

QUANTITATIVE ANALYSIS OF SHAPE VARIATION IN TYPE AND MODERN POPULATIONS OF *MERIDION* (BACILLARIOPHYCEAE)¹

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Subtle differences in valve morphology can indicate sexually isolated populations in diatoms (Bacillariophyceae). Shape descriptors, like Legendre coefficients, have been used to quantify differences in valve outline so that morphologically distinct groups can be recognized. Legendre coefficients were used as shape descriptors to quantify differences in valve outline among five populations in the genus *Meridion* Ag. Two novel populations of *Meridion* from North America, a North American population of *M. constrictum* Ralfs, type material for *M. circulare* (Greve.) Ag., and type material of *M. constrictum* were included in this analysis. Results of a principle components analysis and discriminate analyses on the shape descriptors of all five populations support the hypotheses that the two novel North American populations are undescribed taxa within *Meridion* and that the North American *M. constrictum* can be considered *Meridion constrictum sensu stricto*. A new taxon, *Meridion hohii* Rhode, is described. There appears to be greater diversity within the genus *Meridion* than is currently recognized.

Key index words: Bacillariophyta or Bacillariophyceae; diatoms; Legendre polynomials; *Meridion*; shape analysis; diversity

Abbreviations: DA, discriminant analysis; PCA, principal components analysis

The extent of diatom diversity has been a topic of debate among diatomists since diatoms were first discovered. Estimates of species diversity range from 12,000 species (Hendey 1964) up to 1,000,000 (Mann 1994). The dominant paradigm in understanding diatom diversity has historically included a broad species concept and the idea that most diatom species are cosmopolitan (Bradbury and Krebs 1982, Ross 1983). This both arises from and leads to reports of a given species from a broad range of localities, characterized by a wide range of variability in ecological parameters. Diatom classification and nomenclatural schemes have historically been based almost exclusively on frustule morphology, which is complex and species specific. Consequently,

the need to describe small differences in frustule shape or outline has given rise to an extended and complex terminology (Anonymous 1975, Ross et al. 1979, Barber and Haworth 1981).

Developing a tenable species concept applicable to diatoms has been difficult. Sexual reproduction is rarely observed, and recognition of sexually isolated populations is very difficult. Observation of sexual isolation has indicated that diatom diversity is actually far greater than has historically been estimated. For example, when communities of morphologically distinct subpopulations of *Sellaphora pupula* (Kütz.) Merschk. were observed in sexual reproduction, individuals from different subpopulations were never observed to interbreed (Mann 1984, 1989, 1994, Mann and Droop 1996, Mann et al. 1999). The subpopulations represent morphologically distinct groups within a historically “cosmopolitan” taxon. Morphological differences between these subpopulations are subtle and have been included in the acceptable range of variation for the species (Hustedt 1930, Krammer and Lange-Bertalot 1991a,b, 1997a,b). However, evidence of sexual isolation indicates that they should be recognized as separate species. Further, Geitler (1975) observed no hybridization between closely associated allogamous forms of many species. Although true cosmopolitan taxa surely exist, coupling of sexual isolation with morphological differences indicates that many morphologically variable taxa may be too broadly defined.

Recently, workers have begun to address the issue of quantifying subtle morphological differences between subpopulations. Some attempts to quantify variation rely on traditional measures of valve morphology and cytology, such as length, width, costae density, striae density, protoplast structure, and so on (Stoermer and Sicko-Goad 1985, Fukushima et al. 1988). Identifying discontinuous phenotypic variation becomes a problem when traditional measures of valve morphology overlap. Principal components analysis (PCA) and similar techniques have been used to identify discontinuous variability detectable only when multiple quantitative variables are considered simultaneously (Theriot and Stoermer 1984, Theriot 1987, Theriot et al. 1988, Droop 1994).

Quantitative shape descriptors, such as Fourier or Legendre coefficients, have been used to quantify entire valve outlines (Stoermer and Ladewski 1982, Stoermer et al. 1986, Theriot and Ladewski 1986, Stein-

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man and Ladewski 1987, Mou and Stoermer 1992). Often, differences among valve outlines are easy to detect visually but difficult to quantify or even describe. It is often unclear whether detectable differences are indicative of morphologically distinct groups or are just individual instances along a continuum of morphological variability within a single group. Also, subjective descriptions of valve outlines are often difficult to interpret. The use of shape descriptors allows recognition of morphologically distinct groups based on the entire valve outline. Stoermer and Ladewski (1982) discriminated between valve outlines of the type and modern populations of *Gomphoneis herculeana* (Ehrenb.) Cleve using Legendre coefficients. Mou and Stoermer (1992) used Fourier coefficients to quantify valve outlines in *Tabellaria* Ehrenb.

The genus *Meridion* is particularly amenable to the use of quantitative shape descriptors, because there are only one or two recognized species. If only one species, *M. circulare* (Greve.) Ag., is recognized, then it is argued that there is a continuous gradient in valve outline between the two proposed taxa (Van Heurck 1885, Schoeman 1973); if there are two species, *M. circulare* and *M. constrictum* Ralfs, then characters other than valve outline (e.g. girdle band features) have been used (Williams 1985).

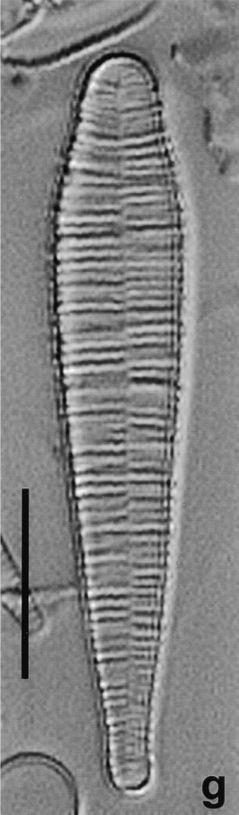
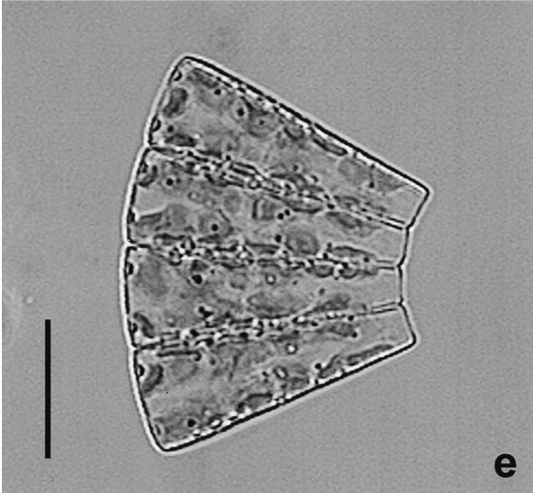
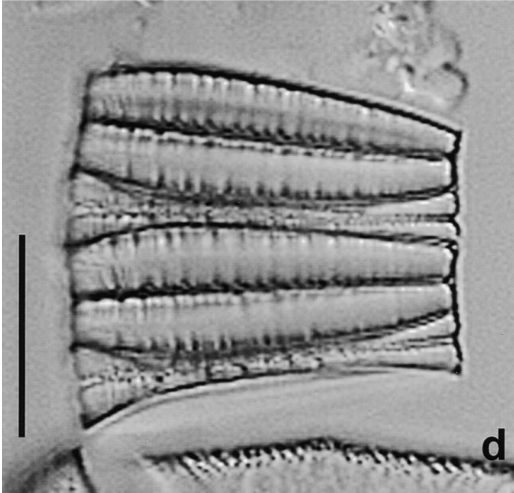
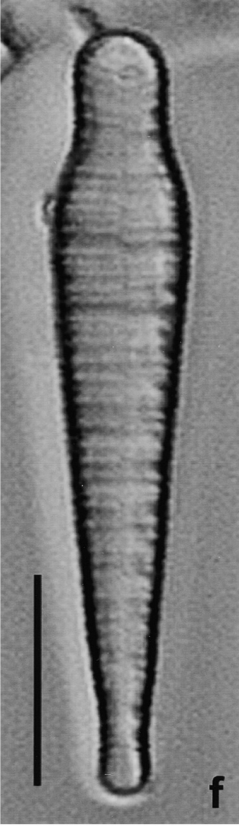
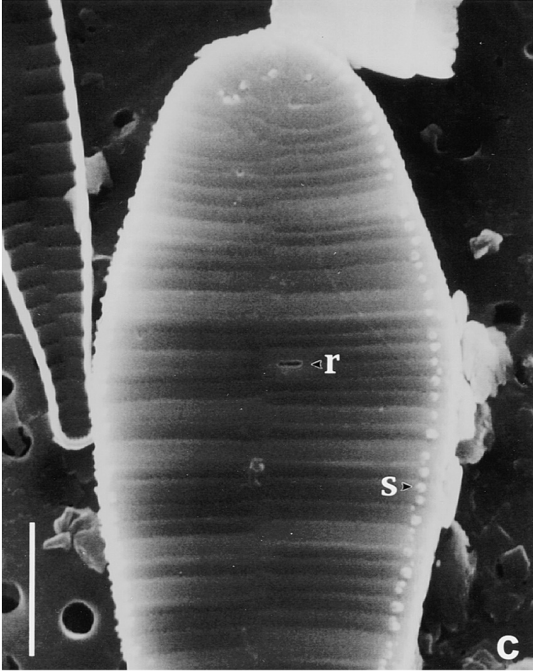
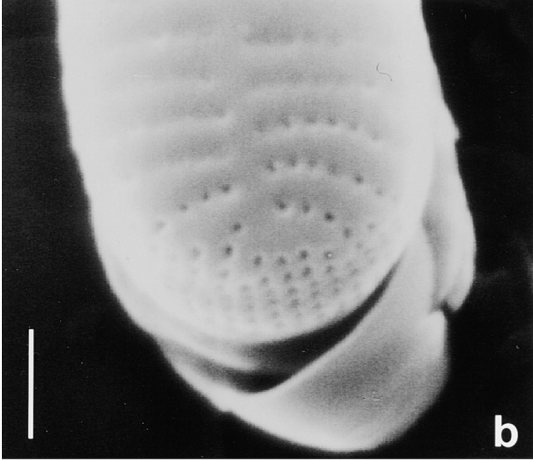
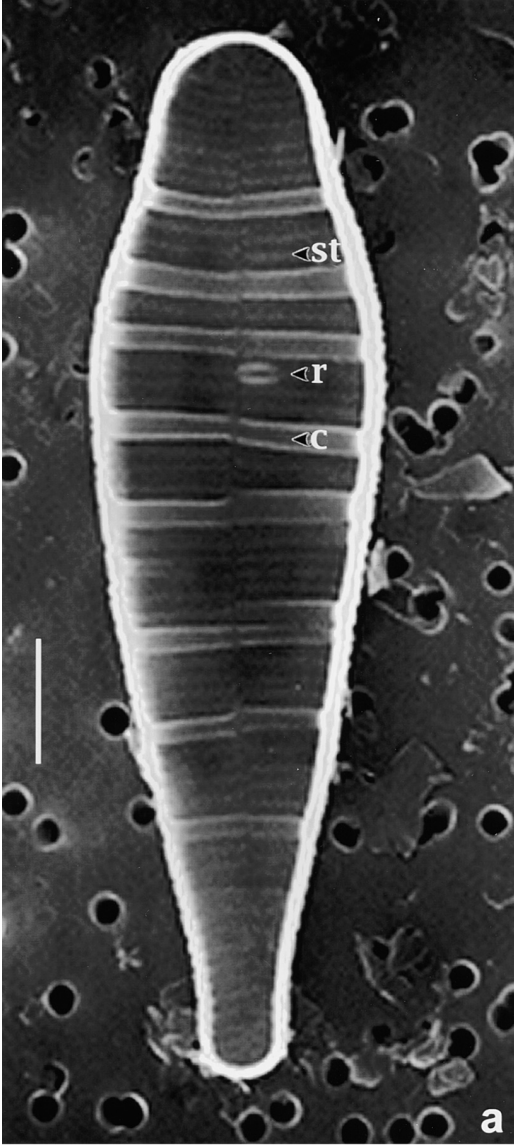
Meridion Ag. is instantly recognizable to most diatomists. Frustules are heteropolar in both valve and girdle views. In valve view, frustules appear clavate with a subcapitate footpole (terminology after Barber and Haworth 1981). Size ranges have been reported at 7–80 μm in length and 4–21 μm wide at the widest point. Costae are well-developed transapically (Fig. 1a). Two to six rows of uniserate striae are usually visible between the costae (Fig. 1a). The striae extend onto the valve mantle. The pseudoraphe is narrow and, at times, indistinct. A rimoportula is present near the headpole apex, oriented parallel to the costae and off center from the valve midline (Fig. 2). The external expression of the rimoportula appears as a simple slit (Fig. 1c). Internally, the rimoportula extends inward to approximately the height of the costae (Fig. 1a). Apical pore fields are formed at both poles by an undifferentiated conglomeration of simple punctae (Fig. 1b). The pore fields extend from the valve face onto the mantle. The apical pore field at the footpole is more developed than the pore field at the headpole. Spines appear at the valve face–margin interface (Fig. 1c). Spines can vary from being small knobs to large and interlocking spatulate structures. In live material, the chloroplasts appear as numerous elliptical

plates (6–12 per cell) (Williams 1985) (Fig. 1e). The characteristic spiral colony formation results from these wedge-shaped cells growing appressed valve face to valve face. Colonies are often found in fragmented semicircular sections, either periphytic or pseudoplanktonic. Periphytic colonies either form with cells attached perpendicular to the substrate by mucilage secreted at the footpole or prostrate in mucilaginous pads (Krejci and Lowe 1987). These periphytic colonies have been described as looking like “staves of a tub” (Ralfs 1843). *Meridion* is reported to have a pronounced seasonality, where it can form macroscopic colonies for a few weeks in late winter/early spring (Krejci and Lowe 1987). Individuals have been reported to produce “innenschalen” (or internal valves), thought to be a form of resting cell (Geitler 1971) (Fig. 1d). The innenschalen are usually acostate (Fig. 1, f and g). Various authors have mistakenly described innenschalen as new species, varieties, and forms (Mayer 1917, Foged 1964).

Both *M. circulare* and *M. constrictum* have been described as cosmopolitan taxa (Hustedt 1938, 1949, Foged 1978, 1981, Krammer and Lange-Bertalot 1991a,b, 1997a,b), although rare in the tropics (Hustedt 1949). Both have been reported from Africa, Asia, Australia, Europe, and North America (Hustedt 1938, 1949, Foged 1964, 1977, 1978, 1979, 1980, 1981, 1982, Patrick and Reimer 1966, Schoeman 1973, Williams 1985, Cumming et al. 1995). They are also reported as occurring sympatrically, with *M. constrictum* being less abundant (Germain 1981). However, in collections from North America, two populations are found that do not strictly conform to descriptions of the currently recognized species. These novel populations, along with the type material and a population from North America that does conform with the descriptions of *M. constrictum*, make up the five populations included in these analyses. Traditional measures of shape (length, width, striae, and costae density) overlap for all included populations; however, visually detectable differences in valve outline were observed. We hypothesize that the two novel populations are undescribed species within *Meridion* and have valve outlines distinguishable from the type populations. We also hypothesize that the North American *M. constrictum* should be considered *M. constrictum sensu stricto*.

This study is the quantification of differences in valve outline between a number of populations in the genus *Meridion* using Legendre coefficients. Two primary questions are addressed. First, we investigate whether an analysis of valve outline using Legendre co-

FIG. 1. (a) SEM showing an internal valve view of WA *Meridion* sp. st, uniserate striae; r, internal expression of the rimoportula; c, costae. Scale bar, 2 μm . (b) SEM of WA *Meridion* sp. showing an external valve view of a footpole with an apical pore field evident. Scale bar, 1 μm . (c) SEM of WA *Meridion* sp. r, external expression of the rimoportula; s, spines. Scale bar, 2 μm . (d) Light microscopy (LM) of WA *Meridion* sp. Girdle view of a partial colony with internal valves evident. Scale bar, 10 μm . (e) LM of a live colony of *Meridion circulare* showing multiple chloroplasts per cell. (f) LM of an internal valve of *Meridion constrictum* from Washington State. Scale bar, 10 μm . (g) LM. An internal valve of WA *Meridion* sp. Note the lack of costae. Scale bar, 10 μm .



efficients is sensitive enough to detect differences in a group with a relatively simple valve outline, such as that observed in *Meridion* species. All previous analyses of valve outline using Legendre coefficients have been on taxa with more convoluted valve outlines, such as *Didymosphenia* (Stoermer et al. 1986). Second, we address whether there is support for the description of new species within *Meridion*.

MATERIALS AND METHODS

Populations from the following localities were investigated:

1. United States: (i) Taft Spring, Hoh River Valley, Olympic National Park, Washington State, T27N R9W S12, collected 30 May 1997. Epiphytic strands on *Chara* sp. K.M. Rhode personal collection nos. 18 and 20. (ii) Taft Spring, Hoh River Valley, Olympic National Park, Washington State, T27N R9W S12, collected 30 May 1997. Sediment. K.M. Rhode personal collection nos. 19 and 21.
2. United States: Sugar Mountain Bog, Avery County, North Carolina, collected 5 July 1995. K.M. Rhode personal collection nos. 181 and 182. Collected by Lynn Brant.
3. Europe, presumably from United Kingdom: "Cold Bath Spring, Mr. Jenner." British Museum Collection nos. 23954 and 23597 (Syntype of *Meridion constrictum*).
4. Europe, presumably from United Kingdom: "Rivulet near Dumbryden Quarries, 1820" British Museum Collection no. 81187 (Holotype of *Meridion circulare*).

Material from the United States was cleaned first in 30% H₂O₂ and then in NHO₃, repeatedly rinsed until a neutral pH was achieved, and then settled onto coverglasses to air dry. The coverglasses were made into permanent slide mounts using Naphrax high-resolution mounting medium. Material used in scanning electron microscope (SEM) observations was dried onto polycarbonate membrane filters attached to aluminum EM stubs and coated with approximately 20 nm of gold/palladium. SEM observations were made using an SEM (model T100, JEOL USA, Peabody, MA) at 25 kV accelerating voltage.

Light microscope observations were made using differential interference contrast illumination with oil immersion optics on a Leica DMRX microscope (N.A. = 1.40) (Leica Microsystems AG, Heerbrugg, Switzerland). Individual valves were imaged using a Sony 3CCD color video camera (Sony Electronics Inc., Park Ridge, NJ). Ten specimens from each population were selected for imaging. Selection criteria included lying parallel to the coverglass in valve view and being free of debris. Individuals were chosen to roughly encompass the complete size range of a given population. Individual valves were arranged before imaging such that they all appear the same length within the imaging field, lying horizontally, with the footpole on the left-hand side of the image. Axes were then superimposed over the images so that the *x* and *y* axes bisect the valve apically and transapically, respectively. Digital image manipulation was performed on a Macintosh computer (Apple, Cupertino, CA) using the public domain NIH Image 1.62 (1998) program.

Fifty data points per 1/2 valve (bilaterally) along the valve outline were taken in the form of *x,y* coordinates. Data points were

normalized to range between -1 and 1 for each individual. These data points were used to calculate 10 Legendre coefficients (P₀ to P₉) per 1/2 valve using custom-written programs (J.L. Pappas, unpublished data) in Mathview 2.50 (1997) mathematics software (Waterloo Maple Inc., Waterloo, ON, Canada). Ten coefficients were used because this number adequately produced a best fit without introducing individual-specific variation. The coefficients were used to reconstruct outlines for representative individuals from each population. These reconstructions were superimposed on the original outline to insure accurate representation.

The P₀ coefficient in each series describes a rectangle of the same size for all individuals (because their length has been standardized) and therefore has no descriptive value with regard to outline and was excluded from subsequent statistical analyses. The remaining coefficients were then used as shape descriptors in statistical analyses. It should be noted that inclusion or exclusion of the first coefficient did not significantly change the results of any of the analyses. However, its exclusion increases the interpretive value of the component loadings in the Principal Components Analysis (PCA).

Principal Components Analysis was used to visualize relative differences (or similarities) in shape across populations. Discriminant analysis (DA) was used to test whether the coefficients could be used to distinguish between populations (Green and Carroll 1978, Afifi and Clark 1996). Standard and jackknifed classification accuracies were calculated for all comparisons (Van Valen 1978). Classification accuracies showed the predicted placement of individuals in populations based on discriminators derived from the Legendre coefficients. Three separate DAs were conducted. The first included all five populations under consideration. The second excluded the WA *M. constrictum*. As it is hypothesized to be *M. constrictum sensu stricto*, its inclusion in a DA with *M. constrictum* may distort the classification accuracies of the other taxa. The third included the WA *M. constrictum* and the type of *M. constrictum*.

RESULTS

Two *Meridion* taxa observed, one in collections made from the Taft Springs complex and one in collections made from Sugar Mountain Bog, did not conform to descriptions made of either species of *Meridion* in the literature. The Taft Springs collection included two distinct subpopulations of *Meridion*. One of the subpopulations conformed with the description of *M. constrictum* (referred to as "WA *M. constrictum*" here). Even though the WA *M. constrictum* fell within the range of variation described for *M. constrictum*, there were consistent noticeable differences in valve outline between it and the type population. Most notably, it was observed that the degree of constriction at the headpole is less for the WA *M. constrictum* (Fig. 2, a-c.). The other subpopulation in the Taft Springs collection (referred to as "WA *M. sp.*") was found to have a valve outline that could be considered intermediate between *M. circulare* and *constrictum*. It also has an unusual rimoportula placement (Fig. 2, l-m.). The rimoportula on each valve typically occurred approximately one fourth to one third of the way down the length of the valve instead of the

FIG. 2. Light micrographs of the five *Meridion* populations included in the analysis. (a-c) *Meridion constrictum* from Washington State (K. M. Rhode personal collection). (d-f) Syntype material of *M. constrictum* (British Museum Collection). (g and h) Holotype material of *Meridion circulare* (British Museum Collection). (i-k) *Meridion* sp. from North Carolina (K. M. Rhode personal collection). (l-n) *Meridion* sp. from Washington State (m.) from holotype slide of *M. hohii* Rhode (CAS 221016) (K. M. Rhode personal collection). Arrows indicate external expression of the rimoportulae. Scale bar, 10 μm.

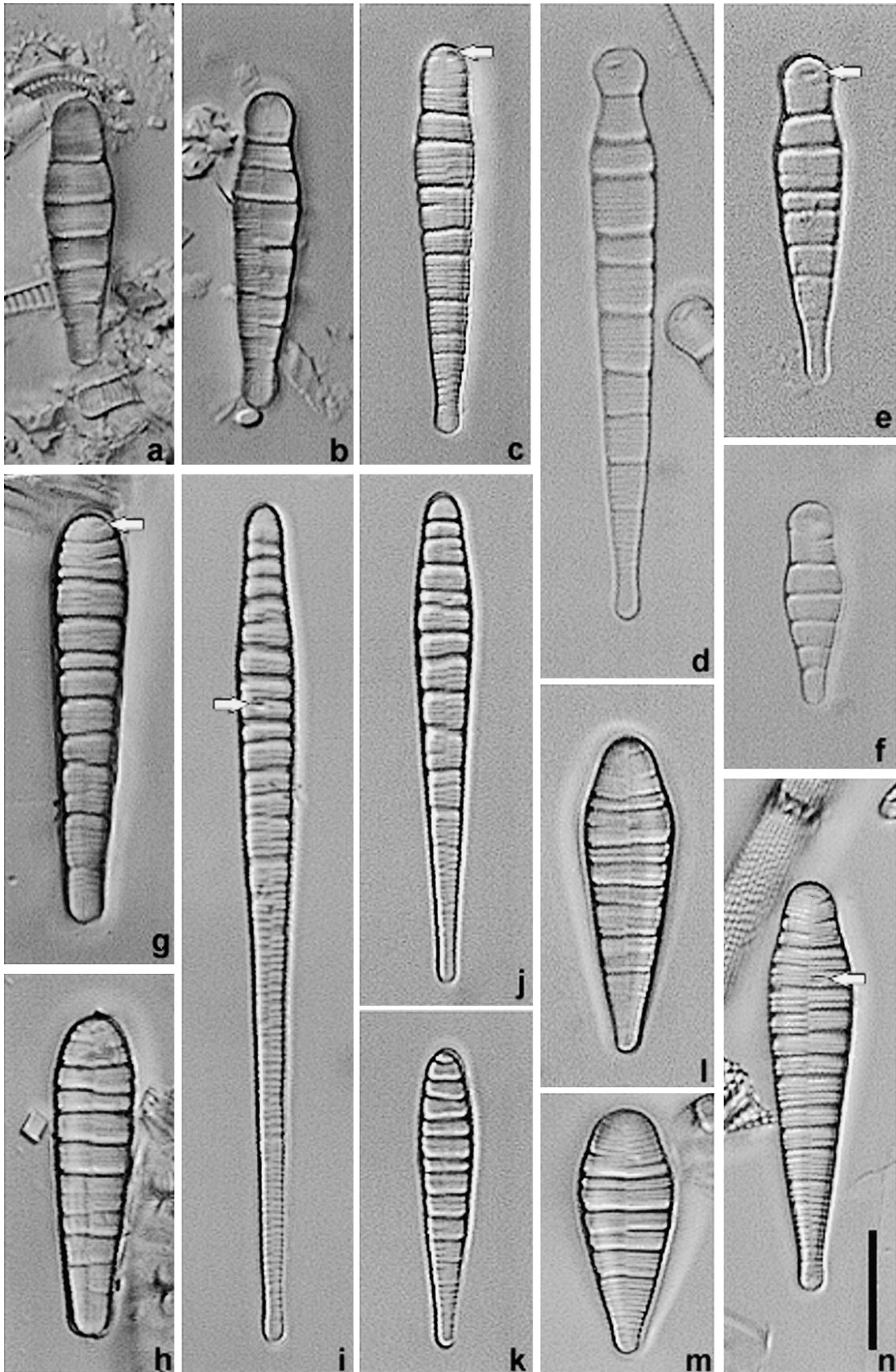


TABLE 1. Results of principal components (PC) analysis on Legendre polynomial coefficients 1–9 for all five populations.

PC	1	2	3	4	5	6	7	8	9
	Component loadings								
P ₁	-0.0151	0.0003	0.0074	-0.0065	0.0013	0.0017	-0.0033	0.0002	-0.0003
P ₂	0.0326	-0.0028	0.0010	-0.0067	0.0002	-0.0001	0.0005	0.0004	-0.0003
P ₃	0.0133	0.0064	-0.0037	0.0032	-0.0016	0.0027	-0.0047	0.0003	0.0006
P ₄	0.0031	0.0171	0.0013	-0.0002	0.0028	-0.0002	0.0013	-0.0006	-0.0020
P ₅	0.0021	0.0044	0.0037	0.0013	0.0016	-0.0016	0.0005	0.0045	0.0024
P ₆	0.0083	0.0011	0.0103	0.0038	-0.0027	0.0021	0.0013	-0.0021	0.0011
P ₇	0.0034	-0.0063	0.0029	0.0039	0.0003	0.0025	0.0002	0.0028	-0.0033
P ₈	0.0077	-0.0051	0.0025	0.0039	0.0064	-0.0029	-0.0020	-0.0017	0.0001
P ₉	-0.0011	-0.0015	-0.0030	-0.0006	0.0049	0.0060	0.0018	-0.0003	0.0014
	Percent of total variance explained								
	60.8872	16.0356	8.0063	5.3748	3.2627	2.5343	1.6518	1.3536	0.9036

Component loadings and percent variance are explained for each PC shown.

usual headpole apex placement of European populations. The Sugar Mountain Bog collection contained a taxon (referred to as “NC *M. sp.*”) whose valve outline was observed to include an attenuated headpole (Fig. 2, i–k.). It also was found to have a rimoportula placement similar to the WA *M. sp.*

The first three principal components (PCs) in the PCA accounted for 60.9%, 16.0%, and 8% of the variability across populations, respectively (84.9% of the total variance) (Table 1). The fourth through sixth PCs accounted for only 5.4%, 3.3%, and 2.5% of the variability, respectively. Inclusion of PCs beyond the third did not contribute substantially to conclusions regarding which shape components were important in understanding shape variability in these populations. Therefore, only the first three PCs were included in further analyses.

Component loadings and variance explained for the first three PCs are shown in Table 1. P₂ had the heaviest loading on the first PC. P₂ described a naviculoid outline (Fig. 3). P₁ and P₃ were also heavily loaded on the first PC. P₁ and P₃ described overall asymmetry and, specifically, asymmetry of the naviculoid shape. P₄ had the heaviest loading on the second PC. P₄ described a bicapitate outline. P₆ had the heaviest loading on the third PC. P₆ described the degree of median inflation. P₁ is also heavily loaded on the third PC. A plot of these first three PCs for all the populations is shown in Figure 4.

Results of DA, including all five populations and all individuals in building the discriminant function, showed a classification accuracy of 84%, a jackknifed classification accuracy of 82%, and a Cohen kappa of 0.80. Cohen kappa is a measure of agreement beyond chance. A Cohen kappa above 0.75 is thought to show a strong agreement beyond chance (Cohen 1960) (Table 2). In the jackknifed classification matrix, individuals from the WA *M. constrictum* population were most frequently misclassified (9/20 individuals). Six were placed with the type population of *M. circulare* and three were placed with the type population of *M. constrictum*. Five individuals from the type population of *M. constrictum* were misclassified; four were placed with the type population of *M. circulare* and one was placed with the WA *M. constrictum* population. Three individuals from the WA *M. sp.*

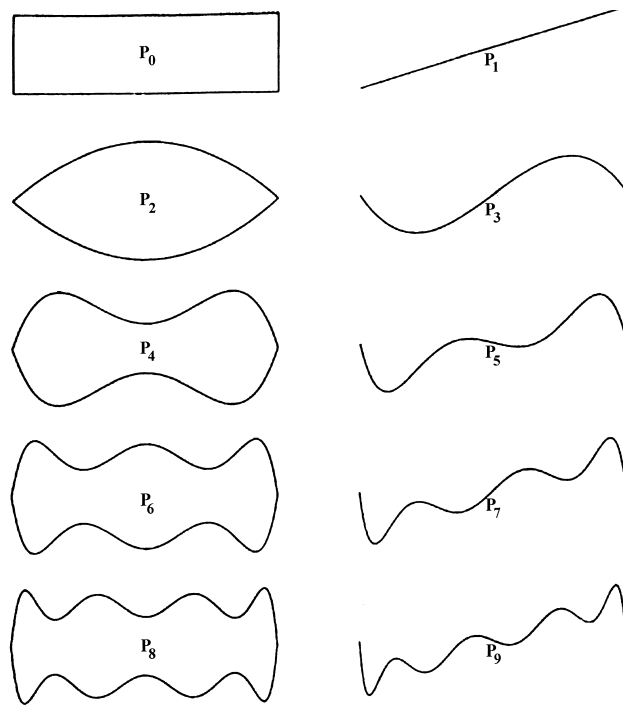


FIG. 3. Shapes constructed from Legendre polynomials P₀ to P₉ without any coefficients. (From Stoermer and Ladewski 1982, with permission.)

population were misclassified; two were placed with the type population of *M. circulare* and one with the WA *M. constrictum* population. One individual from the type population of *M. circulare* was misclassified with the WA *M. constrictum* population. Individuals from the NC *M. sp.* population were never misclassified in any DA conducted as part of this analysis.

A DA on four populations, excluding the WA *M. constrictum*, showed a classification accuracy of 93%, a jackknifed classification accuracy of 88%, and a Cohen kappa of 0.90 (Table 3). In the jackknifed classification matrix, individuals from both the type populations of *M. constrictum* and the WA *M. sp.* population were most frequently misclassified (4/20). All these

TABLE 2. Results of DA including all five populations.

Group	Jackknifed classification matrix					Percent correct
	1	2	3	4	5	
1	11	0	6	3	0	55
2	1	17	0	2	0	85
3	1	0	15	4	0	75
4	1	0	0	19	0	95
5	0	0	0	0	20	100
Total	14	17	21	28	20	82

Cohen kappa value = 0.80.

Classification matrices show predicted placement of individuals based on discriminators derived from the shape descriptors.

1, *Meridion constrictum* from Washington State; 2, *Meridion* sp. from Washington State; 3, type of *Meridion constrictum*; 4, type of *Meridion circulare*; 5, *Meridion* sp. from North Carolina.

misclassified individuals were placed with the type population of *M. circulare*. Two individuals from the type population of *M. circulare* were misclassified as members of the WA *M. sp.* population.

Finally, a DA including just the type population of *M. constrictum* and the WA *M. constrictum* population had the lowest accuracy with a classification accuracy of 88%, a jackknifed classification accuracy of 73%, and a Cohen kappa of 0.075. Individuals from both populations were misclassified with the other. In the jackknifed classification matrix, the WA *M. constrictum* population had seven misclassified individuals and the type population of *M. constrictum* had four misclassified individuals.

Graphs of the PCs showed aggregation into four groups (Fig. 4). The two populations of *M. constrictum* grouped together and showed little separation. There was not perfect separation of the other groups. However, this appeared to have to do with morphological variability associated with the size diminution series and is discussed later. Examination of component loadings for each of the PCs gave insight into what aspects of shape contribute more or less to the distinction of the groups (Table 1).

Perhaps not surprisingly, median inflation, “bicipitatness,” “naviculoidness,” and the degree of asymmetry of these shape components, were the most important aspects of shape contributing to variability across these populations. It appeared that PC1 charac-

TABLE 3. Results of DA excluding the population of *Meridion constrictum* from Washington State.

Group	Jackknifed classification matrix				Percent correct
	2	3	4	5	
2	16	0	4	0	80
3	0	16	4	0	80
4	2	0	18	0	90
5	0	0	0	20	100
Total	18	16	26	20	88

Classification matrices show predicted placement of individuals based on discriminators derived from the shape descriptors.

2, *Meridion* sp. from Washington State; 3, type of *Meridion constrictum*; 4, type of *Meridion circulare*; 5, *Meridion* sp. from North Carolina.

Cohen kappa value = 0.90.

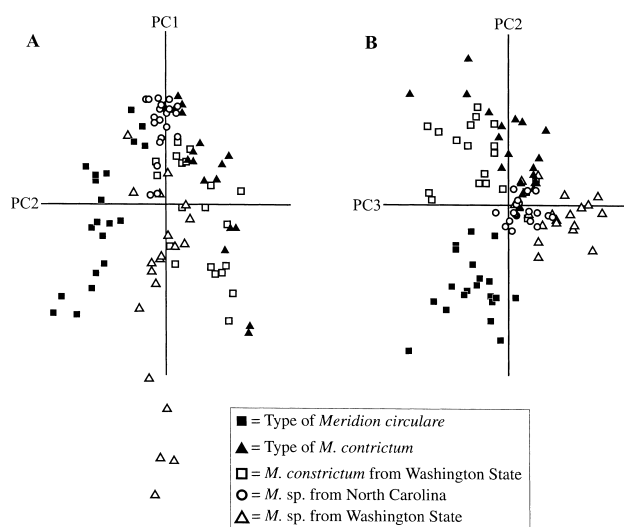


FIG. 4. (A) Plot of PC1 and PC2. (B) Plot of PC2 and PC3. PC, principal component.

terized the degree of transapical asymmetry. The NC *M. sp.*, which are not highly asymmetric transapically, grouped at the positive end of the PC1 axis (Fig. 4), whereas the highly asymmetric WA *M. sp.* tended toward the far negative end of the PC1 axis. The populations of *M. circulare* and *M. constrictum* covered the range of the PC1 axis. The position of a given individual valve depended on where in the size diminution series that individual fell. For these three populations, we observed that individuals are more asymmetric, relative to their length, when they are shorter than when they are longer. Generally, the smaller individuals tended toward the negative end of the PC1 axis, whereas the larger individuals tended toward the positive.

Principle component 2 appeared to characterize the degree of bimodality, or capitateness, of the poles (Fig. 3). The *M. constrictum* populations were found to have distinctly capitate poles and grouped on the positive end of the PC2 axis. *Meridion circulare* was not observed to have capitate poles and fell at the far negative end of the PC2 axis. Again, there was some variation across the size range.

Principle component 3 was harder to interpret. However, P_6 and P_1 were most heavily loaded on it, characterizing the degree of median inflation and the symmetry of that inflation (Fig. 3). In this case, PC3 seemed to describe how “broad shouldered” the individual was. The WA *M. sp.* was found to be broad shouldered, and individuals from that population aggregated at the positive end of the PC3 axis. The other populations fell toward the negative end.

As stated before, overlap between the populations was due, in part, to morphological variability associated with the size diminution series. Generally, for all populations except the WA *M. sp.*, individuals were found to become more similar as they get smaller. It is the case with most diatoms that as they get smaller they

lose valve outline detail and tend more toward an ovoid shape (the "Geitler phenomenon") (Geitler 1932). In this case, WA *M. sp.*, whereas generally becoming more ovoid, also becomes more broad shouldered and transversally asymmetric as it gets smaller (Fig. 2, l–n). Consequently, it was more distinct than the other groups toward the small end of the size range.

The results from DA and PCA mirrored each other. It was possible to discriminate well between all groups except between the two populations of *M. constrictum*. It was possible to discriminate between those two populations but with the lowest accuracy considered significant. This finding is consistent with the hypothesis that these are the same species from different geographic locations. There was enough morphological variability between the two populations that they could be marginally discriminated between but not as well as between what were hypothesized to be different species. Including both *M. constrictum* populations in building the discriminant function and treating them as distinct from one another lowered the overall accuracy of discrimination.

Misclassified individuals from all groups were most often placed with the type population of *M. circulare*. *Meridion circulare* has the simplest outline of the populations included in this analysis. Most of the misclassified individuals from any group were individuals at the small end of the size range. This appears to be the Geitler phenomenon making discrimination of individuals at the small end of the size range difficult.

DESCRIPTION

Characteristics of the WA *Meridion sp.* are distinct enough to warrant its own identity. The following species is proposed:

Meridion hohii Rhode, sp. nov.

Valvae heteropolaris, apicibus rotundatis, capitipolus rostratus, basi subcapitata, 14–38 μm longae, 5–7 μm latae in centro, 6–7.8 μm latae parte latissima. Coloniae spirales formatae. Costae transapicales 4–6/10 μm, striae punctatae 13–19/10 μm, parallelae. Rimoportula praesens 15%–50% secus totum longitudinem valvae.

Valves heteropolar, apices rounded, headpole rostrate, footpole (base) subcapitate, 14–38 μm long, 5–7 μm broad at center, 6–7.8 μm broad at widest part. Spiral colonies formed. Transapical costae 4–6/10 μm, striae punctate 13–19/10 μm, parallel. Rimoportula present, 15%–50% along the length of the valve.

Holotype: Slide CAS 221016 (material CAS 619992) deposited at the California Academy of Sciences.

Type locality: Taft Springs complex, Hoh River valley, Olympic National Forest, Washington State, United States.

Distribution: Currently known only from the type locality.

This taxon differs from *M. constrictum* and *M. circulare* by having a rostrate headpole and rimoportulae placement distal from the headpole.

NC *M. sp.* is also distinct enough to warrant its own identity. A proposed new taxon at the species level is being made by L.A. Brant, Northern Iowa University (personal communication).

DISCUSSION

The hypothesis that the two *Meridion* spp. from North America are unique taxa is supported by our analyses. The inability to discriminate at the small end of the size range is a problem for diatomists generally. Indeed, judging from published micrographs, some reports of *M. circulare* may actually be *M. constrictum* at the small end of the size range (Foged 1978). Studies such as this are only effective if enough of the size range is present in a collection; however, an analysis of valve outline using Legendre coefficients seems to be sensitive enough to use generally on taxa with relatively simple valve outlines.

There appears to be greater diversity than was thought in this once monotypic genus. Species in *Meridion* are distinct enough that most diatomists can instantly recognize them. However, they are also rare enough that most diatomists have not given them much scrutiny. The pronounced seasonality of *Meridion* (Krejci and Lowe 1987) is a contributing factor in this lack of scrutiny. In addition, *Meridion* appears to have a simple morphology compared with many other diatoms. In a character-poor group like this, differences in valve outline become even more important in sorting out taxa. There may be other broadly defined "cosmopolitan" taxa that require closer scrutiny to understand their true diversity and biogeography.

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