells with such different shapes belonged to the same species, although von Stosch (1985) did not hesitate to combine bi- and tripolar specimens in *Odontella retiformis* (A. Mann) von Stosch, using cleaned material alone. Schmid (1997) has shown that the triradiate freshwater diatom *Centronella reicheltii* Voigt can give rise in culture to bipolar cells that are very similar indeed to *Fragilaria crotonensis* Kitton, which co-occurs with *Centronella* in the plankton at various sites worldwide. Her conclusion that *Centronella* is not a separate genus seems fully justified (see also Round *et al.* 1990). Nevertheless, it remains an open question as to whether the triradiate cells are merely teratological, as Schmid suggests, or represent a genetically distinct population, conceivably even a separate species, derived from *F. crotonensis* or its immediate ancestor and dispersing with it. Schulz (1918) noted that several other araphid pennate diatoms that are normally bipolar also seem to be able to produce triradiate cells.

Switching of valve ontogeny between alternative pathways, resulting in the production of different striation densities (as in Stoermer's 1967 study of *Mastogloia*), has recently been demonstrated by McBride & Edgar (1998) in *Gomphonema angustatum* (Kützing) Rabenhorst, in the best example of the Janus cell approach to date. This example is particularly interesting, and to some extent worrying for the taxonomist who relies solely on analyses of cleaned, dead material, because plots of stria density against length (which acts as a proxy for the stage of the life cycle: section III c) show two fairly discrete elongate clusters. The 'coarse' and 'fine' clusters have different stria densities (8–9 vs 13–14 striae in 10 μm in larger frustules), and different regressions of stria density on length (stria density decreases more rapidly with length in the 'coarse' cluster). In smaller frustules, produced towards the end of size reduction, stria densities become more homogeneous, but in larger frustules, the distribution of stria densities is clearly bimodal. This could easily have been interpreted as indicating the existence of two species, with different allometric relationships, if McBride & Edgar (1998) had not been able to demonstrate that Janus cells exist, combining the 'coarse' and 'fine' morphologies. Reimer (1970) also noted wide variation in stria density between valves of the same frustule in several *Gomphonema* Ehrenberg species and it may be that valve development is unusually labile in this genus. Stria structure or density has been observed to vary in response to temperature in *Pseudo-nitzschia seriata* (Cleve) H. Peragallo and *P. multiseries* (Hasle) Hasle, but not in *P. pseudodelicatissima* (Hasle) Hasle (Lundholm *et al.* 1997).

Little information has been published about the plasticity of cytological characteristics, reflecting the lack of interest diatomists have shown in them. Generally, although the size and exact pattern of lobing of the plastids may vary between individuals in a population, the overall position and shape of the plastids and nucleus vary little, except in those centric (and a few pennate) diatoms with many plastids per cell (polyplastidy). The plastids and nucleus move around in the cell during the cell cycle, in patterns characteristic of a species or genus (e.g. Mann & Stickle 1988; Mann 1989c, 1996), and represent significant sources of new taxonomic characters. In polyplastidic diatoms, karyostrophy (clustering of plastids around the nucleus) is widespread, usually as a response to light but also after mechanical stimulation (Franz & Schmid 1994; Makita & Shihira-Ishikawa 1997; Furukawa *et al.* 1998). Such responses are scarcely likely to pose difficulties for species taxonomy. There are a few cases, however, in which significant changes in plastid shape and arrangement occur, either in response to environmental change or accompanying size reduction during the life cycle. Thus, von Stosch (1985) recorded that the two long plastids usually present in *Haslea wawrikae* (Hustedt) Simonsen fragment into small platelets in senescent cells, and Cox (1990) and Geitler (1958c, 1973a) have recorded a reduction in plastid number or arrangement during the life cycles of *Biremis* D.G. Mann et E.J. Cox *in* Round *et al.* and *Eunotia* Ehrenberg species.

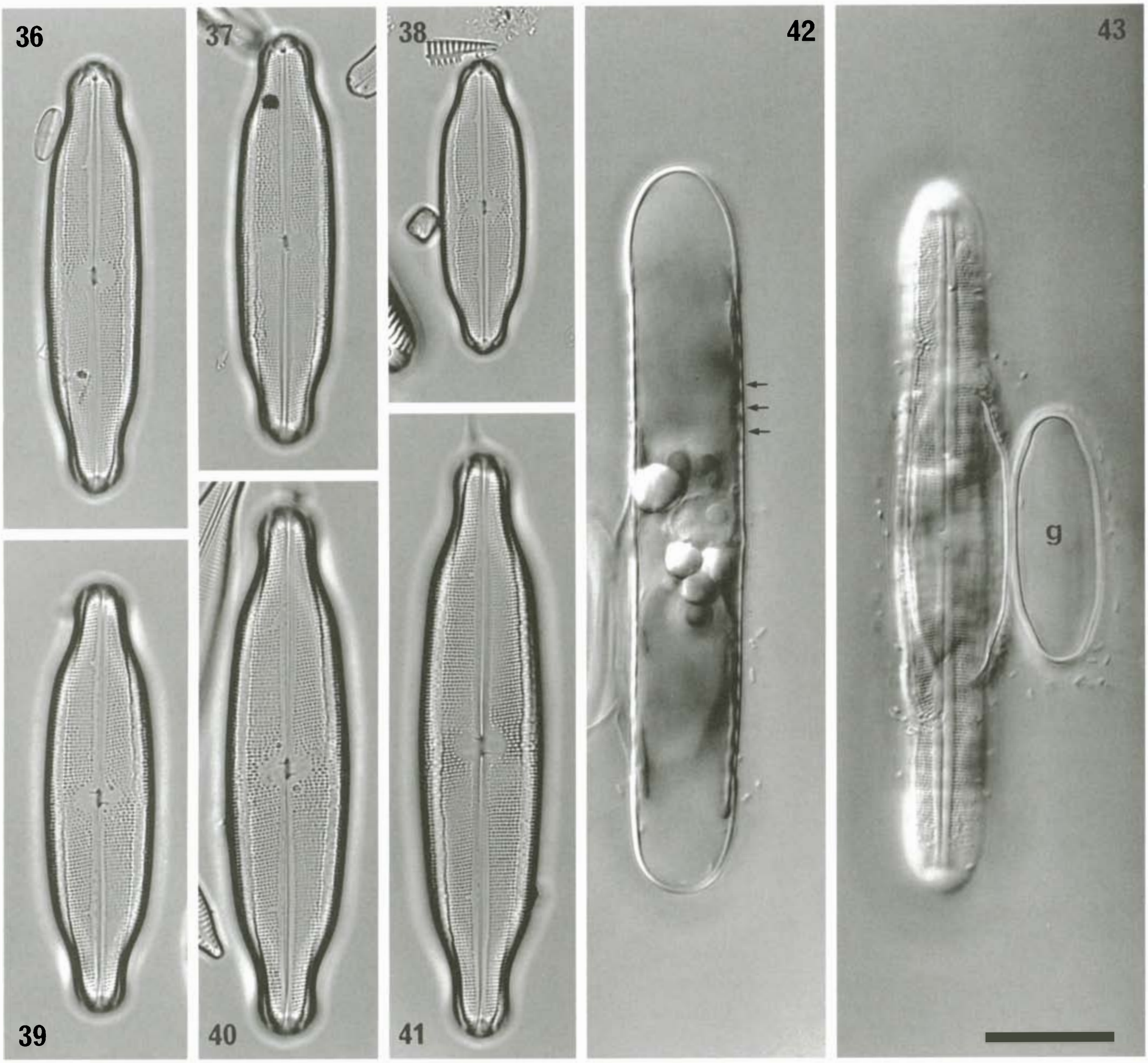
Casual observations and controlled experiments show that colony characteristics often change in response to environmental conditions. Colony characteristics (growth forms) have been shown to change seasonally in some planktonic species. For instance, *Thalassiosira tumida* and *T. ritscheri* (Hustedt) Hasle in Hasle & Heimdal occur as long chains connected by chitin threads during the austral spring, but as single cells at other times (Fryxell 1989), although it is conceivable that this reflects the changing abundance of clones with different growth habits, rather than phenotypic plasticity. In *Achnanthes longipes,* clones with different sexual characteristics exhibit different growth forms in culture. Unisexual and bisexual clones tend to grow dispersed, whereas monoecious clones form dense tufts (Chepurnov & Mann 1997). *Skeletonema costatum* (Greville) Cleve generally occurs in nature in long chains, but Bentley (1958) found that in bacteria-free cultures maintained in entirely synthetic media, *S. costatum* occurred as single cells or, more rarely, in pairs and triplets. Addition of the plant growth substance indole-3-acetic acid at concentrations of c. 10^{-7} to 10^{-8} gl^{-1} led to the formation of eight-celled chains, but growth in undefined Erdschreiber medium produced 50-cell chains, as observed in nature. A curious form of switching between alternative colony forms has been reported in *Amphora coffeaeformis* (C.A. Agardh) Kützing by Garduño *et al.* (1996); control of development seems to be physiological (perhaps linked to life-cycle changes), not genetic, but the exact mechanism and significance of the polymorphism are unclear.

In summary, although more studies certainly are necessary and despite some clear demonstrations of polymorphism and phenotypic plasticity, enough is known to make it unlikely that future research will greatly undermine the reliance taxonomists traditionally have placed on shape, wall structure, striation density, and pattern. Schmid (1994) takes a different view, claiming that, because ontogeny is "highly sensitive to the environment", there are in fact many fewer species than are currently recognized. She has certainly demonstrated some interesting changes in morphology in culture, through changes in culture conditions and treatment with drugs (e.g. see Pickett-Heaps *et al.* 1990), which throw considerable light on morphogenesis. Furthermore, among the papers listed above, there are some that show clearly that taxonomists have been misled by phenotypic plasticity. This seems to be particularly true for planktonic centric diatoms, especially in genera of the Thalassiosirales (*Thalassiosira, Stephanodiscus,* and *Cyclotella*; cf. Figs 30–35). However, only a minority of diatom species are planktonic and the plankton, far more than the benthos, is likely to experience extreme changes in nutrient availability and light climate during the annual cycle; it would not be surprising if their phenotypes prove to be unusually plastic. Many diatoms have been cultured *in vitro* during the 20th century by physiologists and biochemists, so that, if it were common for species or genera to be 'transformed' one into another by changes in temperature or nutrient status, it would surely have been noticed by now. And some claims of phenotypic plasticity seem to be unfounded, or at least, do not have the significance attached to them by their authors, such as the apparent interconversion of *Coscinodiscus concinnus* W. Smith and *C. granii* Gough that was reported by Holmes & Reimann (1966) but was discounted by Boalch (1971) and that has not since been considered to be of taxonomic importance (e.g. Hasle & Syvertsen 1996). Detailed studies of species such as *Sellaphora pupula,* in culture and in nature (Mann 1989a; Mann & Droop 1996; Mann *et al.* 1999), show that apparently minor differences in shape, size, striation density, and pattern have a genetic basis and are faithfully transmitted through the asexual and sexual phases of the life cycle. Mizuno's (1987) experiments on a clone of *Cocconeis scutellum* Ehrenberg likewise demonstrate extreme constancy in striation density and pattern, despite exposure of cultures to temperatures of 5–22°C and different daylengths.

On the other hand, it must be admitted that the stability of many protoplast-, colony-, and electron microscopy-based characters (e.g. polar raphe endings, velum structure, process structure, cingulum architecture) has yet to be tested, although it is likely that many of them reflect genotypic variation (Round 1996a).

Morphological changes brought about during the normal life cycle

As a result of the unique method of cell division and wall formation in diatoms, one of the two daughter cells produced after each division has the same size as the parent cell, where-



Figs 36–43. *Neidium ampliatum,* sympatric demes from Blackford Pond, Edinburgh, Scotland (slide Blackford 18.12.85A). Light microscopy. Scale bar (in Fig. 43) = 20 μm.

Figs 36–41. Cleaned valves, illustrating size reduction (reverse order in Figs 39–41). Note the oppositely deflected central raphe endings, characteristic of most *Neidium* spp., and that the width changes little with decreasing length. Bright field optics.

Figs 36–38. *Minor* deme.

Figs 39–41. *Major* deme.

Fig. 42. *Minor* deme. Expanding auxospore, contained within the perizonium, which is composed of a series of transverse silica hoops (e.g. arrows). The zygotic nucleus is visible at the center. Differential interference contrast optics.

Fig. 43. *Minor* deme. Initial cell with initial epivalve, flanked by the empty thecae of the gametangia ('g' and out of focus, above initial cell). Note that the gametangia are less than one half of the length of the fully expanded auxospore; the gametangial valves are broadly rostrate whereas the initial cell is linear, with bluntly rounded poles. Differential interference optics.

as the other is generally smaller. Consequently, over time, mean cell size in a population decreases (Figs 36–41); this may continue for months or years (Mann 1988a; Jewson 1992a; Potapova & Snoeijs 1997). Sooner or later, however, size is restored via a special cell, the auxospore (Fig. 42), which is generally a zygote, formed after allogamous sexual reproduction (further information is given in a recent review of the diatom life cycle by Edlund & Stoermer 1997). Subsequently, new large valves and girdle bands are produced within the auxospore, producing the first cell (the initial cell) of the next generation; the old, small frustules of the gametangia are cast off, empty (Fig. 43).

Auxosporulation does not occur until cells pass below a critical size threshold and there is then a range of size within which auxosporulation can be triggered, if certain other conditions are met, such as particular daylengths, light intensities, salinities, or temperatures (e.g. see Drebes 1977), or the presence of compatible strains (in dioecious species). In some species there is also a lower size threshold, below which sexual reproduction will not occur whatever the external conditions (Chepurnov & Mann 1997; Drebes 1977). Studies by Geitler (1932) indicated that the life cycle contains several 'cardinal points', which are more or less constant within particular clones or races and can be used to characterize them. These are the size threshold for auxosporulation and the sizes of the fully expanded auxospores (or the initial cells formed within them), and (if applicable) the size threshold below which auxosporulation ceases. Studies by Roshchin and Chepurnov (Roshchin 1994) and Armbrust & Chisholm (1992) show that the life cycle is sometimes much more complex than in the Geitlerian model, and Davidovich (1994) demonstrated a dependence of auxospore size on the sizes of the gametangia (see also Edlund & Stoermer 1997). Nevertheless, although taxonomists will have to be more cautious in using size data than has seemed necessary hitherto, the general principle of using cardinal points to characterize populations or taxa has not been completely undermined. Geitler's idea of a characteristic upper size threshold for auxosporulation apparently is still valid throughout, unless Armbrust & Chisholm's (1992) observations of size changes in *Thalassiosira weissflogii* (Grunow *in* Van Heurck) Fryxell et Hasle cultures do indeed reflect true auxosporulation, as opposed to vegetative enlargement, and are not a peculiarity of this species alone. If there is a characteristic size threshold for auxosporulation and a characteristic range of gametangium size, and if the sizes of the gametangia (auxospore mother cells) and initial cells are correlated, then there must also be a characteristic upper limit and range of initial cell size (Mann *et al.* 1999).

Using the cardinal point approach, Geitler found that several freshwater species are heterogeneous with respect to size. Demes can be found, in allopatry or sympatry, that differ in the lengths of the gametangia and initial cells, and often also in other characteristics, such as striation pattern and density, details of reproductive behavior, and cell attachment (Geitler 1968, 1975, 1977). Similar variation has been reported also by Mann (1988b, 1989a), and Krammer (1997a, 1997b) has taken the bold step of recognizing more or less all such variants as informal or formal taxa.

It has been shown repeatedly that changes in size during the life cycle are frequently accompanied by changes in morphology, either in the valve pattern alone (as in circular centric diatoms) or in both pattern and shape. Shape tends to change in similar ways throughout, suggesting similar, simple control mechanisms (see Mann 1994a). Valves become more isodiametric and rounded; if bipolar, they generally reduce in length much more than width (Figs 36–41, 43) (Geitler 1932; Lund 1945–46; Granetti 1968a, 1968b, 1977; Hostetter & Hoshaw 1972; Tropper 1975; Steinman & Ladewski 1987; Denys & Carter 1989; Round *et al.* 1990). The smallest valves may lack many diagnostic features and become almost indistinguishable from those of other taxa (Hustedt 1937b). Schmid (1990) noted that *Coscinodiscus wailesii* Gran et Angst valves begin to resemble those of *C. asteromphalus* Ehrenberg or *C. granii* towards the end of size reduction. In other cases, however, taxonomically useful characteristics only develop as size reduction proceeds, such as heteropolarity in *Rhoicosphenia curvata* (Kützing) Grunow (Mann 1984b) or *Martyana martyi* (Héribaud) Round (Kawashima & Kobayasi 1995), the broadly rostrate poles of *Neidium ampliatum* (Ehrenberg) Krammer (Fig. 43) (Mann 1984c), and the dorsal indentations of *Eunotia* species (Hustedt 1955; Mayama 1995a, 1995b). Auxosporulation has not been documented in most species, however, and so the full range of size and shape is unknown, making it difficult to interpret differences between populations sampled at different times in different places. In addition, auxosporulation seems often to be episodic, producing distinct size classes, that may or may not overlap (Nipkow 1927; Round 1982; Mizuno & Okuda 1985; Mann 1988a; Jewson 1992a; Potapova & Snoeijs 1997). Thus, if one population is sampled soon after auxosporulation, and another is caught close to the minimal size, it can be a matter of guesswork whether they belong to the same taxon. Hence, better knowledge of the life cycle, derived through more detailed knowledge of wild populations or long-term studies of clonal cultures, has sometimes revealed taxonomic redundancy. Striking examples include the demonstration that '*Anomoeoneis costata*' refers to the initial cells of *A. sphaerophora* (Ehrenberg) Pfitzer (Schmid 1979) and that *Actinocyclus niagarae* H.L. Smith is the initial cell of *Stephanodiscus niagarae* (Edlund & Stoermer 1991). The 'genus' *Amphiraphia* Chen et Zhu, which was placed in its own order by Chen & Zhu (1983) because it possesses a fragmentary raphe along the midline of the valve, in fact represents the initial cells of *Caloneis* Cleve species (Mann 1989b; the generic status of *Caloneis* needs to be established *vis-à-vis Pinnularia*). Different stages of the life cycle have sometimes been described as separate varieties: Kociolek & Stoermer (1988) concluded that *Gomphoneis herculeana* (Ehrenberg) Cleve var. *robusta* (Grunow) Cleve represents part of the life cycle of var. *herculeana.* Except in extreme cases, however, such as '*Amphiraphia*', morphological changes during the life cycle are gradual and continuous (e.g. Figs 36–41). They will only be a problem during species delimitation if taxonomists are incautious in extrapolating from small samples.

Toward the end of size reduction in culture, many of the valves formed have irregular shapes and striation patterns (e.g. Geitler 1932; Granetti 1968c, 1978; Hostetter & Hoshaw 1972; Round 1993; Estes & Dute 1994; Mann *et al.* 1999), which also occurs after vegetative cell enlargement (e.g. von Stosch 1967; Roshchin 1994) [see also the poorly understood life cycle of '*Navicula*' *muscatinei* Reimer et Lee (Lee & Xenophontes 1989)]. These teratological forms are interesting demonstrations of both the potential plasticity of development in diatoms and the constancy of some aspects of structure (e.g. areola structure and occlusions), despite gross abnormality in others (valve shape, position of the annulus, sternum, or raphe, stria pattern). In nature such malformed cells are uncommon, however, and their conspecificity with 'normal' cells in the same samples is usually easily demonstrated (even if culture studies are impossible), by structural similarities of the frustule and protoplast, and the existence of intermediate morphologies.

Physiological and genetic evidence

Only a tiny fraction of the total genotypic variation present within a population or taxon is likely to be manifested morphologically. Physiological and biochemical differences will also be present, as will totally cryptic nucleotide substitutions. Wood & Leatham (1992) reviewed the physiological and genetic data then available on diatoms, most of which concerns marine phytoplankton (but see, for example, Lewin & Lewin 1960). Clones identified morphologically as belonging to the same species can differ in growth responses to temperature and salinity, vitamin requirements, nitrogen metabolism, silicon metabolism, zinc-dependent growth rate, sensitivity to pollutants, chemical composition, the characteristics of photoadaptation, and diel periodicity with respect to several physiological parameters (for references, see Wood & Leatham 1992). More recently, there has been intense study of *Pseudo-nitzschia* species, revealing complex patterns of intra- and interspecific variation in the production of domoic acid, a toxic amino acid (e.g. Bates 1998; Bates *et al.* 1998), and *Phaeodactylum tricornutum* Bohlin strains have been found to differ in the production of external carbonic anhydrase (John-McKay & Colman 1997). However, although it is clear from these investigations that morphological similarity is sometimes a poor predictor of physiological characteristics (with obvious implications for ecological monitoring and paleoecological reconstruction), it is by no means clear what relevance this has for species delimitation. As Wood and Leatham note, most studies deal with only one or a few clones per population, so that it is impossible to know whether the clones are representative, or to determine the relationship between intra- and interspecific variation.

In only a few cases has there been extensive analysis of populations. The best studied species is *Skeletonema costatum,* for which Gallagher has shown that sympatric populations sampled at different times can be genetically differentiated. In Narragansett Bay, Rhode Island, USA, *S. costatum* dominates the phytoplankton in late summer and also in winter, but the populations forming the two blooms are quite different in allozyme banding patterns and physiological characteristics; summer and winter populations seem as distinct genetically as sibling species of *Drosophila* or vascular plants (Gallagher 1980, 1982; Gallagher *et al.* 1984; Gallagher & Alberte 1985). Pilot restriction fragment length polymorphism analysis of chloroplast DNA has also indicated considerable divergence between summer and winter populations (Stabile *et al.* 1995; see also Stabile *et al.* 1990, 1992). However, the taxonomic interpretation of the differences between the populations is uncertain. Gallagher (1980) discussed the possibility that the populations might represent sibling species, but noted some evidence for genetic exchange between them. More recently, after applying different methods of analysis to the original data set, she has come to the conclusion that the summer and winter blooms represent the two ends of a genetic continuum within a single species (Gallagher 1994). Diversity seems to be maintained by seasonal changes in the direction of selection.

Some molecular sequence data for *Skeletonema* show 18S rDNA heterogeneity among clones of *S. costatum* and closely related species. Medlin and colleagues (Medlin *et al.* 1991, 1995; Medlin & Simon 1998) interpret this as evidence for the existence of several cryptic species in the *S. costatum* complex. One group of isolates differed from the others morphologically and probably ecologically, as well as in its 18S rDNA sequence, and this was separated as a new species, *S. pseudocostatum* Medlin (Medlin *et al.* 1991; Castillo *et al.* 1995). This leaves the remainder of *S. costatum* apparently paraphyletic (Medlin *et al.* 1995, fig. 8). The 18S rDNA differences between *S. pseudocostatum* and other *Skeletonema* isolates include compensatory base changes within helices of the molecule (cf. Fig. 44), making it highly unlikely that they are of no significance or are artifacts (Medlin 1997). Coleman *et al.* (1994, 1998) have shown that similar compensatory changes in the internal transcribed spacer (ITS) sequences of Volvocales correlate with the boundaries of biological species (syngens). However, relatively few clones of *Skeletonema* were studied, and although the molecular data certainly demonstrate variation, it is unclear whether this is more or less than one might expect *within* a widespread species. It would be useful to have sequence data from a wider range of isolates and a variety of genes, and to attempt to interbreed different members of the complex.

There are few comparable studies of other diatom species complexes, but Medlin's results with *S. costatum* and *S. pseudocostatum* are consistent with data on *Pseudo-nitzschia* H. Peragallo *in* H. & M. Peragallo species, for which molecular data, immunological characteristics, morphology, and toxicity concur in supporting the separation of *P. multiseries* (which produces the neurotoxin domoic acid) from *P. pungens* (Grunow *ex* Cleve) Hasle (which is nontoxic or produces only small amounts of domoic acid); previously, these had been considered only as forms of the same species (Hasle 1965, 1995; Bates *et al.* 1993, 1998; Douglas *et al.* 1994; Scholin *et al.* 1994; Manhart *et al.* 1995; Hasle *et al.* 1996). In the *Sellaphora pupula* complex, there is significant variation in 18S rDNA and *rbc*L sequences between the sympatric and allopatric gamodemes described in section IV, including compensatory changes in 18S rRNA helices (Fig. 44), and ITS sequences have diverged to such an extent that alignment is problematic, except between the most closely related demes (Mann & Guihal, unpublished data).

Murphy & Guillard's (1976) isozyme study of *Thalassiosira pseudonana* Hasle et Heimdal and *T. weissflogii* was restricted to only 14 clones, as opposed to the 457 clones of *S. costatum* examined by Gallagher (1980). They concluded from the enzyme data that there were three groups of clones, two falling within *T. pseudonana* as it was then defined and one corresponding to *T. weissflogii* (as '*T. fluviatilis*'). The two *pseudonana* groups had different distributions (one neritic, one oceanic) and exemplar clones from each differed physiologically and morphologically. One clone, 7-15, was intermediate between the oceanic and neritic groups, physiologically, morphologically, and in its enzyme banding patterns, suggesting that the clones are not genetically isolated. However, more recent research has suggested that *T. pseudonana* should be divided into three species, *T. pseudonana, T. guillardii* Hasle, and *T. oceanica* Hasle (Hasle 1978, 1983a), which apparently can be distinguished consistently (Hasle & Syvertsen 1996).

Skeletonema costatum and *Thalassiosira pseudonana* are interesting examples, because the impetus for taxonomic revision was generated by physiological and genetic data and only later involved a renewed analysis of morphology. Although few other species have been examined in such detail, there are already hints that *S. costatum* and *T. pseudonana* may not be atypical and that genetic analysis of other planktonic diatoms will reveal previously undetected species. Thus,

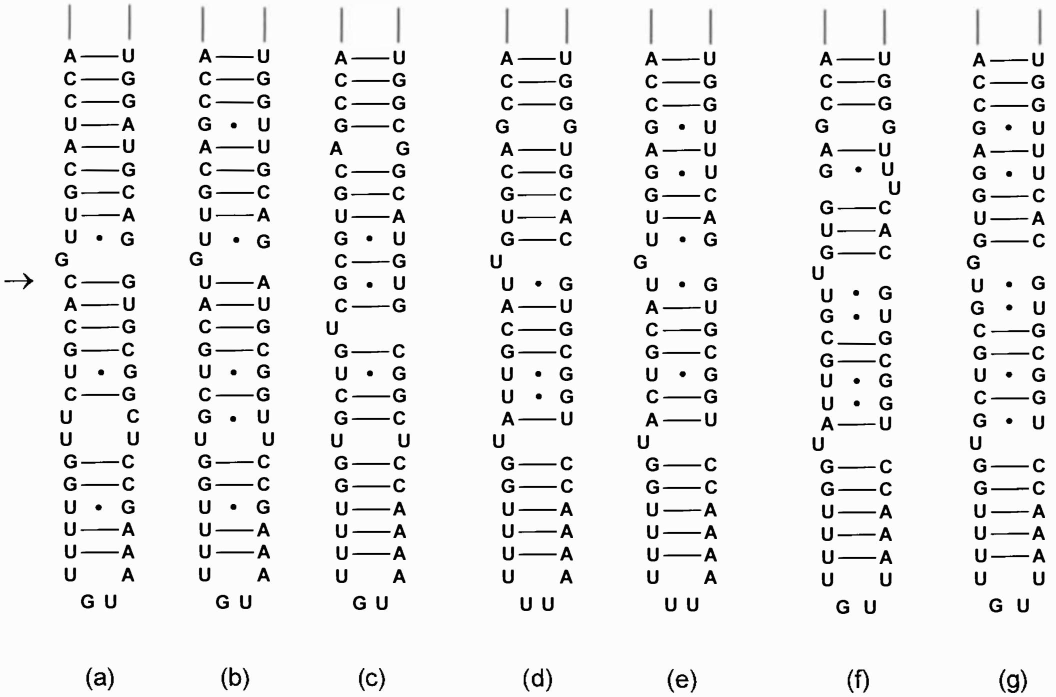


Fig. 44. Secondary structure models for helix 21-1 of small subunit rRNA in *Sellaphora* species. As in other diatoms (cf. Medlin *et al.* 1996; Medlin 1997), helix 21-1 is very variable. However, parts of the sequence are strongly conserved, allowing detection of compensatory base changes (e.g., arrow). (a) *Sellaphora pupula, capitate* deme (clone 11), Blackford Pond. (b) *Sellaphora pupula, rectangular* deme (clone 13B), Blackford Pond. (c) *Sellaphora laevissima* (clone 22Tr), Threipmuir Reservoir. (d) *Sellaphora pupula, elliptical* deme (clone 13R), the pond, Royal Botanic Garden, Edinburgh. (e) *Sellaphora pupula, small* deme (clone 7B), Blackford Pond. (f) *Sellaphora pupula, small-lanceolate* deme (clone 5TM), Threipmuir Reservoir. (g) *Sellaphora bacillum* (clone 9B), Blackford Pond.

even though *Pseudo-nitzschia* is one of the best documented of all marine planktonic diatom genera (e.g. Hasle 1965; Hasle *et al.* 1996), four Californian clones of *Pseudo-nitzschia* were found that failed to react with any of the species-specific large-subunit (LSU) rRNA probes developed by Miller & Scholin (1998) to identify the known *Pseudo-nitzschia* species. This might, of course, indicate intraspecific polymorphism with respect to the target LSU sequences, but a preliminary examination showed that the four clones also differ morphologically from known *Pseudo-nitzschia* species (Miller & Scholin 1998). They may represent three new species. In addition, genetically differentiated strains have been detected in *P. australis* Frenguelli and *P. pungens* (Scholin *et al.* 1994). Skov *et al.* (1997) have demonstrated isozyme variation, apparently accompanied by minor morphological variation, among 10 clones isolated from a bloom of *Pseudo-nitzschia pseudodelicatissima,* but not enough is known to justify taxonomic conclusions.

Soudek & Robinson (1983) made an isozyme analysis of 101 isolates of the common planktonic diatom *Asterionella formosa* Hassall from 32 lakes and rivers in North America and Europe. Wood & Leatham (1992) have pointed out that the number of isolates analyzed per population by Soudek & Robinson was not high (only eight lakes were represented by five or more isolates), so that it is difficult to draw many firm conclusions. There was no clear evidence for cryptic speciation. However, although isolates from the same lake were uniform in their banding patterns, whether they were collected at the same time or not, those from different lakes had significantly different patterns, even if the lakes drained into each other. There was some correlation between banding pattern and geography, with European isolates clustering apart from most North American isolates. The most divergent pattern was found in an isolate from Lake Ohrid (Macedonia–Albania), which was the only lake included in the analysis that predates the Holocene. Clones of *Stephanodiscus niagarae* isolated from different Holocene lakes in North America have different ITS sequences (Zechman *et al.* 1994), but intrapopulational variation was not studied.

Lewis *et al.* (1997) used RAPD analysis to examine genetic variation in North American populations of another freshwater planktonic diatom, *Fragilaria capucina* Desmazières. Here, samples of each population were larger, with 126 clones from seven lakes. Variation occurred both within and between populations, but with few exceptions, clones from the same lake clustered together and apart from those from other lakes. The lakes studied came from a latitudinal transect from Manitoba, Canada, to Texas, USA, but the RAPD data did not correspond in any simple way to geography: variation was not clinal. Populations from Texas clustered more closely with those from North Dakota than with populations from Oklahoma or Kansas. Interestingly too, all but one of the lakes sampled by Lewis *et al.* were reservoirs, which have existed for an even shorter time than the postglacial lakes studied by Soudek and Robinson. Lewis *et al.* also noted that *F. capucina* var. *mesolepta* Rabenhorst from Lake Manitoba did not differ genetically from var. *capucina* isolated from the same lake, suggesting that var. *mesolepta* should be abandoned. Hürlimann & Straub (1991) documented the presence of several morphologically and ecologically distinct demes ('Sippen') within

European *F. capucina,* but whether any of these correspond to the North American populations studied by Lewis *et al.* is unknown; Lewis *et al.* gave no morphological data and cited no voucher specimens.

Interpretation of genetic differences among freshwater diatom populations requires knowledge of the mechanisms of dispersal. For lakes to be colonized by planktonic diatoms within a few years of being formed, which has sometimes been recorded (e.g. by Atkinson 1988) [for references to some other studies, with contradictory results, see Talling (1951)], medium- to long-distance transport of at least a few viable cells must occur quite frequently. In agreement with this, a wide variety of diatom species, including some regarded as truly aquatic (as opposed to those characteristic of soil or terrestrial habitats) were recorded on the island of Surtsey, off Iceland, only 5 yr after its formation through volcanic eruption (Behre & Schwabe 1970). Unfortunately, there have been few direct attempts to determine *how* diatoms are dispersed. Most of the limited evidence was gathered more than 30 yr ago by Schlichting and coworkers (e.g. Schlichting 1960, 1964, 1969; Stevenson & Collier 1962; Parsons *et al.* 1966; Stewart & Schlichting 1966; Milliger & Schlichting 1968; Schlichting & Milliger 1969); see also Atkinson (1970, 1971), Jaworski & Lund (1970), Talling (1951), and van Overeem (1937). These papers show that, for different diatom species, air, insects, or birds can be effective dispersal agents. However, the fluxes of cells between habitats must usually be tiny, compared to the standing crop. Thus, in the early stages of colonization, when population numbers are small, it seems not unlikely that fixation of genes could occur rapidly, through selection and genetic drift, producing the kinds of genetic diversity documented in *Asterionella* and *Fragilaria.* The genetic profile of the population will also, of course, be influenced strongly by the nature of the colonizing cells. But once a population has become established to the extent that it is detectable, which requires there to be many million cells in even a small lake, genetic drift will become much less important as an evolutionary mechanism and the contribution made by new immigrants will also be relatively small, unless they carry selectively advantageous genes. In temperate and polar regions, most lacustrine habitats have been ephemeral on timescales of 10^3–10^5 yr, so that the species that inhabit them have been given repeated opportunities to build up large, essentially infinite populations from small numbers of founders. It seems likely that their population genetics and speciation mechanisms will differ significantly from species of marine diatoms, either in the phytoplankton or phytobenthos, where habitats are more continuous, both spatially and temporally.

The only study to date that has examined the genetic structure of populations with respect to morphological characteristics is a quantitative genetic analysis of the antarctic marine planktonic species *Thalassiosira tumida,* by Wood *et al.* (1987). This revealed that most of the phenotypic variation with respect to selected morphological features (the number of fultoportules surrounding the central annulus, the average number of satellite pores per fultoportule, and the number of marginal rimoportules) was related to ontogeny (life-cycle changes) or enviromental factors (reflecting phenotypic plasticity). The remaining variation was genetic and, although small, would nevertheless be an adequate basis for rapid morphological evolution, given continued directional selection. Johansen & Theriot (1987) found clonal differences in the numbers of central fultoportules in a related species, *T. weissflogii.*

Thus, genetic and physiological data show what one would expect—that diatom species are genotypically diverse, with differentiation between populations that can sometimes be regarded as ecotypic (as in some physiological specializations reviewed by Wood & Leatham 1992) but is sometimes probably selectively neutral (e.g. some rDNA sequence variation). Unexpectedly high genetic variation occurs between populations of a species living in different lakes, even those formed very recently, indicating that dispersal and gene flow cannot prevent divergence. The taxonomic significance of the data is rarely clear, however, usually because of inadequate sampling (this is no criticism of those who did the research, because their studies were not usually undertaken for taxonomic purposes): samples have been too small, or too biased, or were not collected with due reference to geography. Furthermore, it is usually impossible to examine congruence with other datasets, because comparable data on morphology, ecology, reproductive biology, and crossability are not available for the same populations.

Variation in reproductive behavior: Geitler's 'Sippen'

During his long life, Lothar Geitler made many studies of sexual reproduction and auxosporulation in freshwater diatoms, most of which have some relevance for the student of diatom species (for a complete bibliography, see Schmid 1991). His idea of 'cardinal points' has already been mentioned, together with the discovery that different populations of a species can have different cardinal points, that is, different size ranges between initial cells and gametangia. Geitler also discovered that different demes do not necessarily have the same reproductive biology. In his earliest contributions on this theme (Geitler 1927a, 1927b), he showed that there was interdemic variation in the attached freshwater diatom *Cocconeis placentula* Ehrenberg and he returned to this species in several later papers spanning 55 yr (Geitler 1932, 1948, 1952a, 1958a, 1958b, 1973b, 1982). In a small river (Seebach) near Lunz, Austria, Geitler found five sympatric phenodemes of *C. placentula* that differed morphologically and also reproductively (data summarized in 1982). One phenodeme corresponded to a previously described taxon [var. *lineata* (Ehrenberg) Van Heurck] and Geitler described the other four as new varieties (*euglyptoides, klinoraphis, pseudolineata,* and *tenuistriata*). The Lunz demes of *euglyptoides* and *tenuistriata* are sexual and isogamous, *klinoraphis* is usually isogamously sexual but sometimes parthenogenetic, *pseudolineata* is anisogamous, and *lineata* is an obligate apomict, forming auxospores through diploid parthenogenesis. In the only study to date that has examined karyotypes within a single diatom species complex, Geitler established that the diploid chromosome number varies from 20 to 24 in *euglyptoides* and *pseudolineata,* through 28–30 in *klinoraphis* and *tenuistriata,* to 30–32 in *lineata* (Geitler 1973b). A deme morphologically similar to Lunz *klinoraphis* was found at Schladming (Steiermark, Austria), about 115 km from Lunz, but this deme was obligately rather than facultatively parthenogenetic (Geitler 1958a). At Schladming there was also a deme that resembled two other Austrian demes, from Spitz (Nieder-Österreich) and Vienna, respectively. On the basis of morphology, all three could be referred to var. *euglypta* (although with some similarities to var. *lineata* from Schladming and Vienna), but while the Schladming and Vienna demes were sexual and isogamous, the Spitz deme was parthenogenetic. Other demes were also found at other sites in Austria (Geitler 1932, 1958a, 1970a). The pattern of variation in this species is therefore very complex, even in central Europe. Because the *C. placentula* complex has been recorded worldwide (Krammer & Lange-Bertalot 1991b), additional variants probably exist.

It is important to note, however, that these studies of *Cocconeis placentula* were based not on the use of clonal cultures, but on observations of natural populations. This makes interpretation tricky. In particular, it is difficult to judge the significance of differences between *allopatric* demes, especially of vars *euglypta* and *klinoraphis,* because we cannot exclude the possibility that reproductive behavior was influenced by different environmental conditions. The same difficulty also occurs both with respect to the automictic and allogamous demes found in *Denticula tenuis* Kützing (Geitler 1953), because the demes were collected from widely separated localities (Lunz and Schladming), and also in interpreting differences in pairing configuration between demes of *Gomphonema parvulum* (Kützing) Kützing (Geitler 1958c). Is this phenotypic plasticity, or genotypic variation within a single species, or does it reflect the presence of cryptic species?

Where long-term observations of natural populations show consistently that two or more demes occur in the same place at the same time and yet remain distinct, the balance of probability is that they are genotypically differentiated and quite possibly reproductively isolated too. This must apply to the Lunz demes of *C. placentula* (Geitler 1982), *G. angustatum* (Geitler 1963b, 1970b), and *Cymbella cesatii* (Rabenhorst) Grunow *in* A. Schmidt (Geitler 1975). In all these cases, differences in sexual reproduction and auxosporulation are accompanied by morphological or size differences (otherwise, of course, there would be no visible markers by which to distinguish demes when growing intermingled).

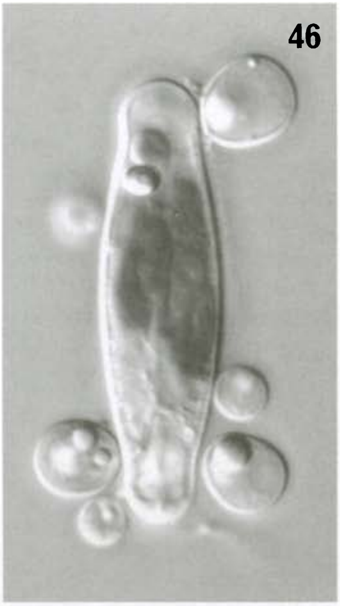
Apart from Geitler, few phycologists have surveyed reproductive behavior in a variety of populations or isolates of the same species. Clones of *Coscinodiscus granii* isolated from the North Sea at different times seem to differ reproductively, with some behaving monoeciously and others exhibiting subdioecy (Drebes 1968, 1977). Similar temporal changes have been reported in the Black Sea (Roshchin & Chepurnov 1999). In *Ditylum brightwellii* (West) Grunow *in* Van Heurck too, there is variation in reproductive behavior: some clones are apparently asexual, restoring size only through vegetative enlargement, but others produce auxospores sexually (von Stosch 1986). French & Hargraves (1986) isolated 70 clones of *Leptocylindrus danicus* (Ehrenberg) Gran and found only two that were capable of the 'normal' life cycle, in which resting spores are formed within the auxospore after expansion; the remainder exhibited enlargement following extrusion of protoplasts from between the epitheca and hypotheca of vegetative cells. The asexual clones differed morphologically from the sexual clones, lacking a central pore (see also Round *et al.* 1990), and were therefore separated into a new variety *apora* (French & Hargraves 1986). Three varieties of *Melosira moniliformis* (O.F. Müller) C.A. Agardh have been studied in some detail; they differ in whether or not the ripe oogonia bend to allow fertilization, and in the method of sperm formation (hologenous vs merogenous) (Roshchin & Chepurnov 1999; for explanations of sperm formation, see Drebes 1977, Round *et al.* 1990). Three varieties of *Achnanthes brevipes* C.A. Agardh have also been studied: vars *brevipes* and *angustata* (Greville) Cleve are allogamous, whereas var. *intermedia* (Kützing) Cleve is automictic. Varieties *angustata* and *intermedia* occur together at Karadag, Crimea, but *brevipes* has not yet been found growing with either of the other two (Chepurnov, unpublished observations).

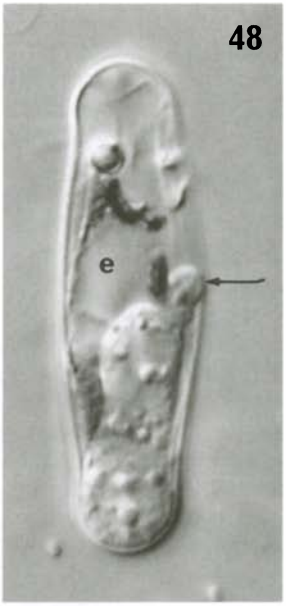
The most intricate pattern of variation in reproductive biology discovered so far is in *Sellaphora pupula.* As noted in previous papers (Mann 1984a, 1989a, 1989c; Mann & Droop 1996), some demes are allogamous (Figs 58–63), but others are automictic or (apparently) wholly asexual. We have recently discovered further, more subtle variation among allogamous demes. In the *capitate* deme (Fig. 53) from Blackford Pond, Edinburgh, Scotland, outbreeding is strictly enforced by dioecy: clones are either male or female and successful auxosporulation occurs only when male and female clones are mixed (Mann *et al.* 1999). Similar behavior has been found in a morphologically similar deme from the Crimea, Ukraine (Chepurnov & Mann, unpublished observations). Elsewhere, inbreeding is permitted via intraclonal (monoecious) reproduction, to a limited degree in the Blackford *small* and *rectangular* demes (Figs 52, 54), and freely in *elliptical* demes from Threipmuir Reservoir, near Edinburgh, and the pond of the Royal Botanic Garden, Edinburgh (RBGE) (Fig. 63) (Mann & Chepurnov, unpublished observations).

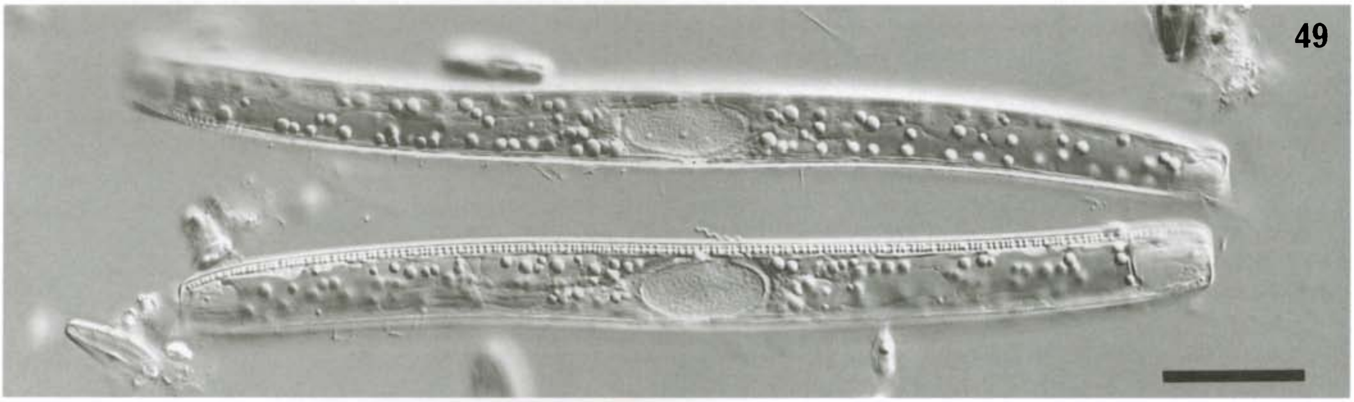
Ecological differentiation and discrimination by parasites

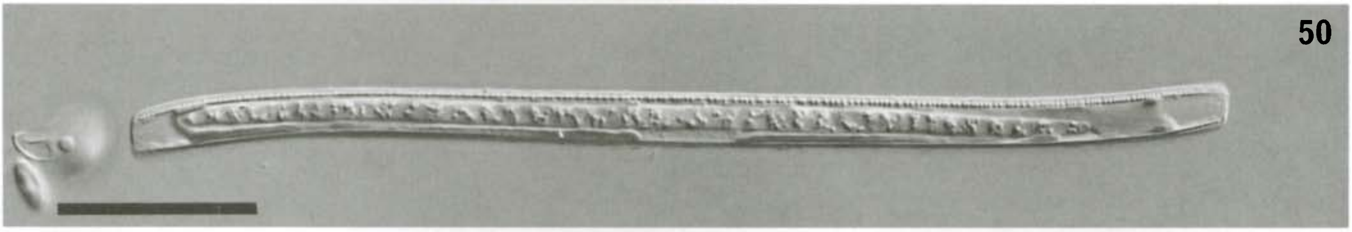
It is, of course, expected that closely related species will differ ecologically (e.g. Van Valen 1976; Hutchinson 1978; Begon *et al.* 1990) and in many groups of organisms such differences are easily found. Diatom ecology is in a relatively primitive state at the species level, however, with few autecological studies, apart from the classic studies of *Asterionella* and *Aulacoseira* by Lund (e.g. Lund 1949a, 1949b, 1954, 1955, 1971; Hughes & Lund 1962), and few quantified analyses of niche separation, apart from resource competition work by Tilman and Sommer (e.g. Tilman 1982; Sommer 1987). This, coupled with changes in classification and poor documentation by ecologists of the communities and species they have observed, makes it difficult to say very much about the niches that particular species occupy.

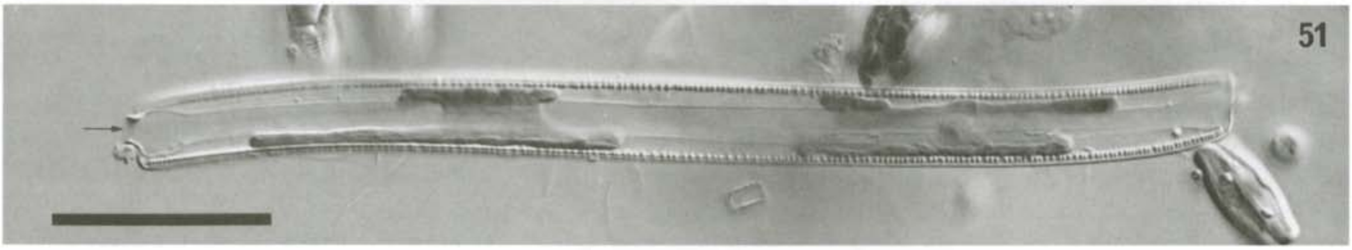
Recently, information has become available as a by-product of paleoecological studies, in which it is essential to characterize the realized niches of taxa in order to be able to develop transfer functions linking the composition of a preserved assemblage to acidity, salinity, total phosphorus, and so on (Stoermer & Smol 1999). Such data seem to confirm, as expected, that closely related taxa do often differ ecologically (here, I am assuming that close correspondence in details of morphology reflects close relationship). Examples are *Staurosira construens* (Ehrenberg) Williams et Round (= *Fragilaria construens*) and its variety *venter,* and *Achnanthidium lanceolatum* de Brébisson *in* Kützing [= *Achnanthes lanceolata* = *Planothidium lanceolatum* (de Brébisson) Round et Bukhtiyarova] and its variety *rostratum,* which separate in the ordinations of Bennion (1995). Earlier, the ecological sepa-











Figs 45–51. Parasitism in freshwater epipelic diatoms from Blackford Pond, Edinburgh, Scotland. Light microscopy, differential interference contrast optics. Scale bars = 10 μm (Figs 45–48) and 40 μm (Figs 49–51).

Figs 45–48. *Sellaphora pupula* demes. Deme names as used by Mann & Droop (1996) (see also Figs 52–57).

Fig. 45. *Small* deme, with single discharged sporangium of ?*Chytridium* sp. (operculum visible at arrow).

Fig. 46. *Lanceolate* deme, bearing many encysted cells of ?*Chytridium* sp., that have penetrated the cell wall and given rise to ramifying systems of 'rhizoids' within the cell.

Fig. 47. *Capitate* deme, bearing encysted cells and a discharged sporangium of ?*Chytridium* sp.

Fig. 48. *Capitate* deme, containing a living, endobiotic oomycete parasite, which is beginning to form its exit papilla (arrow); a second parasite has already discharged and remains as an empty sporangium (e).

Fig. 49. *Nitzschia sigmoidea.* Mating cells in meiotic prophase. *Nitzschia sigmoidea* did not mate with *N. vermicularis* in the same sample.

Figs 50, 51. *Nitzschia vermicularis* cells infected by an endobiotic oomycete. A single elongate parasite cell is present within the diatom in Fig. 50, and Fig. 51 shows a dead host cell after discharge of the oomycete sporangium through an apical papilla (arrow). *Nitzschia sigmoidea* in the same sample remained uninfected.

ration between *T. flocculosa* (Roth) Kützing and *Tabellaria quadriseptata* Knudson, an indicator of strongly acid waters, was important in prompting Flower & Battarbee (1985) to reinvestigate the subtle morphological differences between these species and to confirm that Knudson (1952) had been right to recognize *quadriseptata.*

Allopatric populations of a single species can often be shown to experience different light climates, temperatures, and nutrient availabilities, and the associated flora and fauna are rarely identical. Without physiological studies and reciprocal transplant experiments (which are much easier in macroalgae and vascular plants), however, the significance of ecological differences in allopatry is unclear. In contrast, sympatric demes of the same or closely related species can sometimes betray their ecological differentiation more easily. Thus, among the *Cocconeis placentula* demes at Schladming, Austria, vars *euglypta* and *klinoraphis* showed slight niche separation, with *klinoraphis* occurring only on the leaves of aquatic mosses but *euglypta* occurring also on *Cladophora* (Geitler 1948). Round (1972) found that two sympatric demes of *Sellaphora pupula* had different, essentially complementary patterns of abundance during the year, although the growth periods for each deme were not synchronous between the two small ponds studied, both in the University of Birmingham Botanic Garden. *Fragilaria capucina* populations were studied by Hürlimann & Straub (1991) and seem to exist as a series of demes, which are very subtly different morphologically but have different distributions in nature, although some grow sympatrically. Studies using experimental channels revealed that the demes have different responses to ammonium concentrations.

Parasitism of diatoms by fungi and protozoa is frequent and sometimes brings about catastrophic losses (e.g. Canter 1979; Canter-Lund & Lund 1995). In the present context, the most interesting discovery is that parasites can discriminate between morphologically similar demes of what have traditionally been considered single species. *Fragilaria crotonensis* exists in many subtly different morphologies, among them two that are most easily distinguished by the shape of the cell in girdle view. In 'rod' demes, corresponding to var. *crotonensis,* the cells taper more or less steadily towards the poles, whereas in 'flared' demes (var. *prolongata* Grunow *ex* Van Heurck) the poles are noticeably expanded; chains of 'rod' cells generally have a much wider mucilage envelope than those of 'flared' cells. Scanning electron microscopy reveals further differences, in the orientation of the rimoportule and the size of the apical pore field (Crawford *et al.* 1985). 'Rod' and 'flared' demes occur together in Windermere, Ullswater, Blelham Tarn, and Esthwaite Water in the English Lake District, Lac Léman in Switzerland, and Bureso, Denmark. Among the parasites that infect them are two chytrids, *Rhizophydium fragilariae* Canter and 'species 3', which show complementary preferences. *Rhizophydium fragilariae* infects 'rod' demes, but 'flared' demes remain almost unaffected; 'species 3', on the other hand parasitizes 'flared' demes (Canter & Jaworski 1982, 1983). In both *F. crotonensis* demes, individual clones exhibit different degrees of susceptibility.

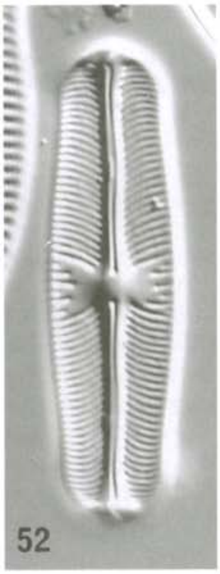
Studies of other planktonic diatoms and their chytrid parasites have also shown a high degree of specificity (e.g. Canter *et al.* 1992; Doggett & Porter 1995), and similar phenomena seem to occur in benthic species, such as *Sellaphora pupula.* In Blackford Pond, Edinburgh, *S. pupula* demes (Figs 52–57) are infected by an operculate, exobiotic chytrid (?*Chytridium* sp.: Figs 45–47) and an endobiotic oomycete (Fig. 48). Three of the six demes (*capitate, rectangular,* and *lanceolate*) are highly susceptible to the chytrid (Table 1; Figs 46, 47). Another deme (*small*) is often infected (Figs 45, 54) but seems to be partly resistant (Table 1), and the large-celled, slow-growing *obese* deme (Figs 55, 62) is almost immune (Table 1); scarcely any information is available concerning the *neat* deme, which is always rare. The oomycete, on the other hand, seems to be able to cause severe infections in only one of the six demes present (*capitate,* Fig. 48), although a single infected cell of *obese* has also been observed. Likewise, another endobiotic oomycete attacks Blackford *Nitzschia vermicularis* (Kützing) Hantzsch *in* Rabenhorst (Figs 50, 51), but 'ignores' the closely related species *N. sigmoidea* (Nitzsch) W. Smith (Fig. 49).

It would be interesting to study species complexes such as *Sellaphora pupula* in relation to the Red Queen hypothesis for the maintenance of sexual reproduction, which suggests that sex is important in allowing hosts to counter the rapid adaptation of shorter-lived parasites to the prevalent host genotypes (Van Valen 1973; Dybdahl & Lively 1998). *Sellaphora pupula* demes show differential susceptibility to parasites and also have different reproductive systems, varying from strong outbreeders through facultative inbreeders to automictic and asexual demes. Parasitism might help explain why so many apparently very similar diatom species coexist within many benthic communities. Coexistence may be promoted by frequency dependent selection: severe infections of parasites such as chytrids or oomycetes cannot develop when their hosts are rare (the chance of a parasite zoospore encountering a new host is too small) [see Kudoh & Takahashi (1990), who give references].

IV. TOWARDS A SYNTHESIS CONCERNING THE NATURE OF DIATOM SPECIES

Interpretation of discontinuous infraspecific variation in sympatry

The work reviewed above suggests that there is often genotypic variation, partly visible, partly cryptic, within groups that have generally been regarded as single species. However, this should not be surprising, because every species is genetically diverse, to a lesser or greater extent. The question is whether the intricate pattern of variation that has been revealed by recent studies is compatible with current species boundaries or whether it requires them to be changed. No general answer can yet be given and in many cases competing hypotheses seem to explain the data equally parsimoniously. For example, the reproductive diversity found by Geitler among allopatric demes of *Cocconeis placentula* var. *euglypta* and *Denticula tenuis* could reflect the existence of cryptic species, or it might just represent infraspecific genotypic variation, or even phenotypic plasticity. The genetic diversity within *Fragilaria capucina* and *Asterionella formosa* may prove to be accompanied by morphological and ecological differentiation and reproductive isolation, and individual demes may perhaps be at least as worthy of recognition at the species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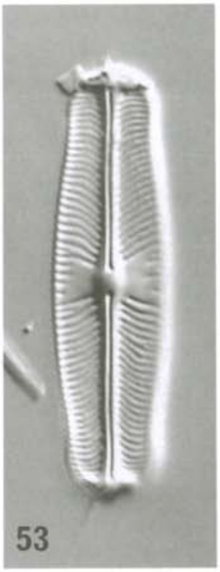
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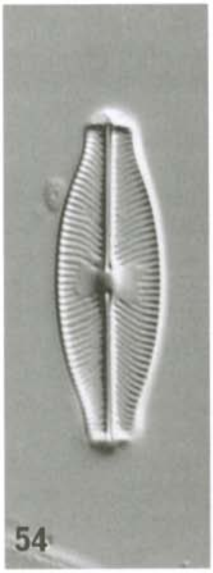
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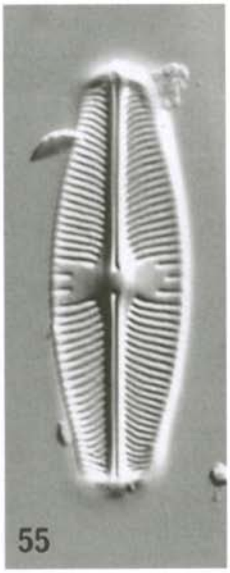
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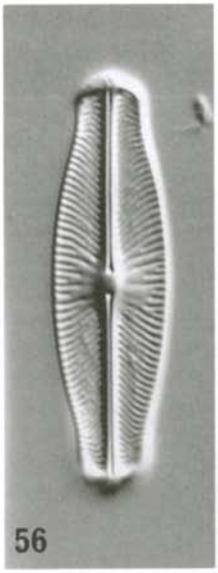
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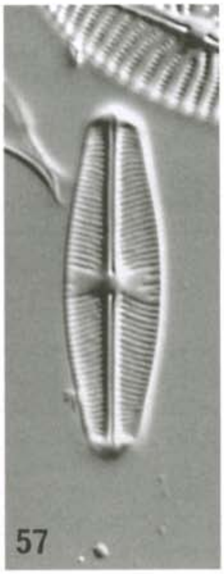
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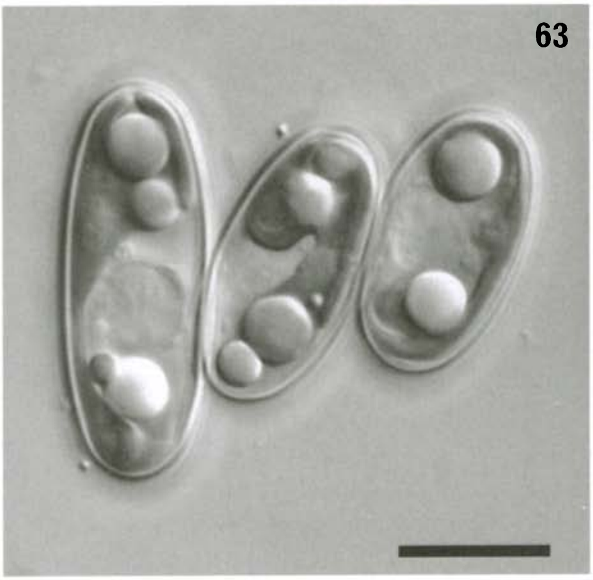
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level as Theriot's new species within the *Stephanodiscus niagarae* complex; or they may simply be populations that have become differentiated through adaptation and genetic drift.

Ambiguity is least if we consider sympatric populations. Here, it is easiest to discount the effects of phenotypic plasticity and polymorphism and to evaluate the significance of discontinuities in the variation pattern. Several examples have already been given where two or more morphologically different demes of a particular species or species complex have been found coexisting in the same locality; these include *Diploneis smithii/fusca, Hantzschia virgata,* and *H. marina,* split into 2 to 20 or more demes at various sites along British sea coasts, and the freshwater epiphytic diatoms *Cocconeis placentula, Gomphonema parvulum,* and *Cymbella cesatii,* at Lunz, Schladming, and elsewhere in Austria. To these can be added various other examples from the literature, including several freshwater epipelic taxa, such as *Neidium ampliatum* (Figs 36–41), *Caloneis silicula* (Ehrenberg) Cleve, *Cymatopleura solea* de Brébisson et Godey, and *Sellaphora pupula* (Figs 52–57), which have been studied in Edinburgh lakes by Mann (Mann 1984a, 1988b, 1989a; Mann & Droop 1996), the brackish to marine epipelic species *Biremis lucens* (Hustedt) Sabbe, Witkowski et Vyverman (Sabbe *et al.* 1995), and the freshwater planktonic species *Tabellaria flocculosa* (Knudson 1953b) and *Fragilaria crotonensis* (Crawford *et al.* 1985). In *Synedra parasitica* (W. Smith) Hustedt, the vars *parasitica* and *subconstricta* (Grunow *in* Van Heurck) Hustedt live alongside each other in eutrophic lakes, attached to *Nitzschia sigmoidea* and other large diatoms [Chang & Steinberg (1988) consider them to be separate species]. In all these species, sympatric demes can be distinguished on the basis of slight differences in shape, size, and striation pattern. It is easy to find other less well-documented cases where similar demes coexist. Our recent examination of benthic samples from Lake Baikal reveals many such cases, for example in *Navicula lacus-baikali* Skvortzow et Meyer (see below and Figs 79–87) and in the *Sellaphora bacillum* (Ehrenberg) D.G. Mann cluster.

It is common, therefore, to find pairs or larger numbers of demes growing together that seem to be closely related on the basis of morphological similarity and that have therefore been classified in the same species. But we should also be careful not to assume that our current taxonomy is always conservative. Examples are also relevant when they concern sympatric demes that are often or always separated into different species by taxonomists, but are nevertheless very closely related. These could include *Pinnularia major* (Kützing) W. Smith and *P. viridis* (Nitzsch) Ehrenberg (Mann 1988b), *Amphora ovalis* and its close relatives *A. libyca* Ehrenberg and *A. pediculus* [*sensu* Krammer & Lange-Bertalot 1986 (Mann 1984a)], *Craticula cuspidata* and *C. ambigua* (Ehrenberg) D.G. Mann (Mann 1988b), or *Nitzschia sigmoidea* and *N. vermicularis* (Figs 49–51). Among the members of the *Stephanodiscus niagarae* complex studied by Theriot (summarized in 1992a), two pairs are sympatric: *S. reimerii* Theriot et Stoermer and *S. niagarae* occur together in several lakes in northern Iowa, USA, and *S. superiorensis* Stoermer et Theriot and *S. niagarae* occur together in Lake Superior, although one is an open water species whereas the other occurs near the shore. *Stephanodiscus yellowstonensis* Theriot et Stoermer, on the other hand, is endemic to a single lake in Wyoming and grows there alone; it is therefore arguable, perhaps, whether it represents a separate species or a locally differentiated population of *S. niagarae,* except by analogy with *S. reimerii* and *S. superiorensis* [there is no information about reproductive compatibility between *S. yellowstonensis* and other *Stephanodiscus* species, and ITS sequence data show little difference between *S. yellowstonensis* and *S. niagarae* from other lakes in the Yellowstone area (Zechman *et al.* 1994)].

Discontinuities in the variation pattern between sympatric genodemes of the same or closely related species could exist for the following reasons:

1. Divergent (disruptive) selection. Intermediate genotypes (and hence phenotypes) are produced through recombination and sexual reproduction, but are removed by selection.
2. Polymorphism and canalization. Intermediate phenotypes cannot be produced because development is canalized, flipping between alternative ontogenetic trajectories.
3. The populations are in disequilibrium. One or all of the

←

Figs 52–63. *Sellaphora pupula.* Deme names as used by Mann & Droop (1996). Light microscopy, differential interference contrast optics. Scale bar (in Fig. 63) = 10 μm.

Figs 52–57. Six demes from Blackford Pond, Edinburgh, Scotland, cleaned valves (slide East 16/4).

Fig. 52. *Rectangular* deme (allogamous).

Fig. 53. *Capitate* deme (allogamous). The *rectangular* and *capitate* demes are similar in shape and striation density, but differ in size (at any particular length, *rectangular* is c. 1 μm wider than *capitate*) and in details of valve morphology near the poles.

Fig. 54. *Small* deme (allogamous).

Fig. 55. *Obese* deme (allogamous).

Fig. 56. *Lanceolate* deme (apparently asexual): note the 'shadow striae' extending in toward the central nodule at the center.

Fig. 57. *Neat* deme (?autogamous).

Figs 58–63. Mating between sympatric and allopatric populations of morphologically similar demes.

Fig. 58. *Capitate* deme, paired gametangia in a seminatural mixed population from Blackford Pond, during meiosis II.

Fig. 59. *Capitate* deme, backcross between Blackford female clone 6 (smaller cell, to right) and the hybrid male clone [(24bts + 11)2], obtained by crossing clone 24 from Bryntsevskij stavok, Crimea, Ukraine, with clone 11 from Blackford Pond. Cells in meiotic prophase.

Fig. 60. *Small* deme, paired gametangia in a seminatural mixed population from Blackford Pond.

Fig. 61. *Small* deme, mating between cells from clone 6B (from Blackford Pond) and clone 17D (larger cell, to left), from Dunsapie Loch, Edinburgh, Scotland. Cells in meiotic prophase.

Fig. 62. *Obese* deme, triplet of gametangia in a seminatural mixed population from Blackford Pond.

Fig. 63. *Elliptical* deme, mating between clones 22D (from Dunsapie Loch) and 3R (from the pond, Royal Botanic Garden Edinburgh). In the triplet, two cells of 22D (smaller cells, center and right) bond to each other, and one bonds also to a cell of 3R (left); this behavior is possible only in demes capable of monoecious reproduction. All cells in meiotic prophase.

Table 1. Parasitism of *Sellaphora pupula* demes by an operculate chytrid (cf. *Chytridium* sp.: Figs 45–47). Counts of healthy, infected, and dead cells in seminatural populations 3–8 d after collection of mixed epipelon from Blackford Pond, Edinburgh, Scotland. Deme names as in Mann (1989a) and Mann & Droop (1996): see also Figs 52–57. Note the very low rate of infection of the *obese* deme.

Deme	Healthy	Infected[1]	Dead[2]
22 Apr 1988			
rectangular	4	28	4
capitate	2	113	24
small	5	6	2
obese	103	2	0
lanceolate	0	1	0
neat	1	0	0
25 Apr 1988			
rectangular	0	1	10
capitate	4	2	16
small	4	2	4
obese	53[3]	2	2
18 Jan 1996			
rectangular	8	10	0
capitate	110	51	4
small	43	6	2
obese	109	3[4]	0
lanceolate	213	192	9
20 Feb 1996			
rectangular	10	3	3
capitate[5]	61	25	7
small	21	1	0
obese	262	2[4]	0
lanceolate	218	39	19
20, 21 Feb 1996			
rectangular	1	3	3
capitate[5]	17	62	36
small	20	6	3
obese	85	2[4]	0
lanceolate	20	68	60

[1] Infected cells can bear one to many parasites.

[2] Infected cells were counted as dead once they bore at least one discharged sporangium (cells have never been observed to recover from infection once the parasite has penetrated the cell wall and produced intracellular rhizoids).

[3] One cell contained an endoparasite resembling the oomycete often found infecting the *capitate* deme.

[4] Chytrids were seen attached or adjacent to *obese* cells, but apparently without penetration of the diatom.

[5] *Capitate* cells were also infected by an endobiotic oomycete (Fig. 48), whether or not they were simultaneously infected by *Chyridium.*

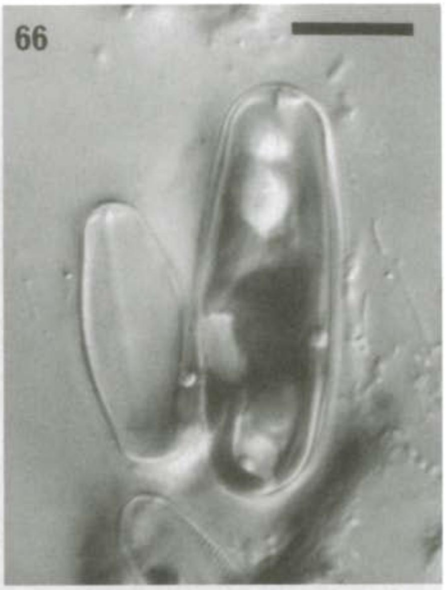
demes are recent immigrants that have either arrived *en masse* or built up their populations vegetatively over the period since colonization. There has been insufficient time for integration and selection to produce a new equilibrium assemblage.

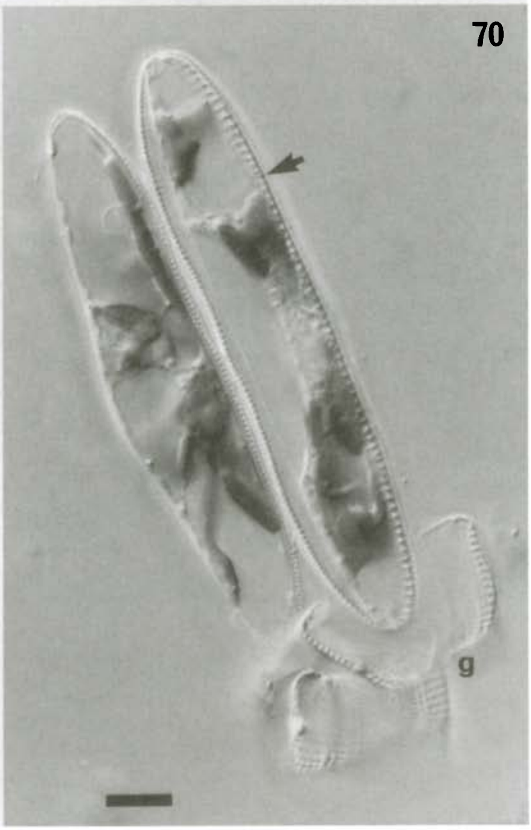
4. The demes are reproductively isolated. Their gene pools are separate and intermediate genotypes and phenotypes cannot arise, except through convergent evolution.

All four reasons may operate in some circumstances, but the only one for which there is any direct evidence is possibility 4. The idea of canalized development (possibility 2) grows out of observations of polymorphism such as in *Mastogloia* (Stoermer 1967; see above). Here, alternative morphologies (*smithii* and *elliptica-dansei* valves) can be produced within the same clone, as shown by the existence of cells possessing one valve of each type. Valves with intermediate morphologies were not found. It is easy to imagine how a developmental switch of this kind, operating at any stage of the life cycle as a phenotypic response to some unknown internal or external factor, might become fixed in the 'on' or 'off' position, as a result of selection for the trait in question. What is at present a plastic response within clones could then become assimilated genetically, to produce clones with constant *smithii* or *elliptica-dansei* morphology. Although such clones might still interbreed, *smithii* or *elliptica-dansei* morphologies would segregate in their progeny and natural populations would therefore contain no Janus cells. There would be no obvious link between the two morphologies although they would be mere character differences such as green vs yellow seeds in peas. It is quite possible that the genetic assimilation and canalization of phenotypic responses (Waddington 1957, chapter 5) is involved in the formation of new diatom species, but with few exceptions the sympatric demes studied so far *are* reproductively isolated. Furthermore, they often differ in many, very diverse respects (e.g. reproductive biology, size, shape, morphology, parasite sensitivity), which are unlikely to be controlled by a single gene.

Possibility 3 may seem highly implausible in microalgae, being much more likely in mobile, social animals that attain sexual maturity only after many years, such as humans. However, the idea should not be dismissed lightly in diatoms, because of the length of the life cycle. It may take 5 or more years in nature for cells of a clone to reduce in size sufficiently for most of them to pass the sexual size threshold (Mann 1988a; Jewson 1992a). Thus, a deviant cell arising in a particular habitat or arriving from elsewhere could build up a large, distinct local population, even if it later proved fully compatible with the preexisting population. A trivial example of this is in *Cocconeis* populations, where misshapen cells are not infrequent and can give rise to large colonies. Here the deviant cells apparently arise through unequal or abnormal cytokinesis and thus their morphologies have no genetic significance, which is obviously untrue of the interdemic differences discussed in previous sections, but the same principle applies. However, against possibility 3, we may note that morphologically distinct, sympatric demes can have a longevity greatly exceeding any reasonable estimate of the life cycle. As noted previously, Droop (in preparation) has demonstrated that *Diploneis smithii/fusca* demes have been present for at least 140 yr on the Isle of Cumbrae, West Scotland.

Compelling evidence has accumulated to support possibility 4: sympatric demes are often reproductively isolated from each other. This has been shown for the Blackford Pond demes of *Neidium ampliatum, Caloneis silicula,* and *Cymatopleura solea* (each represented by two demes: e.g. Figs 36–38, 39–41), and for the four allogamous demes of *Sellaphora pupula* (e.g. Figs 58, 60, 62; Mann 1984a, 1989a; Mann & Droop 1996; Mann *et al.* 1999). In *N. ampliatum* many thousands of pairs have been observed (from 19 January to 19 February 1996 alone, 4719 pairs were counted in seminatural populations) and in only two cases so far has pairing been found between cells of different demes (Fig. 67). In these mixed pairs the cells proceeded through meiosis and formed gametes, but fertilization did not occur. Less extensive observations indicate similar isolation between sympatric demes of *Caloneis silicula, Cymatopleura solea,* and *Sellaphora pupula* in other eutrophic parkland lakes in Edinburgh (Figgate Loch,





Figs 64–70. Hybridization in pennate diatoms. *Sellaphora* deme names as used by Mann & Droop (1996). Light microscopy, differential interference contrast optics. Scale bars = 10 μm.

Figs 64–66. *Sellaphora pupula.*

Fig. 64. *Large* deme from Threipmuir Reservoir, near Edinburgh, Scotland. Paired cells in seminatural populations, meiotic prophase.

Figs 65, 66. Mating between the *large* and *tidy* demes in mixed, seminatural populations from Threipmuir Reservoir.

Fig. 65. Paired gametangia, meiotic prophase; *large* gametangium to right.

Fig. 66. Zygote, formed within *large* gametangium (right).

Fig. 67. *Neidium ampliatum.* Mating between the *major* (left; cf. Figs 39–41) and *minor* (cf. Figs 36–38, 42, 43) demes from Blackford Pond; gametangia containing two gametes (clearly visible in the *minor* cell, right). Plasmogamy did not occur.

Figs 68–70. *Achnanthes brevipes.* Mating between vars *brevipes* and *intermedia* (see text).

Fig. 68. Variety *brevipes* clone 7 (broader, lanceolate cell to left) × var. *intermedia* clone 4, early meiotic prophase.

Fig. 69. Variety *brevipes* clone 6 (squat cell to left) × var. *intermedia* clone 2, early meiotic prophase.

Fig. 70. Variety *brevipes* clone 6 × var. *intermedia* clone 2, two initial cells of F_1 generation, still associated with the gametangial frustules (g). The right-hand cell has produced its initial epivalve (arrow).

Dunsapie Loch, St Margaret's Loch), and experiments by A.M. Roshchin and V.A. Chepurnov (personal communication) show that *Melosira moniliformis* vars *moniliformis* and *subglobosa* Grunow (which grow together at Karadag, Black Sea) are also incompatible. In addition, no mating has been observed between sympatric populations of closely related species, such as *Nitzschia sigmoidea* (Fig. 49) and *N. vermicularis, Amphora ovalis, A. copulata,* and *A. pediculus, Cymatopleura solea,* and *C. elliptica* (de Brébisson *ex* Kützing) W. Smith, *Sellaphora laevissima* (Kützing) D.G. Mann, *S. bacillum,* and *S. pupula* (D.G. Mann, unpublished observations), or *Licmophora ehrenbergii* (Kützing) Grunow and *L. abbreviata* C.A. Agardh (V.A. Chepurnov, unpublished observations). Earlier, Geitler found no evidence of interbreeding between sympatric demes of *Cocconeis placentula* (with one exception, discussed below), *Achnanthes lanceolata, Cymbella cesatii,* and *Gomphonema angustatum* (Geitler 1927b, 1958a, 1970b, 1975, 1980, 1982).

Reproductive barriers were detected initially (e.g. Mann 1984a) through studies of natural or seminatural populations (I use 'seminatural' to describe mixed natural populations that have been manipulated in the laboratory or kept in rough culture). With such studies there is always the risk that any capacity for interclonal and interdemic mating will be masked by overwhelming numbers of intraclonal matings, if the diatom is relatively immobile and homothallic. Recently, therefore, we have studied sexual reproduction in culture, first to determine the mating system, and then to test compatibility between clones belonging to different demes. In several cases, demes have been found to possess mechanisms (e.g. dioecy) that hinder or prevent inbreeding (Mann *et al.* 1999), and these guarantee that observations of mixed natural populations will faithfully reflect compatibility between different demes. But aside from this, direct attempts to cross sexually mature clones of different sympatric demes have failed in all cases so far, just as in seminatural populations. Experiments have involved the Blackford demes of *Caloneis silicula* and *Neidium ampliatum,* three of the Blackford demes of *Sellaphora pupula* (*small, capitate,* and *rectangular*), and several sympatric demes of *S. pupula* from Threipmuir Reservoir, near Edinburgh. In one case, however, an interesting interaction has been observed between different demes of *S. pupula.* In mixtures of female clones of the *capitate* deme (Fig. 53) and male clones of the *rectangular* deme (Fig. 52), or of male *capitate* with female *rectangular,* there was a stimulation of movement and apparent attempts to pair, although there was no bonding between cells and no transition to meiosis (Mann *et al.* 1999). These observations suggest that parts of the mate-recognition system are still common to the two demes, which seem to be the most closely related of the *S. pupula* gamodemes studied so far, judging by 18S rDNA, ITS, and *rbc*L sequence comparisons (Mann *et al.,* unpublished observations).

On the whole, then, observations of (semi-) natural populations and experiments indicate that discontinuities in the variation pattern within sympatric populations are accompanied by reproductive isolation. There are three known exceptions to this generalization. Geitler (1958a) discovered hybridization within the Lunz populations of *Cocconeis placentula,* between vars *pseudolineata* and *euglyptoides.* In addition, he reported that some cells had intermediate morphologies, suggesting that they might be hybrids or the result of backcrossing between the F_1 hybrids and *pseudolineata* or *euglyptoides.* However, intermediate morphologies were rare and very few certain cases of hybridization were found among many pairs studied, and so it seems that substantial reproductive barriers do exist between the two demes. Quite different behavior was found later in *Gomphonema* populations in the Lunz Untersee. Here, Geitler (1969, 1979) reported hybridization between sympatric demes of what he called *Gomphonema constrictum* Ehrenberg *ex* Kützing and its variety *capitatum* (Ehrenberg) Van Heurck (these are not separated by Krammer & Lange-Bertalot 1986, who include both within *G. truncatum* Ehrenberg). Most remarkable was the fact that copulation did not occur within a deme but almost always (with only two exceptions among several hundreds of pairs) between a *constrictum* cell and a *capitatum* cell. Geitler observed few initial cells, however, and does not say whether these progressed past the formation of the initial epivalve. It is possible, therefore, that the F_1 was nonviable; abortion of initial cells after formation of the initial epivalve but without formation of an initial hypovalve occurs in the F_2 of crosses between allopatric varieties of *Achnanthes brevipes* (see below), perhaps because of unequal segregation or other irregularities at mitosis [the first mitosis in the initial cell is a necessary trigger for the formation of the initial epivalve (Geitler 1963a; von Stosch & Kowallik 1969)]. In contrast, sympatric populations of *G. constrictum* vars *capitatum* and *constrictum* in the Heustadelwasser, near Vienna, seem to be reproductively isolated, because here, although *constrictum* is again allogamous, *capitatum* is automictic (fusion takes place between sister gametes in unpaired gametangia). Geitler's observations of the Heustadelwasser demes were made at different times, however, and so it is impossible to know how the demes would have interacted if they had become sexual synchronously, as at Lunz (Geitler 1951, 1952b).

The final example of crossing between morphologically distinct, sympatric demes, concerns two demes of *Sellaphora pupula* from Threipmuir Reservoir, near Edinburgh. Paired cells of the *large* and *tidy* demes were illustrated by Round *et al.* (1990) and are also shown here (Figs 65, 66; for comparison, intrademic mating of *large* is shown in Fig. 64). In this case, in contrast to Geitler's *Gomphonema constrictum,* both demes seem to be allogamous (automixis has never been observed in either of them) and, in mixed populations, pairing occurs both within and between the two demes. However, as with *Gomphonema,* no information is available concerning the viability of hybrid progeny. Zygotes have been observed in many cases, but whether these develop into viable initial cells is unknown. So far, attempts to produce hybrids using clonal cultures have been unsuccessful.

In conclusion, studies of sympatric populations indicate good, although not exact congruence between prezygotic reproductive barriers and the limits of the genodemes established using morphological, developmental (e.g. during sexual reproduction and auxosporulation), ecological, and parasitological data. Kociolek (1997) has suggested that our data on *Sellaphora pupula* amount to "convincing evidence" that this species is heterogeneous and needs to be split (see also the comments of Cox 1997). It is tempting to be swayed by the compliment and, if all we are aiming for is a local taxonomy, applicable to Blackford Pond or Threipmuir Reservoir, or any other small area, we could certainly recognize each deme as a separate species. But systematics aims for a global taxonomy and so studies of sympatric populations are not enough; allopatric demes must also be examined, to see whether conclusions reached from studies of sympatric demes have more general validity. Very little research of this kind has been done, even within relatively well-studied taxa such as the *Sellaphora pupula* complex, and this is why we still hesitate to describe new species within *Sellaphora,* despite the arguments in favor of this that we have made in several papers (Mann 1984a, 1989a; Mann & Droop 1996).

Extension to allopatry

The task in studying sympatric demes is to establish the extent and nature of differences between sets of organisms: to look for discontinuities in the pattern of variation. In contrast, the main problem in studying allopatric populations is to establish common identity. So, if we wish to extend discussion to cover allopatric demes, the first step is to look for cases where morphologically extremely similar demes occur in different places. This may seem a trivial task: after all, almost the whole of ecology and paleoecology is based on recording, counting, and measuring individuals of the same species in different places, and one would therefore hope to be able to rely on a large body of previous research to help guide the extrapolation from local taxonomies to a global taxonomy. Unfortunately, in most cases it is impossible to know what other people have meant by a particular name (cf. Spamer & Theriot 1997) and even published photographs are often inadequate to allow one to say with any degree of certainty whether they represent demes known to be present elsewhere. Each deme must be documented in detail and compared carefully with every other deme, with respect to as many different characters as possible, both morphological and nonmorphological.

An extra difficulty in interpreting whether or not two allopatric demes are the same is that their local characteristics will almost certainly be molded by competition with close relatives. Demes may differ more strongly when living sympatrically than when living apart, as a result of character displacement (e.g. Brown & Wilson 1956; Taper & Case 1992; Schluter 1994). Hence, the characteristics used to distinguish between *Sellaphora pupula* demes in Blackford Pond may not work when applied to populations of the same demes growing separately elsewhere.

Victor Chepurnov, Stephen Droop, and I have begun to work intensively on allopatric demes of *Sellaphora, Achnanthes,* and *Diploneis* species. In *S. pupula,* we have found that demes very similar to those found in Blackford Pond also occur in other eutrophic lakes with highly organic, silty sediments (Mann & Droop 1996). For example, the *small, capitate,* and *rectangular* demes seem to be widespread in the UK. Although we have carried out no statistical tests (e.g. discriminant analysis), it seems to be impossible in many cases to determine the provenance of any particular valve from its morphology alone. Molecular sequence data for the *small* deme from Blackford Pond and Dunsapie Loch show near identity for 18S rDNA and a 400-base-pair (bp) section of *rbc*L; the *elliptical* deme from the Royal Botanic Garden pond and *cf. elliptical* (see below) from Threipmuir Reservoir are also almost identical for the same sequences. Furthermore, the accompanying diatom flora is often very similar, suggesting that ecological differences are minimal. And when cells of allopatric populations are mated, they seem to be fully compatible, producing viable offspring. We have made experimental crosses between *small* demes from two lakes (Blackford Pond and Dunsapie Loch, both in Edinburgh; Fig. 61), *rectangular* from three lakes (Blackford Pond, Threipmuir Reservoir, and Balgavies Loch, the last lying c. 80 km away from the other two), and *capitate* from two lakes (Blackford Pond and Bryntsevskij stavok, Crimea, Ukraine; Fig. 59). In all cases, a vigorous F_1 was produced. In some cases, for example, with Blackford and Ukrainian clones of *capitate* demes, we have obtained an F_2 generation and also backcrossed the F_1 with Blackford and Ukrainian clones (Fig. 59).

In these cases, therefore, we have a consilience between morphological, ecological, and reproductive data, suggesting that, in a global taxonomy, it might be appropriate to recognize *capitate, small,* and *rectangular* as separate species. However, the number of lakes studied is small and in other demes we have discovered complications that suggest that it is premature to draw firm conclusions. Thus, in two Edinburgh lakes, Dunsapie Loch and the pond of the RBGE, there are apparently identical demes that we refer to as *elliptical. Elliptical* is monoecious (Fig. 63) and mates with itself vigorously in monoclonal culture, which makes it difficult to maintain clones in culture and make crosses between them. Nevertheless, we have been able to show that Dunsapie and RBGE clones are interfertile, by using clones with cells of different sizes, that is, at different stages of the life cycle (Fig. 63). A third morphologically similar deme, *cf. elliptical,* with 18S rDNA and *rbc*L sequences very similar to those of RBGE *elliptical* (e.g. two base differences in c. 400 bp of the *rbc*L gene, contrasting with at least eight between sympatric *capitate* and *rectangular* from Blackford Pond), occurs in Threipmuir Reservoir and also shows vigorous monoecious reproduction. However, the initial cells produced monoeciously by Threipmuir *cf. elliptical* are much smaller than those produced by the Dunsapie and RBGE demes. Dunsapie clone *22D* produced initial cells with a mean length of 50.7 μm (± SD 2.18) from gametangia of c. 19 μm, whereas in Threipmuir clone *7Tm,* similar-sized gametangia produced initial cells with a mean length of 42.95 μm (± SD 2.58). Alongside this, there seemed to be less tendency for Threipmuir *cf. elliptical* to mate with Dunsapie or RBGE *elliptical* than for the latter two to mate with each other, as judged by the relative frequencies of intra- and interdemic pairings. Nevertheless, *cf. elliptical* and *elliptical* are compatible, at least to the extent that cells can pair, undergo gametogenesis, and produce zygotes; the viability of the F_1 is as yet unknown. A further clone from Diss Mere, Norfolk (eastern UK) was isolated and resembled the Edinburgh *elliptical* clones both morphologically and in its vigorous monoecy. It proved impossible to make crosses between Diss *elliptical* and other demes because all cells were used up in intraclonal reproduction, but the sizes of the initial cells (mean length 51.4 μm, produced from c. 23-μm gametangia) suggest that this deme was a 'true' *elliptical,* belonging with the Dunsapie and RBGE demes. *Elliptical* and *cf. elliptical* may differ ecologically. Dunsapie Loch, RBGE pond, and Diss Mere are all highly eutrophic, parkland lakes with almost black, silty sediments, whereas Threipmuir Reservoir is less productive, lies in a catchment area dominated by heathland, sheep pasture, and ombrotrophic bog, has strongly colored peaty water, and sediments that are a mixture of red-brown muds and sand.

In stark contrast to the above results, *Achnanthes longipes* clones from Panama and the Black Sea have proven to be unable to produce viable offspring, although they are sexually compatible (V.A. Chepurnov, unpublished results). Cells of different clones pair and can form zygotes but, at least in the culture medium used (based on Black Sea water, salinity 16 psu), the initial cells do not progress beyond formation of the initial epivalve and die. Detailed studies of morphology have not yet been carried out, but there is no gross difference between the clones.

In all of the above, the allopatric demes are extremely similar morphologically. We have also tried to make crosses between dissimilar allopatric demes and Davidovich & Bates (1998) reported attempts to cross *Pseudo-nitzschia multiseries* with *Pseudo-nitzschia pseudodelicatissima.* So far, crosses between dissimilar *Sellaphora pupula* have failed, regardless of whether the demes are allopatric or sympatric, but admittedly, fewer than 10 demes have been studied and not in every combination. The two *Pseudo-nitzschia* species also proved to be incompatible. In contrast, however, two allogamous varieties of *Achnanthes brevipes* are capable of crossing in culture. We isolated clones of *A. brevipes* var. *brevipes* from a salt marsh pool at Dunstaffnage, near Oban, West Scotland, and introduced them into mixed culture with clones of var. *intermedia* from the foreshore of the Firth of Forth at Gosford, in eastern Scotland. The cells differ in size and shape but hybridize freely to produce an F_1 (Figs 68–70). The F_1 has been grown successfully in culture but proved unable to complete its life cycle: gametes were produced and sometimes fused, but the zygotes were nonviable, either in attempts to produce an F_2 or in backcrosses with parental clones. It seems, therefore, that these demes of *intermedia* and *brevipes* have diverged to such an extent that gene flow between them is impossible. Perhaps prezygotic isolation mechanisms have not evolved because the demes rarely or never meet in nature, but much further research is necessary, first to establish that other clones of *intermedia* and *brevipes* behave similarly, and second to determine whether the varieties are always isolated from each other geographically or ecologically, or whether they sometimes grow sympatrically. Crosses have also been attempted between allopatric demes of vars *angustata* and *brevipes,* and between *angustata* and *intermedia* (*intermedia* and *brevipes* were derived from the localities mentioned above; *angustata* came from Karadag, Crimea). No hybridization occurred. In the Black Sea at Karadag, var. *intermedia* occurs sympatrically with var. *angustata.* Here, *intermedia* is automictic (Roshchin & Chepurnov 1993; Roshchin 1994; Chepurnov, unpublished observations) and it is therefore reproductively isolated from *angustata*; var. *brevipes* does not occur at Karadag.

These examples show that it is not easy to extrapolate from a local taxonomy to a global one. In some cases (the *small, capitate,* and *rectangular* demes of *Sellaphora pupula*), there is good agreement between morphological, ecological, and mating data over a wide geographical area. Elsewhere, different data sets seem to conflict. However, the example of *Achnanthes brevipes* shows how further information may enable conflicts to be resolved: the failure of hybrid *intermedia* × *brevipes* to backcross or produce an F_2 tends to suggest that these two are independent species, not a single, morphologically variable species, as might have been thought from the ease of producing a hybrid F_1. Of course, our results are few in number and hopelessly incomplete, but at least they demonstrate the kinds of questions we can ask and expect to answer using simple methods.

One possibility we must entertain is that some diatom species may be 'ochlospecies' (from *ochlos,* an unruly mob), which Cronk (1998) has defined, following F. White, as "very variable (polymorphic) species, whose variation, though partly correlated with ecology and geography, is of such a complex pattern that it cannot be satisfactorily accommodated within a formal classification". The concept of ochlospecies arose from studies of *Diospyros* (tropical African trees), where some species were found to be highly variable, often with two or more distinct, nonintergrading forms present in a particular locality. Other variants could be found at other localitites, "but taken together all the forms intergrade and the classification breaks down . . . Similar variants may occur in widely separated localities and appear to be polytopic in origin" (Cronk 1998). Variation is thus nonhierarchical, although apparently not as a simple result of hybridization or of hybridization followed by apomixis, as in agamic complexes in genera such as *Crepis* or *Rubus* (Stebbins 1950). Cronk suggested that ochlospecies may result when a species with wide ecological tolerance spreads rapidly into new areas, promoting geographically unstructured variation, through genetic drift in founding populations, strong selection as the species colonizes new habitats and climatic zones, and the conservation of mutations in an expanding population; the presence of discrete variants in a single locality could reflect disruptive selection. Because sympatric members of *S. pupula* complex are reproductively isolated, and because similar allopatric demes (e.g. *capitate*) do seem to be 'the same' (i.e. they are not polytopic in origin), based on morphological identity and the capacity to mate, *S. pupula* does not seem to fit the concept of ochlospecies as developed by White and Cronk. However, other diatoms may indeed be ochlospecies, and species complexes such as *S. pupula* may have had their origins as ochlospecies; if so, the history of speciation may in some cases be unrecoverable.

Speciation, evolution, and biogeography

Even though most phycologists never observe sexual reproduction in diatoms (partly because the length of the vegetative phase is so much greater than the period spent in sexual reproduction, and partly because of the tendency to treat diatoms as invisible and inconsequential before they have been boiled in oxidizing acids!), there is now overwhelming evidence that the evolutionary diversification of diatoms has taken place predominantly within sexual lineages. No family or genus, or even a species-rich section of a genus, is known in which all the species are asexual or parthenogenetic (data summarized in Geitler 1932, 1973b, 1985; Drebes 1977; Roshchin 1994). Even in a group such as *Nitzschia* sect. *Lanceolatae,* where agamic complexes might be suspected to occur because of the taxonomic intransigence of the group [cf. angiosperms such as *Taraxacum, Hieracium* (Stebbins 1950)], the literature contains more records of sexual reproduction than of automixis, apomixis, or parthenogenesis (Geitler 1932, 1973b). During the last 15 years, we have recorded allogamous sexual reproduction in 29 species and demes in Blackford Pond, including most of the common epipelic species. In contrast, only five species and demes have proved to be autogamous or asexual. Autogamy was found in one *Nitzschia* species and possibly in the *neat* deme of *Sellaphora pupula* (Fig. 57). Taxa that seem to be asexual are the *lanceolate* deme of *S. pupula* (Fig. 56), *Caloneis amphisbaena* (Bory) Cleve, and *Craticula ambigua*; in these no sexual reproduction has ever been observed in natural or seminatural populations, despite extensive observations at every time of the year, and size reduction seems not to occur. Other species present in Blackford Pond are so rare or have been studied so little that the lack of observations of sexual reproduction means nothing.

Furthermore, in most sexual diatoms, sex is not facultative, as it can be in other algae, because it is inextricably linked to the restitution of size following relentless diminution during the vegetative phase. Only a few diatoms have been shown to be able to suspend the process of size reduction *and* yet to maintain a sexual life cycle: examples are found in marine *Achnanthes* species, where size reduction can arrest above the sexual size threshold [*A. brevipes* cf. var. *angustata* (V.A. Chepurnov, unpublished observations)] or size can be maintained apparently indefinitely through cycles of vegetative enlargement [*A. longipes* (von Stosch 1965; Roshchin & Chepurnov 1992; Roshchin 1994)], although this behavior has only been observed in culture. Other examples of vegetative enlargement have been reported by von Stosch (1965, 1967, 1985, 1986) and this process may not be unusual among centric diatoms living in the marine plankton. But the vast majority of diatom species are neither centric nor planktonic and in most of these sex seems to be an integral part of the life cycle, enforced at regular intervals, although these may be several years apart (Mann 1988a; Jewson 1992a). Therefore, most speciation events in diatoms must occur in organisms with frequent, obligate sex. Richardson (1995) has emphasized, correctly, that natural diatom populations resemble those of other microalgae in that they will almost always consist of many fewer genotypes than individuals (except perhaps after mass auxosporulation), as a result of mitotic division and colony fragmentation. However, in my view Richardson's emphasis on mutation and asexuality is misleading. In most diatom species, after one to several years of size reduction, *every* surviving individual of *every* lineage must reproduce sexually or die. Diatoms are some of the most sexual organisms on earth; our problem in understanding them is that we do not invade their privacy often enough. Diatoms are also (unusually for algae) diplonts. Hence, as we gather more information about diatom speciation and population genetics, it will probably be more appropriate to draw analogies with higher animals (and many higher plants), than to make comparisons with asexual or parasexual organisms such as bacteria or (apparently) Euglenophyta, or with the many groups of haplontic unicellular algae (e.g. van den Hoek *et al.* 1995).

The prevalence of sex also gives us reason to believe that distinctions between hierarchical and reticulate variation will exist in nature, at least in sympatry, and the evidence discussed in previous sections shows how we may be able to arrive at a Waltonian consensus about the limits of species. It seems fair to conclude that diatom species, as they have traditionally been defined, are probably often heterogeneous, containing several entities that are separable morphologically, genetically, ecologically, and reproductively. We should therefore expect that future research will greatly increase the numbers of species that are recognized, perhaps to the c. 200,000 suggested by Mann & Droop (1996) (see also John & Maggs 1997). Thus, the species inflation that is so evident in recent papers by Lange-Bertalot and his colleagues is probably more justified than the earlier tendency to combine species (see above). But, of course, every case must be judged on its own merits.

My final topic is: how do species arise? Closely related demes can coexist in the same lake. They are usually allogamous, sexual organisms and they are often separated reproductively, by prezygotic isolation mechanisms. Have they evolved sympatrically or have they become sympatric secondarily, after evolving parapatrically or allopatrically? How do demes coexist and why can we tell them apart? How does reproductive isolation arise and how is it maintained? [Interestingly, there is now evidence for particularly rapid change in fertilization proteins in several animal and plant groups, offering some insights as to how reproductive isolation can develop in organisms that lack visual courtship rituals, physical genitalia, or cytogenitalia, or animal vectors of gametes or gametophytes (Vacquier 1998)].

These questions form a compelling agenda for future research. They also raise issues that are relevant to much of this review, which I have delayed addressing but cannot ignore any longer. These are the determination of homology and relationship. We assume that the diversity of living organisms has been produced by genetic drift and by natural selection, operating on inherited characteristics, which are liable to change through genetic processes such as point mutation, recombination, transposition, and inversion. However, these processes are largely unobserved today and wholly unobservable in the past. Except in a few (usually artificial) cases, relationships and homology can only be inferred from the patterns of distribution of characters in living organisms and fragmentary dead ones (fossils), according to the Darwinian principle of descent with modification. By relationships, I mean genealogical or phylogenetic proximity; homology I take to be a fundamental identity between two structures (including parts of semantide molecules), which although they may be very different in form or function, are evolutionary transformations of a single structure or type of structure possessed by an ancestral organism. The least arbitrary and most explicit method for determining relationships is the cladistic approach. Initially, I failed to understand fully the basis of cladistic methodology and its power. Although I do not believe that the support given to the phenetic approach in Round *et al.* (1990) was wholly misplaced and I still believe that paraphyletic groups have a place in formalized classifications (cf. Cavalier-Smith 1998), I have come to accept that cladistics offers the best way to analyze and resolve relationships. My comments below on the difficulties of using cladistics in studies of speciation and species relationships should not, therefore, be taken as an attack on cladistic principles, but rather as a despairing commentary on the practical difficulties attending application of the principles in studies of species relationships in diatoms.

The cladistic approach has at its heart the principle that each classification (as expressed in a cladogram) and hypothesized phylogeny should constitute a parsimonious explanation or summary—indeed, the *most* parsimonious summary—of the pattern of variation in inherited characteristics, based on comparisons of homologous structures. Homology can be estimated to some extent by detailed knowledge of the structure in question and its development, but in the end, it depends on knowledge of phylogeny. Hence, to some extent the cladistic approach is one of reciprocal illumination, requiring repeated cycles of character analysis and scoring, application of an algorithm to discover parsimonious summaries of the data matrix (cladograms), and examination of the character transformations implied by the cladograms to see whether initial hypotheses of homology need to be revised. For example, one might initially assume that the compressed photosynthetic organs of vascular plants ('leaves'!) are all homologous, on the basis that they are lateral to the shoot, possess some kind of vascular trace, generally have abundant stomata, and fulfil a similar function. But if subsequent analysis of living and fossil plants were to produce cladograms suggesting that the major lineages of vascular plants have been derived independently from leafless ancestors resembling the Silurian *Cooksonia* or Devonian *Horneophyton,* the assumption of homology between different kinds of leaf would become highly questionable, except perhaps at a 'higher' level, as vascularized axes (Kenrick & Crane 1997). Then, 'leaves' would need to be replaced by two or more new sets of putative homologues and the cladistic analysis begun again. Turning to examples among heterokontophytes, there is a remarkable similarity between the spines produced by the marine planktonic diatom *Corethron* and those found in the freshwater chrysophyte (synurophyte) *Mallomonas plumosa* Croome et Tyler. Both organisms produce long straight spines that bear sharp barbs along their length, and they also produce complex hooked spines. The similarity is obvious and, if anything, becomes more striking with closer scrutiny. It would not be unreasonable, therefore, to treat the straight spines as homologous in these two algae, likewise the hooked spines, as suggested by Crawford & Round (1989). However, 18S rDNA data for heterokontophytes do not suggest a close link between diatoms and synurophytes (e.g. Cavalier-Smith & Chao 1996; Saunders *et al.* 1997), nor do they indicate that *Corethron* is basal within the diatoms (Medlin *et al.* 1996). Cavalier-Smith and Chao's maximum likelihood 18S rDNA tree suggests that, for *M. plumosa* and *Corethron* spines to be homologous, we would have to assume that both types of spine were present in the ancestor of all pigmented heterokontophytes, but were lost independently in raphidophytes, eustigmatophytes, xanthophytes and brown algae, pelagophytes, and chrysophytes, and in all the basal diatom lineages except that leading to *Corethron.* Although a formal cladistic analysis has not been carried out, it seems extremely unlikely that this hypothesis of homology can be sustained without grossly blunting Ockham's razor. A recent *rbc*L analysis of heterokontophytes (Daugbjerg & Andersen 1997) places the diatoms closer to the synurophytes than the 18S rDNA data does, but even so homology of spines is unlikely.

The problem in applying cladistic approaches to studies of species and speciation in diatoms, as opposed to studies of relationships between higher taxa, is twofold. First, cladistic methodology is not suited to dealing with nonhierarchical variation and will detect false homoplasies where relationships are reticulate. This is why phylogenetic species concepts advocated by cladists emphasize that species are minimal taxa ["smallest diagnosable clusters" (Cracraft 1983)]—the smallest groupings that are hierarchically related to each other (Davis 1997). Cladistic techniques and algorithms can be applied below the species level, but the cladograms that result must be interpreted with great caution: lack of congruence between the patterns of variation in different characters is to be expected in sexual organisms and does not in itself require the iterative reevaluation of characters and homology that has to be undertaken in studies of higher taxa.

Secondly, cladistic methodology is poorly suited to dealing with quantitative, continuously varying characters such as length, width, outline shape, linear or areal densities of striae, pores, or spines, which are often almost the only characters available to taxonomists within species-rich genera such as *Cyclotella, Thalassiosira, Navicula* Bory, *Sellaphora* Mereschkowsky, *Fallacia* A.J. Stickle et D.G. Mann, *Amphora* Ehrenberg *ex* Kützing, *Nitzschia, Surirella,* and many others (e.g. compare Figs 52–57; SEM provides little extra information in this case). Kitching *et al.* (1998) state that continuous, quantitative characters "should only be excluded if the cladistic analysis cannot handle such data or if it can be shown empirically that those characters convey no information or phylogenetic signal relative to other characters in the data matrix", but they also note that quantitative characters are excluded from many cladistic analyses and that "in almost all reported analyses, it is the clear-cut qualitative characters that delimit groups unambiguously". The problems lie in coding and the treatment of character-state transitions.

Although it is sometimes possible, with difficulty, to make plausible attempts to code some quantitative characters for cladistic analysis within a small group of species, such as the *Stephanodiscus niagarae* complex (Theriot 1992a), more extensive or less cautious analysis of morphological variation among species of a genus is likely to fail. If quantitative characters are included, character coding becomes increasingly arbitrary as more taxa are included, except in the happy but unlikely chance that intermediate values are missing for some parameter, allowing gap coding: "to the extent that two taxa being compared do not overlap in a quantitative feature, discrete states can be postulated to exist" (Theriot & Serieyssol 1994; see also Theriot 1992b). Perhaps, for instance, there is a group of species that exhibits stria densities of anything between 5 and 15 striae in 10 μm and a second group where stria densities take values between 20 and 35 striae in 10 μm, but perhaps there are no species with between 16 and 19 striae in 10 μm. We could then treat stria density as a two-state character, with states A (5–15 striae in 10 μm) and B (20–35 striae in 10 μm). However, it does not seem reasonable that a diatom with 15 striae in 10 μm should be coded as identical to one with 5 striae in 10 μm, but different from one with 20 in 10 μm. Alternatively, a larger number of character states could be distinguished (segment coding), but again one is left wondering whether this would have any genetic or taxonomic meaning. Rae (1998) has argued for coding based on statistical tests of significance of differences between taxa for each metric character. If two taxa have statistically inseparable distributions for a particular metric character, they pass the 'first test of homology' (i.e. raw similarity), and are coded as having the same character state; homology is then tested further, by parsimony analysis of the whole data matrix, to see which character states fulfil the congruence test. How, though, does one sample statistically and characterize a species or higher taxon, as opposed to a local population, when local populations of a species themselves often differ significantly from each other with respect to these same metric characters (and will never be identical)? And if a series of statistically separate states is found and quantitative variation is coded as a multistate character, should the character states be treated as unordered or ordered? Treating them as ordered may make a great deal of difference to the resulting trees and is often regarded as unwise, at least in a first analysis; yet it seems unreasonable to treat the states of a metric character as simple alternatives, when they have an inherent arrangement (small to large, sparse to dense, and so on) and probably have a complex, additive genetic basis (e.g. Falconer 1981, chapter 6).

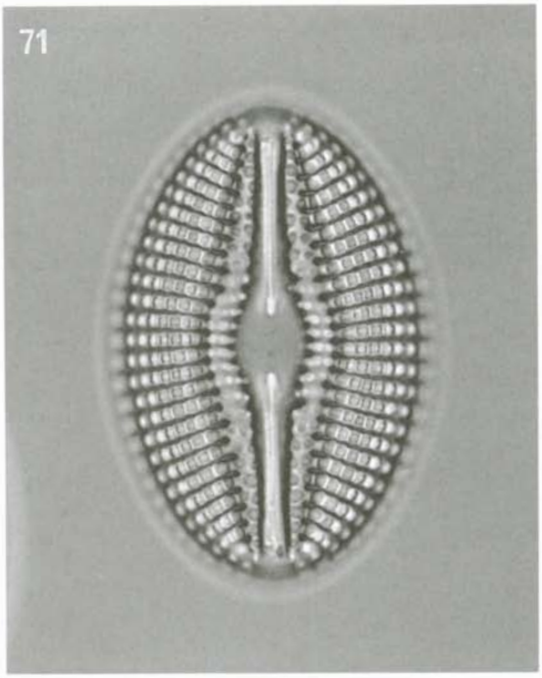
If quantitative characters were accompanied by many qualitative, presence/absence characters, and if the total number of characters greatly exceeded the number of taxa in the analysis, one might have some confidence that phylogenetic signal might emerge in cladistic analysis, above the noise produced by poorly informed coding, and that reiteration of the coding-parsimony analysis-recoding cycle might generate robust cladograms. But quantitative characters *predominate* within many diatom genera or species groups [e.g. among the taxonomically useful features of Thalassiosiraceae listed by Theriot & Serieyssol (1994)], making it difficult to be optimistic about the outcome of any cladistic analysis that either does or does not include them. Yet, because features such as size or stria density clearly reflect genotypic variation and will contain information about homology, to ignore them is unacceptable (Kitching *et al.* 1998; Rae 1998).

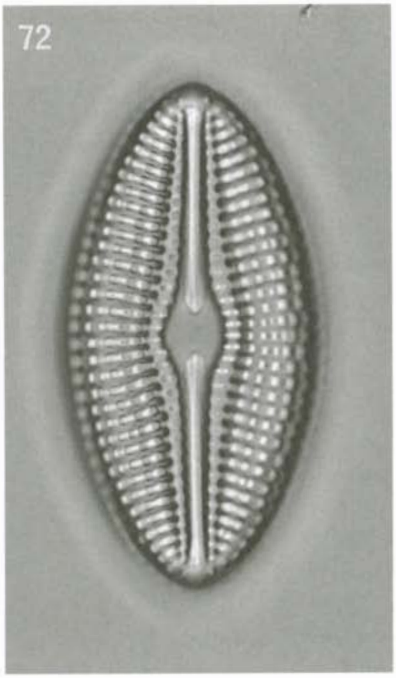
These difficulties make me doubt whether the time and effort needed to construct cladograms for groups of closely related species, using morphological data alone [e.g. those presented by Kociolek & Stoermer (1989a)], is spent optimally. In Kociolek and Stoermer's analysis, nodes are supported by only one or two character-state transitions, and 'quantitative' characters are omitted, except for auxospore size, which is broken into two characters and four character states, even though it is clear that the data available were limited for some taxa (for 10 of 17 species, Kociolek and Stoermer gave no range for auxospore size, suggesting that only a single auxospore was measured). And yet it is hard to see how this analysis could have been improved substantially, especially because several of the taxa included are only known as fossils. We can only make progress in understanding the historical aspects of speciation when we can show with confidence that clades are monophyletic, based on the presence of several distinctive derived characteristics (synapomorphies). In many diatom genera, morphology simply does not offer enough characters for this to be possible, even if the genus is of only modest size. Thus, I believe that in many cases, although morphological and other 'conventional' data are still valuable and should be included in phylogenetic analyses, *significant* progress will be achieved only by introducing molecular approaches, because these alone can yield the large, independent data sets whose congruence enables confident assessment of relationships, phylogeny, and homology among tens or hundreds of species. Even then, of course, it will be possible for us to be misled, as the land-snail example shows (section I; Clarke *et al.* 1996) and because of homoplasy.

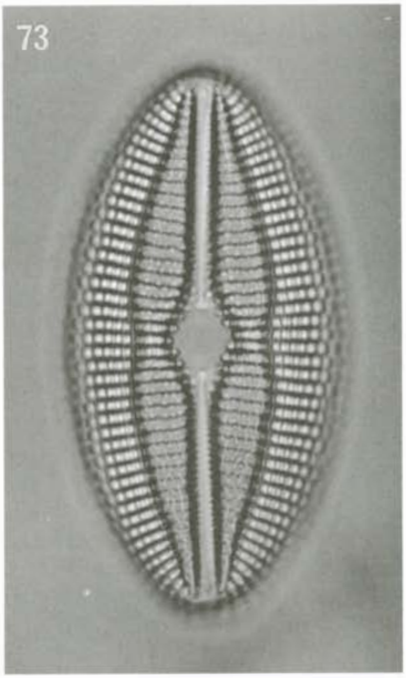
In fossil taxa, the prospects are bleak indeed for robust construction of classifications and phylogenies at the species level, unless there are sufficient modern relatives to provide corroboration via molecular and other nonsilica data. Williams's (1996) study of fossil *Tetracyclus* Ralfs was exemplary, but still yielded few unambiguous conclusions—and this is a genus in which the frustule is unusually complex and provides an unusually large number of discrete, qualitative characters. Others have attempted to reconstruct phylogeny without the rigor of cladistic analysis, such as in Yanagisawa & Akiba's (1990) treatment of *Denticulopsis* Simonsen, *Crucidenticula* Akiba et Yanagisawa, and *Neodenticula* Akiba et Yanagisawa. Although Yanagisawa and Akiba did not discuss how they assessed relationships and evolutionary history, they seem to have performed an informal phenetic analysis of morphological data, which they then interpreted using the stratigraphical and geographical distributions of taxa. It is possible that this is the best that can be done, because *Denticulopsis, Crucidenticula,* and *Neodenticula* offer few qualitative characters amenable to cladistic analysis. However, even though the fossil record of these marine planktonic diatoms is particularly good, one can have only modest confidence that the methods used by Yanagisawa and Akiba will yield approximate truths about phylogeny and speciation. Unfortunately molecular data cannot be obtained, because there are few extant representatives of *Denticulopsis, Crucidenticula,* and *Neodenticula,* which reached their greatest diversity in the Middle Miocene. Similar comments apply to Yanagisawa's (1996) study of the extinct genera *Rossiella* Desikachary et Maheshwari, *Bogorovia* Jousé, and *Koizumia* Yanagisawa.

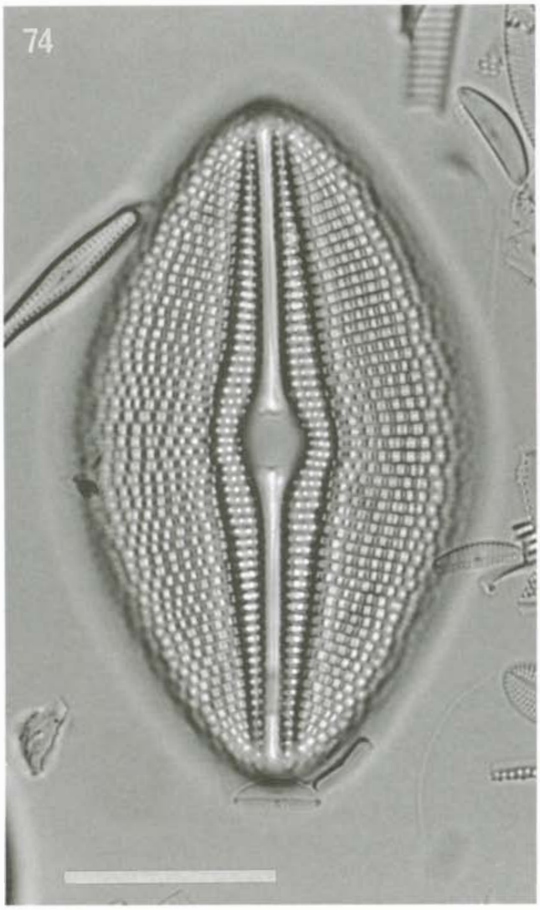
This is not to say that fossils cannot provide useful data about the evolution and speciation of diatoms. The long and detailed fossil record, especially during the Tertiary, provides excellent opportunities for understanding the pattern and time-scale of morphological evolution. Perhaps more than in any other group of organisms, it should be possible to develop a full 'evolutionary synthesis' for some diatoms, using morphological, cytological, reproductive, and molecular data for extant organisms, and crossing experiments, as well as studies of morphological variation among fossil diatoms, the stratigraphic record, and biogeography. Where morphology offers suitable characters, the recently developed 'stratocladistic' approach can be used to reconcile phylogenies estimated from character data with the fossil record (Julius & Stoermer 1996; Fox *et al.* 1999).

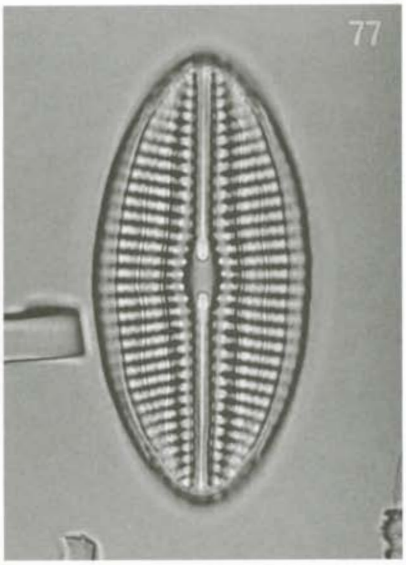
The potential of historical approaches has been appreciated for some time. Small (1945a, 1945b, 1946, 1948a, 1948b, 1948c, 1949a, 1949b, 1950a, 1950b, 1951, 1952a, 1952b, 1952c, 1952d) developed an elaborate theory of quantitative evolution, based on a huge volume of data on the geological occurrence of diatom taxa (in the earlier papers he reports a survey of the stratigraphic ranges of all 7288 species listed by Mills 1933–35!), supported by data on various other groups of plants and animals. Small came to the conclusion that species of diatoms fall into two groups: 'permanent' species, with life spans of c. 100 million years, and 'evanescent' species, lasting less than 1 million years. He suggested that the life span of each species reflected inherent genetic factors, not the effects of chance or natural selection, making a species "ba-

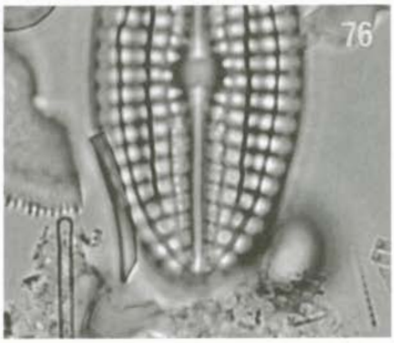


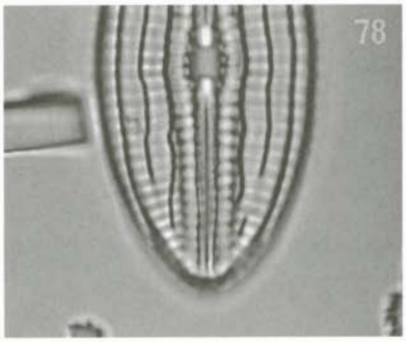












Figs 71–78. Rare or endemic species of *Diploneis* from Lake Baikal, Siberia. All from 33 m depth, Ol'khon Gate, Mid Basin, except Fig. 74. Light microscopy, bright-field optics. Scale bar (in Fig. 74) = 20 μm.

Fig. 71. *Diploneis late-elliptica* Skabichevskij. E 2810.1/2.

Fig. 72. *Diploneis* sp. E 2810.1/2.

Fig. 73. *Diploneis* cf. *baicalensis* Skvortzow et Meyer. E 2810.1/2.

Fig. 74. *Diploneis* sp. Cape Valukan, North Basin. E 2861/1.

Figs 75, 76. *Diphoneis jasnitskii*: two foci. Note the longitudinal ridges present toward the outside (dark lines, Fig. 76), contrasting with the otherwise fairly similar *D. mauleri*. E 2810.2/3.

sically and innately stable for a certain stable-period, after which the specific pattern ceases to be capable of exact reproduction'' (Small 1952a). Evolution appeared to proceed 'monopodially'. Long-lived species gave rise to a series of more ephemeral species at fairly regular intervals, but the ephemeral species themselves did not speciate; even in the long-lived species speciation was rare, occurring every 7 million years on average. Speciation was suggested to take place through rapid, radical change in one organism, via a 'specific mutation' (cf. Goldschmidt 1940), which then gave rise to a new 'pure line' through vegetative cell division; hence varieties would rarely be 'incipient species'. Small's papers contain a mixture of bizarre and intriguing ideas and deserve more attention than they have been given in the last 50 years. For example, the claim that allogamous pennate diatoms have shown a higher speciation rate than the centric diatoms (Small 1950a) has not obviously been contradicted by new data and is worth discussion and explanation. However, Small's analysis was certainly flawed, through its dependence on a poorly sampled and patchily dated fossil record, treated inconsistently by different taxonomists with divergent views on species circumscription. Furthermore, his ideas on abrupt ('punctuated') speciation, which should not be dismissed *a priori,* are nevertheless contradicted by two recent studies. Koizumi & Yanagisawa (1990) documented gradual development of asymmetry in *Fragilariopsis doliolus* (Wallich) Medlin et Sims [previously *Pseudoeunotia doliolus*; see Medlin & Sims (1993)] during the last 2 m yr, and Theriot (1992a) has demonstrated the gradual divergence of *Stephanodiscus yellowstonensis* from a *S. niagarae*-like ancestor. The mechanism that Small proposed for abrupt speciation—mutation in a single individual, which then perpetuates itself indefinitely, establishing a new species—is unlikely in outbreeding sexual species (most diatoms probably fall into this group) and untenable for obligately dioecious species, such as *Rhabdonema adriaticum* Kützing (von Stosch 1958), *Licmophora ehrenbergii, L. abbreviata, Striatella unipunctata* (Lyngbye) C.A. Agardh, *Haslea subagnita* (Proshkina-Lavrenko) Makarova et Karaeva, and *Nitzschia longissima* (de Brébisson) Ralfs (Roshchin 1994), and some *Sellaphora pupula* demes (e.g. *capitate,* Fig. 53; Mann *et al.* 1999); here a new species, arising through a macromutation in a single individual, would initially contain only one sex. It could be argued, of course, that this is precisely why 'permanent' species speciate and 'evanescent' species do not. However, further speculation is pointless until Small's analysis has been repeated with better data, and it is unlikely that anyone will consider this a priority in the foreseeable future.

In some cases, we probably know enough about the variation pattern and about the geographical distributions of taxa to be able to say something about the origins and spread of species. The diatom flora of Lake Baikal has been documented in some detail by Skvortzow & Meyer (1928), Mejer (1930), Skvortzow (1937), Skabichevskij (e.g. 1984), and others, and many of the taxa found are described and illustrated in standard Russian diatom floras (Proshkina-Lavrenko *et al.* 1950, 1951). As a result, many of the claims for high endemism within the Baikal flora are probably justified, at least for the larger species, such as the remarkable series of endemic *Diploneis* species (Figs 71–78; Skabichevskij 1936, 1952; Skvortzow 1937). If these distinctive diatoms occurred elsewhere (apart perhaps from other lakes in the Baikal region), they would almost certainly have been noticed and recorded. In most cases, however, we have no idea where or how the Baikal endemics arose. They may have evolved in Baikal, either from other endemic species or from invading, more widespread species, in the same way that *Stephanodiscus yellowstonensis* seems to have evolved from a *S. niagarae*-like ancestor in Yellowstone Lake, Wyoming (Theriot 1992a). In some cases, possession of unusual features (putative synapomorphies) suggests links between endemic Baikal taxa and more widely distributed species, such as the longitudinal canal structure in *Diploneis jasnitskii* Skabichevskij (Figs 75, 76), which links it to the more widespread *D. mauleri* (Brun) Cleve (Krammer & Lange-Bertalot 1986, fig. 109: 12–14). Alternatively, endemic species may be paleoendemics—relictual species that enjoyed wider distribution during the Tertiary period, as Skvortzow (1937) suggested for several taxa. So far, however, there is no clear evidence for this and Skvortzow's examples need to be reassessed.

We have recently been studying the *Navicula lacus-baikali* complex (Figs 79–87), which has not been reported from anywhere except Lake Baikal. Two characteristics seem to be present in all *N. lacus-baikali* and absent from almost all other freshwater *Navicula* (*sensu stricto*) species, suggesting that the *N. lacus-baikali* complex is monophyletic. One is the interruption of the striae by longitudinal hyaline areas (Figs 81–87) and the other is a slight but distinct heteropolarity of the raphe: the terminal raphe fissures curve differently at the two poles (Figs 79, 80). The second feature is shared with *N. reinhardtii* Grunow *in* Van Heurck (Cox, in press), which also resembles *N. lacus-baikali* in its relatively coarse striae and size but lacks its hyaline areas. *Navicula reinhardtii* seems to represent the sister group for the *lacus-baikali* complex, rather than the superficially similar marine species related to *Navicula finmarchica* (Cleve et Grunow) Cleve, which Witkowski *et al.* (1997) suggested should be separated into a new genus, *Fogedia* Witkowski *et al.* The hyaline lateral areas of *N. lacus-baikali* are distinctive and the valves are robust and large. It is therefore highly unlikely that *N. lacus-baikali* has been overlooked elsewhere and it seems to be a true endemic. But *N. lacus-baikali* is not uniform morphologically and individual samples of epipelon often contain two or three distinct demes (e.g. Figs, 81, 82 or 84, 85), separated by shape, size, and striation density [none of the demes correspond exactly to the varieties described by Skvortzow (1937), which seem to be heterogeneous]. Coexistence in sympatry of demes with different valve shapes (making phenotypic plasticity an un-

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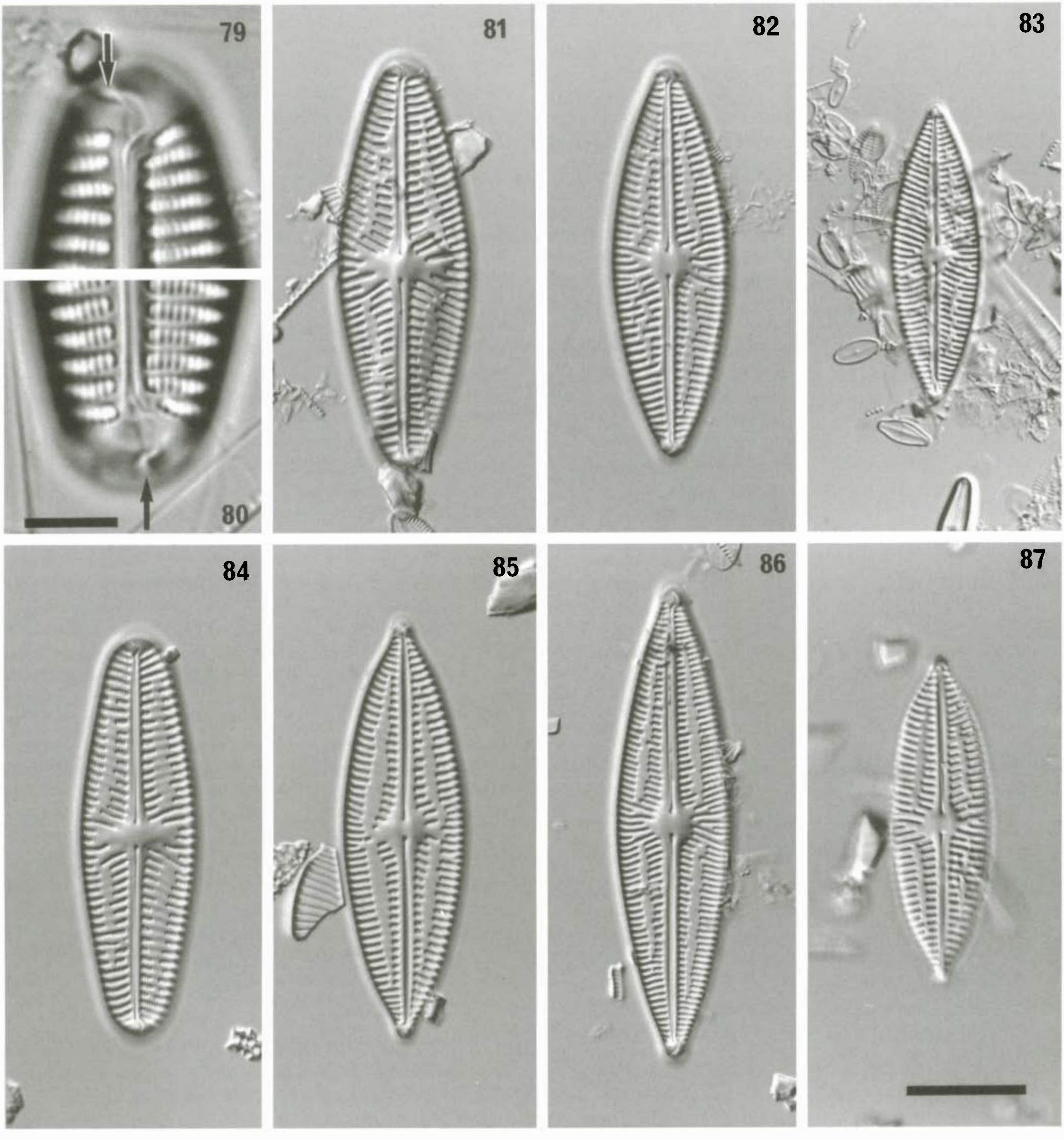
Figs 77, 78. *Diploneis meyeri* Skabichevskij, two foci. Note the prominent longitudinal ridges present externally (dark lines, Fig. 78; compare Fig. 76). Conspecificity with *D. jasnitskii* is possible (as an extreme example of polymorphism), given the great similarity in valve outline (shape and size) and the presence in both diatoms of external longitudinal ridging, but it is made unlikely by the combination of differences in stria density, stria, and longitudinal canal structure. E 2810.1/3.



Figs 79–87. The *Navicula lacus-baikali* complex, from Lake Baikal, Siberia. Light microscopy, differential interference contrast and bright-field optics (Figs 79, 80). Scale bars = 5 μm (Figs 79, 80) or 20 μm (Figs 81–87).

Figs 79, 80. Both ends of the same valve, showing heteropolarity with respect to the raphe system; at the top (Fig. 79) the terminal raphe fissure is hooked more strongly toward the secondary side of the valve (left) than at the opposite pole (arrows).

Figs 81, 82. Sympatric demes from 20 m depth, Peschanaya Bay, South Basin, Lake Baikal, slide E 2799/1. The deme shown in Fig. 81 is characterized by larger size, coarser striation, and obtuse, as opposed to acute, valve poles.

Fig. 83. Small-celled deme with dense striation from 20 m depth, Cape Orlovyj, North Basin, slide E 2975.

Figs 84–86. Demes from the Ol'khon Gate, Mid Basin.

Figs 84, 85. Demes coexisting at 33 m depth, one with linear–lanceolate valves with obtuse poles and coarse striation (Fig. 84), the other with lanceolate valves with slight shoulders subapically, apiculate poles, and slightly denser striation. Slide E 2810.1/3.

Fig. 86. Deme from 14 m depth, with lanceolate valves and dense striation. Slide 2811/1.

Fig. 87. Compare to Fig. 85. Valve from 18 m depth, Bajkal'skoe, North Basin, slide E 2941.

likely explanation) suggests that they may be reproductively isolated species, like the Blackford Pond demes of *Sellaphora pupula.* The demes present at one site do not always correspond to those present elsewhere in Lake Baikal (compare Figs 81, 82 with Fig. 83 and with Figs 84, 85), although sometimes they do (it is quite possible that Figs 85 and 87 represent different stages in size reduction within the same deme) and so it is quite likely that *N. lacus-baikali* will need to be split into half a dozen or more species. Although other explanations are possible, the simplest interpretation for the variation pattern and distribution of *N. lacus-baikali* is that it has evolved and diversified in Lake Baikal or the Baikal rift. Cheremisinova (1973) records *N. lacus-baikali* from Pliocene deposits of the Tunka depression, a filled-in lake basin just south of modern Baikal and so speciation need not have been strictly sympatric (unfortunately, the photograph provided by Cheremisinova does not allow detailed comparison with extant demes).

The Baikal flora demonstrates the important point, largely neglected until recently (Mann & Droop 1996), that although many freshwater species may well be cosmopolitan (as claimed in some floras, e.g. Hustedt 1927–66; Krammer & Lange-Bertalot 1986, 1988, and others), many are not. Apart from planktonic species (which comprise the minority of marine diatom species), the marine diatom flora has not been so well documented, but here too endemic species and ecotypes exist, e.g. in the Caspian and Black seas (Karayeva & Makarova 1973; Proshkina-Lavrenko and Makarova, cited *in* Guillard & Kilham 1977) and also in the Baltic (see below).

In freshwater, endemism is not well developed in the glaciated areas of northern Europe and North America, or at least is rarely obvious, but ancient lakes and ancient islands (continental fragments, such as New Caledonia, New Zealand, Tasmania, or Madagascar) seem to have their own endemic taxa, in addition to an admixture of more widespread species (e.g. Kociolek & Stoermer 1993; Lange-Bertalot & Moser 1994; Moser *et al.* 1995, 1998; Vyverman 1996; Kociolek *et al.* 1997; Vyverman *et al* 1997, 1998). Kociolek *et al.* (1998) believed that there are several species endemic to western North America, including *Navicula walkeri* Sovereign, which is apparently restricted to California and Oregon, where it has existed since the Pliocene or earlier. In some cases, there appear to be 'species flocks'—peculiar, highly diverse assemblages of related species that are restricted to a particular area—although these are less well developed than the flocks of fish and invertebrates found in some ancient lakes (see Martens *et al.* 1994) or the sea (Johns & Avise 1998). Hustedt (1935, 1937–39, 1942, *in* Huber-Pestalozzi 1936, 1942; Vyverman 1996) described 38 taxa of *Surirella* that seem to be endemic to the Tertiary lakes of Indonesia, and *Surirella* and related diatoms have also diversified in the East African rift lakes (Hustedt *in* Huber-Pestalozzi 1942; Ross 1983; Cocquyt 1998), Lake Ohrid (Jurilj 1948, 1954), and Lake Baikal (Skvortzow 1937; Hustedt *in* Huber-Pestalozzi 1942). Another group showing evolutionary radiation in Indonesia is the cluster of 19 '*Denticula*' taxa related to *Denticula vanheurckii* Brun, described by Hustedt (1935, 1937–39) (these species are more closely related to the Epithemiaceae than to *Denticula sensu stricto,* which is now placed in the Bacillariaceae; Round *et al.* 1990). Other flocks include the *Sellaphora* species of the East African rift lakes (Müller 1910), and *Brachysira* Kützing in New Caledonia (Lange-Bertalot & Moser 1994).

These radiations are remarkable and pose many interesting questions. Why, for instance, do several groups of ancient lakes have large clusters of endemic *Surirella* species, whereas the myriad newer lakes of the Northern Hemisphere can muster only about as many species between them (Huber-Pestalozzi 1942; Krammer & Lange-Bertalot 1988)? And why has the *Sellaphora pupula* group apparently diversified much more than the *S. bacillum* group in the East African Great Lakes, whereas the reverse seems to have occurred in Lake Baikal (Mann, unpublished observations)? Why did *Tetracyclus* diversify around the Pacific rim more than elsewhere (Williams 1996; Williams *et al.* 1998). However, in most cases, discussion is limited by taxonomic bias and inconsistency, and by a lack of reliable information about geographical distributions. There has undoubtedly been a tendency among many diatomists to 'coax' their taxonomy into a European or North American mold, assuming that most species are cosmopolitan. Hagelstein (1939) noted that in Puerto Rico "endless differences in size, outline, and striation, from published descriptions and figures, have caused difficulty at times in making determinations, and the author has frequently been tempted to propose new species". Unfortunately, he not only resisted this temptation but also chose not to document the "endless differences". Without repeating his study there is no way of knowing if he was right or whether Puerto Rico (or the Caribbean generally) is in fact rich in endemic species.

Hence, there is an urgent need for careful biogeographical studies (not least because paleoecologists need to know whether information about the ecological preferences of taxa is transferable between regions or continents), based on critical revisions of genera and backed by voucher specimens and iconographs (see also Round 1998). It will also be necessary to check that biogeographical patterns have not been materially altered by humans in recent centuries. Kociolek & Stoermer (1988) have documented loss of *Gomphoneis eriense* (Grunow) Skvortzow et Meyer var. *eriense* from the North American Great Lakes during the last 120 y and its restriction to western North America, and *G. herculeana* var. *herculeana* has disappeared from some of the Great Lakes during the same period; more recently *Stephanodiscus niagarae* has been lost from Lake Ontario (Julius *et al.* 1998). Several cases of introductions have been documented among marine phytoplankton, such as *Coscinodiscus wailesii* and *Odontella sinensis* (Greville) Grunow in British coastal waters (see Guillard & Kilham 1977; Boalch 1987), and Harper (1994) has suggested that the ubiquitous freshwater planktonic diatom *Asterionella formosa* may have been introduced to Australasia by Europeans.

The kinds of difficulties that limit our ability to distinguish biogeographical patterns also apply to discussion of the stratigraphic range of 'species'. Most records cannot be trusted, unless backed by good photographs. However, among marine plankton, ranges of <0.5 m yr [e.g. several *Denticulopsis* species, including *D. okunoi* Yanagisawa et Akiba, *D. miocenica* (Schrader) Simonsen, *D. ovata* (Schrader) Yanagisawa et Akiba, *Thalassiosira brunii* Akiba et Yanagisawa] to >6 m yr [e.g. *Denticulopsis hyalina* (Schrader) Simonsen, *Nitzschia rolandii* Schrader] are well documented (Akiba 1985; Yanagisawa & Akiba 1990, Tanimura 1996). Yanagisawa (1996) gives ranges of 13–14 m yr for *Rossiella paleacea* (Grunow) Desikachary et Maheshwari and *Bogorovia punctulata* Yanagisawa, and long ranges have also been reported for *Delphineis surirella* (Ehrenberg) Andrews (Andrews 1981) and *Perissonoë trigona* (Grunow) Andrews et Stoelzel (Andrews & Stoelzel 1984). Sims's recent (1998) revision of tripolar diatoms formerly referred to *Triceratium* Ehrenberg or *Sheshukovia* has revealed three species, now referred to *Medlinia* Sims, that persisted from the Upper Cretaceous (Campanian) until the Eocene, some 20 m yr later. In other cases, the reported range must be treated with caution. For example, *Sellaphora pupula* and *S. americana* (Ehrenberg) D.G. Mann are recorded alive today and as far back as the Miocene (Glezer *et al.* 1974), but the heterogeneity of modern populations and the likelihood that they are not conspecific (see above) suggests that the fossil records may refer to several different lineages, rather than to single species. Some extant taxa have been recorded from the Eocene or even from the Cretaceous (Schrader 1969; Glezer *et al.* 1974), such as *Stephanopyxis turris* (Greville et Arnott *in* Gregory) Ralfs *in* Pritchard, but these need reinvestigation, to establish that the fossil and living specimens are indeed similar and that there is no evidence of lineage splitting. *Paralia* (previously *Melosira*) *sulcata* (Ehrenberg) Cleve used to be cited as a species that had existed since the late Cretaceous (e.g. Glezer *et al.* 1974), whereas recent accounts treat it as several species with shorter stratigraphical ranges, although one of these, *P. crenulata* (Grunow) Glezer, still has a range from the late Cretaceous to the early Oligocene (Glezer *et al.* 1992).

Although most known endemics are associated with ancient habitats, divergence and speciation can apparently take place rapidly, over periods of 10^3–10^4 yr or less. According to Theriot (1992a) the evolution of *Stephanodiscus yellowstonensis* from *S. niagarae*-like antecedents occurred between 12,000 and 3800 BP, which suggests that it would not be unreasonable to look for endemic taxa in other lakes in temperate regions. Recently, Snoeijs & Potapova (1998) documented the presence of distinctive populations of *Diatoma* Bory in the Baltic Sea, including ecotypes of *D. vulgaris* Bory and *D. moniliformis* Kützing and what seems to be an endemic species, *D. bottnica* Snoeijs. The current salinity regime of the Baltic stabilized only about 3000 yr ago, suggesting that this might be the age of the Baltic *Diatoma* populations, but even if they arose earlier and tracked the complex salinity changes in the Baltic by migrating backwards and forwards, they are unlikely to be older than Theriot's *Stephanodiscus* species, because the whole area was covered by the Fennoscandian ice sheet. Rapid speciation over similar timescales has been reported in other groups, such as the flock of cichlid fish in Lake Victoria, which contained more than 200 species until the extinctions of the last 30 yr and which seems to have evolved in the last 12,000 yr (Johnson *et al.* 1996; Kaufman *et al.* 1997). Sometimes little genetic divergence is found between populations of metazoa that show clear, genetically based differences in ecology and morphology, suggesting rapid adaptive divergence, and recent experimental studies of fish, lizards, and insects also indicate that adaptive changes can happen extremely quickly (Orr & Smith 1998). Genetic data for *Asterionella formosa* and *Fragilaria capucina* in man-made lakes hint that detectable genetic differences can arise between large populations of planktonic diatom species in c. 10^2 yr (Soudek & Robinson 1983; Lewis *et al.* 1997; see above). Thus, if the high frequency of diatom endemism in ancient habitats is real and not an artifact of sampling or taxonomists' fancy, it is unlikely to be because long periods of isolation are a necessary precondition for speciation. Rather, it suggests either that ancient habitats tend to be special in some respect other than longevity (lakes Baikal and Tanganyika are exceptionally deep, New Caledonia has large areas of ultrabasic rock, and so on), or that long-term stability of habitats allows finer niche partitioning among species. As in other groups of organisms, however, time and isolation will almost certainly promote endemism (cf. Coesel 1996; Coleman 1996; Tyler 1996; Vyverman 1996).

In other groups of plants, polyploidy is considered to be an important evolutionary process (Stebbins 1950, 1971). Polyploids are usually at least partially isolated by reproductive barriers from their diploid ancestors, however, allopolyploidy can restore normal meiotic function in hybrids that otherwise would be sterile through failure of the chromosomes to pair regularly. In several diatoms, the formation of autopolyploid auxospores has been observed directly (Geitler 1927b, 1932; Mann & Stickle 1991; Mann 1994b; Chepurnov & Roshchin 1995) (Mann and Chepurnov have also made unpublished observations of autopolyploid auxospores in *Caloneis silicula, Amphora libyca,* and *Achnanthes brevipes* vars *angustata* and *intermedia*), and Geitler has demonstrated variation in chromosome number within the *Cocconeis placentula* complex (see above; Geitler 1973b). Chromosome numbers have been reviewed for diatoms by Kociolek & Stoermer (1989b) and vary from $2n = 8$ to $2n = 128$–130. Some further counts, also indicating a wide range of chromosome numbers, have since been reported by Giri and others (Giri *et al.* 1990; Giri & Chowdary 1991; Giri 1992; and see Agrawal & Chaudhary 1996), but many of these are unconvincing, judging by the photographs provided. The evidence is thus sparse but nevertheless demonstrates conclusively that polyploidy and aneuploidy have occurred during diatom evolution. Just how important they have been will not become clear until new methods have been developed for studying diatom karyotypes rapidly and accurately. Two problems must be overcome. First, the brittle silica frustule makes it impossible to produce squash preparations in the normal way. Second, in many diatoms, the chromatin forms a dense ring around the central spindle at metaphase, in which individual chromosomes can be distinguished only with difficulty or not at all (e.g. see Mann & Stickle 1989; Round *et al.* 1990).

So far, there is little evidence in diatoms for truly cryptic (sibling) species, that is, species that are morphologically almost identical but reproductively isolated. In the best-investigated species complex, *Sellaphora pupula,* we have not yet found any cases in which demes are morphologically identical but unable to mate, although some of the demes (e.g. *capitate* and *rectangular*) are certainly very similar (Figs 52, 53). Medlin & Simon (1998) consider that there may be cryptic species in the *Skeletonema costatum* complex, but no mating experiments have yet been made to corroborate the molecular sequence data. In contrast, cryptic species (syngens) are well known in several chlorophyte microalgae, including *Pandorina morum* (Coleman 1959, 1977; Coleman *et al.* 1994), *Eudorina elegans* Ehrenberg (Goldstein 1964), *Volvulina steinii* Playfair (Carefoot 1966), and *Chlamydomonas moewusii* Gerloff (Wiese & Wiese 1977), and also in the heterotrophic dinoflagellate *Crypthecodinium* Biecheler and several ciliates, for example, the *Paramecium aurelia* O.F. Müller complex and *Tetrahymena pyriformis* (Ehrenberg) Lwoff (Sonneborn 1975; Beam & Himes 1987; Preparata *et al.* 1992; Beam *et al.* 1993). In the desmid *Closterium ehrenbergii,* reproductive isolation between syngens is accompanied by a degree of morphological differentiation (Ichimura 1981, 1996; Ichimura & Kasai 1990), but this seems to be less pronounced than in *Sellaphora pupula.* On the other hand, in another desmid, *Micrasterias thomasiana* Archer, although there are restrictions on mating between clones drawn from different populations, almost all clones can be considered to be part of the same syngen, in spite of morphological differences among them (Blackburn & Tyler 1987). The diatom data are far too incomplete for us to be able to say that cryptic species do *not* exist in diatoms, but it seems clear from the evidence available that speciation in diatoms *has* often been associated with morphological divergence and it is interesting to ask why.

At a gross level, it is sometimes possible to correlate morphology and habitat, so that one can suggest that a particular feature has some adaptive significance. For example, attached diatoms are often wedge-shaped (as in *Licmophora, Gomphonema, Gomphonemopsis* Medlin *in* Medlin et Round, and so on) and Medlin (1991) has argued that this may minimize drag. However, the subtler aspects of morphological variation have no explanation and it strains belief that every twist, curve, or prong has direct adaptive significance. Diatom species often have different nutrient requirements and different responses to pH, salinity, and temperature—the modern, highly successful industry of paleoecological reconstruction depends on it (Stoermer & Smol 1999)—but at first sight it is not at all obvious why such differentiation should be associated with morphological change. Furthermore, as noted elsewhere (Mann 1997), because diatoms have no sight and because mating does not involve geometrical fit between 'cytogenitalia', morphological differences will not in themselves bring about reproductive isolation, except perhaps in some raphid diatoms (e.g. *Neidium*), where plasmogamy takes place through narrow copulation apertures or tubes formed at characteristic positions along the girdle (Mann 1984c), so that large differences in size between copulating cells could make it impossible for sexual union to be consummated (cf. the difficulties of a Chihuahua and Irish Wolfhound). On the whole, however, speciation in diatoms, insofar as it involves the development of prezygotic reproductive isolation, must be a biochemical affair. I suggest, therefore, that many of the morphological differences between closely related species are accidental: they are by-products of physiological and ecological differentiation, brought about because of the unique life cycle and morphogenesis of diatoms.

To illustrate how this might occur, consider two populations, initially identical, but subject to different selection pressures: population A experiences a consistently higher silicate : phosphate resource supply ratio than population B. In time, assuming genetic variance with respect to silicon and phosphorus utilization and metabolism, and assuming that energy and materials used in silicon metabolism do not at the same time enhance phosphate metabolism (and *vice versa*), so that there has to be some kind of 'trade-off' during adaptation, we might expect the populations to diverge, such that, on average, B cells become better able than A cells to survive at low silicate concentrations but less able to survive at low phosphate concentrations. Conversely, A cells should on average become better able to survive at low phosphate concentrations but less able to survive at low silicate concentrations (see Tilman 1982) [Kilham (1994) discusses the possibility of 'superspecies', that would compete well for both limiting nutrients]. There are two ways (not mutually exclusive) in which B cells could become better able to cope with low silicate. One is to use less and the other is to become more effective at obtaining silicate when it is present at low concentrations. The latter need have no morphological effect (although it might, if uptake were promoted by changes in the surface area : volume ratio); the former almost certainly would. In some cases, it is known that silicate deficiency causes a morphological response in the phenotype, for example, through failure to add later-formed parts of the valve in *Thalassiosira* and *Cyclotella* (Belcher *et al.* 1966; Hasle *et al.* 1971; Booth & Harrison 1979; Schmid & Schulz 1979). In addition to this truncated development (paedomorphosis), use of less silica in the cell wall will often have other effects, especially in pennate or bipolar centric diatoms. Several pieces of evidence indicate that shape changes during the life cycles of pennate diatoms result from a relatively simple, physical interplay between the turgor of the protoplast and the flexibility of the cell wall (Mann 1994a). Thus, anything that affects the flexibility of the cell wall, such as its degree of silicification, is likely to influence the ontogenetic trajectory of shape ('Formwechsel') during the life cycle and also the rate at which size reduction occurs, shortening or lengthening the life cycle. Changes in osmotic relationships, for example, as a result of growth in different salinities, will operate similarly. Jahn's (1986) studies of *Gomphonema augur* Ehrenberg and Taylor's (1996) preliminary work on *Sellaphora pupula* both showed a change to narrower valves in clonal cultures, as a response to elevated salinity. The simplest, although untested, explanation is that cell turgor was reduced at higher salinities, producing less deformation of the girdle at cell division and hence narrower valves (Mann 1994a). Thus, in diatoms, selection for physiological traits will often have the by-product of morphological change, because of the tight coupling between morphology, wall flexibility, and cell turgor.

Selection for changes in wall flexibility, cell turgor, or both could arise for other reasons. For example, chytrid and oomycete parasites enter diatom cells primarily by penetrating between different frustule elements (e.g. Beakes *et al.* 1988); they cannot dissolve the silica itself. The ability of a parasite to infect a cell must therefore be related to cell turgor and the strength, structure, and flexibility of the cell wall, especially in the girdle region where infection usually occurs. In turn, changes in girdle thickness and flexibility will alter the trajectory of shape change as cells decline in size from auxospore to gametangium. Thus, the evolutionary 'race' between parasite and host, like nutrient uptake and use, is likely to have indirect, essentially nonadaptive consequences for cell shape. In other circumstances, there may be selection for larger or smaller size, perhaps through selective predation (see Reynolds 1984, 1997; Sommer 1987), or because of the physiological concomitants of size (e.g. by altered surface area : volume ratios): [Potapova & Snoeijs (1997) discuss some interesting aspects of this with respect to the life cycle of *Diatoma moniliformis*]. These too are likely to have effects on shape, except in circular diatoms, again because of the intimate link between size and shape brought about by the peculiarities of diatom cell division.

In turn, shape changes are likely to be accompanied by adjustments in pattern. As Schmid has emphasized (e.g. Steucek & Schmid 1989; Schmid 1994), the diatom frustule must be viewed as a mechanically satisfactory solution to the conflicting problems of achieving sufficient strength to withstand the outward pressure of the turgid protoplast, shear stress brought about by water movements, and internal tension; and allowing the exchange of material (water, ions, organic secretions, and so on) between cell and environment. Producing any kind of wall is energetically expensive (e.g. see Raven 1983) and diverts resources away from the production of energy-capturing cell components, so it is likely that selection will favor wall structures that are economical to produce. And this in turn means that shape, size, and pattern will change together, tending towards the minimal use of materials consistent with the necessary strength and porosity.

If these ideas have any validity, we might predict that cryptic species will be rare among pennate and bipolar centric diatoms, but could be common in centric diatoms with circular valves, because here physiological and ecological specialization is less likely to lead automatically to morphological change.

V. CONCLUSIONS

History suggests that in many cases, diatomists might just as well have been classifying scraps of wallpapers as diatoms. Diatom taxonomy has developed largely without a conceptual basis, using a restricted range of characters drawn from just one part of the phenotype (the valve). Differences in valve morphology have been used to separate taxa without any significant attempt to understand how these differences are produced during ontogeny, without much understanding of how the differences have developed during evolution (character-state transformation), and without insight into the adaptive significance of differences. To some extent, none of this matters. If diatoms are predominantly sexual, meiotic organisms, there will be a level at which reticulate variation, produced through dispersal of vegetative cells and gametes, copulation, meiotic segregation, and recombination, is replaced by hierarchical variation, brought about because genes cannot move between lineages, so that newly evolved features are restricted to the lineage within which they arise. And one can be aware of a boundary between reticulate and hierarchical variation without understanding why the boundary exists, and this is why species (the minimal groupings among which relationships are hierarchical) were recognized long before the discovery of meiosis and the advent of modern genetics, before the significance of sexual reproduction began to become clear, and before the development of a theory of evolution by natural selection. Thus, because diatoms are sexual, meiotic organisms, we should, in theory, be able to develop and agree upon a species-level taxonomy on the basis of data on variation in the phenotype, without recourse to population genetics and mating experiments, just as we could classify wallpaper (the analogue to reticulate variation among individuals of a species might be color variation along and between rolls, with slight differences in dye mixing and quantity).

Theoretical expectations about the development of a robust and uncontroversial species taxonomy are rarely met, even in sexual organisms (except in mammals and birds), partly because the boundary between hierarchical and reticulate variation is not sharp, but mainly because our knowledge of the variation pattern is poor, so that detecting any kind of boundary is next to impossible. In diatoms, this becomes obvious after glancing through taxonomic descriptions of species, which are often based on only a few individuals and rarely cover all stages of the life cycle; it is also evident from the lack of agreement between different taxonomists, or even between papers written by the same taxonomists, considering similar evidence at different times (section II d). It will always be difficult to be confident about species boundaries, if all that is available is a smattering of morphological data, haphazardly gathered from eclectic samples of natural populations that can change more in 6 mo than angiosperm communities do in a millenium. For some angiosperms, gymnosperms, and metazoa, every individual of a particular population, sometimes even every individual of a species, can be observed, counted, and characterized. This can never be done for diatoms and diatom taxonomy will always lag well behind the taxonomy of long-lived, macroscopic organisms, but our sampling certainly could be better.

The ecological importance, ubiquity, and utility of diatoms make it essential to improve upon the species taxonomy developed over the last 200 yr, including the products of the last 15 yr of vigorous activity (section II d). Defining and circumscribing species is not an esoteric activity, with no relevance to science and life. The importance of clarifying species boundaries is shown most clearly in groups of organisms with high economic or medical significance (Brasier 1997; Lane 1997), which can even include diatoms (e.g. Bates *et al.* 1993, 1998; Scholin *et al.* 1994). But in fact, species definitions affect everyone who uses the names of organisms, from ecologists and paleoecologists to biochemists and molecular biologists. Cracraft (1997) pointed out that "endangered, distinct populations ranked as subspecies, or not given formal rank at all, will generally carry less political and conservation significance than those ranked at the level of species" and the same is true in other fields too: rightly or wrongly, species are treated as the lowest, and often the *only* taxonomic category worth bothering about.

I have argued here and elsewhere (Mann 1982, 1990) for pluralism in the use of valve, girdle, protoplast, reproductive, and other characters in diatom taxonomy, and it is depressing that, even now, 'diatom' is treated as synonymous with 'silica valve' by many diatomists. However, it is unrealistic to expect that valve morphology will be replaced as the *main* source of data in species taxonomy, for four reasons. Valve morphology provides continuity with past taxonomies; it is easily described; it can be assessed more quickly and cheaply than other aspects of the phenotype; and it is always available (contrast physiological data, which can be gathered only if the organism can be cultured). Although molecular genetic methods are becoming widespread, easy, and inexpensive, and sample the genotype directly, it is doubtful whether they will ever replace morphology for the primary characterization and identification of diatom species and populations, except in the few taxa that have economic or medical significance (e.g. *Pseudo-nitzschia*).

How, then, can we use our old, blunt tools to build Utopia? The two-pronged approach to diatom systematics (and relevant aspects of morphogenesis, genetics, and so on) that has evolved over the past two centuries is basically sound, although it needs a reversal of thinking and some fine-tuning. Historically, we have combined broad, general surveys of variation with detailed research on a few convenient (e.g. *Phaeodactylum tricornutum*) or abundant (e.g. *Skeletonema costatum*) species; the broad surveys necessarily came first. In species taxonomy, this now needs to be reversed, at least in terms of priorities, even if the two approaches continue in parallel. The immediate priority is to gain a profound knowledge of the nature, origin, and maintenance of the variation pattern in several species complexes (model systems) selected from freshwater and marine habitats to represent the major lineages of diatoms, different growth forms, and different mating systems. This knowledge can then be used to guide the search for species limits elsewhere, using less intensive (and admittedly less sure) approaches. The data reviewed here suggest that taxonomists have seriously underestimated the numbers of diatom species, even among organisms already discovered, essentially because they did not know how intently they had to look before species boundaries would appear; population differences within species also seem to be much greater than was expected (Gallagher 1980, 1982, 1994; Soudek & Robinson 1983; Gallagher *et al.* 1984; Gallagher & Alberte 1985; Lewis *et al.* 1997). I gave an analogy in 1987: "Consider a grassy hillside. Seen from far away it appears smooth, the slope changing gradually from place to place. Approach closer and terraces and scarps appear, the visible manifestation perhaps of a forgotten agriculture, or of solifluction in colder periods long ago. Walk over the hillside and your ankles notice the miniature steps and pocks made by soil creep and rabbits . . .". Studies of model systems are not definitive, except in relation to the systems themselves, but they help us to start playing in the right ballpark as we catalogue diatom diversity on a global basis and they can give confidence that classifications will not be overturned as easily and quickly as I have documented for *Nitzschia* (section II d).

In Edinburgh, we have begun to develop model systems, using various freshwater epipelic diatoms, especially *Sellaphora* spp., while Theriot has concentrated on planktonic *Stephanodiscus.* However, we are very far from understanding any of these and there is the considerable danger that our results are unrepresentative. Work done by Roshchin and Chepurnov on the mating system in *Achnanthes longipes* and *A. brevipes* (e.g. Roshchin 1984, 1994; Roshchin & Chepurnov 1993; Chepurnov & Roshchin 1995; Chepurnov & Mann 1997, 1999) would form a strong basis for studies of variation and speciation in attached marine littoral diatoms, and Gallagher and Medlin's studies of *Skeletonema* are also foundational (section III d).

While the model systems are being worked out in detail, those who continue to catalogue diversity on a broader scale must plan and document their work more carefully, so that it is transparent and repeatable. Taxonomic research—indeed, most types of research on diatoms—should be backed by voucher specimens and photographic evidence of the taxa studied, and the voucher specimens should be deposited in accessible collections, in an institute with a proven record of responsible curation (which unfortunately excludes many universities). Several important diatom collections (e.g. of Adolf Schmidt and B.W. Skvortzow) have already disappeared and others are effectively inaccessible. Better sampling, analysis, and characterization of natural populations are also needed. The extra work (and publication costs!) this will involve can be minimized by taking full advantage of new technology, especially digital image capture, storage, and transmission, which make it possible to build huge virtual libraries of diatom images and morphometric data (Bayer & Droop, in preparation). Easy access to such databases should help avoid inconsistency and redundancy in species taxonomy, and also prevent 'taxonomic drift', as usage of a particular taxon name moves away from the original, typified concept (Mann 1998).

Final thoughts? There are a lot of diatom species (God must like them almost as much as beetles: *pace* Haldane); humans find it difficult to tell them apart, other diatoms don't; but perhaps a Compleat Diatomist can get to know their ways.

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