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VARIATION AND POLYMORPHISM IN DIATOMS: THE TRIPLE HELIX OF DEVELOPMENT, GENETICS AND ENVIRONMENT. A REVIEW OF THE LITERATURE

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ABSTRACT. – The dogma that diatom cell walls are faithfully reproduced without variation from generation to generation is questioned. We suggest that there are many sources of variation in diatom cell wall morphology, and this polymorphism can be size-dependent and size-free. We discuss three major sources of variation, namely, genetic, ontogenetic and environmental, and present a survey of the literature to support our argument. We also suggest that this variation may be adaptive or circumstantial. It is important for those interested in diatom taxonomy, systematics, and ecology to recognize intraspecific variation in diatom taxa, and the implications variation holds for these disciplines. We call for renewed and robust research programs focused on each of the three major sources of infraspecific variation in diatoms.

INTRODUCTION

Is the correspondence between variability within a taxon and the classification systems we have developed for diatoms as good as we think it is? Put another way, what degree of variation or polymorphisms do diatom taxa express, and does that breadth of expression relate to the classification systems we have constructed? This question, at very specific levels, has occupied many members of the diatom community, including taxonomists, ecologists, paleoecologists and stratigraphers, for quite some time.

Students have been told somewhere in their education about diatoms that variation is negligible. "… most diatoms divide to produce valves that are virtually identical to the parent valves…", Round *et al.* (1990, p. 84) represents a popular explanation of the continuity in diatom cell walls between generations. This has included the idea that reproduction of the cell walls from one generation to the next is done so faithfully, that diatoms may be used as test objects for light and electron microscopes (Hustedt 1949, 1956). The general feeling is that some records of polymorphisms do exist, however, in his review of species concepts in diatoms, Mann (1999) gave little space to discussing polymorphism. This phenomenon has usually been considered as limited in number, the range of the polymorphism is not so extreme as to modify the foundations of our systematic schemes, and the more disparate cases have been called into question (Mann 1999).

While Mann (1999) discounts the ranges of variability in the diatoms, especially those situations where variation may appear extreme, relative to accepted classification systems, variation is the main source of evolutionary novelty (Futuyma 2005) and it is best to understand it and develop observational and experimental approaches to understanding it, rather than deny or downplay its existence and role in diatom evolution. As practicing diatomists, we know that there exists variation in diatom cell walls, and though a summary of those examples and the potential sources of that variation has been generated (Mann 1999, Cox 2002), a reconsideration of those cases, and others not referenced or published since that time, might be appropriate. Hence the impetus for this contribution.

Cox (2002) has, we believe, correctly identified three sources of variation: development, genetic and environment. This is aligned with the provocative book by Lewontin (2002) that reminds us of the many sources of variation, and the tempering effects of that breadth of sources on the promises of the molecular age. In this paper we review and attempt to summarize the various sources of variation as documented in the literature and attributed to either development, genetics or environment, and compare the variation expressed by taxa with the classification system now in use by the diatom/phycological community, a classification system based in large part on the structure of the glass cell walls of diatoms (e.g., Smith 1872, Round *et al.* 1990, Nikolaev & Harwood 2002) and/or molecular sequences of genes (e.g., Sims *et al.* 2006, Sörhannus *et al.* 1995, Kooistra & Medlin 1996).

At this point we should point out that variation in diatom frustular morphology may roughly fall into two categories, which we will term adaptive and circumstantial. Perhaps the most commonly recognized types of adaptive variation are found in several small species of *Stephanodiscus* that are common in eutrophic waters, where gross variations in valve morphology regularly occur during one growth cycle (Håkansson & Stoermer 1984, Stoermer & Håkansson 1984, Theriot *et al.* 1988). These adaptations appear to confer clear selective advantage, in that they provide these species with means of reducing their requirements for silicon (through alterations in valve structure), and modifying their sinking rates (through colony formation).

Examples of circumstantial variation include the morphological responses of some diatom species to various forms of physical and chemical stress. Examples might include morphological variations associated with ephemeral environments, such as Janus valves and other types of deformities associated with osmotic stress as colonies dry. As discussed later, various chemical insults may also produce morphological variation to the point of making species difficult to identify (Stoermer & Andresen 2006). It might be argued that the fact that morphological variation occurs in these cases reflects the ability of these species to survive inimical conditions and is, in fact adaptive.

Sources of variation

Variation associated with Development

Development is viewed here as the process of ontogeny associated with both vegetative cell division and sexual reproduction. Kociolek & Williams (1987) discussed the interpretation of ontogeny in a unicell, and gave several examples of ontogenetic sequences for diatoms throughout the life cycle. Variation in diatom developmental process may be viewed as those where change is more likely to occur, because the developmental pathway is less established (channelized, cf. Futyuma 2005), resulting in polymorphisms of degree. An example is the process of size diminution. These are compared with processes that might have a deeper phylogenetic basis, for example nuclear division and resulting valve morphogenetic implications. These features are likely more channelized, resulting in discrete outcomes.

i. Size diminution and valve variation

The best-known variation in diatoms is that which occurs during the life cycle. This variation is so well documented, that certain "laws" have been formulated to express the widely known phenomenon. Because of the rigidity of the glass cell walls, and their bipartite nature, vegetative cell division usually results in the production of daughter valves that are smaller than the parent valves. With subsequent cell divisions, populations decrease in size. This phenomenon is known as the MacDonald-Pfitzer hypothesis (MacDonald 1869, Pfitzer 1871). A few taxa have appeared not to follow this rule, as documented by Wielding (1948).

Geitler (1932) further refined our understanding of the variation associated with the implications of the MacDonald-Pfitzer hypothesis with the concept of a range of sizes that define the largest cell size and the size at which sexual reproduction is initiated. He termed these sizes the "cardinal points" in the cell cycle, and thought these points to be specific for a taxon. Several authors have considered this approach in more recent work, including Mann (1986) and Kociolek & Stoermer (1988a, b). Geitler added additional details to our understanding of the variation in shape of pennate diatoms through cell diminution, describing the phenomenon that with size reduction, specimens were more rounded, with length decreasing proportionately faster than breadth. The rules of MacDonald, Pfitzer and Geitler have been documented across great taxonomic breadth: centric and pennate, marine and freshwater, fossil and Recent.

Work on centric diatoms has demonstrated size diminution with cell division. Examples include *Aulacodiscus* species (Burke 1970), *Stephanodiscus suzukii* (Tuji & Kociolek 2000), *Cyclotella meneghiniana* (Schulz 1971, Schulz & Trainor 1970), *Asteromphalus orientalis* (Rivera & Barrales 1994), *Cyclotella polymorpha* (Meyer & Håkansson 1996) *Stoermeria* (Kociolek *et al*. 1996), and *Coscinodiscus concinnus* (Holmes & Reimann 1966). The study by Meyer and Håkansson is remarkable as an example of the typological concepts inherent in species concepts held by some diatomists. In this work the authors describe a diatom that expresses morphologies of *C. radiosa* on one valve, and *C. planetophora* on the other (while co-occurring with diatoms with the morphologies of these two species only). The conclusion reached by the authors was to create a new species for the form with both morphologies. Differences between auxospores and vegetative valves have been shown generally by Hustedt (1927-1966) and in *Melosira* (now *Aulacoseira*) by Crawford (1975).

A number of studies have described the changes in valve ornamentation associated with size diminution. Some authors have shown the relationship between number of processes and diameter, for example in *Aulacodiscus* species (Burke 1970), *Arachnoidiscus ornatus* (Kobayashi *et al*. 1998) and *Thalassiosira* (Johansen & Theriot 1987). The number, shape, and orientation of rays in *Asteromphalus sarcophagus* change with regard to size (Rivera & Barrales 1994). Teubner (1995) demonstrated a positive correlation between diameter and stria length in *Cyclotella* species. In this remarkable study, 55 % of the frustules examined demonstrated heterovalvy. Theriot (1987) and Theriot & Stoermer (1981, 1984) developed techniques to examine the size-related variation versus size-free variation in frustular features of *Stephanodiscus* species. In some cases the changes are not simple continua, and this has been documented in relatively recent species (e.g., Tuji & Kociolek 2000) and in fossil species (Edgar *et al*. 2004). In centric taxa that are not circular in outline, size diminution may be accompanied by shape changes. This was documented in the taxon *Stoermeria californica* Kociolek *et al*. (1996).

In pennate diatoms, changes in the life cycle from auxospores through size diminution can be associated with numerous morphological features. Auxospore morphology may differ not only in being the maximum size of a taxon (see Geitler 1932, Mann 1986), but also differences in shape and symmetry. For example, see gomphonemoid diatom auxospores that are cymbelloid (Passy-Tolar & Lowe 1995, Kociolek & Stoermer 1988a) and curved and undulate auxospores of *Diatoma moniliformis* (Potapova & Snoejis 1997). Other specific morphological structures, such as gomphonemoid species that vegetatively have stigmata whose sauxospores are astigmate, and taxa that have bilobed apical pore fields in vegetative cells that are entire in the auxospores (Passy-Tolar & Lowe 1995, Kociolek & Stoermer 1988a, b). Hustedt (1927-1966) suggested that diatom morphology was vulnerable to environmental influences in the development of auxopsores and initial valves, and that modifications that occurred at this early ontogenetic stage would be carried through the cell cycle. These modifications would be reversed, according to Hustedt, after the next round of sexual reproduction.

A general, predictable, pattern of shape change associated with size diminution was formulated by Geitler (1932). With size reduction, valves tend to lose undulations and become more elliptical in outline. This has been substantiated in numerous studies with both descriptive (e.g., Wallace & Patrick 1950, Mizuno 1987, Kociolek & Stoermer 1988a, Subba Rao & Wohlageschaffen 1990, Williams *et al*. 1999) and quantitative approaches. Solliday (1994) noted differences in outline of *Surirella utahensis* that seemed to be unrelated to size. With the quantitative approach, Stoermer & Ladewski (1982) and Stoermer *et al*. (1986a) documented shape change in *Gomphoneis* taxa across space and time, while Tropper (1975) reconstructed valve outline of *Achnanthes hauckiana* with regression analysis. Multivariate statistics were used to describe the shape of valves of *Tabellaria* (Theriot & Ladewski (1986), *Didymosphenia geminata* (Stoermer *et al*. 1986b), *Gomphonema augur* (Jahn 1986), and *Eunotia pectinalis* (Steinman & Ladewski 1987). Droop (1994, 1995) has used a statistical approach to document differences between species of *Diploneis*, and Goldman *et al*. (1990) examined quantitative shape change in *Surirella fastuosa*. Though differences in diatom shape have been described by adjectives, the above studies have shown that quantitative expression of shape changes and differences is possible, allowing statistical evaluation of differences in these features that are otherwise defined by descriptive terms only.

Relationship of valve structure to size in pennate diatoms have been described in numerous, diverse taxa. Reimer (1954) showed that several *Nitzschia* species fit within the type population of *N. frustulum*, potentially reflecting differences within one taxon relative to size (see also Wendker 1990). Cocquyt (2000) provided bivariate plots of length versus alar canal width in *Surirella brevicostata*.

At the lower end of the size scale, it has been hypothesized that a "cardinal point" is reached where sexual reproduction is initiated (and after which the cell cannot become sexual) (Geitler 1932, Mann 1986). However, it is known that cells do continue to divide beyond this lower "cardinal point" and that morphological changes accompany the continued size decrease. Many of the cells become teratological, (Kümmerformen) and this has been documented by Geitler (1932) for *Eunotia formica* and by Estes & Dute (1994) and Schmidt (1975) for *Synedra ulna*, among many others.

ii. Morphogenesis

Our understanding of the process of diatom valve morphogenesis, and variations in the process within a single genotype, have been forwarded by the work of Volcani (1981), Schmid (1979, 1980, 1994), Meene & Pickett-Heaps (2004), Pickett-Heaps *et al*. (1990) Mann (1984) and Cox (2002). There has been a rich history, initiated in the era of light microscopy (Lauterborn 1896), but more fully developed in the era of transmission and scanning electron microscopy, of progress in understanding the valve morphogenesis (Pickett-Heaps *et al*. 1984).

While data from these studies have been viewed to develop a better understanding for phenomena for specific groups (e.g., Mann 1981, 1983, 1984), the number of taxa actually studied is quite modest, and a broader synthesis of current results is wanting.

The differences resulting from variation in development in diatoms can range from small, intrataxon features, to differences that have traditionally separated different species or even genera. In some of these cases, it would appear that new investigations into the delineation of taxa, based on the reversibility of variation, are warranted. For instance, should we continue to make the distinctions between the genera *Hantzschia* and *Nitzschia*, based on the orientation of the raphe positions on a frustule when that feature is variable within a single taxon? For example, *Nitzschia alba* has been shown to develop typical *Nitzschia* frustules, that is, with the keel bearing the raphe system being placed atop one another of each valve (on the same side of the frustule). However, it is also able to develop frustules where the keel of valves are orientated opposite from each other within a frustule, a feature used to distinguish the closely related genus *Hantzschia* (Lauritis *et al*. 1967, Kociolek & Williams 1987).

A number of studies has documented not only the process of morphogenesis, but also the roles a variety of chemicals, and their interaction with the environment, can play in the developing cell wall (Cohn *et al*. 1989, Schmid 1997, 2009)

Genetic variation

We live in a time when documenting the sequences of genes and other molecules is happening at a fast pace, helping to unlock clues of everything from phylogenetic history to the turning on and off and regulation of a wide variety of metabolic pathways and systems. While a wide variety of studies have used molecular and biochemical data to generate hypotheses about diatom relationships (e.g., Kaczmarska *et al.* 2005, Kooistra *et al.* 2004, Bruder & Medlin 2008, see Sims *et al.* 2006 for others), thereby documenting variability across taxa (e.g., Sarno *et al.* 2005), very few studies have documented intraspecific variation of diatoms. In some instances where supposedly closely related taxa are not found to be closely related (even "the same species" may come in widely different parts of a phylogenetic tree), this is not a shortcoming of genetics *per se*, but perhaps the identification skills of the individuals being used to develop molecular sequences or perhaps taxon sampling (Theriot *et al.* 2009).

Historically, the work by Gallagher (1982) and Stabile *et al.* (1990) demonstrated variation among clones and within-populations of *Skeletonema costatum* across time (seasons) in Narragansett Bay, Rhode Island. Murphy & Guillard (1976) showed variation in electrophoresis banding patterns within and between species of the genus *Thalassiosira*. Bourne *et al.* (1992) showed tremendous variability in molecular sequence data for clones identified as *Cyclotella meneghiniana*. This has been subsequently documented by Beszteri *et al.* (2005). Soudek & Robinson (1983) and Lewis *et al.* (1997) documented variation across geographic space for *Asterionella formosa* and *Fragilaria capucina*, respectively, although the morphologies of the populations appeared nearly identical. Wood *et al.* (1987), working with *Thalassiosira tumida*, were able to identify a genetic component to variation associated with morphology. They noted the amount of variability is high, and argued that in the context of directed evolution (intense, directional selection), significant morphological change could occur across relatively short time intervals.

In terms of assessing variation in taxa with regard to molecular sequences, an excellent overview of the situation is provided in Mann & Evans (2007). *Ditylum brightwellii* (Rynearson & Armbrust 2004, 2005, Rynearson *et al.* 2006) and *Pseudo-nitzschia multiseries* and *P. pungens* (Evans *et al.* 2004, 2005, respectively; Casteleyn *et al.* 2009) have been shown to exhibit high degrees of variability in certain repetitive segments of their DNA. Different populations of these taxa appear to be physically isolated from others, despite their occurrence in relatively small areas/water bodies.

However, in most cases, results have revealed that specimens/cultures/etc., thought to be the same species, have high degrees of sequence differences, and after the review of the specimens shows morphological differences between them. Mann & Evans (2007) have referred to this phenomenon as "pseudocryptic species". It has been demonstrated in species of *Skeletonema* (Manhart *et al.* 1995, Medlin *et al.* 1991, Kooistra *et al.* 2006), *Eunotia* (Vanormelingen *et al.* 2007, 2008) *Pseudo-nitzschia* (Casteleyn *et al.* 2008; Cerino *et al.* 2005) and *Sellaphora* (Evans *et al.* 2008). Recently, Kaczmarska *et al.* (2009) have related genetic sequences, sexual pairing and reproduction with the biogeography on the araphid, benthic diatom *Tabularia fasciculata*.

Variation with respect to environmental variables

During cell division and subsequent cell wall morphogenesis, environmental conditions can influence how the cell wall is laid down, to the point of the diatom producing valve features that are different from the valves produced under different environmental conditions. A wide range of environmental variables has been identified to affect cell wall morphology, and this literature is extensive. This list is not exhaustive, but variables that have been analyzed include salt: concentration and osmotic effects, (e.g., *Cyclotella,* Tuchman *et al.* 1984, Schultz 1971, Håkansson & Chepurnov 1999, *Mastogloia*, Stoermer 1967, *Thalassiosira*, McMillan & Johansen 1988, *Coscinodiscus*, Nagai & Imai 1999, *Skeletonema,* Paasche *et al.* 1975, Marsot *et al.* 1983, *Stephanodiscus,* Geissler 1982, and others, e.g., Li & Chang 1979). Silica concentration may have striking effects (e.g., *Stephanodiscus*, Theriot 1987, *Thalassiosira*, Booth & Harrison 1979, Mann 1999; Vrieling *et al.* 1999). Temperature: (*Rhizosolenia*, Hustedt 1927, *Thalassiosira*, Syvertsen 1977, *Cyclotella*, Hustedt 1938/9, 1956, Geissler 1970a, b) and the covariant seasonality: (*Chaetoceros*, Karsten 1905-7, *Gomphoneis minuta,* Kociolek & Stoermer 1988a) may also be important.

Several authors have referred to morphological effects of pH: (*Eunotia,* Hustedt 1938-1939, *Fragilaria*, McFarland *et al.* 1997), although these may be confounded by the effects of metals such as aluminum (*Asterionella*, Gensemer 1990, Gensemer *et al.* 1993a, b, 1995); Selenium (Doucette *et al.* 1987), copper (Morel *et al.* 1978, Rijstenbil *et al.* 1994), cadmium (numerous taxa, Adshead-Simonsen *et al.*1981, Gold *et al.* 2003, Nassiri *et al.* 1997, Torres *et al.* 2000, Morin *et al.* 2007, 2008a-c), as well as other heavy metals (Behra *et al.* 2002, Berland *et al.* 1977, Lazinsky & Sicko-Goad 1990, Pérès 2000, Sicko-Goad & Stoermer 1979, Smith 1983, Ruggiu *et al.* 1998, Rachlin *et al.* 1983, Williams & Mount 1965, Jensen *et al.* 1982) and other chemicals (e.g., Safonova *et al.* 2007, Schmitt-Jansen & Altenburger 2005, Spurck & Pickett-Heaps 1994). These may also be expressed as morphological differences in different habitats. For example soil forms were identified by Lund (1945, 1946) were much smaller than the same species he identified from aquatic habitats, and may have different stria pattern. Morphological variation has also been attributed to general trophic status (Murakami & Kasuya 1993, Yang & Duthie 1993). *Fragilaria capucina* was shown to have different morphologies in different experimental water quality conditions (Hürlimann & Straub 1991; see also Andresen & Tuchman 1991, Antoine & Benson-Evans 1986, Feldt *et al.* 1973, Gomez & Licursi 2003). Morphological variaton has also been attributed to geography: Wimpenny (1966) reports wider range of cells in *Chaetoceros* in northern latitudes than in tropics, though he cautioned that this might be due to less grazing of smaller cells in northern latitudes than in tropics. We also consider it likely that some reported consistent morphological differences apparently correlated with geography may prove to un-recognized pseudo-cryptic species.

There is a long history of relating diatom communities, and incorporating the presence of deformities, with pollution, including trophic state (e.g., Besch *et al.* 1970, 1972, Deniseger *et al.* 1986, Dickman 1988, Prygiel 2002, Cattaneo *et al.* 2004, Reavie *et al.* 2005, Morin *et al.* 2007, 2008a, b, Nunes *et al.* 2003, Tapia 2008, Smucker & Vis 2009). Theriot & Stoermer (1984) noted the differences in *Stephanodiscus* morphology related to Si:P ratios in various regions of the Great Lakes. Different races of *Fragilaria capucina sensu* Lange-Bertalot were related to trophic state (see Hürlimann & Straub 1991).

Outcomes

Size-free variation

There have been several studies that demonstrate differences between individuals that seem to be unrelated to either size diminution. These differences present in the same samples seem to rule out environmental effects. It is possible that these differences, many times expressed without regard to size, are due to genetic differences but this area has not been explored. A remarkable example is the valve outline differences shown by Solliday (1994) for *Surirella utahensis* in sediments from Mono Lake, California. Also, the non-siliceous cells of *Phaeodactylum tricornutum* may be bilaterally symmetrical as well as tri-radiate. Borowitzka *et al.* (1977) and Borowitzka & Volcani (1978) have demonstrated three different morphotypes for this taxon. Schmid (1997) showed that the triradiate genus *Centronella*, known from European waters, can become bilaterally symmetrical, closely resembling the commonly distributed species *F. crotonensis*. Gemeinhardt (1926) showed the various placement of labiate process in species of *Diatoma* and *Tabellaria*.

Functional heterogeneity

There are many examples of functional heterogeneity in diatoms, in both single cells and chain-forming taxa. Perhaps the most commonly cited example is to be found in the monoraphid diatoms, which has been shown to be a grade of morphological similarity not a monophyletic clade (e.g., Cleve 1895, Kociolek & Stoermer 1986, Mayama & Kobayasi 1989, Medlin & Kaczmarska 2004). In these groups, one of the valves has a raphe and the second valve is without a raphe. Via cell division and morphogenesis, frustules first have two valves, both bearing a raphe, but the rapheless valve is developed via a secondary filling in with silica of the raphe slit (Boyle *et al.* 2004, Andrews 1981, Kociolek & Williams 1987). *Chaetoceros* valves may have setae that are of differing lengths (or absent; Karsten 1905-1907). *Aulacoseira* chains will at certain points develop separation valves with different spination or "end valves" that are dome-shaped and without interdigitating spines, ending the development of the chain. It is thought these valves are produced to induce cell sinking and spore formation (Edlund *et al.* 1996). Valves with the same morphology may have a different organization of girdle elements. For example, Johnson & Rosowski (1992) showed 4 variations in valvocopula and pleurae structure and arrangement in *Pleurosira laevis*.

Teratologies: Deformities in the cell wall structure

Differences in the structure of valves from the typical condition are well known in diatoms. Cox (1891) outlined 3 types of cell deformities: those in outline (illustrated by Cox in the genus *Surirella*), multiple centers of origin (of in the number of annuli in "centric" diatoms) and asymmetries of structures (extra stigmata, raphe discontinuities, extra raphe slits, etc.). It has been recognized for a long time that diatom valve deformities are more common in cultured specimens (Lockwood 1893, Miquel 1893, Drum 1964, Hostetter & Rutheford 1976, Torgan *et al.* 2006). Barber & Carter (1981) and McLaughlin (1988) have detailed many teratologies in natural populations and identified 7 different causes of these teratologies. These include:

1. Environmental causes (pollution, pH)
2. Crowding (culture)
3. Parasitism
4. Sex
5. Minimal sizes
6. Other external factors (light, temperature)
7. Genetics

Hustedt (1927-1966) discussed the susceptibility of auxospores during environmental change, and the impact environment could have not only on the morphology of the auxospore/initial valve, but also on the rest of the cell line. He also suggested that this could be reversed during next cell cycle. Hostetter & Howshaw (1972) showed that the number of deformities increased with decreasing cell size in *Stauroneis anceps*, and excellent SEM illustrations of this phenomenon have been presented by Estes & Dute (1994).

Janus cells

Contrary to Mann's (1999) downplaying of this commonly-reported type of polymorphism (to the point he even dismisses published accounts of the phenomenon), there are many interesting illustrations of Janus cells in diatoms. Deriving from the two-faced Greek god Janus, the term indicates frustules with differing morphologies between the two valves. The phenomenon has been observed across the diversity of diatoms, including early diatom clades as well as derived raphid pennates. Examples include *Triceratium* (the two different valves on the frustule prompted Brun (1896) to propose a new genus *Capsula* for the condition*), Cyclostephanos* (Hickel & Håkannson 1987), *Stephanodiscus* (Kling 1992) *Cyclotella* (Teubner 1995), *Discostella stelligera* (Haworth & Hurley 1986), *Mastogloia* (Stoermer 1967), *Gomphonema* (McBride & Edgar 1998) and *Nitzschia* (Lauritis *et al*. 1967). This phenomenon can also be widespread within populations, not just found in a few, "weird" frustules. Teubner (1995) demonstrated the appearance of Janus valves in over 50 % of the population of *Cyclotella* valves (exhibiting features of four different taxa!).

It is these areas of variability that most diatomists have spent their time wrestling with whether the variation they see can be circumscribed within a single taxon or should be attributed to more than one taxon. The assumption has been most of the time that for any taxon, taxonomists group things together within some range of continuous variation, and make distinctions between (split out) things where we see discontinuous variation. The situation related to Janus cells suggests that all the variation within a taxon is not necessarily continuous. That is, whether the feature is stria organization and density, relative placement of raphe system, or valve organization, there are not intermediate conditions between the character states expressed. Thus, in these cases where different, non-continuous states are present within a taxon, reversibility is assumed, that is, with a shift in environmental conditions, or later in the cell cycle, the variation can shift back. If reversible, we can show this is part of the same life cycle, we would assume the forms/morphologies are part of the same taxon. This leads to the idea of an "ontogenetic species concept" (see Mann & Kociolek 1990). The "differences" expressed in this variation are still recognizable at the species, or at the very most, genus, levels. Almost everyone (except maybe Brun in the case of *Capsula*), have thought these types of reversible, non-continuous expressions of variation to be a part of the same species.

Interactions. Development and Environment

There are other types of morphological variation expressed by some diatoms where the differences in expression have been questioned as to whether the forms are part of the same genus, or of different, more general taxonomic hierarchy.

Symbioses

Diatoms are known to form symbioses with a number of different hosts. In some cases the symbiosis is a long-established one, and the integration of the diatom into the host nearly complete. For example, diatoms have been identified as the symbiotic partner with dinoflagellates, through its characteristic division of its nucleus as well as rRNA (Dodge, 1971, Chesnick *et al*. 1997). In other cases, the symbiosis seems to be a relatively recent phenomenon. Diatoms have entered into relationships with foraminifera. While inside the foraminifera, the diatoms do not express their siliceous frustules. When teased out of the forams, the diatoms lay down a glass cell wall (Lee *et al*. 1979, 1980). Thus, the environment in which the diatoms have developed heavily influences their morphology.

Resting spores

Resting spores are produced by a broad group of diatoms, marine and freshwater, across the diversity of the evolutionary tree of diatoms. They are thought to be produced during times of stress. Round *et al*. (1990) illustrate the variety of ways resting spores may be produced. A number of papers have been recently published on spores, and their quite dissimilar appearance from vegetative cells (e.g., Suto 2004a-c, 2005, 2006). The typical situation is that marine resting cell forms are quite different from vegetative cells; freshwater forms almost indistinguishable from vegetative cells. For example, in the marine diatoms, *Chaetoceros* produces spores that have been identified as separate genera (the genera *Periptera, Omphalotheca* and *Xanthiopyxis* are really spores of *Chaetoceros*, Hargraves & French 1983, see also Suto references above). Resting spore formation can be effected by the chemical composition of the water (e.g., Oku & Kamatani 1995).

Some data challenging the notion that marine spores are different from vegetative cells while spores formed by freshwater species are nearly indistinguishable from vegetative forms include *Eunotia soleirolii*, whose spores lack a raphe system altogether and resemble some members of the Fragilariaceae (Stosch von 1967, Stosch von & Fecher 1979) and *Nitzschia monoensis* where the thick, unornamented spore is nothing like the finely structured vegetative valves (Jones 1987, Kociolek & Herbst 1992). In marine diatoms, *Thalassiosira nordenskioeldii* and *Detonula confervaceae* spores are very similar to vegetative cells (Syvertsen 1977).

Innenschalen

Innenschalen are internal valves, produced as single valves within a frustule or as entire frustules within a frustule. There can be variations in the way and number of nuclear divisions that occur to produce Innenschalen (Geitler 1953). They are thought to be similar in function to resting spores. This phenonmenon can occur across broad taxonomic catagories, especially amongst pennate diatoms. Examples include, *Melosira dickeii* (Krammer & Lange-Bertalot 1991), *Meridion* (Kociolek & Lowe 1993), *Eunotia* (Hustedt 1927-1966), *Achnanthes* (Geitler 1980), *Amphora* (Anderson 1975), *Rhopalodia*, *Nitzschia* and *Hantzschia* (Liebisch 1930, Geitler 1980). In the case of *Meridion*, the Innenschalen look very similar to "normal" valves in terms of size/proportion, but they many times have different stria densities and may lack features that diagnose the genus or group (in this case, presence of costae; Kociolek & Lowe 1993).

Extreme Variation

In the genus *Spumorbis*, Komura (1998) reported two forms of frustules, one form where the valves are morphologically somewhat similar, and the other where they are organized entirely differently. The structure on one of the valves resembles *Coscinodiscus*, the other having structures that are reminiscent of *Aulacodiscus*-two different orders in the classification scheme of Round *et al*. (1990). Witkowski *et al*. (personal observations) have identified valve morphologies that are similar to *Paralia* and *Costopyxi*s, representing two different families on the same filament. Kociolek & Spaulding (2002) described the presence of *Actinocyclus* frustules within filaments of *Ellerbeckia*. Though Crawford (2004) suggested the latter phenomenon was due to frustules of nearly the same size falling entirely within the filaments of *Ellerbeckia*, at a rate of nearly 20 % of the population, additional data on this phenomenon across many disparate groups of diatoms suggests Mann's discounting a similar situation described by Wood (1959) may have been hasty at best.

Summary

The reports on variation in diatoms, as expressed in the polymorphism of the cell wall, are not rare occurrences. Nearly every group of diatoms, including freshwater, estuarine and marine, and across the diatom tree of life, have been investigated and shown to express subtle to wide ranges of variation. Variation is the heart of the evolutionary process. Diatomists need to consider this variation of the cell wall, its sources and expressions of variation. Some variation is quite subtle, such as shape or density of ornamentation. Other variation can be extreme, such as those cases were different valves or ornamentation may not coincide with the established classification scheme. In these latter cases, while healthy scrutiny is warranted, it cannot be discounted. The literature shows suggests that the expression of variation can cross many different levels of established taxonomic hierarchy, from species through orders.

While we have a significant amount of data today, the study of diatom polymorphism is, in our opinion, significantly under-studied, and does not have the level of activity it did even 10 years ago. Few studies explore the sources of variation in diatom morphology, and many fewer still examine variation from an experimental point of view. The genetic and development aspects of diatom variation are in need of additional research, and the interplay between these two factors, and the environment, are also areas of potentially fruitful research.

One area that is receiving significant attention is the application of diatom variation, especially to detecting the impacts of environmental degradation on diatom morphology. This implies the association of deformed valves with current or circumscribed species. Thus, in terms of species concepts, relating the morphologies expressed to environmental stress is important. Because of the promise it offers, we believe further development of this concept to water quality indices and assessment will continue.

Interpretations of morphological variation in diatoms for an overall understanding of classification system are important. We are still assessing the range of variation that can be expressed within a taxon, and incorporating that knowledge into our classification systems. And while those working with molecular techniques are attempting to characterize taxa by relatively short sequences of amino acids for a few genes, it must be kept in mind that whatever those sequences are, the way they interact through development and response to the environmental milieu in which an organism may find itself is important. This 'triple helix' (Lewontin 2002) of genetics, environment and development are not only independent sources of variation, but the interactions between them account for the organisms we see (morphologically, physiologically, ecologically).

The observations of Komura (1998), Kociolek & Spaulding (2002), and Witkowski *et al*. (personal observations) on fossil forms suggest that expression of morphological variation may have been greater earlier in the evolution of some groups. While ontogenetic/developmental studies may help determine the extent and mechanisms of variation in diatom morphology, the fossil record may be as, or more fruitful in elucidating a deeper understanding of diatom relationships and classification. For a group such as the diatoms, where a significant degree of the group's morphological diversity is extinct, the fossil record may play an important and unique role in determining the phylogenetic basis of the diversity of form, more so than the current trends in molecular biology.

Diatomists should reconsider the role of polymorphism and the explicit assignment of variation to potential sources, and the potentially important role polymorphism might play in the divergence of taxa. Understanding morphological variation and its basis in the genetic makeup of taxa is still relatively primitive. While an understanding of either development or genetic variation is not complete, it is a requirement for a better understanding of the degree of variation expressed in diatom taxa, and the tempo and mode of evolution in the diatoms.

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