PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Volume 56, No. 10, pp. 99–106, 4 tables April 29, 2005

Taxonomy and Ecology: Further Considerations

John Patrick Kociolek
Diatom Collection, California Academy of Sciences
875 Howard Street, San Francisco, CA 94103; Email: pkociolek@calacademy.org

In this overview, points of the initial publication by Kociolek and Stoermer are reviewed and expanded upon, noting the gulf between the disciplines of taxonomy and ecology and the modest ways the two areas currently intersect. Some research areas for synergy are suggested. Previously published data on diatom community structure are assessed in terms of decreasing taxonomic resolution. The varying levels of taxonomic refinement are compared to the original data, and argue for the finest degree of taxonomic resolution. The final session of the workshop is summarized related to the desirability and implementation of on-line taxonomic resources, especially floras.

The publication of our paper on the need for a marriage of diatom taxonomy and ecology (Kociolek and Stoermer 2001) prompted a wide range of comments and responses directed to us, some constructive, some not, and was one of the most requested either of us have ever published. It also prompted the gathering/workshop, which generated the series of papers included herein. The workshop was developed to foster dialogue on the general topic of describing and promoting ways for taxonomists and ecologists to collaborate. Despite some initial cultural hurdles, by the end of the workshop participation by the entire group was open, honest and constructive.

The present report has three objectives: First, it reviews, amplifies and (hopefully) clarifies some of the points made in the earlier paper related to integrating taxonomic and ecological studies. Second, an example is based on previously published data showing the relationship (and dependency) on ecology and relative to fine- and coarse-grained taxonomy. Lastly, one of the areas of extensive discussion that coalesced the opinions of many in the final workshop session is summarized and discussed; namely the potential and desirability of flexible, on-line taxonomic products, particularly floras.

Taxonomy and Ecology-More differences than similarities

Tradition is one of the greatest barriers separating the disciplines of Ecology and Taxonomy. The number of strictly taxonomic (versus morphological/ultrastructural) papers in the diatom literature is relatively modest, compared to the number of papers with ecology as a focal point. And the breadth of places for publications of ecological papers far exceeds the relatively smaller number of publication venues for taxonomic works. Taxonomic works rarely contain any specific ecological data-cursory summaries are usually the most offered. When included, ecological data have rarely been used to substantially forward our knowledge about the taxonomy of specific entities. Many ecological studies use taxonomy as a means to an end, but the species lists (usually containing many errors in names and authorities) usually suggest a continuation of previous approaches (and errors) rather than any serious analysis of taxonomic results (though many more diatoms are being seen by ecologists than taxonomists). Finer-grained taxonomy and the current state of flux in freshwater diatom nomenclature appear to offer difficult hurdles for ecologists. The formal structures of our discipline help to perpetuate the gulf between taxonomists and ecologists. At meetings of the international society, oral presentations are arranged to separate presentations by ecologists and taxonomists; the two groups usually meet as they pass by each other going into/out of their respective sessions.

The divide between taxonomy and ecology is reflected not only in the outright absence of taxonomists in the area of ecology, but in the approaches the two groups have to taxonomy. Although, of course, there are exceptions to the stereotypes/generalizations I offer here, I would suggest that the goal of most taxonomists is what I call "correct taxonomy," that is trying to understand the morphological variability through the ontogeny of the cell and cell cycle (Kociolek and Williams 1986), what the circumscribed taxon should be called in the context of other taxa. Assignment of the taxon under study with in the Linnaean hierarchy not only offers an information storage-retrieval system (so that other data, including ecological data) can be compared and used in a wide range of studies, including comparative autecology, comparisons across space and time, alien species), but also predictive value so the hierarchy system should express the phylogenetic/evolutionary position of the taxon (Kociolek 1998). These typical taxonomic studies are usually organized and presented in stylized formats and with jargon, which appear arcane to ecologists. The back-and-forth that can result from such studies suggest more uncertainty than certainty (recall the numerous exchanges related to the proposal of the genus *Naviculadicta* — e.g., Moser et al. 1995, Kociolek 1996). The result of these debates is a wait-and-see stance from ecologists using the taxonomy, such that the impact of much of the primary literature is delayed unnecessarily. Even when the fervor of discussion has died down, and an approach has more or less been settled upon, some have found it difficult to embrace the consensus (e.g., Camburn and Charles 2000).

To achieve their research agenda, ecologists, on the other hand, focus attention on "consistent" taxonomy, making sure that the entities they encounter in the light microscope can be reliably applied to their respective group, hopefully representing some "real" biological entity. Ecologists face the challenge to avoid "shoe-horning" specimens into already-established taxon names, and to ensure their "consistent" grouping have some biological reality.

Another way taxonomists and ecologists are separated relates to their search for places to conduct their research programs. Ecologists, for the most part, seem to be attracted to systems that have been in some way impacted, usually by the activities of human beings. A driver towards these systems and their related questions may be funding, as governments (locally, regionally, nationally and internationally) seek understanding to possible impacts and remediation required. Taxonomists tend to seek out non-impacted situations to explore and conduct their research programs. It is usually these places that support native and undescribed taxa (e.g., Moser et al. 1995, 1998; Metzeltin and Lange-Bertalot 1998), and it has been suggested that an understanding of the biogeography of freshwater diatoms has been clouded by the impacts of the human species on the distribution of species (Kociolek and Spaulding 2000). Due to human disturbance, taxonomists are less likely to encounter species that might bear on the questions they pose. Thus, an issue so basic as where we work helps to divide taxonomists and most ecologists. It should be noted, however, that as ecologists seek to understand "pristine" or "unimpacted" situations, and the structure of communities found in those types of habitats, partnering with taxonomists in the investigation of those systems would be a wonderful setting for the marriage of taxonomy and ecology.

A common concern of those using diatoms to estimate water quality is the (in)ability to identify every individual encountered in their slides/counts. Many times the specimens are rare, or in cases of taxa where the entire population has nearly synchronized division, thus encountering many individuals, but who occupy a narrow range of variation. It is well documented that two or more distinct taxa may overlap morphologically, especially at the small end of the size range (Stoermer et al. 1986; Theriot and Ladewski 1986; Geitler 1932). Thus, although it may be impossible for the practicising ecologist to undertake studies to understand the full range of variation in a taxon (thus providing insights into the identity of the taxon), it must also be realized that closely related species share many similarities (hence the close evolutionary relationship), and thus it might be difficult to separate/identify isolated individuals. An analogy might be the difficulty to identify deciduous trees to species when leaves are off the tree, but easier when leaves and flowers are out.

Thus, whereas the current state of ecological and taxonomic research is of two nearly independent fields, their interrelationships are at best utilitarian, with any dependency in terms of relationships driven by taxonomists supporting ecologists with flora (rare, actually) or serving as "hired gun" identifiers of individual or groups of species.

We believe that this separation of disciplines does not have a long, sustainable future. Integration of the two disciplines is a goal worth pursuing, with the payoffs of a more rigorous, robust enterprise (more students, more positions, research impacts and more funding) that approaches answers to questions posed by ecologists and taxonomists. Areas that are and should integrate these approaches include paleolimnology-done successfully, evolutionary ecology (especially of ecologically pristine areas), conservation biology, co-evolution, and biogeography.

Taxonomic resolution and its impacts on ecological interpretations

The interplay between taxonomy and ecology perhaps finds no closer relationship, the marriage is not more intimate, than the use of diatoms in the assessment of ecological conditions. A myriad of approaches has evolved since the early ideas of Kolkwitz and Marsson (1908) to apply diatoms to understanding freshwater ecology in particular, especially focused on human impacts (pollution). Excellent overviews of these appoaches can be found in Patrick and Roberts (1979), Cholnoky (1968) and Stoermer and Smol (2001).

In quantitative approaches, early workers suggested robust analyses (robust in the sense of statistics/mathematical models) required enumeration of thousands (in some cases tens of thousands) of valves to achieve reliable results (e.g., Patrick et al. 1954; Hohn 1961; Hohn and Hellerman 1963; Patrick 1968). Since the days of these extensive identification and enumeration methods, efforts were made to save time in the analysis of samples and to essentially reduce/minimize cost (because many of these studies were by now in the U.S. being funded by government agencies) but derive "correct" assessments of water conditions. This has led to a variety of approaches where counts are reduced to a certain number of valves (e.g., Stevenson and Pan 2001; 300–600/sample seems to be settled upon without too much debate) or until no new taxa have been encountered (e.g., Charles et al. 2002; assuming richness plays some role in the analysis/understanding of water quality).

Although the effort has focused on reducing the number of valves to count (yet still achieving a correct assessment), few studies have looked at ways to reduce taxonomic resolution and still achieve a "correct" understanding of water quality. In other words, does all the "fuss" made by taxonomists to identify and separate taxa at the level of species, variety and form (and this is being done with renewed vigor-e.g. Lange-Bertalot and Metzeltin 1996; Reichardt 1999 as good examples) contribute in a substantitive way to our understanding of water quality?

In the era when scientists were exploring myriads of ways to apply diatoms to water quality studies, complete data sets were often published (e.g., Hohn and Hellerman 1963; Patrick 1968; Patrick and Roberts 1979), as opposed to the summary statistics and data plots seen in most "modern" analyses.

To explore whether taxonomic resolution, i.e. coarse or fine-grained taxonomy, mattered in the interpretation of ecological data, we selected data sets published by Patrick (1968) on Darby Creek, Pennsylvania (USA). For each data set, we calculated species richness and Shannon-Wiener diversity, for three conditions, including the data set as presented (with identifications made by Patrick and finest taxonomic resolution presented in the paper at that time (what we have termed "ALL") and two levels of reduced taxonomic resolution. In one case, we subsumed all subspecific epithets into the species ("SPECIES") and then all species and subspecific epithets subsumed into genera ("GENUS"). The richness and diversity calculations were then ranked for each of the 8 stations based on the three different levels of taxonomic resolution. We then made the assumption that the complete or "ALL" dataset, with the finest level of taxonomic resolution most closely representing the relative ecological conditions of the eight samples. We then compared these relative relationships with those derived from approaches with more coarse-grained taxonomies, to see how well they might serve as proxies for the finest-level of taxonomic resolution. We should note here that the finest-grained taxonomy applied in 1968 probably does not represent the finer distinctions made today.

In Table 1 are listed the richness and diversity measures for the eight samples provided in Patrick (1968) for "ALL," "SPECIES" and "GENUS." The eight samples are then ranked from most to least rich, and from most to least diverse in Table 2. The richness and diversity measures are provided for pennate taxa only in Table 3. Ranking of the pennate taxa measures is provided in Table 4.

The data suggest that the samples were relatively rich, in the data including pennate and centric taxa, with total taxa numbers ranging from 101 to 112 in the ALL samples, 84-98 taxa in the SPECIES samples and 19–23 taxa in the GENUS samples. Diversity ranged from 4.5170 to 4.9641 in ALL samples 4.2581 to 4.6687 in SPECIES samples and 2.4761 to 2.8527 in the GENUS samples. In the rankings, sample 8 was the richest in all calculations, whereas sample 6 (ALL, SPECIES) and sample 7 (GENUS) were poorest in terms of taxa. Interestingly, in terms of diversity, sample 3 was most diverse in each of the three sample calculations, whereas sample 8 (the richest in terms of number of taxa) was the least diverse in all three calculations. Assuming the ALL samples best approximated the "true" condition, SPECIES rankings of richness matched exactly the ALL calculations, whereas GENUS matched only 50% of the rankings. For diversi-

TABLE 1. Comparison of Richness and Shannon-Weiner Diversity including all taxa.

Sample	*Richness*	*Diversity*
Sample 1		
ALL	105	4.6555
SPECIES	88	4.3523
GENUS	22	2.6942
Sample 2		
ALL	104	4.6967
SPECIES	88	4.4337
GENUS	21	2.7002
Sample 3		
ALL	103	4.9641
SPECIES	87	4.6687
GENUS	20	2.8527
Sample 4		
ALL	111	4.6429
SPECIES	95	4.366
GENUS	23	2.5449
Sample 5		
ALL	108	4.8087
SPECIES	94	4.4895
GENUS	21	2.776
Sample 6		
ALL	101	4.8705
SPECIES	85	4.5502
GENUS	21	2.747
Sample 7		
ALL	107	4.7037
SPECIES	92	4.3687
GENUS	19	2.6464
Sample 8		
ALL	112	4.517
SPECIES	98	4.2581
GENUS	23	2.4761

TABLE 2. Ranking of samples by ALL, SPECIES only and GENUS only for Richness and Shannon-Weiner Diversity with all taxa included. "#shared" shows the number of rankings that are in agreement with All taxa.

Richness All	*Richness Species*	*Richness Genus*	*Diversity All*	*Diversity Species*	*Diversity Genus*
8	8	8	3	3	3
4	4	4	6	6	5
5	5	1	5	5	6
7	7	5	7	2	2
1	1	6	2	7	1
2	2	2	1	1	7
3	3	3	4	4	4
6	6	7	8	8	8
#shared with ALL		4 out of 8		6 out of 8	3 out of 8

TABLE 3. Comparison of Richness and Shannon-Weiner Diversity including pennate taxa only.

Sample	Richness	Diversity
Sample 1		
ALL	94	4.3976
SPECIES	79	4.0794
GENUS	19	2.2934
Sample 2		
ALL	95	4.4671
SPECIES	80	4.1681
GENUS	18	2.2619
Sample 3		
ALL	95	4.7224
SPECIES	79	4.389
GENUS	17	2.4439
Sample 4		
ALL	102	4.3962
SPECIES	86	4.0926
GENUS	20	2.1704
Sample 5		
ALL	100	4.6403
SPECIES	86	4.2801
GENUS	18	2.4285
Sample 6		
ALL	93	4.6821
SPECIES	78	4.3588
GENUS	18	2.578
Sample 7		
ALL	99	4.4825
SPECIES	83	4.0871
GENUS	16	2.2709
Sample 8		
ALL	102	4.262
SPECIES	88	3.9695
GENUS	20	2.0455

TABLE 4. Ranking of samples by ALL, SPECIES only and GENUS only for Richness and Shannon-Weiner Diversity with pennate taxa only included. "#shared" shows the number of rankings that are in agreement with All taxa.

Richness All	*Richness Species*	*Richness Genus*	*Diversity All*	*Diversity Species*	*Diversity Genus*
8	8	8	3	3	6
4	4	4	6	6	3
5	5	1	5	5	5
7	7	2	7	2	1
2	2	5	2	4	7
3	1	6	1	7	2
1	3	3	4	1	4
6	6	7	8	8	8
#shared with ALL	6 out of 8	2 out of 8		4 out of 8	3 out of 8

ty, SPECIES matched 75% of the rankings of ALL, but GENUS matched ALL in less than 40% of the rankings.

In data including pennate taxa only, richness ranged from 93–102 taxa in ALL, 79–88 in SPECIES and 16–20 in GENUS. Diversity ranged from 4.2620 to 4.7224 in ALL, from 3.9695 to 4.3890 in SPECIES and from 2.0455 to 2.4439 in GENUS. In the rankings, data for pennates only mirrored the total taxon scores, while sample 8 being the most rich, and sample 6 being least rich in ALL and SPECIES and sample 7 least rich in the GENUS calculation. Likewise, sample 3 was the most diverse and sample 8 (the most species rich) was least diverse. Order of ranking of samples in terms of richness, 6 of the 8 rankings of SPECIES were the same as ALL, whereas only 2 of 8 were the same between GENUS and ALL. Order of ranking of samples in terms of diversity, as in pennate and centric taxa, showed less correspondence between SPECIES and ALL (4 out of 8) and GENUS and ALL (3 out of 8).

These data seem to suggest that even modest changes in taxonomic resolution can lead to large changes in the relative ranking of samples (up to 50% difference). In other words, reduced taxonomic resolution does not provide accurate prediction of relative rankings of water condition. The surprising result of an inverse relationship between species richness and diversity suggest even the most common measures of water quality analysis may require further critical evaluation. Further analysis is needed, with robust statistical power, on the impacts of reduced taxonomic resolution on predicting the relative rankings of water conditions.

CREATING MODERN TAXONOMIC TOOLS FOR A LARGE, INTERNATIONAL USER COMMUNITY

The workshop discussed at length ways in which taxonomic information can best be conveyed to the broad community of diatomists, serving both taxonomists and ecologists (and others as well). Praise was evident for projects like the Süsswasserflora (Krammer and Lange-Bertalot 1986–1991), with its great taxonomic and geographic breadth, detailed taxonomic information, and incredible photo documentation. A second project also hailed by the workshop participants, though more restricted in scope, was the series on diatoms from the Baltic Sea (Snoeijs and co-workers, 1993–1998). The project succinctly brings together illustrations with listings of important literatures and helpful comments into a common, useful format. It also represents a collaboration of scientists from different labs, countries and perspectives.

Shortcomings of traditional floras include the lack of tying images or distributions explicitly to specimens in publicly accessible collections, uncertainty or lack of studies documenting synonymies, lack of detailed geographic summaries, the static nature of data and the high cost of the published volumes.

Given the limited number of formally trained taxonomists and systematists worldwide (Kociolek and Stoermer 2001) and the increased possibilities for interaction and collaboration afforded by the internet, many workshop participants saw the opportunities and benefits of developing an on-line flora. This concept has been discussed in part by Kociolek (accepted). Such a flora could also be linked to/integrated into other information systems that are already in place or in development that offer templates for achieving additional goals (offering the ability for users to provide comments and feedback, allowing the flora to create dialogue and be a dynamic entity for several possible communities; see one example dealing with the freshwater diatoms of south Florida (and the system in place at Academy of Natural Sscience, Phildelphia [ANSP] as current examples). The call for on-line tools such as floras was recently presented in *Science* (Wheeler et al. 2004).

Information that can be an integral part of an on-line flora include name (linked to databases on nomenclature), description, important references (linked to on-line literature databases), verified distributions (linked to collection/herbarium databases), reported distributions (linked to literature databases), images (linked to image databases), types (linked to collection databases) and the person(s) responsible for the entry information. There is currently being developed enough information infrastructure available on-line such that an on-line flora is possible. It is time for members of the diatom community to work towards producing this much-needed tool—a tool that would serve both taxonomists and ecologists.

Literature Cited

Charles, D., C. Knowles, and R.S. Davis, eds. 2002. *Protocols for the Analysis of Algal Samples Collected as part of the U.S. Geological Survey National Water-Quality Assessment Program*. Report No. 02-06. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA. 124 pp.

Cholnoky, B.J. 1968. *Die Ökologie der Diatomeen in Binnengewässern*. J. Cramer, Lehre, Germany. 699 pp.

Geitler, L. 1932, Die Formwechsel der pennaten Diatomeen (Kieselalgen). *Archiv für Protistenkunde* 78:1–226.

Hohn, M. 1961. The relationship and population density in diatom populations from Silver Springs, Florida. *Transactions of the American Microscopical Society* 80:140–165.

Hohn, M., and J. Hellerman. 1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. *Transactions of the American Microscopical Society* 82:250–329.

Kociolek, J.P. 1996. Taxonomic instability and the creation of *Naviculadicta* Lange-Bertalot in Moser and Lange-Bertalot, a new, catch-all genus of diatoms. *Diatom Research* 11:223–224.

Kociolek, J. P. 1998. Does each genus of diatoms have at least one unique feature? *Diatom Research* 13:177–179.

Kociolek, J.P. (In press.) Some thoughts on the development of a diatom flora for freshwater ecosystems in the continental United States and a listing of Recent taxa described from U.S. freshwaters. *Hydrobiologia*. Festschrift for Rex Lowe.

Kociolek, J.P., and S.A. Saulding. 2000. Freshwater diatom biogeography. *Nova Hedwigia* 71:223–241.

Kociolek, J.P,. and E.F. Stoermer. 2001. Taxonomy and ecology: A marriage of necessity. *Diatom Research*

16:433–442.
Kociolek, J.P,. and D.M. Williams. 1987. Unicell ontogeny and phylogeny: Examples from the diatoms. *Cladistics* 3:274–284.
Kolkwitz, R., and M. Marsson. 1908. Ökologie der pflanzliche Saprobien. *Berichte der Deutsche Botanischen Gesellschaft* 26:505–519.
Krammer K., and H. Lange-Bertalot. 1986. Bacillariophyceae. Naviculaceae. 2/1. *In*: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds., *Süsswasserflora von Mitteleuropa* . Gustav Fisher, Stuttgart, Germany. 876 pp.
Krammer K., and H. Lange-Bertalot. 1988. Bacillariophyceae. Bacillariaceae, Epithemiaceae, Surirellaceae. 2/2. *In*: H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds., *Süsswasserflora von Mitteleuropa* . Gustav Fisher, Stuttgart, Germany. 596 pp.
Krammer K., and H. Lange-Bertalot. 1991a. Bacillariophyceae. Centrales, Fragilariaceae, Eunotiaceae. 2/3. *In*: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds.,.*Süsswasserflora von Mitteleuropa*. Gustav Fisher, Stuttgart, Germany. 576 pp.
Krammer K., and H. Lange-Bertalot. 1991b. Bacillariophyceae. Achnanthaceae. Kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema. 2/4. *In*: H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds., *Süsswasserflora von Mitteleuropa.* Gustav Fisher, Stuttgart, Germany. 437 pp.
Lange-Bertalot, H., and D. Metzeltin. 1996. Indicators of Oligotrophy. 800 taxa representative of three ecologically distinct lake types. Carbonate, oligodystrophic, weakly buffered soft water. *Iconographia Diatomologica* 2:1–396.
Metzeltin, D., and H. Lange-Bertalot. 1998. Tropical diatoms of South America I. About 700 predominately rarely known or new taxa representative of the neotropical flora. *Iconographia Diatomologica* 5:1–695.
Moser G., A. Steindorf, and H. Lange-Bertalot. 1995. Neukaledonien. Diatomeenflora einer Tropeninsel. *Bibliotheca Diatomologica* 32:1–340.
Moser G., H. Lange-Bertalot, and D. Metzeltin. 1998. Insel der Endemiten. Geobotanisches Phänomen Neukaledonien. *Bibliotheca Diatomologica* 38:1–464.
Patrick, R.M. 1968. The structure of diatom communities in similar ecological conditions. *The American Naturalist* 102:173–183.
Patrick, R.M., and N.A. Roberts. 1979. Diatom communities in the Middle Atlantic states, U.S.A. Some factors that are important for their structure. *Nova Hedwigia*, *Beiheft* 64:265–284.
Patrick, R.M., M. Hohn, and J. Wallace. 1954. A new method for determining the pattern of the diatom flora. *Notulae Naturae* (259):1–12.
Reichardt, E. 1999. Zur Revision der Gattung *Gomphonema*. Die Arten *G. affine/insigne, G. angustatum/micropus*, *G. acuminatum* sowie gomphonemoide Diatomeen aus dem oberoligozän in Bohmen. *Iconographic Diatomologica* 8:1–203.
Snoeijs, P., ed. 1993. *Intercalibration and Distribution of Diatom Species in the Baltic Sea*, vol. 1. Opulus Press, Uppsala, Sweden. 129 pp.
Snoeijs, P., and S. Vilbaste, eds. 1994. *Intercalibration and Distribution of Diatom Species in the Baltic Sea*, vol. 2. Opulus Press, Uppsala, Sweden. 125 pp.
Snoeijs, P., and M. Potapova, eds. 1995. *Intercalibration and Distribution of Diatom Species in the Baltic Sea*, vol. 3. Opulus Press, Uppsala, Sweden. 125 pp.
Snoeijs, P., and X. Kasperoviciene, eds. 1996. *Intercalibration and Distribution of Diatom Species in the Baltic Sea*, vol. 4. Opulus Press, Uppsala, Sweden. 125 pp.
Snoeijs, P., and N. Balashova, eds. 1998. *Intercalibration and Distribution of Diatom Species in the Baltic Sea*, vol. 5. Opulus Press, Uppsala, Sweden. 143 pp.
Stevenson, R.J., and Y. Pan. 2001. Assessing environmental conditions in lakes and streams with diatoms. Pages 11–40 *in* E.F. Stoermer and J.P. Smol, eds., *The Diatoms. Application for Environmental and Earth Sciences*. Cambridge University Press, Cambridge, UK. 469 pp.
Stoermer, E.F., T.B. Ladewski, and J.P. Kociolek. 1986. Further observations on *Gomphoneis*. Pages 205–213 *in* M. Ricard, ed., *Proceedings of the 8th Symposium on Living and Fossil Diatoms*, Paris, 1984.
Stoermer, E.F., and J.P. Smol, eds. 2001. *The Diatoms. Application for Environmental and Earth Sciences*. Cambridge University Press, Cambridge, UK. 469 pp.

THERIOT, E., AND T.B. LADEWSKI. 1986. Morphometric analysis of shape of specimens from the neotype of *Tabellaria flocculosa* (Bacillariophyceae). *American Journal of Botany* 73:224–229.

WHEELER, Q.D., P.H. RAVEN, AND E.O. WILSON. 2004. Taxonomy: Impediment or Expedient? *Science* 303(5656):285.