

A Study of *Gomphonema augur* Ehrenberg:

The Structure of the Frustule and its Variability in Clones and Populations

Etude de *Gomphonema augur* Ehrenberg: Structure du frustule et variabilité en clones et en populations

by

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With 3 plates and 1 text table

Abstract: *Gomphonema augur* Ehrenberg is found in very low numbers as "Aufwuchs" in urban canals in Berlin; numbers increase slightly in late fall and winter in contrast to most other *Gomphonema* species. The morphological and ecological characteristics of this taxon are little known in spite of the fact that it is generally considered to be widely distributed. To establish some of its features one clone of *G. augur* and one of a taxon of a much larger cell size, thought to be closely related, were isolated and cultivated under different conditions such as a higher salt content and higher temperature. Features discernable using the light microscope — size, shape and striae — were compared with those of the populations from which the clones were taken; observations on the living cell as well as ultrastructural descriptions will be published elsewhere. The results show that the features vary between the different parts of the clone but are similar in the parallel treatments of the two clones. Apart from disturbances in the striae typical shape features tend to get shifted under stress although the general outline of each clone is conserved.

These findings are compared with data in literature and with related taxa.

Key-words: diatoms, *Gomphonema augur*, variability, valve structure, clones, cultures, populations.

Résumé: *Gomphonema augur* Ehrenberg s'observe parfois en très petit nombre comme "Aufwuchs" dans les canaux urbains de Berlin; sa quantité s'accroît légèrement à la fin de l'automne et pendant l'hiver contrairement à d'autres espèces. On sait peu de choses sur les caractères morphologiques et écologiques de ce taxon bien qu'on le dise extrêmement répandu. Pour distinguer certains de ses caractères on a isolé un clone de *Gomphonema augur* d'un autre taxon semblable mais de plus grande longueur et on les a cultivés dans des conditions différentes, notamment à des salinités et à des températures plus élevées. Les caractères visibles sous le microscope photonique — grandeur, forme et striation de la valve — sont comparés à ceux des populations naturelles; la cytologie et l'ultrastructure feront l'objet d'une autre publication. Les résultats montrent que les caractères varient dans les diverses parties d'un clone mais ils sont semblables dans les traitements parallèles des deux clones. Mise à part la désorganisation du schéma typique des stries sous l'influence du stress, le contour du clone est conservé. Ces résultats sont comparés avec la littérature et avec les taxons apparentés.

Mots-clefs: diatomées, *Gomphonema augur*, variabilité, structure de la valve, clones, cultures, populations.

Introduction

Several *Gomphonema* species are important components of the “Aufwuchs” in urban canals in Berlin throughout the year. *Gomphonema augur* Ehrenberg, however, is generally found in very low cell numbers increasing slightly in late fall and winter when other species decline. This taxon is easily distinguished by the typical V-shape of the valve face, being widest near to the cuneate head pole. The variability of these features as well as the ultrastructural morphology and ecological characteristics of this taxon, however, are little known in spite of the fact that it is generally considered to be widely distributed (see keys and descriptions in Hustedt 1930, Cleve-Euler 1955, Patrick & Reimer 1975, Germain 1981).

In early January when the population seems to be at its peak, another taxon of larger cell-size has been observed for several years in very low but constant cell numbers. It is conspicuous because of its variable shape as it sometimes either resembles *G. augur* var. *gautieri* Van Heurck (see i.e. Mayer 1928) or one of the many “*turris*”-forms that have been described under different names: i.e. *G. acuminatum* var. *turris* (Ehr.) Cleve (sensu Germain 1981, or Schmidt 1902 Pl. 239, Fig. 33) depending on the position and relative dimensions of the apical pole. Hustedt’s argument (1938: 438) that the “*turris*”-form is not a separate taxonomic entity but only a shape variation (“Grenzvariation”) of *G. acuminatum* Ehr., *G. gracile* Ehr., *G. augur* and *G. lanceolatum* Ehr. (Hustedt 1930 and 1938) respectively and his note of a joint occurrence of this form with their respective taxa would mean that the taxon under consideration is closely related to *G. augur*. (in this paper it is therefore called *Gomphonema* cf. *augur*). Since transitional shapes among the long valves seem to occur (see Cleve-Euler 1955: 176 and Schmidt 1902 Pl. 240 Fig. 1-6 for transitions between *G. augur*, *G. acuminatum*, *G. turris*) but no overlap lengthwise to the typical *G. augur* was found, the question arose as to how much these taxa can vary in their shape, i.e. whether these taxa are a homogeneous entity, including the valves of initial cells as well as those after a number of cell divisions (see also Rudzki 1965).

Material and Methods

The samples which served as a basis for the clones and populations were taken on December 6th, 1983, and January 6th, 1984, from the rocky bank of the Westhafenkanal, an urban canal in Berlin (West) of β - α mesosaprob water quality, connected with the river Spree. The populations were found mainly in big clusters on stalks as “Aufwuchs” on *Cladophora*. The clone of *G. augur* was isolated from the December sample and the one of *G. cf. augur* in January. These clones were cultured in sterilized and filtered habitat water at 15 °C, a light/dark cycle of 12 hours and about 2,000 Lux; the water of the January sample had a pH of 7.6, conductivity of 644 μ S/cm and contained 50 mg Cl/l. NaCl was added to one part of each clone in a single incident to raise the chloride level to 750 mg/l (hereafter referred to as ‘medium Cl’) and 2050 mg/l (hereafter called ‘max. Cl’) respectively.

Another part was cultured at 27°C and a light/dark cycle of 10/14 hours with approximately 1200 Lux (hereafter called 'higher temperature'). 'Control 1' was grown parallel in time to 'medium Cl', and 'control 2' parallel to 'higher temperature'; timewise the part 'max. Cl' lies between these two. For *G. cf. augur* the parts 'medium Cl' and 'control 2' were not analyzed. All parts of the clones were grown for 15 days, cleaned in hot H₂O₂ and rinsed. For LM they were embedded in Naphrax, analyzed with a Leitz Dialux 20, NPL FL Objective Oil 100 and photographed with Agfa-Ortho 25. For each experiment 50 valves were measured with LM but due to the limited numbers of *G. cf. augur* in the natural population only 32 valves were used. The valves were grouped into half scale units (1 scale-unit = 0.9 μm).

Results

Size

As can be seen in the table the length within each of the two populations of *G. augur* varies considerably, but their mean values are similar. The breadth is more constant and is very similar to the population of *G. cf. augur*. Cells in this population are much longer but vary less than those of *G. augur* including even the one smallest valve (see table). The greater length of *G. cf. augur* in correlation to the same breadth as *G. augur* results in a higher length-breadth-ratio of 1: 4.5 and 1: 2.7 respectively. Whereas the length and breadth of the two natural populations of *G. augur* are positively correlated with a high statistical significance - a reduction of length is accompanied by a reduction in breadth — there is only a little positive correlation of no statistical significance in *G. cf. augur*.

Table: Quantitative features for the clones and populations

	LENGTH					BREADTH					CORRELATION	
	min - max (μm)	diff. (μm)	mean value** (μm)	s	vc %	min - max (μm)	diff. (μm)	mean value** (μm)	s	vc %	r	L:B
<u>Gomphonema augur</u>												
Population: Dec.	25.2 - 42.7	17.5	33.5 ± 1.9	4.74	14.1	11.2 - 14.4	3.2	12.5 ± 0.2	0.59	4.7	+ 0.69***	2.7
: Jan.	23.4 - 44.1	20.7	33.8 ± 2.0	5.29	15.7	10.8 - 13.5	2.7	12.4 ± 0.2	0.55	4.4	+ 0.57***	2.7
Clone: control 1	34.6 - 36.9	2.3	35.8 ± 0.2	0.53	1.5	12.1 - 13.0	0.9	12.7 ± 0.1	0.24	1.9	- 0.4**	2.8
: control 2	32.4 - 36.4	4.0	34.5 ± 0.3	0.85	2.5	11.7 - 13.5	1.8	12.8 ± 0.1	0.33	2.6	+ 0.07	2.7
: high temp.	32.4 - 36.0	3.6	34.4 ± 0.4	0.94	2.7	10.8 - 12.6	1.8	11.6 ± 0.3	0.35	3.0	+ 0.07	3.0
: medium Cl	31.5 - 35.1	3.6	34.0 ± 0.3	0.80	2.3	11.7 - 13.0	1.3	12.3 ± 0.1	0.37	3.0	- 0.16	2.8
: max. Cl	30.6 - 36.9	6.3	33.7 ± 0.5	1.38	4.1	9.4 - 11.7	2.3	10.5 ± 0.3	0.66	6.3	+ 0.73***	3.2
<u>G. cf. augur</u>												
Population Jan.	47.7 - 63.0	15.3	57.8 ± 1.1	2.81	4.9	11.7 - 13.5	1.8	12.8 ± 0.2	0.43	3.4	+ 0.23	4.5
Clone: control	49.1 - 52.2	3.1	50.8 ± 0.3	0.66	1.3	12.1 - 13.0	0.9	12.5 ± 0.1	0.28	2.3	+ 0.03	4.1
: high temp.	46.8 - 49.9	3.1	48.3 ± 0.3	0.82	1.7	11.2 - 12.6	1.4	11.8 ± 0.1	0.28	2.4	- 0.01	4.1
: max Cl	45.4 - 51.3	5.9	49.1 ± 0.6	1.45	3.0	9.4 - 12.1	2.7	10.9 ± 0.3	0.64	5.8	- 0.09	4.5

s = standard deviation

vc = coefficient of variation

r = correlation of length and breadth

*** highly significant

** significant

Measurements of the isolated clone of *G. augur* lie to the center of those of both natural populations (see plate I); 'control 1' is well above their mean values. 'Control 1' is conspicuous for the lowest variation of length and breadth, whereas 'control 2' (about 3 weeks later) varies more. In addition, these cells are shorter and slightly broader than those of 'control 1'. Cells that were exposed to 'higher temperature' are very similar in their length as well as in their correlation of length and breadth to their parallel 'control 2', breadthwise they are generally more slender. This results in a higher length-breadth ratio than all other parts except 'max. Cl'. Cells from 'medium Cl' concentration are decisively shorter (almost 2 μm) in their mean value and also somewhat more slender than in the parallel 'control 1'. Cells from 'max. Cl' concentration that timewise lie between 'control 1 and 2' are the most variable of all samples (see plate I). The highly significant positive correlation of length and breadth is even higher than for the natural populations. In terms of length the measurements of the cells span more than the entire range of all other treatments; the mean value is closest to 'medium Cl' but the coefficient of variation is highest by a factor of 2-3. Cells are also the most slender and the respective coefficient of variation as well as the length-breadth ratio is the highest of this clone.

Similar comments can be made of *G. cf. augur* as can be seen in the table and in plate I. In contrast to *G. augur* this clone lies directly between all three natural populations as regards length somewhat above the smallest valve of the population. The 'control' is the longest of the three samples of this clone. In its breadth and in its standard deviation for length and breadth it is much like 'control 1' of *G. augur*. The valves of the cells exposed to higher temperatures are generally smaller than in the 'control', probably due to the later generation; in this it also compares well to its counterpart in the other clone. As in the other clone of *G. augur*, cells in 'max. Cl' span the widest area in length, are the most slender (see plate I) and the standard deviation for length and breadth is the highest for this clone. The mean value for the length is between that of the 'control' and the cells grown at 'higher temperature' as might be expected since it was cultured later than the former but earlier than the latter. The mean value of the breadth compares well with its counterpart in the *G. augur* clone. In no part of the *G. cf. augur* clone a correlation between length and breadth was found; therefore — in contrast to *G. augur* where at least some negative or positive correlation was detected — correlation is of no significance for *G. cf. augur*.

Shape

Another feature that normally falls into line with those quantifiable characteristics as length and breadth is the shape of the valve outline: a qualitative feature that can barely be expressed and is difficult to analyze in pictures but maybe better evaluated by mathematical functions in the future (see Stoermer & Ladewski 1982). This feature is of importance for the entire genus *Gomphonema* since identification keys depend almost entirely on the outline due to the lack of easily distinguishable differentiating valve features. Except for the stigma or isolated punctum, striae that

often don't coincide and the inexact undulations of the valve margin, *Gomphonema* is considered to be symmetrical at least about the apical axis. The taxa studied in this paper are pronouncedly heteropolar (see plate II and III). The foot pole where the stalk is attached is generally slender, bluntly rounded and protracted, sometimes more or less capitate. The margins of the valve tapering to the footpole are often concave. Since the stigma and therefore the central area is not situated in the middle of the valve but slightly above with a ratio between the two halves of around 45 : 55 (see also Torika 1930), the valve is always widest in the upper part, somewhere between the central area and the apical pole with a convex margin in *G. augur* or with two widest parts connected with a more or less concave margin in *G. cf. augur*. The head pole is markedly cuneate but never capitate. The way it is linked to the widest part of the valve make up for the "shoulders".

In the populations (see figs 1-6, 9-12) it can be seen that the typical broad V-shape of *G. augur* is not very stable (fig. 3); in addition, the width of the head and foot pole and the margins (see undulations in fig. 2) may vary somewhat. In the clone of *G. augur* (figs 7-8, 13-24) it is obvious that the broad V-shape is absent. The valves are club-shaped, forming more rounded shoulders than in the populations. Additionally, the valves of 'control 1' (figs 7, 8) and '2' (figs 19, 20) have very narrow long protruding foot poles. Except for the smaller size and less concave lower valve margins, the valves of 'medium Cl' (figs 13, 14) are similar in shape to the controls. The valves of the cells exposed to 'higher temperature' are strongly club-shaped (figs 21-24), extremely concave margins connect with the long, slender foot pole, and the head pole is generally very broad and not rounded. The biggest shape change is visible in cells of the 'max. Cl' part (figs 15-18): varying from a small and sometimes cuneate apex (i.e. fig. 17) to only a trace of it (fig. 18). Shoulders are almost absent and taper gently into a slender, sometimes slightly capitate, foot pole (fig. 17). The head pole of many valves is out of focus suggesting, that it might be bent out of the valvar plane.

The shape variation is even more pronounced in *G. cf. augur* (see plate III) mainly expressed in extra undulations. In the populations the outline varies from a V-shape (fig. 26) with a pronouncedly protracted head pole (fig. 27) to a lanceolate shape with the widest part at the central area tapering into the head pole without a break and showing undulations but no shoulders (fig. 25); between these all transitions are found (figs 28-31). The clone as seen in the valves of the 'control' (figs 37, 38) represents one of these transitional forms having a long and slender head pole, shoulders but with the widest part in the middle and concave margins connecting it to the poles. There is another slightly convex undulation towards the foot pole. The valves of cells cultured at 'higher temperatures' (figs 32-36) look basically the same as those of the 'control'. As in the other clone, the cells of 'max. Cl' are the most variable; most valves are more slender in all parts concerned. The protruded head pole tends to become acute (fig. 40, 41) or almost non-existent (fig. 42), only few valves have broad shoulders and the middle is not much wider than the shoulders. The once strong heteropolarity is diminished: the upper part becomes more slender as the lower part gets wider. Additionally, more asymmetrical undulations are observed (fig. 42).

Striae

The number of striae per 10 μm , is difficult to quantify since different results can be obtained from the same valve if the data is taken from the margin, along the raphe and/or across the central area, towards the foot or head pole; even the symmetrical sides of the valve can yield different results. To get the highest and the lowest density of striae possible, the striae were counted in the LM per 10 μm on the side with the stigma along the margin of the valve: first in the middle across the central area and secondly as close as possible to the foot pole. Only range data of the populations and clones are given.

The lowest density of striae was counted in the populations. *G. cf. augur* has 7-9 around the central area and 10-13 at the foot pole; both populations of *G. augur* are similar with 8-10 to 11-13 with the exception of a few valves in the December sample which were much more densely striated (11 to 16); the opposite valves were “normally” striated though. The next higher density, 9 striae per 10 μm , was found in the valves of those cells that were exposed to ‘higher temperature’. In some valves there were rudiments of additional striae at the margin of the valve (especially in *G. cf. augur*). However, due to a defective arrangement of striae just around the central area in many of these valves, also very high numbers — up to 15 for *G. augur* — were counted; sometimes the striae had disintegrated and were uncountable. By contrast, the numbers of striae at the foot pole were regular. The valves of the other parts of the clones of *G. augur* were more densely striated, around 10-13 to 12-15. The same holds true for *G. cf. augur* where only the footpole with 11-14 has fewer striae.

Both taxa have one isolated punctum — a stigma — on one side of the valve. There is a tendency for more isolated punctae (apparently not stigmata) being formed either by the opposite central stria or by the four striae that border the central area. Those extras are found in 21% of the valves for *G. cf. augur*, 36% for *G. augur* in the natural populations (mostly 1, sometimes 3). They appear more regularly in all parts of the clones varying from 64-100% of all counted valves. The lowest percentage and amount are found in the valves of the ‘max. Cl’ part of *G. augur*; the highest, often indefinite number, in cells exposed to higher temperatures, due to a disturbance in the striae.

Discussion

A comparison of the measurements of the clone and natural populations of *G. augur* shows that they fit well into those given in literature (for a discussion of the possible identity of *G. cf. augur* see introduction). The size of 23-44 μm by 9.5-14.5 μm is within the range given by Germain (1981: 20-50 μm by 10-15 μm), van der Werff & Huls (1957-1974: 17-50 μm by 8-15 μm), Cleve-Euler (1955: 17-50 μm by 10-15 μm), a little wider than Patrick & Reimer’s (1975: 17-50 μm by 9-13 μm) and generally larger than Hustedt’s (1930: 17-40 μm by 8-13 μm). Stria counts are lower in the natural populations (8-13/10 μm) than in literature (all around 10-12 to 12-15) but similar to the clones (10-15/10 μm); differences might also be due to the method

of measuring (see discussion under striae). All authors agree on the typical V-shape of the valve and a protruded head pole; only in Schmidt (1902 Pl. 240 figs 7-9) valves with almost no shoulders and an acute head pole are drawn that resemble some of the cultivated valves. More recently a *G. augur* has been illustrated that also lacks shoulders and has its greatest breadth close to the middle (Fungladda et al. 1983). In a different study (Carter & Denny 1982) smaller specimens of *G. augur* have been reported that bridge the gap between the typical *G. augur* and *G. parvulum* var. *lagenula* (Kütz.) Hustedt. To accommodate the forms that are more slender (7-10 μm) Lange-Bertalot (1979, also see the discussion there) created the taxon *G. pseudoaugur* which also includes *G. apicatum* Ehrenberg sensu Mayer (1928). The same measurements as for *G. augur* but with different shapes fit the description of *G. apicatum* sensu Patrick & Reimer (1975: 110) which has an acute head pole, and of *G. carolinense* Hagelstein (1938) which is supposed to have both ends capitate and up to 5 additional stigmas (the drawing in Patrick & Reimer is very different from Hagelstein's). Also *G. sphaerophorum* Ehrenberg might be related as mentioned in Patrick & Reimer (1975) but its head pole is strongly capitate. Since the clones of *G. augur* may become more slender, lose their typical head pole (but never become capitate) and have extra isolated punctae, additional features have to be found to establish the relationship of these taxa.

The results of this study on the two taxa — the variability of valve structures visible in LM — give hints about the plasticity of those features. As expected, the variability is greater in the clones cultivated under various conditions in comparison to the populations from which they were isolated. The variability of the length for example, the most significant feature in the natural populations plays only a minor role in the clones. This is not surprising since the measured individuals are only a section of a large population whereas the clones were cultivated under a time limit. The length-reduction of the clone over a time-span is quite obvious in the different parts of the clone cultivated later (see cells of 'control 1 and 2'). The length-reduction of the valves of *G. augur* grown in 'medium Cl' does not fit into this scheme but this may either be due to an error in method — although care was taken to isolate only cells of the same generation — or an increase of Cl-content results in a sudden decrease in length indicated also in the parts 'max. Cl' (though cultivated a little later). The bigger *G. cf. augur* though, in spite of its variability, is never as long as *G. augur* either in population or in any cells of the cultures. The other size factor, the breadth, a surprisingly steady feature across the two taxa in the populations, aside from the normal slight decrease caused by cell division, reacts more to stress imposed by the culturing conditions; less in the parts exposed to 'higher temperature' and 'medium Cl' but most in 'max. Cl' parts of both clones (see also Geißler 1970b). This is probably due to the osmotic stress of the medium — a subject investigated by Schmid (1979). The same stress resulted probably in the loss or deformation of the head pole as well as in additional undulations of the valve margin. The cells in 'medium Cl' must be able to compensate much of this stress since, except for a length reduction, the shape looks much like the controls. A different stress that cannot be compensated for must be imposed by 'higher temperatures' since those parts are even more slender than 'medium Cl' and have a

high coefficient of variation (see Table) but the number of valves with disorderly transapical striae and even dislocated raphe is much more conspicuous. The habitat water might be a less suitable medium in the warmth (temperature of the habitat was around 4 °C). The medium might also be the cause for the different shapes of the valves as compared with the populations, the number of deformations in the valve pattern already in the controls and the early death of both clones. In addition, other environmental factors had changed: limited amount of water, no water movement, no competitors, different light quantity and quality. It may be supposed that under culturing conditions stress factors are imposed and some are even removed and affect the correlation of length and breadth. Whereas the cells of 'control 1' of *G. augur*, probably less damaged by cultivation than those of 'control 2', show a negative correlation that had been found before for *Gomphonema* (see Kolbe 1927: 81), the natural populations and the cells under obvious stress, 'max. Cl', have similar positive correlations. Since no significant positive or negative correlation for the other three parts were found and the other taxon shows none of this, the basis for a hypothesis is small. The number of striae also seems to be affected, that means they are becoming more dense in culture than in natural populations. The differences are however, only slight and difficult to quantify. The occurrence of rudimentary additional striae and cells where one valve has a much finer striation indicate that this feature might have a higher variability than found in the experiments.

The feature that initiated this study, the variability of the shape, does not yield a clear cut answer. In culture, the quality of typical features of the shape such as protracted footpole, apical pole, undulations and position of greatest breadth is variable but valves tend to be more generally rounded lanceolate and less extremely heteropolar. The general outline, however, is conserved and typical for each clone. For example, although in the clone of *G. augur* the typical V-shape is lost and the widest part is close to the central area with a reduced breadth, the valve still has a widest part somewhere in the upper part of the valve. This stability is even more marked in *G. cf. augur*. Even if the shoulders get very narrow, the two wide parts are discernable. A more slender middle than shoulders was never found, although this might have been expected by the great variation of this feature in the population. Several reasons might account for this: first, the plasticity of a single clone is much less than that of a natural population; second, although all features including length and breadth of the valve are in a cluster, the selection of valves for the population is entirely subjective and therefore the population might be heterogeneous and not representing a natural gene pool; third, the cultivating medium was not optimal; fourth, the mother valve regulates the shape during cell division, i.e. the daughter valve can only keep the outline or become smaller. That even an outline deformation is handed down without harm to the viability of the cells was seen in another experiment (for other species see Geißler 1970b: 657, for a discussion of teratologies see Geißler 1970a: 534). But it seems clear that cells with small shoulders cannot transform into cells with broad shoulders or vice versa since transitions must result in smaller valves; but the different forms were of the same size. Therefore, the individual valves of the extreme shapes could not be direct sister

valves but only later parallel descendants of the same auxospore showing a heteromorphology at least in shape (on polymorphism of a different *Gomphonema* see Germain & LeCohu 1981).

The question of the identity of *G. cf. augur* is even harder to answer. As can be seen in the parallel culture conditions shown in the table and the text figure, both taxa react in a similar way to the same stresses in their size, behaviour under culture conditions, such as growth form, and in the maximum possible salt content as well as valve patterns. But the disparity in length between these two taxa is conserved and the undulation that links the two widest parts in the valves of *G. cf. augur* is never lost. However, it was not cultured long enough to see if the gap in length is bridged and the concave margin lost when the valve gets smaller. The two pictures of a valve of *G. cf. augur* 'max. Cl'. (fig. 39) and of *G. augur* population (fig. 2) might serve as a hint that undulations might be lost or acquired in both taxa. But certainly a bigger gene pool and different culturing conditions, in addition to ultrastructural research and a study of the living cell, are necessary to clear up the identity of the taxa concerned and their relationship to allied taxa.

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Explanation of Plates

Plate I

Variability of length and breadth for the valves of clones and populations of *Gomphonema augur* and *Gomphonema cf. augur*.

Plate II

Variability of the shape of the valves of *Gomphonema augur* (fig.: 1000×) populations: fig. 1-6 and 9-12. Clone - control 1: fig. 7-8, medium Cl: fig. 13-14, max. Cl: fig. 15-18, control 2: fig. 19-20, higher temperature: fig. 21-24.

Plate III

Variability of the shape of the valves of *Gomphonema cf. augur* (fig.: 1000×) population: fig. 25-31. Clone - higher temperature: fig. 32-36, control: fig. 37-38, max. Cl: fig. 39-42, (fig. 37 + 40 interference contrast).





