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Morphology, taxonomy and distribution of *Stephanodiscus triporus* Genkal et Kuzmin and related taxa

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Abstract
Stephanodiscus triporus Genkal et Kuzmin was described in 1978 based on a study from the phytoplankton of Volgograd Reservoir having used transmission electron microscope. This species is small, diameter 3.7-10.6 µm, the number of striae 14-30 in 10 µm, the number of areoles 30-60 in 10 µm and differs from other species of the genus by the presence of three satellite pores of the single central fultoportula. Later a new species was described from the materials of "Lazy Lagoon" (Iowa, USA) *S. vestibulis* Håkansson, Theriot et Stoermer, similar in morphology to *S. triporus*. A large population of the species (*S. vestibulis*) has been found in Lake Balaton and occurred in different Hungarian and French waters as well. Detailed comparison of *S. triporus* and *S. vestibulis* based on our results and literature shows a very close similarity of both taxa. Therefore we reinvestigated the type material of both species and compared the results to the Hungarian and French specimens. Knowing the differences and similarities, conventional and geometric morphometric analysis were carried out comparing the species to its morphologically closest taxon *S. minutulus* as well. There is a continuum between diameter, number and morphology of striae, position of valve face fultoportula with three satellite pores, presence of vestibulum having the more or less same shape of *S. triporus* and *S. vestibulis*. Therefore we suggest that *S. vestibulis* is conspecific with *S. triporus* and regard the first as synonym of last.
Key words: distribution, morphology, *Stephanodiscus triporus, S. vestibulis*, taxonomy

Introduction

Centric diatoms are one of the most important communities of phytoplankton in large rivers and their reservoirs, the biomass of planktonic Bacillariophyceae can reach 90% of the total phytoplankton (e.g. Kiss & Nausch, 1988; Kožova *et al.*, 1982; Ohapkin *et al.*, 1997; Ščerbak *et al.*, 1992, more relevant references in Supplementary references = Sr 25). In this regard, researchers pay great attention in recent years to genus *Stephanodiscus*, and many small-sized new species have been described that are hardly determinable with light microscope like *S. makarovae* Genkal (Genkal, 1978), *S. perforatus* Genkal et Kuzmin (Genkal & Kuzmin, 1978), *S. parvus* Stoermer et Håkansson (Stoermer & Håkansson, 1984), *S. delicatus* Genkal (Genkal, 1985, 2004), *S. binatus* Håkansson et Kling (Håkansson & Kling, 1990), *S. inconspicuus* Makarova et Pomazkina (Makarova & Pomazkina, 1992), *S. hankensis* Genkal et Ščur (Genkal & Ščur, 2000), *S. chantaicus* Genkal et Kuzmina (Genkal & Kuzmina, 1992). The systematic position of some of the above mentioned species was clarified in further studies, and they were reduced to synonymy (Kobayasi *et al.*, 1985; Genkal & Korneva, 1990; Genkal, 2004, 2007, 2010).

Stephanodiscus triporus Genkal et Kuzmin was described in 1978 based on a study from the phytoplankton of Volgograd Reservoir used transmission electron microscope. According to the description, this species has a small-sized diameter 3,7-10.6 µm, the number of radial striae 14-30 in 10 µm, the number of areoles 30-60 in 10 µm. Areolae are randomly in centre, uniseriate on valve face and biseriate close to the valve margin. Interstriae end in spines. There is a ring of marginal fultoportulae and a single rimoportula between them. *S. triporus* differs from other species of the genus by the presence of three satellite pores of the single central fultoportula. The species occurred in other Volga' reservoirs, in the River Volga itself, in Lake Sevan (Armenia) and Lake Pertozero (Karelia; Genkal & Kuzmin, 1978).

Later a new species was described from the materials of "Lazy Lagoon" (Iowa, USA) *Stephanodiscus vestibulis* Håkansson, Theriot et Stoermer (Håkansson *et al.*, 1986), resembling in morphology to *S. triporus*. According to the description, *S. vestibulis* has a small-sized diameter 4-11 µm, the number of striae 12 -14 in 10 µm. Central area convex or concave, areolae having domed cribra. Punctae are disorganized or form striae in the central area, arranged in fascicles of 2 to 4 striae towards to the valve face/valve mantle junction. Spines are arranged in a ring near the valve face /valve mantle junction. One valve face fultoportula is located in the central area with three satellite pores. Several marginal fultoportulae are on the mantle, each is located beneath every third or fourth spine. The external opening of each marginal fultoportula is partly surrounded by an arch, the structure porch-like or resembling a "vestibule". One rimoportula is located a little above the ring of spines, with an external tube. Internally has the lip-like part inserted on an interfascicle near the junction of valve face/valve mantle.

Stephanodiscus vestibulis was later recorded in several lakes: Lake Michigan Potato, White Ash and North White Ash lakes, (USA); Big Lake, Grat Slave Lake, Trout Lake, Lake Manitoba, Lake Ontario (Canada); Lake Kitaura, Lake Biwa, Sayama pond (Japan); River Naktong (Korea); Paleo-Kathmandu Lake (Kathmandu); Brejo do Espinho Lagoon (Brazil); Greifen and Pfäffikon Lakes (Switzerland); and in rivers: Voltoya River (Spain); Bec d'Able River (France – these records are shown on Fig. 39; more references in Sr 1, 2, 3, 5, 6, 13, 20, 21, 26, 27).

A new variety of *S. triporus* has been described based on TEM and SEM studies from the phytoplankton of Rybinsk Reservoir of River Volga in 1990 as *S. triporus* var. *volgensis* Genkal, which differed from the type species in smaller diameter (3.7-8.7 µm) and the presence of a large areola at the centre (Genkal & Korneva, 1990). At the same paper the diameter of valve (5.8-12.1 µm), the number of striae in the 10 µm (14-20), the number of valve face fultoportula (1, sometimes 2) and the number of satellite pores (usually 3, sometimes 2 or 4) for *S. triporus* var. *triporus* were also clarified. Later the SEM studies clarified that the "large areola" of *S. triporus* var. *volgensis* is the impression of the valve face fultoportula of daughter cell and it exists on *S. triporus* var. *triporus* as well. Genkal (2013) refer *Stephanodiscus triporus* var. *volgensis* to the synonym of the type variety. Both varieties frequently occur together and were found in the River Volga (Genkal & Kuzmin, 1978); Kuiybishev Reservoir (Pautova *et al.* 2009, Genkal & Korneva, 1990; Genkal, 1992; Genkal et al., 2006). *S. triporus* was recorded (mainly from the territory of former Soviet Union) in rivers: Danube, Oka (a tributary of the Volga), Neva, Izhora (a tributary of the Neva), Ob, Irtysh, Delingde and Taz (Western Siberia), Angara, Yenisei, Selenga, Amur (Genkal & Levadnaja, 1980, Genkal & Kuzmina, 1984; Genkal & Naumenko 1985; others in Sr), River Danube near the Black Sea (Genkal *et al.*, 2009), River Danube (Hungary, Kiss & Genkal, 1993), River Morava (Slovakia, Marvan *et al.*, 2004); in reservoirs: Revdinskoie (Middle Urals), Narvskoie, Tsimlyanskoe and Kanevskoie (Ukraine in Sr 9), in lakes: Sevan (Armenia) Ladoga, Baikal, Hanka (Far East), Pertozero (Karelia), lakes of Estonia, Delingde (Western Siberia), Lake Erie (Michigan (Genkal & Kuzmin, 1978; Genkal & Laugaste, 1985; Genkal & Nikulina, 1991 others in Sr 8, 9, 10, 11, 13, 15, 17, 18, 22, 25); Curonian Lagoon Baltic Sea (Genkal & Dmitriyeva, 2005),

Having analysed the micrographs found in literature and our own samples taken from several water bodies in Europe, more and more similarities were found between *Stephanodiscus triporus* and *S. vestibulis*.

The aim of this study is to make an amended morphological characterisation of *S. triporus* and to show the similarities with *S. vestibulis*.

Materials and methods

During this study on the one hand the type material of *Stephanosdiscus triporus* and *S. vestibulis* were re-examined; on the other hand, our own samples taken from several waters were investigated. Type material of *S. triporus* originated from type locality (Volgograd Reservoir), deposited to the Institute Biology of Inland Waters of Russian Academy of Sciences, Borok. Isotype slides (No. 134 and 135) and SEM holder (No. H. Håkansson 352) of *S. vestibulis* were got from diatom collection of Botanischer Garten und Botanisches Museum Dahlem, Freie Universität Berlin.

Phytoplankton samples were taken from below the water surface from Lake Balaton in 2010 June at Siófok for the detailed analysis. The species was found in several other Hungarian water bodies as well (Table S1), but only a few cells. To study the Russian and Estonian population of *S. triporus*, a lot of phytoplankton samples were taken from rivers, reservoirs and lakes from the territory of former Soviet Union (Table S1).

Samples from Russian and Estonian waters were treated according to Balonov (1975) as follow. 1 g of potassium bichromate ($K_2Cr_2O_7$) was dissolved in100 ml of hot sulfuric acid (H_2SO_4). 0.5 to 1 ml of this oxidizer was put to the concentrated sample and cooked for 2-3 minutes, then washed with distilled water and centrifuged at 2000 rpm for decantation. All this washing procedure was repeated 3-4 times. Hungarian and

French samples were cleaned with hydrochloric acid and hydrogen peroxide, subsequently washed three times with distilled water. Portions of samples were filtered through a 3 µm-mesh polycarbonate membrane and fixed on SEM stubs with double stick carbon disk, which were then coated with gold-palladium (105 s, 18 mA) and investigated with Hitachi S-2600N scanning electron microscope (in case of Hungarian populations and type materials) and with JSM-25S (in case of Russian and Estonian populations). For SEM analysis of French populations, cleaned samples were filtrated through polycarbonate membrane filters with a pore diameter of 3 µm, mounted on stubs, sputtered with gold (40 nm) with Modular High Vacuum Coating System (BAL–TEC MED 020) and studied with a Leica Stereoscan 430i.

For LM analyses, diatom slides from aliquots of samples were mounted with Naphrax® mounting medium and observed with an Olympus IX70 inverted light microscope equipped with differential interference contrast (DIC) optics at 1500X magnification. LM photos were obtained using an ARTRAY digital camera (Model: ARTCAM-500MI). The micrographs of French populations were taken using a Leica DMRX light microscope with a Leica DC500 camera.

Structural elements of the valves were measured and analysed using scanning electron micrographs following the paper by Genkal (1977, 1984), taking into account of Theriot (1987). Terminology followed Anonymous (1975), Ross *et al.* (1979) and Theriot & Serieyssol (1994).

Conventional morphometrics

The following morphological characters (variables) of the frustule were analysed and measured on SEM micrographs (Fig. 1): valve diameter (DIA), valve face diameter (VFD), number of fasciculae (FAS), number of marginal fultoportulae (MFN), uniseriate areolae distance (UAD), uniseriate areolae number (UAN), biseriate areolae distance (BAD), biseriate areolae number (BAN), number of areolae in a stria at the margin (NAS), distance between valve face fultoportula and rimoportula (FRD), width of labium of rimoportula (WLR). Uniseriate and biseriate areolae distance and number were calculated by the following: we measured the length of the shortest and the longest uniseriate and biseriate areolae (and also counted the number of areolae of them) of every specimen and their means were used as UAN, UAD, BAN or BAD respectively. Valve face diameter was measured between two opposite spines. Most of these morphological parameters selected to the conventional morphometric analysis were suggested by Tapia *et al*. (2004).

Principal component analysis was applied for the conventional morphometric characteristics of outside using the software Past version 1.78 (Hammer *et al.*, 2001). Data were standardized. To compare the characters of *S. vestibulis* and *S. triporus* to the morphologically closest taxon (*S. minutulus*), we measured 50 specimen of a Hungarian population (collected from Lake Széki near Devecser in 2009, N 47^{o} 7,843', E 17^{o} 28,644') of *S. minutulus* as well.

We also tested population of type material of *S. vestibulis* and *S. triporus* (t or Welch-test) to look for statistical equalities in every morphometric characters (Welch-test has been applied when the estimated variance was not equal). For the above analysis we measured 50 specimens from Lake Balaton, 9 from French population, 15 from type material of *S. vestibulis*, 50 from type material of *S. triporus* and 50 specimens of *S. minutulus* from Lake Széki.

Geometric morphometrics

To analyse the inside characters, 9 landmarks were placed inside of the valve (Fig. 2) and digitized using tpsDig2 software (Rohlf, 2004; Rohlf & Slice, 1990). The 9 selected landmarks were the followings: 1:the right base of rimoportula (RP) at the edge of valve; 2: the middle of valve face fultoportula; 3: distant satellite pore of valve face fultoportula from the rimoportula, 4: satellite pore of valve face fultoportula to the left of the third landmark; 5: the end of the labium slit of RP to the valve centre; 6: the other end of the labium slit of RP; 7: the top of marginal fultoportula (MFP) to the right of the RP; 8: the top of left satellite pore of MFP to the right of the RP; 9: the top of right satellite pore of MFP to the right of the RP. The Cartesian coordinates of the cells were aligned (translated, rotated and scaled) by the Procrustes generalized orthogonal least-squared superimposition procedure (Generalized Procrustes Analysis, GPA, Rohlf & Slice, 1990). To determine whether the amount of variation in shape of our geometric morphometric dataset is small enough to permit statistical analysis the slope of the regression line of tangent space distances against Procrustes distances and their uncentred correlation coefficient were calculated using tpsSmall (Rohlf, 2003). The slope of the regression line was 0.98806, the correlation coefficient 0.99996, and inspection of the scatter of points revealed no large deviations of single points. These were accepted as indications of a good fit.

Allometry was also investigated by a multivariate regression of shape variables onto diameter. These analyses were performed using TpsRegr 1.31 (Rohlf 2005).

Canonical Variates Analysis (CVA) was carried out to distinguish individual groups using tangent space Procrustes coordinates. Mann-Whitney U test was used to test whether the medians of *S. vestibulis* and *S. triporus* type materials are different. For this test we used the Euclidean distances of landmarks coordinates from the origo. The CVA and Mann-Whitney test were performed in PAST ver.1.74.

To compare the characters of *S. vestibulis* and *S. triporus* to the most similar species (*S. minutulus*), we measured 50 specimens from Lake Balaton, 4 from French population, 8 from type material of *S. vestibulis*, 40 from type material of *S. triporus* and 15 specimen of *S. minutulus* from Lake Széki. To analyse shape differences, the relative warp scores were used as an ordinary multivariate dataset.

Distribution of species is shown on sketch a map of Hungary and the World used the ESRI ArcInfo 9.3 GIS program.

Results

Reinvestigation of type material of Stephanodiscus triporus

The type material of *Stephanodiscus triporus* was relatively dense in valves; therefore 32 SEM micrographs were taken from outside view and 16 from inside view. Valves are radially striated; the slight elevation or depression of valve face, the valve face fultoportula or the elongated tube of rimoportula is rarely seen with LM (Figs 3-5). Valves are usually almost flat (Figs 3, 4) or slightly convex/concave (Figs 5). The range of diameter was 6.8-9.9 µm (Fig. 17).

During the SEM studies, in the type material (Figs 8-11) most of valves were flat (Figs 8, 9), but some slightly convex/concave valves have been found as well (Fig. 11, Tab. 2). The number of radial fasciculae is 27-42 (radial striae are 10-15 in 10 µm) . Interstriae end with short spines (sometimes they are almost “absent”). The shape of areolae is usually round on valve face, but can be elongated or irregular close to the margin (Fig. 9). They are located randomly in the valve centre, internally covered with domed cribra (Figs 10, 11). The single row of areolae (UAN: 3.5-6.5) becomes double (BAN: 2-6.5) at the edge of valve face. The pore of a single valve face fultoportula is seen near the centre (Fig. 8), sometimes difficult to distinguish between the areolae. The valve face fultoportula has 3 satellite pores internally (Figs 10, 11). There are marginal fultoportulae (internally with 3 satellite pores) on every second to fourth interstriae below a spine (Figs 9,10); the number of marginal fultoportulae is 9-15 (Fig. 17). The external opening of marginal fultoportulae is usually surrounded partially by arched structure (like a narrow vestibule Figs 8, 9, 16). Vestibule is sometimes not developed completely or can be wide. The single rimoportula is situated above the ring of marginal fultoportulae (Figs 10, 11). It has a relatively long and large tube externally in the ring of spines (Figs 9, 16) and a small labium internally oriented more or less perpendicularly to interstria (Figs 10, 11) or sometimes in different angle (supplementary SEM micrographs of all investigated materials are awailable at first author for request).

Reinvestigation of type material of Stephanodiscus vestibulis

The type material of *Stephanodiscus vestibulis* was poor in valves; therefore only 6 SEM micrographs were taken from outside and 5 from inside view. (Because of the sparseness of the type material, for further analysis the published micrographs by Håkansson were also measured).

Valves are radially striated, the elevation or depression of valve face is usually pronounced, and the elongated tube of rimoportula is rarely seen with LM. Valves are usually convex/concave (Figs 6, 7). Only one valve was found with slight elevation in LM. The range of diameter was 5-9.3 µm (Fig. 17). In the type material 10 strongly convex/concave (Figs 12-15) and one slightly convex valves have been found with SEM (Table 2). The number of fasciculae is 24-39 (radial striae are 11-15 in 10 µm - Fig. 17). Interstriae end with short spines. The shape of areolae is usually round on valve face, but can be elongated or irregular close to the margin. They are located randomly in the valve centre, internally covered with domed cribra (Fig. 15). The single row of areolae (UAN: 3.5-6.5) becomes double (BAN: 2.5-5.5) at the edge of valve face (Figs 13, 14). The pore of a single valve face fultoportula is seen near the centre (Fig. 14), sometimes it is difficult to distinguish between the areolae (Fig. 13). The valve face fultoportula has 3 satellite pores internally (Fig. 15). There are marginal fultoportulae (internally with 3 satellite pores - Fig. 15) on every second to third interstriae below a spine (Figs 13, 15); the number of marginal fultoportulae is 6-11. The external opening of marginal fultoportulae is usually surrounded partially by arched structure (like a narrow vestibule – Figs. 12-14). The single rimoportula is situated in the ring of marginal fultoportulae. It has a relatively long and large tube externally in the ring of spines (Figs 13, 14) and a small labium internally oriented more or less perpendicularly to interstria (Fig. 15).

Morphological characterisation of Stephanodiscus triporus/vestibulis based on new investigations

Recent materials were investigated and morphologically analysed from Lake Balaton (8 LM and 107 SEM micrographs), from six lakes or reservoirs and from a river (27 SEM micrographs) of Hungary, from two rivers of France (7 LM and 24 SEM micrographs). Valves are radially striated, the elevation or depression of valve face is seen, several valve have flat valve face, and the elongated tube of rimoportula is seen on some part of valves with LM on Hungarian (from Lake Balaton) (Figs 18-19, 21-23) and French populations as well (Fig. 20).

Valves are usually convex/concave (Figs 24-26), but many valves were flat (Fig. 27) or slightly convex/concave in Hungarian (Fig. 29) and in French population as well. In the material from the Lake Balaton 47% of specimens were flat, 18% were strongly convex/concave and 35% were slightly convex/concave, while in the French population 5% of specimens were flat, 80% were strongly convex/concave and 15% were slightly convex/concave (Table 2).

On the Russian EM pictures taken mainly by Genkal (have been found mainly in Russia from other localities, then type one) similar ratios of strongly convex/concave and slightly convex/concave valve were found, and a flat valve occurred only as a single record (Table 2).

Diameter varied between 3.7-12.5 µm (Fig. 17). The number of fasciculae is 23-65 (radial striae are 11-21 in 10 µm). Interstriae end with short spines. The shape of areolae is usually round on valve face (Figs 24-27, 30), but can be elongated or irregular close to the margin, or in some cases zig-zag slits (Fig. 31). They are located randomly in the valve centre, internally with domed (Fig. 28) or flat (Fig. 29) cribra. Areolae not or partly seen or striae are irregular on heavily silicified valves (Fig. 31). The single row of areoles (UAN: 2.5-11.5) becomes double (BAN: 0-7.5) at the edge of valve face. The pore of a single valve face fultoportula is seen near the centre (Figs 25-27, 30), sometimes difficult to distinguish between the areolae (Fig. 24). The valve face fultoportula has 3 satellite pores internally (Figs 28, 29, 33). There are marginal fultoportulae with 3 satellite pores internally on every second to third (rarely forth, fifth) interstriae below a spine, the number of marginal fultoportulae is 4-14. The external opening of marginal fultoportulae is usually surrounded partially by arched structure (like a narrow vestibule Figs 26, 27, 30). The single rimoportula is situated above the ring of marginal fultoportulae. It has a relatively long and large tube externally in the ring of spines (Figs 25-27, 30) and a small labium is internally oriented more or less parallel to interstria (Figs 28, 29) or sometimes more or less perpendicularly in case of Lake Balaton and only the latest one position was in case of French specimens and specimens from other Hungarian waters.

Conventional and geometric morphometric analysis

To look for statistical equalities in the measured conventional characters of *Stephanodiscus triporus* and *S. vestibulis* specimens found in type materials, we used t (or Welch) test. The diameter differs in the two populations and those characters which are in relationship with the diameter, like valve face diameter and the central fultoportula distance from the rimoportula, but the other characters do not differ (Table 3).

Considering multivariate regression of shape variables on diameter, this gave significant results (Wilks' lambda= 0.123; p = 5.591E-034) indicating the allometry.

The results of the Principal Component Analysis on conventional morphometric dataset of outside characters clearly demonstrated the overlapping of the type material of *S. vestibulis* and *S. triporus* populations along the first and second PC axis (Fig. 34). French and Hungarian populations partly overlap with them. *S. minutulus* partly overlaps with Hungarian population and segregates from the others. The explained variance for the first axis ($\lambda 1$) is 54.4 %, 20.0 % for the second axis ($\lambda 2$) and 13.1 % ($\lambda 3$) for the third axis. PCA revealed that the first 3 factors explain almost all the variability (87.5 %) in the correlation matrix.

Fig. 35 shows the results of CVA based on the geometric morphometric dataset. The Canonical Variates Analysis clearly segregated *S. minutulus* from all other groups (Wilk's $\lambda = 0.01647$, $p << 0.0001$). *S. vestibulis* and *S. triporus* type material and French population well overlapped, while only a small degree of overlap was observed with the Hungarian population. The first two canonical axes explained 64.7 % and 31.7 % of the variation, respectively.
In case of all landmarks of two type material, the Mann-Whitney test was not significant, so the difference in their medians is small (Table 3).
The specimens from type material of *S. vestibulis*, *S. triporus* and French population presented similar relative warp grids (Fig. 36 B, C, D), while the population of Lake Balaton (Fig. 36 A) and *S. minutulus* (Fig. 36 E) differ from them. The population of Lake Balaton differs from the others in the angle of the interstria to the labium of rimoportula. The population of *S. minutulus* differs from the others in the shape of the marginal fultoportulae (*S. minutulus* has longer marginal fultoportula) and the position of satellite pores (the angle of them is 180^o in case of *S. minutulus*, while 120^o in the others) of valve face fultoportula
Because the type material of *S. triporus* was taken only in one sampling site, we investigated the real variability of this species by summarizing some morphological elements measured in populations found in the area of former Soviet Union (Lake Leegu - Estonia, Kiev' Reservoir,,Ivankovo Reservoir, Lake Baikal, Rybinsk reservoir, and Cheboksary reservoir). The range of diameter is 4-12 µm, the number of fasciculae is 25-48, the number of marginal fultoportulae is 5-16.and (1)2-3(4) areolae can be found at the end of striae (Fig. 37). On the EM pictures from the Russian waters published by Genkal more or less the same ratio of strongly convex/concave and slightly convex/concave valves were found, but only one flat valve was recorded.

Distribution of S. triporus and S. vestibulis

In a four-year long project several Hungarian waters were studied on the eastern part of Hungary. Besides this we studied the Lake Balaton as well. During these studies we frequently found *S. vestibulis/triporus* in Hungarian waters, also in lakes and rives (Fig. 38). There was only one Hungarian occurrence of the species before this study (in River Danube), although e.g. the phytoplankton of Lake Balaton has been regularly studied since 1960s, but only with light microscope. Our first thought was that the species is invasive, but we reinvestigated (with SEM) a phytoplankton sample from Lake Balaton collected in 1997 (earlier it was studied only with LM) and now we found the species in it. To collect the data from literature, we can see that it is a widespread species in lakes, reservoirs, rivers and sea (close to delta – Fig. 39).

Discussion

The selection of the morphological parameters

Most of the selected morphological parameters were choosen on the bases of suggestion of Tapia *et al*. (2004). Some other characters are mentioned in taxonomical papers (e.g. Theriot 1987) as important to delimit particular *Stephanodiscus* species, like width of a spine at its base, numbers of spines, width of labiate process at its base, horizontal width of the small rim encircling the valve.

The number of spines usually has no taxonomical importance in the genus *Stephanodiscus* (here at *S. triporus* also) and spines can break off in several cases (their postaments are hardly seen) therefore difficult to count them exactly. The same statement was written in (Tapia *et al*. 2004). We should mention that spines are situated usually at the end of each interstria, therefore the number of spines is usually equal with that of “costae” and rows of striae. The variability of width of spine at its base is rather small and practically impossible to measure it correctly.

We measured the width of labiate process at its base as well, but its vaiability was smaller then confidence of measuring, therefore we did not use it in the analysis.

In one hand practically impossible to measure (strictly) correctly the width of the small rim and it is not seen well in most of our valves. On the other hand to measure it is important if we investigate the degree of valve silicification, but the degree of valve silicification is not a taxonomical key character and estimation of its degree was not our goal.

The variability of selected morphological parameters

The diameter of cells (6.8-9.9 µm) and the number of striae (10-15 in 10 µm) in the presently examined type material of *S. triporus* were much less variable than in the original description (3.7-10.6 µm and 14-30 in 10 µm; Genkal & Kuzmin, 1978). However, a large range of morphological variability was detected when analysing the samples taken from several different localities by describers. Obviously, the type material was less variable because it was taken from a single sampling site (Volvograd reservoir).

Notwithstanding, the typical characters could be found on almost all specimens, like the well developed external tube of the rimoportula, the vestibulum, the typically swollen, wide labium, and the three satellite pores of the valve face fultoportula. Most cells were flat, few were slightly convex/concave, but no strongly convex/concave valves were found. *S. triporus* is originally described to have a flat valve surface (Genkal & Kuzmin, 1978). This could be expected as the description was based on TEM observations, where the convex or concave nature of the valve surface can hardly be detected. We should note, that two strongly convex, one slightly convex and one flat valve can be revealed by the detailed investigation of the original TEM pictures. In the following publications from Russia both strongly and slightly convex/concave valves are seen together with flat ones (Genkal & Korneva, 1990; Genkal, 1992; more in Sr 9, 10, 12, 13, 14, 16, 17, 19, 22) . Analysing in detail the “whole” population from a lake or river and taking many SEM micrographs the “whole” range of morphological variability of a given species can be found. The population from Lake Balaton showed the highest variability, where all types of valve surface was found. In our opinion, these populations demonstrate well that the valve face of this species can be characterised by continuity from strongly convex/concave to completely flat.

Stephanodiscus triporus was also found by Houk in 1987 (Houk, pers. comm.) in the reservoir Nove Mlyny in south Moravia (leg. Petr Marvan 22.9.1987) and in the locality Trstena (dead arm of Danube) in west Slovakia (leg. Maria Horecka 11.11.1987). The valve diameter of the population was 5.7-8.5 µm, and number of striae was 10-16 in 10 µm. On his unpublished SEM micrographs the central part of the specimens was both strongly and slightly convex/concave.

The diameter of cells in the presently investigated type material of *Stephanodiscus vestibulis* was smaller (5-9.3 µm), while the stria number was more variable (11-15 in 10 µm) than in the original description (4-11 µm and 12-14 in 10 µm; Håkansson *et al.*, 1986). The specimens investigated by SEM were strongly convex/concave, albeit some slightly convex/concave cells were found during the LM observations flat specimens were not found. The low number of *S. vestibulis* specimens on the stub of original material may be responsible for the low morphological variability. However, the characteristic features could be found on each specimen, like the well developed tube of the rimoportula (this could be seen on a few specimens in LM as well), the vestibulum, the typically swollen, wide labium, and the three satellite pores of the valve face fultoportula. In the original description of *S. vestibulis*, and on the SEM figures only strongly convex/concave valvae appear (Håkansson *et al.*, 1986). The various morphological descriptions and SEM micrographs from the different parts of the world characterise *S. vestibulis* uniformly as a species with strongly convex/concave valve surface (Håkansson & Kling, 1989; Gotoh *et al.*, 1998; Tuji & Houki, 2001; Håkansson, 2002; Naya *et al.*, 2007). This may be due to the pre-expectation of the observers searching for specimens resembling on original description and micrographs. In the publication of Gotoh *et al.* (1998) specimens have also slightly or strongly convex/concave valves, with 6-13 µm diameter, stria numbers 12-15 in 10 µm and marginal fultoportulae numbers 3.4-6 in 10 µm. Tuji & Houki (2001) found the species in eutrophic Lake Biwa, with diameters of 4-11 µm, and stria numbers 11-14 in 10 µm. The specimens in the pictures are strongly convex/concave forms. Naya *et al.* (2007) found the species in eutrophic Lake Kitaura. The specimens in the pictures have similarly strongly convex/concave valves, with 6-8.5 µm diameter and number of striae 12-14 in 10 µm. The characteristics of the vestibuli and the rimoportula are well visible on all published SEM micrographs, together with the three satellite pores of the valve face fultoportula. All the above mentioned characteristics are in good accordance with our type material investigations and the population in the Lake Balaton.

As we can see on Fig. 17 the conventional morphometric characters of the population from Lake Balaton shows the highest variability. Interestingly, the stria density has a wider range than in the other investigated populations, but overlap with them. Similarly, if this is compared to reported stria numbers of *S. triporus* and *S. vestibulis* in the literature, the population of Lake Balaton completely overlaps with them. In the Hungarian populations all valve face types occurred from flat forms to slightly and strongly convex/concave ones. In the pictures recorded from the two French populations strongly convex/concave, slightly convex/concave and flat specimens were also found, thus the continuity could be detected likewise. In the Lake Balaton population the areolae remained a single line even near the spines as well on some valves, while at some other cases the single line areolae remained very short (consisting of 1-2 areolae). On about half of the specimens the labium was more or less parallel with the interstria; on the other ones it was perpendicular to the interstria. This is well visible on the relative warp grids, where the mean position of the rimoportula relative to the mantle is illustrated by points 5 and 6. Some specimens occurred in the French population zig-zag slits were found instead of round areoles. The reason of this was the strong silification.

A broad morphological disparity is characteristic in several cases among centric diatoms. The two forms of *Stephanodiscus hantzschii* Grunow (*S. hantzschii* Grunow f. *hantzschii* and *S. hantzschii* f. *tenuis* (Hustedt) Håkansson et Stoermer can be found frequently together in the same population, even on the same frustule (e.g. epivalva is fo. *hantzschii,* hypovalva is fo. *tenuis* - Casper et al. 1987). *Cyclotella hispanica* Kiss, Hegewald et Acs is a polymorphic species, the valve face morphology can be different on the same frustule (e.g. epivalva with flat valve face, hypovalva with triangular depressions-elevations – Kiss et al. 2002). The most thorough study of *Stephanodiscus minutulus* type material and cultured material is available (Theriot & Jones 2009). *S. minutulus* forms flat, weakly concentrically undulate and strongly concentrically undulate valves, like *S. triporus*.

Effects of some environmental variables to the cell morphology

There are several examples in the literature that some environmental variables affect the algal cell morphology. *Cyclotella meneghiniana* showed morphological variation during a period of heavy pollution (highly nutrient-rich conditions or other "extreme" environments). Investigations revealed changes in the number of valve face fultoportulae, in the shape of the striation and the costae, and in the position and shape of the satellite pores of the mantle fultoportulae. They tentatively interpreted this diatom to be a form of *C. meneghiniana*, adapted to change of nutrients (Håkansson & Korhola 1998).

Shirokawa et al. (2012) studied the effect of salinity to the developmental plasticity of *Cyclotella meneghiniana*. They found that the numbers of valve face fultoportulae were significantly increased in all strains in seawater.

Phenotypic plasticity of *Synura echinulata* was investigated using geometric morphometrics to describe qualitatively and quantitatively phenotypic plasticity of silica scales cultured at four combinations of light intensity and temperature. Silica scales of *S. echinulata* exhibited considerable environmentally induced plasticity, but taxonomically relevant characters remained unchanged (Němcová *et al.* 2010). Our materials from Lake Balaton and France were also influenced by change of light conditions and temperature (see more chemical variables of Lake Balaton in Duleba *et al*. 2012).

Martín-Cereceda & Cox (2011) found that the valve morphology of a *Thalassiosira* isolate changed with variation in the salinity and silicate concentration of the medium. In this paper they gave a good review of literature about phenotypic plasticity of Thalassiosiraceae.

The results of the conventional and geometric morphometric analysis clearly show that the characters of French population and type materials of *Stephanodiscus triporus* and *S. vestibulis* overlap most intensively. The characters of the population from Lake Balaton differ slightly from these with only partial overlapping. The characters of the species did not overlap with its most similar morphological relative, *S. minutulus*. *S. minutulus* externally (Figs 40, 41) differs from *S. vestibulis* and *S. triporus* in the external opening of marginal fultoportulae (short tube vs. vestibulum), the lack of a strongly developed outer rimoportula tube (in case of *S. minutulus*, while *S. triporus* has it) and in the shape of the valve face; internally (Figs 42-43) in the number of satellite pores of the valve face fultoportula (2 vs. 3) and in the internal size of the tube of marginal fultoportulae (relatively large vs. small, Table 4). However, only some of these characters could be involved in the statistical analysis.

Landmark-based methods in diatom morphology

The landmark-based methods were used in solving problems associated with the morphological separation of diatom species e.g. by Beszteri *et al.*, (2005), Potapova & Hamilton (2007) and Novais *et al.* (2009). In our relative warp grid analysis we could indirectly illustrate the third satellite pore accompanying the valve face fultoportula of *S. vestibulis* and *S. triporus*, and the larger marginal fultoportulae of *S. minutulus*. The two satellite pores in *S. vestibulis* and *S. triporus* are directed in a 120^{o} angle, as the third pore has enough space only in this arrangement; meanwhile the two satellite pores of *S. minutulus* are in an 180^{o} angle.

The taxonomic position of Stephanodiscus triporus and related taxa

On the bases of our study we concluded that *S. vestibulis* is identical in morphology with *S. triporus.* They have a similar range of valve diameter, number of striae in 10 µm, number of rows of areolae, number of satellite pores of valve face and marginal fultoportulae. The main distinguishing feature of *S. vestibulis* is the presence of small arches on the valve mantle similar to the lobby (vestibule), which cover the outer hole of marginal fultoportulae. This feature is typical for *S. triporus* in type material (Figs 8, 9, 16) as well. We should mention this characteristic which was not clear and not described in the firs paper about *S. triporus* (Genkal & Kuzmin, 1978) because only TEM studies were done that time and it was also not mentioned during description of *S. triporus* var. *volgensis* (Genkal & Korneva, 1990). The structure of vestibule was later recognised on the bases of SEM investigations, and shown in several SEM micrographs (Genkal *et al.*, 2006, 2010; Genkal & Golokolenova, 2008; Genkal & Popovskaja, 2008a, 2008b; Genkal & Trifonova, 2009).

As Håkansson *et al.* (1986) note there is a small deepening (close to the valve face fultoportula) of the central fultoportula on some valves of *S. vestibulis* (similar in size to large areolae), presented by other authors, too (Gotoh *et al.*, 1998; Tuji & Houki, 2001). The micrographs about *S. vestibulis* valve centre show it strongly convex or concave on first description (Håkansson *et al.*, 1986), other researchers published micrographs of the species with a less pronounced concentric convex-concave area of the valve centre (Gotoh *et al.*, 1998; Tuji & Houki, 2001). In our material sometimes can be seen almost flat valve (Fig. 27).

In our opinion, the facts above suggest that *S. vestibulis* is conspecific with *S. triporus* and *S. vestibulis* is the synonym of *S. triporus.*

Distribution of Stephanodiscus triporus

Previous to our investigations only a single Hungarian report of the species has been found; Kiss & Genkal (1993) observed it in the River Danube and identified as *S. triporus* according to TEM pictures. Its occurrence in the Lake Balaton has not been reported previously, although several authors regularly perform phytoplankton investigations in the Lake (among others Tamás, 1961, 1975; Tóth & Padisák, 1978; Vörös, 1982, others in Sr 23, 24) . However, these were LM investigations, by which it is almost impossible to differentiate the species from *S. minutulus*. Kiss & Padisák (1990) made a single EM study in the Lake Balaton, in which the species could not be found. Unfortunately the earliest sample that we have from Lake Balaton was collected in 1997. Hence we can not prove its earlier occurrence in the Lake Balaton. However we suppose that *S. triporus* is not an invasive species, but it can be mistaken using only LM in the studies.

The species was recorded from eutrophic freshwaters of western North America, Japan and Korea (Gotoh *et al.*, 1998), but we found it in waters with different trophic level (e.g. Lake Balaton is oligo-mesotrophic – Bolla *et al.*, 2010), so we think it has wide ecological valence for the trophity.

Emended diagnosisof Stephanodiscus triporus

According to our and literature data we give an emended diagnosis of *S. triporus*.
Stephanodiscus triporus Genkal et Kuzmin emend. Genkal, Kiss and Ács
Syn.: *S. vestibulis* Håkansson, Theriot et Stoermer, *S. triporus* var. *volgensis* Genkal.

Cells are solitary or in short chain. Valves are usually concentrically convex-concave, sometimes almost flat with a diameter of 3.7-12.5 µm. The number of fasciculae is 23-65 and the number of radial striae (in 10 µm) is 10-21(30), composed by round or elongated areolae, or sometimes zig-zag slit (26-61 in 10 µm). Interstriae end spines. Areolae in the valve centre are located randomly. The single row of areoles becomes double-triple, or rarely quarter at the edge of valve face, or very rarely remains single. A single fultoportula is seen near the centre with 3 satellite pores internally (rarely 2 or 4). Its round external opening is slightly elevated like a tiny volcano. Opposite to this elevated opening a small depression can be seen (the space of connecting valve face fultoportula). There are marginal fultoportulae with 3 satellite pores on every second to fifth interstriae below a spine. The external opening of marginal fultoportulae is usually surrounded partially by arched structure (vestibule) which is sometimes not developed completely. The single rimoportula is situated above the ring of marginal fultoportulae with small labium oriented perpendicularly to interstria or in different angle, having a relatively long and large tube externally. Distribution: in oligotrophic to eutrophic Asian, European, North and South American lakes, reservoirs and rivers.

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Figure captions:

Table S 1. The list of those Hungarian, French, Russian and Estonian waters where the species was found by us with GPS coordinates.

Table. 2. The morphological variability of valve face of *Stephanodiscus triporus* and *S. vestibulis* on SEM micrographs of our study and found in the literature.

Table 3. Results of t- or Welch-test and Mann-Whitney test in population of *Stephanodiscus triporus* population versus of *S. vestibulis*

Table 4. Differential diagnoses of *Stephanodiscus triporus.*

Fig. 1. Conventional morphometric characters of *Stephanodiscus triporus* (shown on external valve face).

Fig. 2. Selected landmarks (shown on internal valve face of *Stephanodiscus triporus*).

Figs 3-16. LM and SEM micrographs of *Stephanodiscus triporus* (Figs 3-5, 8-11, 16) and *S. vestibulis* (Figs 6-7, 12-15) type material. Scale: 2 µm; black arrowhead: external tube of rimoportula; white arrowhead: valve face fultoportula; black arrow: valve face fultoportula; white arrow: the inverse place of valve face fultoportula.

Fig. 17. Box-plot diagram of measured conventional parameters with outliers. HU: Hungarian data, FR: French data, TV: type material of *Stephanodiscus vestibulis*, TT: type material of *S. triporus,* MI: *S. minutulus.* See other abbreviation in the text. The minimal and maximal values, median, the 25-75 percent quartiles are shown.

Figs 18-33 LM and SEM micrographs of investigated populations from Lake Balaton (Figs 18-19, 21-23, 24-29, 32-33) and French populations (Figs 20, 30, 31) . Scale: 2 µm 18-29, 1 µm: 30-33; Black arrowhead: rimoportula, white arrowhead: vestibule; black arrow: valve face fultoportula; white arrow: the inverse place of valve face fultoportula.

Fig. 34. Plot of the principal component scores 1 and 2, based on the conventional morphometric dataset. Group outliers are connected by lines. inverse triangular: population from Lake Balaton, triangular: French, diamond: type material of *Stephanodiscus vestibulis*, point: type material of *S. triporus*, square: *S. minutulus.*

Fig. 35. Plot of the Canonical Variates Analysis based on the geometric morphometric dataset. Group outliers are connected by lines. See abbr. on Fig. 34.

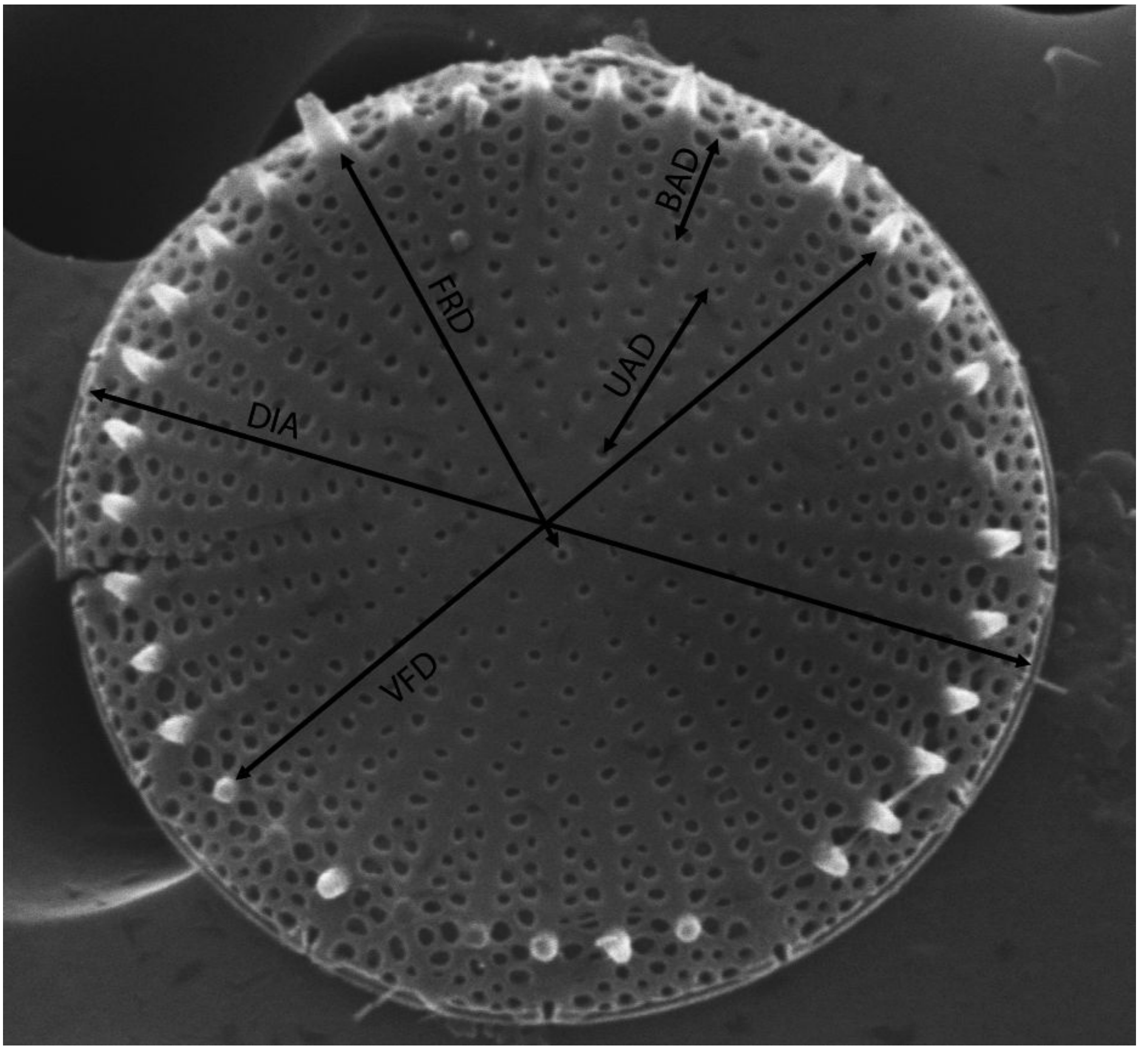
Fig. 36. Grids of relative warps with the average shape of population from Lake Balaton (A), French population (B), *Stephanodiscus vestibulis* type material (C) *S. triporus* type material (D) and *S. minutulus* (E). F: landmarks 1 to 9 (see Fig. 2).

Fig. 37. Box-plot diagram of measured conventional parameters in the area of former Soviet Union, with outliers. IV: Ivankovo reservoir, KI: Kiev's reservoir, LE: Lake Leegu, Ba: Lake Baikal, RY: Rybinsk reservoir, CH: Cheboksary reservoir. See other abbreviation in the text. The minimal and maximal values, median, the 25-75 percent quartiles and the outliers are shown.

Fig. 38. Distribution of *Stephanodiscus triporus/vestibulis* in Hungarian waters.

Fig. 39. The world-wide distribution of *Stephanodiscu triporus* (black circle) and *S. vestibulis* (hollow circle) based on our study, references and Supplementary references data.

Figs 40-43. SEM micrographs of *Stephanodiscus minutulus*. Scale: 2 µm. Black arrowhead: rimoportula, white arrowhead: external tube of marginal fultoportula.



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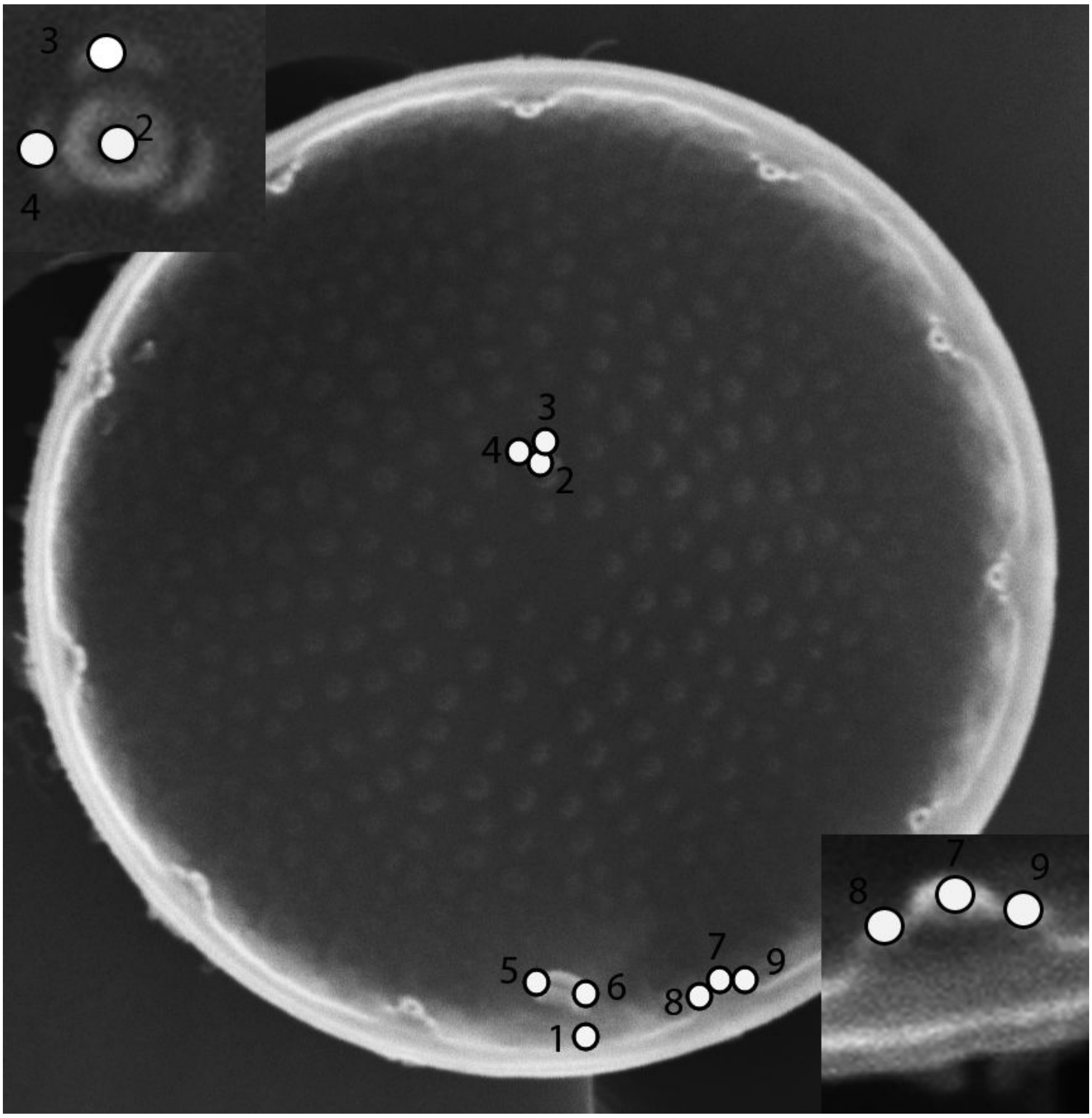

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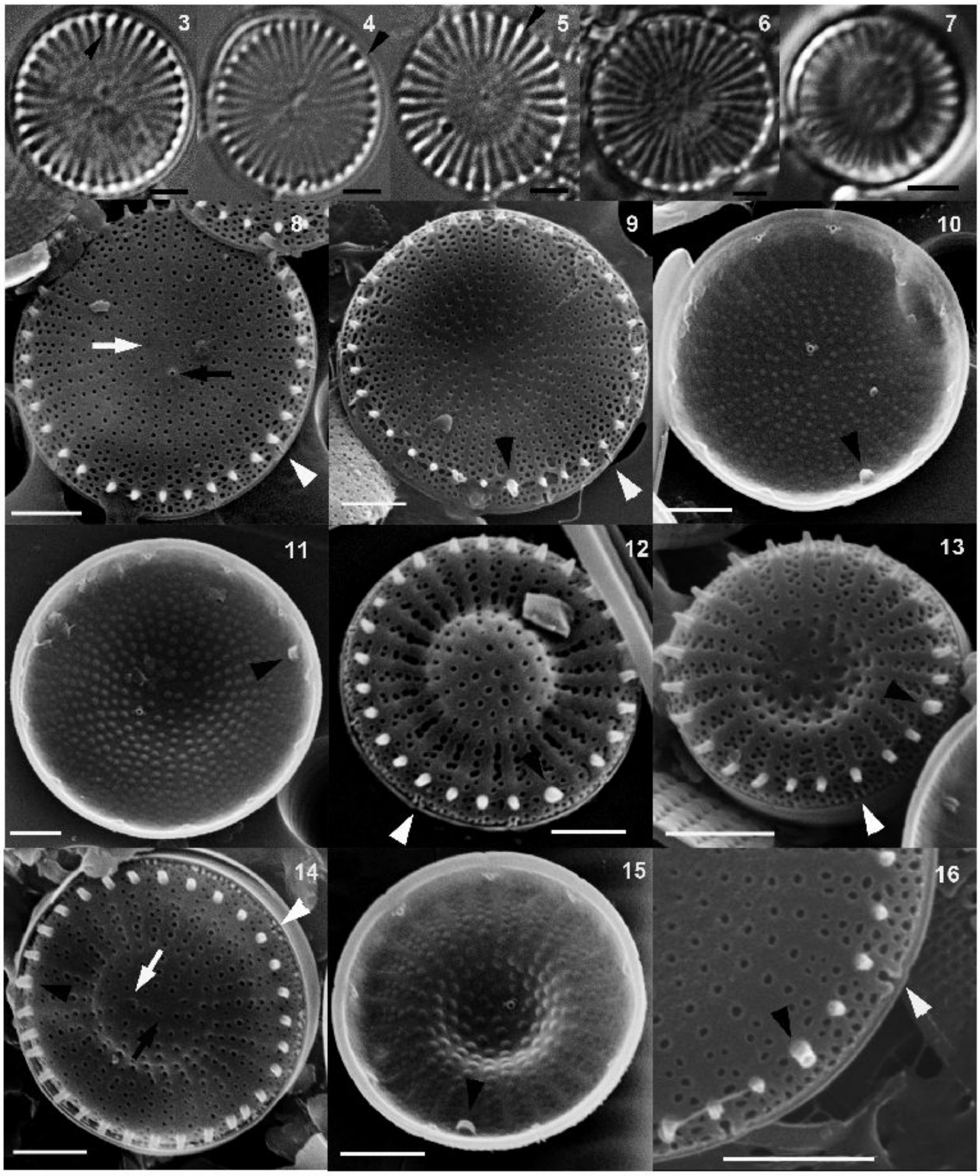
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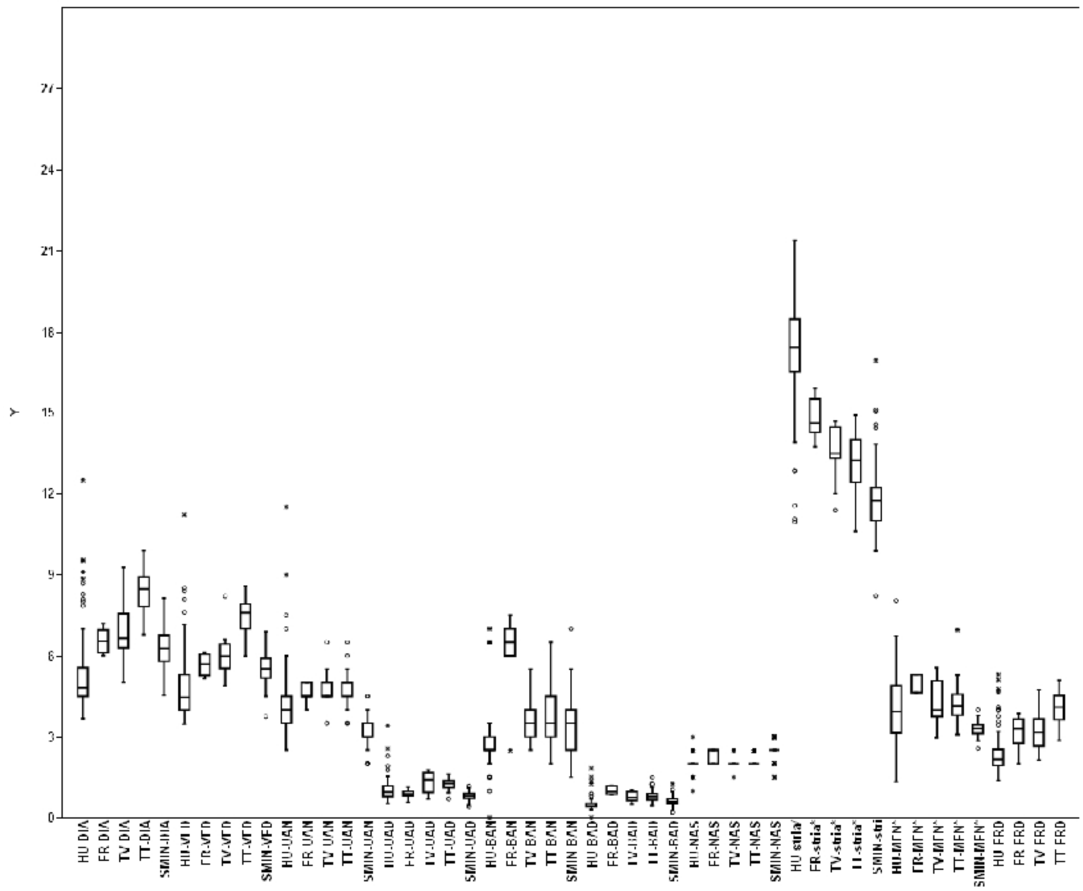
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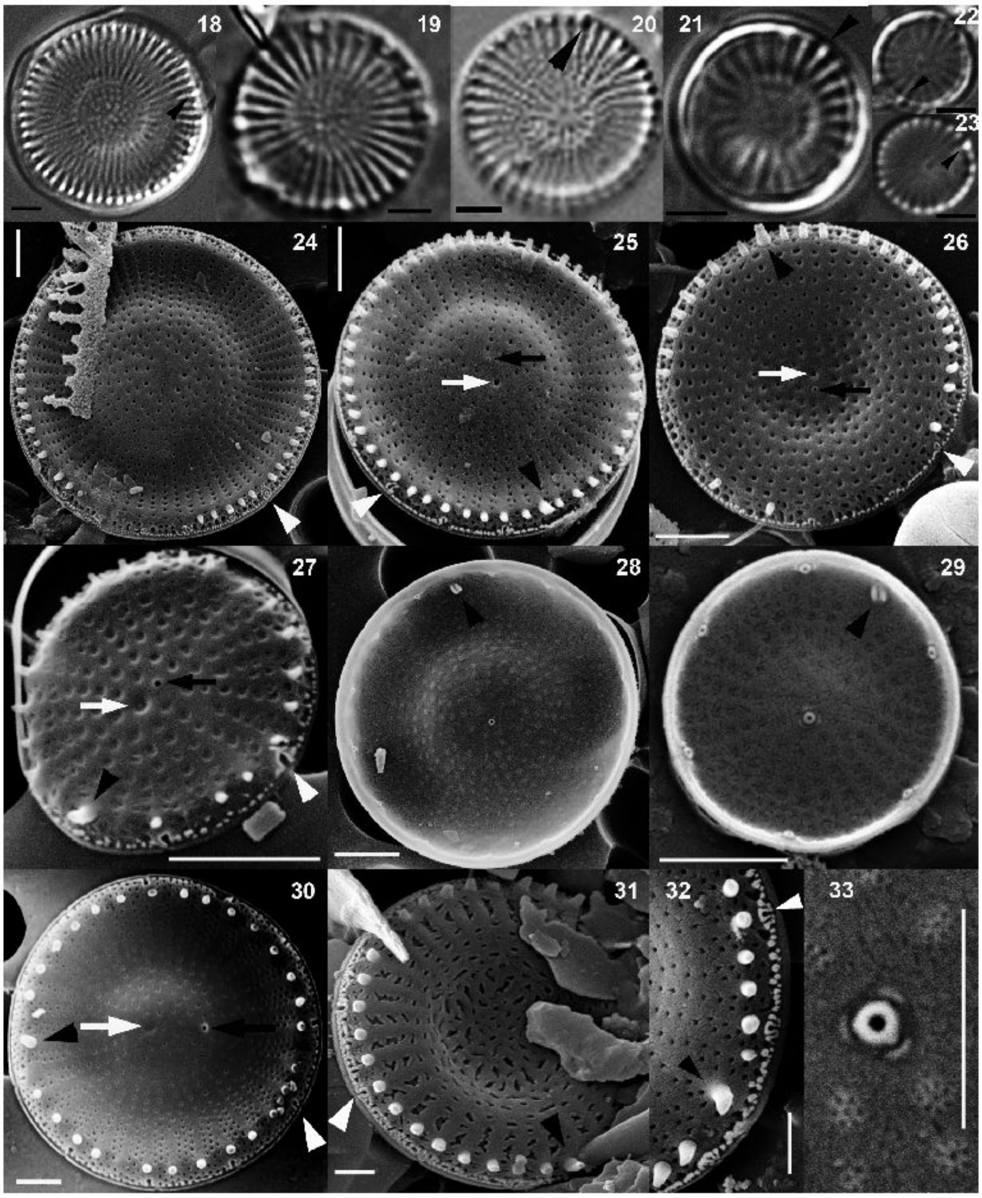
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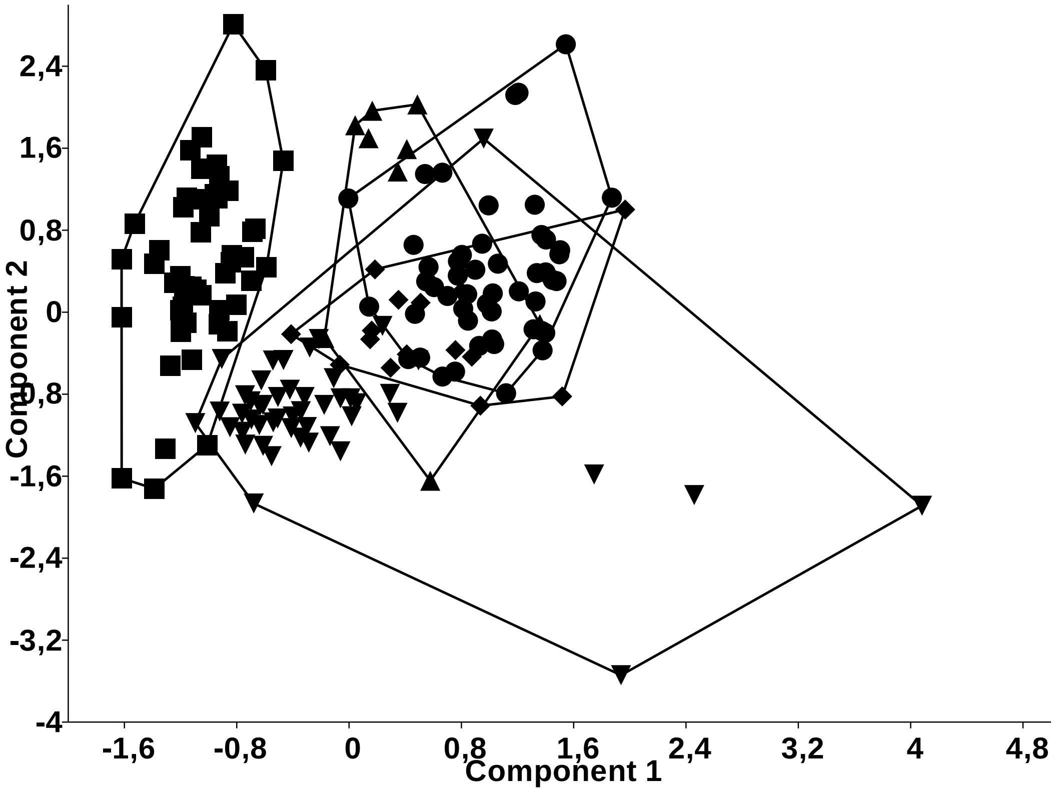
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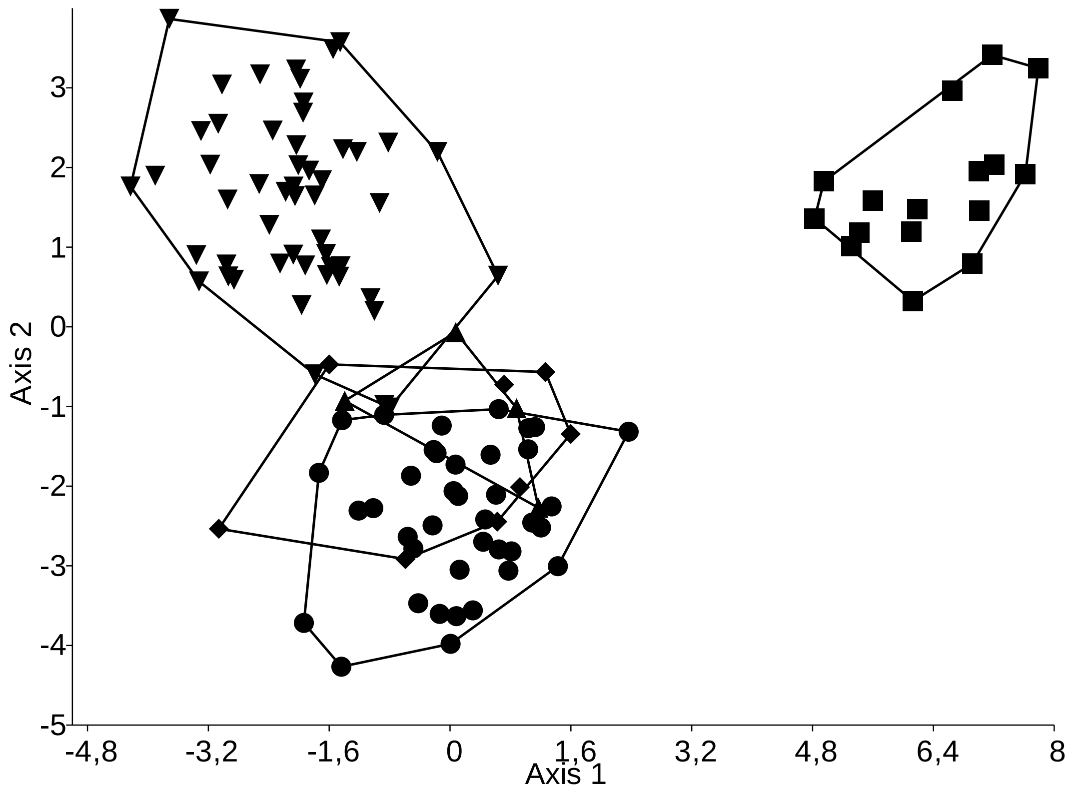
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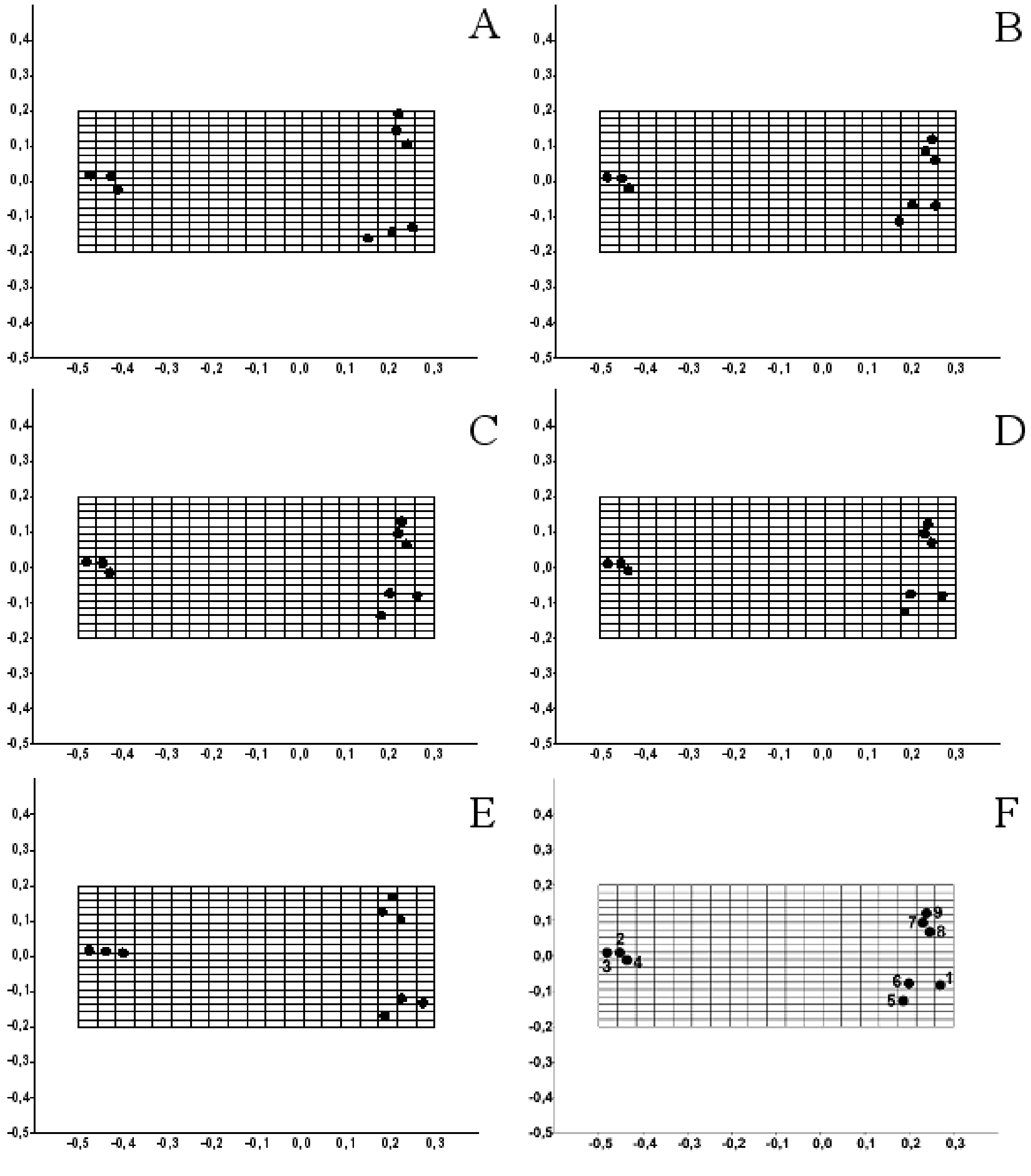
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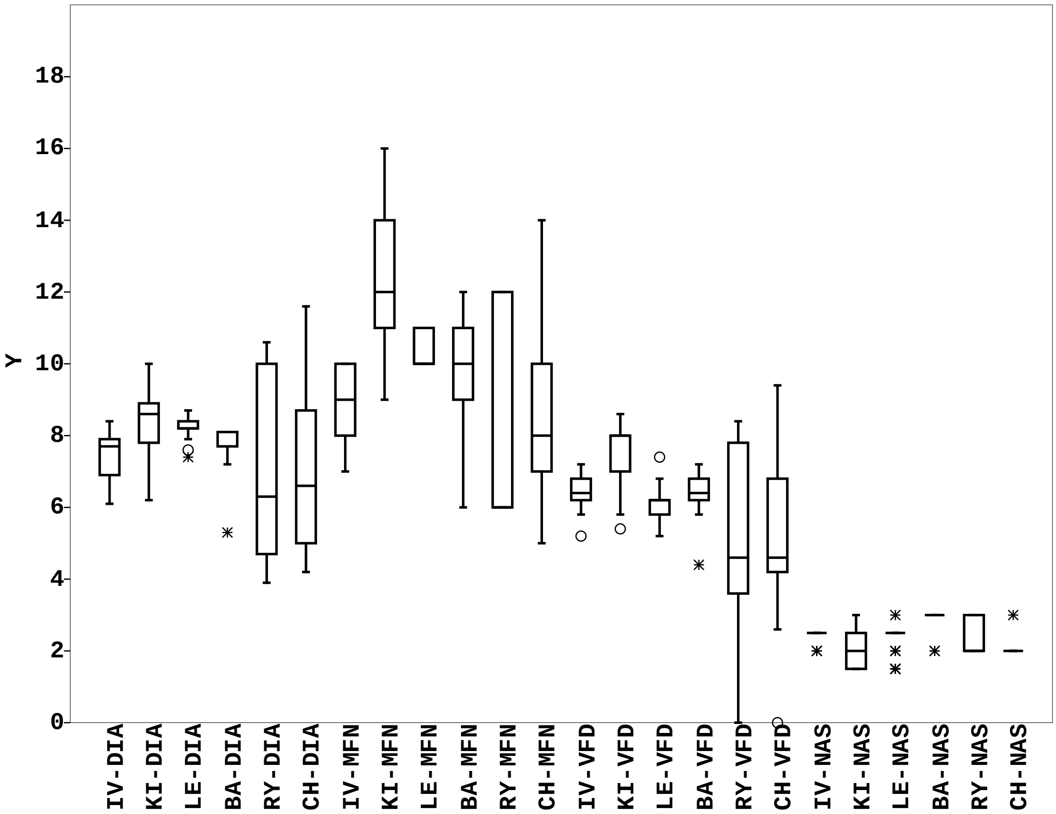
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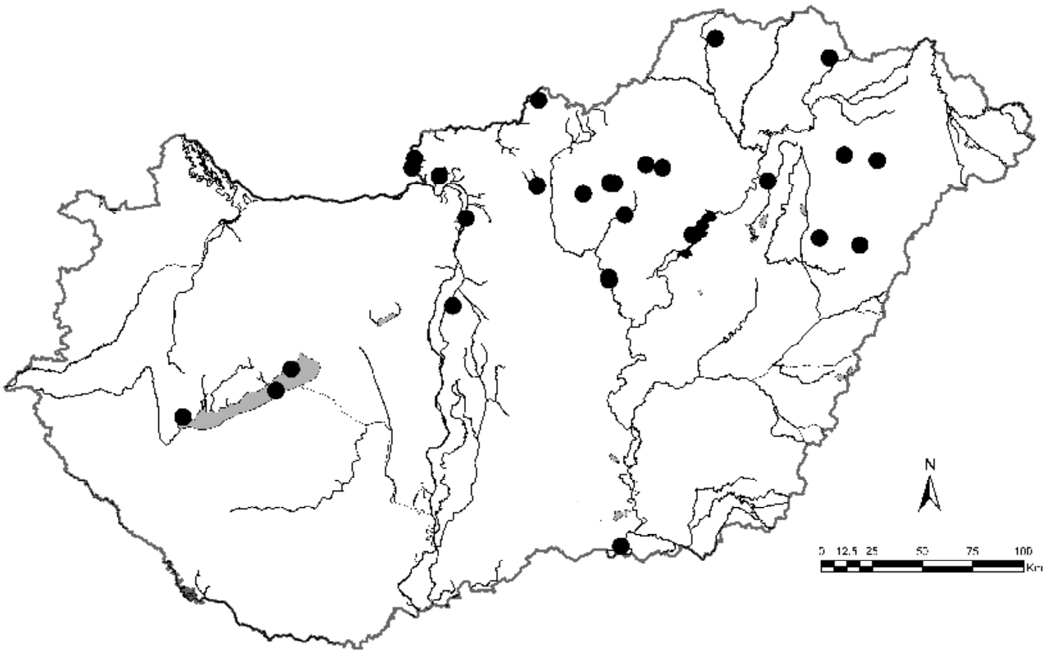
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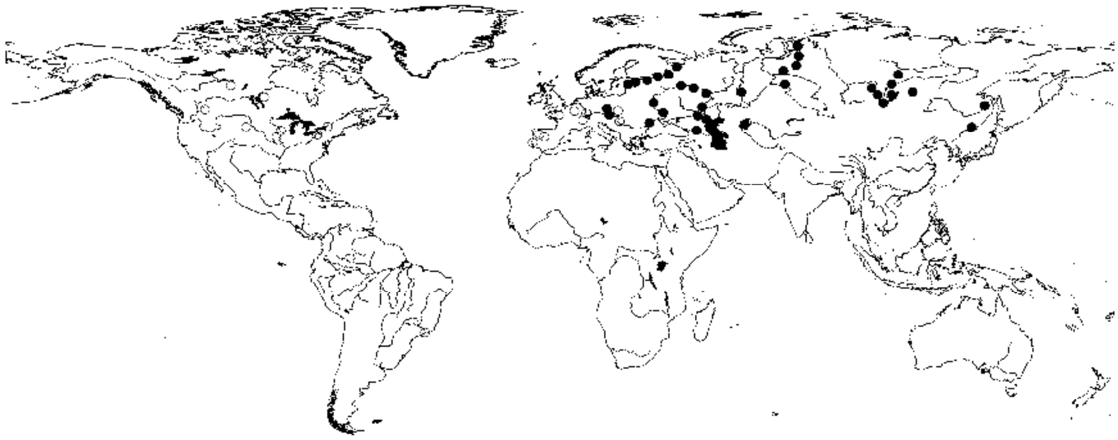

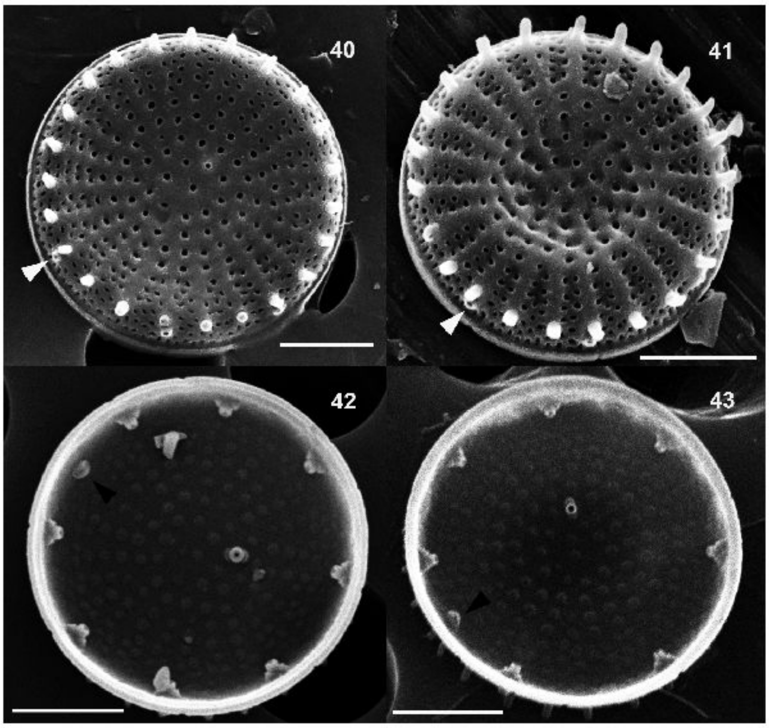

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N	**E (or W in case of France)**	**Water bodies**
47^o 40,26	20^o 10, 07	River Tarna
46^o 11,26	20^o 06,46	River Tisza

47° 23,39	20° 03,27	River river
47° 53,14	18° 45,41	River Ipoly
47° 51,08	18° 56,36	Malomvölgyi and Kis-Hanta creek
47° 55,47	18° 46,41	Ganádi creek
47° 48,51	20° 6,29	Domoszlói reservoir
47° 30,40	21° 42,56	Fancsikai reservoir
47° 46,12	19° 53,49	Gyöngyös-Nagyrédei reservoir
47° 53,534	21° 50,448	Harangodi reservoir
47° 34,741	20° 36,704	Kiskörei reservoir
48° 11,24	19° 36,20	Komravölgyi reservoir
47° 53,21	20° 19,8	Laskóvölgyi reservoir
47° 48,36	20° 4,51	Markazi reservoir
48° 21,44	21° 34,37	Lake Megyer-hegyi
47° 52,42	20° 25,26	Ostorosi reservoir
47° 48,38	19° 35,42	Palotási reservoir
48° 27,15	20° 47,37	Rakacai reservoir
47° 53,718	21° 40,856	Lake Szelkó
47° 33,699	21° 27,276	Szörf reservoir
47° 47,984	21° 8,319	Lake Templom
47° 16,19	19° 01,57	Lake Wizard’s
46° 45,36	17° 16,49	Lake Balaton at Keszthely
46° 53,12	17° 52,51	Lake Balaton at Tihany
46° 58,58	17° 58,48	Lake Balaton at Siófok
58° 21,924	27° 16,841	Lake Leegu
56° 34,52	36° 21,57	Ivanovskoye reservoir
50° 55,497	30° 30,828	Kiev’s reservoir
52° 11,598	107° 39,399	Lake Baikal
58° 22,03	38° 26,115	Rybinsk reservoir
56° 18,064	46° 42,826	Cheboksary reservoir
47° 0,788	1° 6,955	Sèvre Nantaise River at Tiffauges
49° 4,769	1° 6,849	LaVire River at Gourfaleur

	strongly convex	slightly convex	strongly concave	slightly concave	flat
S. triporus type material		10		8	30
S. triporus Lake Balaton	2	18	18	21	52
S. triporus Hungarian waters	5	1	9	8	4

S. triporus (Genkal & Kuzmin, 1978)	2	1			1
S. triporus from Russia*	13	9	4	7	1
S. triporus from Trstena (Houk, pers. comm.)	2	1	2		
S. triporus & *S. vestibulis* Lake Michigan (Genkal & Popovskaya, 1997)			1+1		
S. vestibulis type material	4	1	6		
S. vestibulis from Sèvre Nantaise River (France)	4		7		1
S. vestibulis from Vire River at Gourfaleur (France)	2	1	3	2	
S. vestibulis (Håkansson *et al.*, 1986)	1		2		
S. vestibulis (Håkansson & Kling, 1989)	1		1		
S. vestibulis (Gotoh *et al.*, 1998)	4		1		
S. vestibulis (Håkansson, 2002)	2				
S. vestibulis (Naya *et al.*, 2007)	2				
S. vestibulis (Tuji & Houki, 2001)	1		2		
Sum *S. triporus*	**22**	**39**	**32**	**44**	**89**
Sum *S. vestibulis*	**21**	**2**	**23**	**2**	**1**

inside	**Differ?**	**$P_{95\%}$**	**test**
DIA	Yes	0,02	Welch
WLR	**No**	0,12	Welch
MFN	**No**	0,13	Welch
FRD	Yes	6,07E-07	t
outside			
DIA	Yes	3,76E-05	Welch
UAN	**No**	0,65	t
UAD	**No**	0,51	Welch
BAN	**No**	0,15	t
BAD	**No**	0,15	t
VFD	Yes	4,28E-08	t
FRD	Yes	0,0001	t
FAS	**No**	0,31	t
landmarks			
L1	**No**	**0,91**	Mann-Whitney
L2	**No**	**0,60**	Mann-Whitney
L3	**No**	**0,77**	Mann-Whitney
L4	**No**	**0,60**	Mann-Whitney
L5	**No**	**0,99**	Mann-Whitney
L6	**No**	**0,83**	Mann-Whitney
L7	**No**	**0,37**	Mann-Whitney
L8	**No**	**0,39**	Mann-Whitney

L9	**No**	**0,33**	Mann-Whitney

	S. triporus	*S. minutulus*
Diameter (µm)	**3.7-12.5**	**4-12**
No. of striae in 10 µm	**10-21(30)**	**8-17(20)**
No. of marginal fultoportulae in 10 µm	**1.4-8**	**2.5-4**
No. of areolae in a stria at margin	**(1)2-3(4)**	**(2)3-4**
External opening of marginal fultoportulae	**Vestibulum**	**Short tube**
External tube of rimoportula	**Large**	**Short**
No. of satellite pore of valva face fultoportula	**3**	**2**
No. of satellite pore of marginal fultoportula	**3**	**2**
Position of marginal fultoportula	**On every 2nd to 5th interstriae, below a spine**	**On every 2nd to 5th interstriae, below a spine**
Valva face	**Usually concave or convex, sometimes flat**	**Flat or slightly concave or convex**