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VIE ET MILIEU OF FRESHWATER DIATOMS. COMMENT ON CURRENT ISSUES IN DIATOM ECOLOGY AND FLORISTICS

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FRESHWATER EPIPHYTES
pH TOLERANCE
DIATOM IDENTIFICATION
STABILITY OF MORPHOLOGY

ABSTRACT. – Some problems arising from the sampling and recording of diatoms from acidic freshwater, epiphytic habitats are discussed. This led to further study of data assemblages recorded from more general low pH sites and suggestions for more definitive clusters of diatoms related to narrow pH ranges. Finally, some brief thoughts on the identification of diatoms and the stability of diatom morphology at the species level.

ÉPIPHYTES D'EAU DOUCE
TOLÉRANCE AU pH
DIATOMÉES
IDENTIFICATION
STABILITÉ MORPHOLOGIQUE

RÉSUMÉ. – Quelques problèmes apparus lors de l'échantillonnage et du recensement des Diatomées des eaux acides et des habitats épiphytes sont discutés. Ceci mène à des études plus étendues d'ensembles de données recueillies dans des stations à pH généralement bas, ainsi qu'à des suggestions pour des séparations plus nettes des Diatomées liées à des games de pH étroites. Enfin quelques brefs avis à propos de l'identification et la stabilité de la morphologie des Diatomées au niveau de l'espèce sont exposés.

Very few attempts have been made to sample epiphytic diatoms, though every macrophyte in both freshwaters and marine habitats supports an attached flora of diatoms often associated with species from other algal groups. One notable study concentrating on *Tabellaria* growing on *Phragmites* in lakes in Cumbria (Knudson 1957) has never been followed up. I was alerted to the problem on reading a recent paper by Nygaard (1999) recording a long list of "epiphytic" species in the Danish lake Grane Langsø. This listing raises important questions which I wish to pursue in the light of my studies of diatoms in ponds, lakes and rivers where the epiphytic flora usually tends to be dominated by a few (3–4) species. Some of the important prime users of the basic floristic data on diatoms are applied scientists involved in methods for studying water pollution, river/lake management, etc., and it is essential that the exact site where the diatoms grow is specified and when recording the species on microscope slides the species names are correct.

Diatom species have very specific requirements in terms of habitat – the species "know" exactly where they can grow. However, because waters are not stationary, species can be circulated to varying degrees by water, animal, etc. movement. Thus casual (contaminating) species can occur in any sample. Epiphytes are, by definition, attached though not all are immobile, and when released from their attachment structure some can be highly motile, e.g. *Gomphonema* spp. In my opinion samples should be of single hosts but when this is not possible the individual hosts should be separated not lumped as a single entity as in Nygaard (1999). Gentle washing will help to remove contaminants. The presence of green filamentous algae or other epiphytes should be treated separately. Hopefully the result will be a sample containing few contaminants – no sample will ever be completely free of stray organisms. In some water bodies the host plants become surrounded by a loose mucilage (I believe largely produced by the epiphytes) and in this mucilage other algae including non-attached diatoms can live. The mucilaginous community has been termed the metaphyton (see Behre, 1956 & 1966 for detailed study and Round 1981 for a brief comment).

Table I is taken from Nygaard (1999) and records the relative frequency of epiphytic diatoms on ten samples of a mixture of *Isoetes* spp. and *Sphagnum* spp. plus an unnamed macro-alga growing in the acidic waters of Grane Langsø at 0.25 and 11.25 m depth. Of the over 50 diatoms recorded, only *Eunotia bilunaris*[*] (16.9%), *Eunotia*

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[*] The species listed by Nygaard do not have authorities for the specific names and therefore it would be improper for me to add such, since I do not know which floras Nygaard was using. Other references do have them mentioned.

Table I. – Relative frequency of diatoms epiphytic and in plankton in Grane Langsø based on July samples (from Nygaard 1999).

Diatoms	11.25 m depth	0.25 m depth	plankton 0-10 m
Achnanthes minutissima	0.806	5.13	0
Achnanthes lanceolata	0	0.136	0
Aulacoseira alpigena	0.242	0.157	0
Aulacoseira granulata	0	0.03	0
Aulacoseira islandica	0.242	0.188	0
Aulacoseira lacustris	2.82	0.628	0
Aulacoseira laevissia	0.242	0	0
Aulacoseira lirata var. *lirata*	5.238	0.753	0
Cocconeis placentula var. *euglypta*	0.242	0.282.	0
Cocconeis placentula var. *linearis*	0	0.209	0
Cymbella amphicephala var. *hercynica*	0	0.136	0
Cymbella gracilis	0.242	2.05	0
Cymbella hillarii	0	0.03	0
Cymbella leptoceros	0	0.03	0
Cymbella perpusilla var. *striatior*	0	0.06	0
Cymbella silesiaca	0.242	1.39	0
Eunotia arcus	0.242	0	0
Eunotia bilunaris	16.92	2.51	0
Eunotia incisa	0.242	1.773	0
Eunotia implicata	3.384	2.51	0
Eunotia serra var. *diadema*	0.242	5.23	0
Eunotia ssp.	27.397	36.5	0
Fragularia ulna var. *acus*	0.242	0	0
Frustulia rhomboides var. *saxonica*	0.242	15.17	0
Hantzschia amphioxis	0	0.3	0
Navicula heimansii	0.242	0.188	0
Navicula heimansioides	0	0.973	0
Navicula jaernefeltii	0.242	0.09	0
Navicula lobeliae	0.242	0.04	0
Navicula pupula	0.967	0.09	0
Navicula tuscula	0	0.03	0
Neidium affine var. *affine*	0	0.03	0
Neidium affine var. *longipes*	0	0.09	0
Neidium densestriatum	0	0.43	0
Nitzschia linearis var. *tenuis*	0.242	0.544	0
Nitzschia microcephala forma	0.242	0.06	0
Pinnularia braunii	0	0.06	0
Pinnularia dactylus	0.242	0.03	0
Pinnularia divergentissima forma	0.242	0.03	0
Pinnularia gentilis	0.242	0.28	0
Pinnularia gibba	0.967	0.533	0
Pinnularia major	0.967	0.03	0
Pinnularia mesolepta var. *gibberula*	0	0.03	0
Pinnularia microstauron morphotype 1	0.242	0.240	
Pinnularia microstauron morphotype 2	0.242	0.345	0
Pinnularia subcapitata	2.42	0.74	0
Pinnularia subgibba	0	0.06	0
Pinnularia sudetica	0.242	0.157	0
Pinnularia viridis	0.242	0.21	0
Stauroneis anceps var. *hyalina*	2.176	0	0
Stauroneis phoenicenterum	0.242	0.9	0
Surirella biserta var. *constrictum*	0.242	0	0
Surirella linearis	0.242	0.25	0.25
Tabellaria flocculosa	28.2	17.36	0
Tabellaria fluccolosa var. *sterionelloides*	0	0	0.08

spp. (23.3%) and *Tabellaria flocculosa* (28.2%) are at all abundant at 11.25 m and they are typical members of the epiphytic flora in acidic lakes. At 0.25 m depth *Eunotia* spp. (36.5%), *Frustulia rhomboides* v. *saxonica* (15.17%) and *Tabellaria flocculosa* (17.30%) can be added to this acidic flora. Many interesting problems arise from the perusal of this list. The obvious first comment is that the *Eunotia* and *Tabellaria* are non-motile, both attaching by means of extruded mucilage pads, whereas *Frustulia* is a biraphid motile genus, but here it is almost certainly the form which lives in mucilage tubes, though why it does not build populations at 16.5 m is not clear. This raises my first concern – microscopic observation of collections in the live state is desirable – this would have clarified the microhabitat of *Frustulia* and also the exact status of the *Eunotia* spp. which in the case of *E. bilunaris* is an attached epiphyte (personal studies – text in preparation) but exactly where do the other 40-plus species grow. In my opinion the separation of rare species in a population from the contaminants should be essential basic ecological practice. Are there any rare but truly epiphytic species in Nygaard's list ? I offer the following comments. Of the non-motile species listed, *Achnanthes minutissima* in some form may be epiphytic but the exact site may be on other microscopic algae, and the acid waters do not favour the small forms of this taxon which is a completely chaotic mix, probably of individual species still requiring proper study – it's inclusion in a list of indicator organisms is almost certainly useless. *Achnanthes lanceolata* is not a species expected in acid waters and may be a mistaken identification. The *Aulacoseira* species are characteristic of acid waters but are not epiphytic – they almost certainly occur as filaments of cells floating on the surface of the sediments and should not be in a list of epiphytes, at least not until someone observes populations strictly associated with host plants. *Cocconeis placentula* is rare here due to the chemical nature of the water – though it is common as an epiphyte in alkaline situations, but the same comments apply as to *A. minutissima* – many *placentula* variants require extensive study – records have little value until the taxonomy is sorted out. *Cymbella* species are often components of epiphytic sites but only *C. gracilis* on this list is. Dare I say it, but *Cymbella* species are some of the most difficult to identify with confidence and since Nygaard's time have been split into at least six genera – often very difficult to distinguish. *Fragilaria* (not *Fragularia*) *ulna* is another problem in taxonomy and Nygaard was almost certainly not aware of this. Not only was it in *Synedra* for at least 150 years (and in my view should still be there), now it is proposed that the name be changed again to *Ulnaria* (Kütz.) Compère (2001) in complete disregard of the advice in the International Code of Nomenclature to preserve, where possible, commonly applied names (see the Code). Of the remaining taxa in Nygaard's list – from *Hantzschia* down to *Surirella* – all are biraphid, motile forms associated with sediments and thus contaminants. One species merits further comment and this is *Hantzschia amphioxy*, only recorded at 0.25 m depth and not surprising since it is probably the commonest of all soil diatoms – a most remarkable feature of its distribution is why it is not (or perhaps rarely) washed into permanently submerged sites. In over 50 years observation I have never recorded more than an occasional valve in lakes or rivers but in almost every wet place on soils it can be found. Finally, only two genera (*Eunotia* and *Tabellaria*) are common in the acidic epiphyton of Grane Langsø.

The site at 0.25 m depth has the larger flora representing a greater contribution of species from stones and more varied sediments, etc. whilst at 11.25 m probably only a uniform fine organic sediment is common. In addition, light limitation may operate at the lower depth.

Comparing the overall Nygaard data with other recent studies, e.g. Eloranta (1988) who combined epiphyton and epilithon (using the unfortunate term periphyton) recorded a small pool of species, *viz. Anomoeoneis* (*Brachysira*) *brachysira* (Bréb.) Grun., *Eunotia lunaris* (Ehrenb.) Bréb., *E. tenella* (Grun.) Hust., *E. veneris* (Kütz.) O. Müll., *Frustulia rhomboides* v. *saxonica* (Rabenh.) De Toni, *Navicula cari* Ehrenb., *Tabellaria flocculosa* (Roth) Kütz. and *T. quadriseptata* Knudson which are all components of the pool of species common to acid lakes. A later study from a more widespread sampling of lakes ranging from Lappland south to the Tatra mountains (Eloranta & Kwandrans 2002) also revealed a low species richness (21–25) species) with acidophilic and acidobiontic elements. Cluster analysis enabled these workers to refine the distribution into five clusters of species which were scattered over the regions though neither pH values, conductivity nor total phosphate levels were sufficiently correlated with the clusters to give useful ecological characterisation.

My own observations on diatom epiphytes from U.K. acid waters confirms the dominance of *Tabellaria flocculosa* (Roth) Kütz., *Eunotia* species, particularly *E. incisa* Greg., *Peronia fibula* (Bréb. *ex* Kütz.) Ross, *Cymbella aequalis* W. Sm., *C. gracilis* (Ehrenb.) Kütz., but *Frustulia rhomboides* (Ehrenb.) De Toni and *F. rhomboides* v. *saxonica* Rabenh. are abundant, though never dominant, and part of an unattached flora. A regular occurrence of two biraphid spp., *Navicula heimansii* Van Dam & Kooyman and *Brachysira brebisonnii* R. Ross in Hartley suggest a small, probably motile, element in the flora.

As implied by Eloranta & Kwandrans there is simply a pool of acid-loving species in lakes of pH below (6.0) 5.5 but their presence or absence in any one lake is determined by microhabitat factors such as host specificity (sand grain/higher plant host – this latter requires correlating at the species level), sediment type (epipelon), stone type (epilithon) compounded by as yet unknown chemical features. If we are to use terminology such as acidophilic/ acidobiontic then these must be defined by pH ranges or some other character of the environment – the controlling mechanisms lie in the dual environment of physical position and chemical status of the water – the "milieu".

A brief consideration of the chemical "milieu" is warranted.

There is much data in the literature on pH ranges of individual diatom species but space restricts a widespread analysis. I have therefore selected one detailed study of 178 sites based on the flora retrieved from each lake by sampling the surface (most recent) sediment from the deepest point (Stevenson *et al.* 1991). This method of sampling collects all the diatom species, only some of which are epiphytic. I have extracted two sets of species, those (non-planktonic) occurring in more than 100 sites and therefore forming a widepread (Scandinavia/ U.K.) pool of common acid-loving species. They are together with their pH, *Achnanthes* (*Psammothidium**) *marginulata* Grun. in Cleve & Grun. (5.2), *A.* (*Achnanthidium*) *minutissima* Kütz. (6.3), *Brachysira brebissonii* R. Ross in Hartley (5.3), *B. vitrae* (Grun.) Ross in Hartley (5.9), *Cymbella hebredica* (Grun. ex Cleve) Cleve (5.1), *C. lunata* (W. Sm. in Grev.) (5.1), *C. perpusilla* A. Cl. (5.2), *Eunotia exigua* (Bréb. *ex* Kütz.) Rabenh. (5.1), *E. naegelii* (5.0), *E. pectinalis* v. *minor* (Kütz.) Rabenh. (5.4), *E. tenella* Grun. in V. Heurck (5.2), *Fragilaria virescens* Ralfs (5.7), *Frustulia rhomboides* (Rabenh.) De Toni (5.2), *F. rhomboides* v. *saxonica* (Rabenh.) De Toni (5.1), *Navicula leptostriata* Jørgensen (5.1), *N. madumensis* Jørgensen (5.4), *Peronia fibula* (Bréb. ex Kütz.) Ross (5.3), and *Tabellaria flocculosa* (Roth) Kütz. (5.4). Of these the most widespread is *T. flocculosa* in 171 sites and we could term these *T. flocculosa* lakes or alternatively lakes with pH between 5.0–6.0, that is an acidophilic group. But *Achnanthidium minutissima* falls outside this group in terms of pH. As mentioned above this is not yet a useful indicator species owing to the chaos in the taxonomy. Further analysis of this excellent compilation of data could profitably extract the less common species which must have additional constraints outside that of pH. Can a truly acidobiontic cluster be determined from the Stevenson *et al.* data? There is a problem in that, within the whole set (178 sites) a much smaller number of sites can be classed as acidobiontic (the species only occur in 4 to 88 lakes) compared with a 100+ in the acidophilic series. This does not however affect the outcome. If we assume an upper pH limit (5.0) for these, then we have two former *Achnanthes* species, *Psammothidium austriaca* Bukh. & Round (1996) (4.9), (*A.*) *P. austriaca* (Hust.) Bukh. & Round (1996) (4.9), *Asterionella ralfsii* W. Sm. (4.9), *Brachysira serians* (Bréb. *ex* Kütz) Round & Mann (4.8), *Eunotia bactriana* Ehrenb. (4.7), *E.* cf. *minima* (no attribution) (4.9), *E. microcephala* Krasske *ex* Hust. (4.7), *E. microcephala* v. *tridentata* (A. Meyer) Hust. (4.7), *E. schwabei* Krasske (4.7), *E. trinacria* Krasske (4.8), *E. perpusilla* Grun. in Van Heurck (4.7), *Fragilaria* cf. *oldenburgiana* (?) (4.7), *Navicula cumbriensis* Haworth (4.9), *N. hoefleri sensu* Ross & Sims (4.9), *N. madumensis* (4.9), *Pinnularia rupestris* Hantzsch in Rabenh. (4.9), *Semiorbis hemicyclus* (Ehrenb.) Patrick in Patrick & Reimer (4.8), *Oxyneis* (*Tabellaria*) *binalis* (Ehrenb.) Grun. in Van Heurck (4.7). The noteworthy features of these "*Eunotia* lakes" (acidobiontic) are that the pH range is restricted (4.7–5.0) and that with one exception they occur in less than 50 of the 178 sites and that not one of an extreme acid tolerant group of species (i.e. below pH 4.5 and mainly below pH 3.0) occur. This latter group is only common in acidic, often volcanic waters (see the extensive Japanese literature, the most recent of which are Idei & Mayama 2001 and Jordan 2001). Sites in Stevenson *et al.* (1991) above pH 6.0 are characterised by low occurrence (less than 50 sites) and there is a high probability that these species are contaminants from adjacent waters. This is probably a major problem in interpreting data from the deepest sediments. I have used the phrases "*Tabellaria*" and "*Eunotia*" lakes though I think it preferable to use acidophilic and acidobiontic, since these terms can be related to a discrete physical range. Although I have used the pH data in Stevenson *et al.* (1991 for this comparison, pH measurements are somewhat variable (dependent on variation due to instruments, time of day, season, etc.) and species complement may be a more reliable indicator.

Having discussed the "milieu" briefly, the "vie" is equally important and this encompasses at a basic level – taxonomy – the enabling science without which we cannot discuss ecology.

The problems of identification have been hinted at above and cannot be pursued here since this involves lengthy checking of literature and samples, but individual corrections using the post-1990 literature should be possible, and indeed is essential for subsequent work. Unfortunately the literature is scattered and often not available outside major libraries/centres of diatom studies. This is a particular problem for applied studies since it is unrealistic to expect all laboratories to have the up-to-date literature, indeed in some instances there is hardly any literature. My early work relied on the floras of Hustedt: at first his 1930 book and then the more complex but regrettably not complete Rabenhorst Flora (1927–1966) which on the whole characterised individual species (with occasional varieties and forms) and illustrated the size range without further complication. This was followed by the American flora of Patrick & Reimer (1966, 1975) which took a somewhat different approach with single illustrations of most taxa, often taken from original slides and often using European type slides – an uncomplicated system, which is excellent if species are stable entities with little variation (see below). Then the much more complex treatment by Krammer & Lange-Bertalot (1987, 1988, 1991a, b) and numerous subsequent publications, all using a multi-sampling approach resulting in multiple illustrations of the "same" (?) diatom from different habitats. This adds massive complications, e.g. of taxa mentioned above such as *Achnanthes minutissima*, and equally of the alkaline species *Gomphonema parvulum* (Kütz.) Kütz. or *Cocconeis placentula* Ehrenb. which are correctly referred to as clusters of forms (Sippen) – whilst others such as *Cocconeis pediculus* Ehrenb. is a monotonous taxa without any apparent variability. Other species, e.g. *Navicula gregaria*

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* Genera in brackets are new names, established by the author in later publications.

Donk. is referred to as a problematic taxon but the illustrations in numerous publications using worldwide samples reveals an entity exactly as in the Figs 27–31 in Schoeman & Archibald (1966) and many later illustrations – a stable entity from diverse regions of the world – there are, however, some other closely related forms which can confuse this concept but they are not as thoroughly studied. Most recently I have been impressed by papers on *Cyclotella ocellata* Pantocsek (Edlund *et al*., 2003) and *Stephanodiscus suzukii* Tuji & Kociolek (emend. Kato, Tanimura, Fukusawa & Yasuda) (Kato *et al*. 2003). The *Cyclotella* work, whilst discussing cell size range/auxospore size range in great detail, nevertheless reveals a general stability of form in the species. The *Stephanodiscus* work follows the course of *Stephanodiscus* species with an assessment of the light microscopic morphological variation over a considerable period of time represented in a 385 cm core. Again, the slight morphological variation did not appear sufficient to disturb the concept of this equally stable species. If the stability of form of these two is common to the majority of diatoms, and all my experience suggests that this is so, then the total number of species is *extremely* high with many taxa not yet adequately described.

In conclusion, one should be wary of long lists of species from "single" or "double" microhabitats (e.g. the *Isoetes*/*Sphagnum* used by Nygaard) – some taxa may be dominant only on the *Isoetes* or vice versa. Observation of live samples should always precede preparation of cleaned material. Care has to be taken when recording pH values but sites with values below 5.0 do seem to contrast markedly in floristics from those at 5.0–6.0. Stability of diatom frustule morphology is greater than would be deduced from data in floras where mixing of material from often unknown habitats and widely spaced geographical locations gives a confusing picture – especially for applied workers without the means to pursue intricate taxonomy.

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