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Static allometry of unicellular green algae: Scaling of cellular surface area and volume in the genus *Micrasterias* (Desmidiales)

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Running title: Allometry and S:V scaling of *Micrasterias*

Abstract

The surface-area-to-volume ratio of cells is one of the key factors affecting fundamental biological processes and, thus, fitness of unicellular organisms. One of the general models for allometric increase in surface-to-volume scaling involves fractal-like elaboration of cellular surfaces. However, specific data illustrating this pattern in natural populations of the unicellular organisms have not previously been available. This study shows that unicellular green algae of the genus *Micrasterias* (Desmidiales) have positive allometric surface-to-volume scaling caused by changes in morphology of individual species, especially in the degree of cell lobulation. This allometric pattern was also detected within most of the cultured and natural populations analysed. Values of the allometric S:V scaling within individual populations were closely correlated to the phylogenetic structure of the clade. In addition, they were related to species-specific cellular morphology. Individual populations differed in their allometric patterns and their position in the allometric space was strongly correlated with the degree of allometric S:V scaling. This result illustrates that allometric shape patterns are an important correlate of the capacity of individual populations to compensate for increases in their cell volumes by increasing the surface area. However, variation in allometric patterns was not associated with phylogenetic structure. This indicates that the position of the populations in the allometric space was not evolutionarily conserved and might be influenced by environmental factors.

Keywords: allometry; Desmidiales; geometric morphometrics; green algae; surface-to-volume ratio

Introduction

Scaling of the surface area (S) and volume (V) of three-dimensional objects with identical shape, but varying size, occurs according to the well-known geometric power law defined as $S = k \cdot V^{2/3}$, where k represents the deviation of the object from a spherical shape (Huxley, 1932). Thus, when the organism is growing isometrically, its S:V ratio decreases according to the two-thirds power law function. For unicellular organisms this involves 2/3 scaling of the cellular surface that inherently affects the rates at which it can take up resources from the environment, as well as dispose of any excreted substances. It has repeatedly been shown that different cellular S:V ratios of various taxa and communities of microorganisms correspond to different ecological strategies and niches in natural habitats (e.g. Irwin *et al.*, 2006; Soininen & Kokocinski, 2006; Finkel *et al.*, 2009; Neustupa *et al.*, 2013). This has led to an expanding array of studies investigating the community structure of unicellular microalgae based on their morphological classification using volume, surface area, or other shape descriptors (Finkel *et al.*, 2007; 2009; Law *et al.*, 2014). Notably, Finkel *et al.* (2007) showed that the long term changes in size structure of marine phytoplankton over the Cenozoic reflected changes in estimated sea surface temperature. Decrease in water temperature, leading to lower stratification and, consequently, higher nutrient loads to the upper layers, was accompanied by an increase in median cell size of major phytoplankton groups. Conversely, temperature increase led to lower nutrient levels and smaller phytoplankton cells with higher S:V ratios. This pattern of cell size dynamics directly dependent on water temperature and nutrient availability was also confirmed in a study based on a global data set of recent marine phytoplankton (Mousing *et al.*, 2014). Likewise, the decrease in phytoplankton size in relation to lower nutrient availability was observed in large stratified lakes (Finkel *et al.*, 2009). In addition, Neustupa *et al.* (2013) illustrated that mean cell size of the phytobenthic desmidiacean green algae in acidic wetlands decreased with decreasing water pH that lead to lower availability of key nutrients.

However, besides changes in species structure that lead to shifts in mean cell size the overall S:V ratio of natural communities can be also influenced by within-species, size-related changes in cellular morphology. In fact, shape variation of the unicellular organisms typically is size-dependent, both within and among species. This results in allometric relationships in which the scaling exponent (α) of the power law function is significantly different from 2/3 (Okie, 2013). Allometric shape changes can be differentiated into ontogenetic allometry related to infraspecific growth processes, static allometry reflecting shape variation among individuals at a given ontogenetic stage, and evolutionary allometry resulting from differences among species with different phylogenetic position (Klingenberg, 1998; Pélabon *et al.*, 2014). Recently, a model was presented, highlighting three general strategies for increasing the surface area of living cells: (1) surface elaboration (fractalization), (2) geometric shape dissimilitude, such as elongation or flattening, and (3) surface internalization (Okie, 2013). While the first two mechanisms are inherently related to cellular shape change, surface internalization, accomplished typically by increasing the number of mitochondria, may be shape independent. Okie's (2013) model illustrated that allometric surface-to-volume scaling at the cellular level may lead to exponents lower than 0.67, but also to linear relationships (i.e. exponents of approximately 1.0), or even supralinear scaling, using the above mentioned strategies. However, positively allometric S:V scaling, implying that exponents are significantly higher than 0.67, was not always ascertained in various natural assemblages of the unicellular organisms, such as phytoplankton or microphytobenthos. Despite apparent interspecific geometric dissimilitude of these organisms, Niklas (1994) illustrated that the scaling exponents of the surface area with respect to cellular volume were close to 0.67 in a data set compiled from literature records of the surface areas and volumes of freshwater and marine microalgae. This has been supported by simulations illustrating that the two-thirds S:V scaling power law applies to a set of simple geometric objects, such as prolate and oblate spheroids, or terete cylinders, differing in their aspect ratio, thus approximating the observed morphological variability of many unicellular microalgae, such as diatoms or chlorophycean green algae (Niklas, 1994). However, Reynolds (2006) obtained an S:V scaling exponent $\alpha = 0.82$ for a set of frequently distributed phytoplankton taxa with body volumes spanning across six orders of magnitude and cellular shapes varying from spheres and ellipsoids to cylinders or their combinations. He suggested that an increased S:V scaling exponent was the result of evolutionary pressure for stabilizing the S:V ratio of the phytoplankton organisms, which possibly may constitute the single most influential factor governing the morphology of planktonic microalgae.

Conversely, allometric changes in surface elaboration of unicellular organisms have so far received much less attention. Although Okie (2013) suggested that an increased cell size of microorganisms should be positively related to the depth and frequency of their surface convolutions, this hypothesis has never been explicitly tested. However, there are several common groups of unicellular eukaryotes that typically have elaborated shapes, including lobes, incisions, or processes, which could be allometrically related to cell size. Many of these taxa belong to a group of phototrophic protists, traditionally called "green algae", i.e. microalgae classified to several lineages of the Chlorophyta and Streptophyta (Leliaert *et al.*, 2012). Their mature cells are typically surrounded by polysaccharide walls, resulting in rigid cellular shapes. Most notably, the desmids (Desmidiales, Zygnematophyceae), a streptophytan group comprising more than 5000 species, typically have delicately elaborated cells with numerous successively divided incisions and lobes (Brook, 1981; Coesel & Meesters, 2007). Because of this complexity, vegetative cells of several desmid genera, such as *Micrasterias*, *Euastrum*, or *Staurastrum*, have been considered to be the morphologically most complicated cells, i.e. deviating the most from a spherical shape, within the entire plant kingdom (Brook, 1981). Desmid cells are typically composed of two bilaterally symmetric semicells. They reproduce by asexual mitotic division in the isthmus plane, their narrowest central part. The daughter cells then develop a new, younger semicell. Growth of the semicells involves gradual development of species-specific incisions and lobes and is terminated by deposition of the secondary cell wall that includes rigid polysaccharide microfibrils (Coesel & Meesters, 2007). Consequently, each cell is composed of 2 unequally old semicells, whose morphology is fixed once their growth phase is finished. From a morphological point of view, the semicells form tightly integrated units. Neustupa (2013) illustrated that the average morphological difference between two mature *Micrasterias* semicells of a single desmid cell is more or less the same as the difference among semicells from different cells in a single population. Therefore, semicells may be taken as fundamental units for the morphological analysis of desmids. Most desmid species grow in the microphytobenthos of oligotrophic wetlands and peatlands (Coesel & Meesters, 2007; Neustupa *et al.*, 2013). In these habitats they often form a dominant phototrophic component of the microbial community. Additionally, they may be cultivated relatively easily in asexually reproducing clonal strains and these genetically homogenous populations can be kept in cultures on a long-term basis. These characteristics make desmids a suitable model group from among the unicellular eukaryotes for investigating the evolutionary dynamics of surface elaboration as a possible mechanism for allometric manipulation of the S:V ratio of cells.

The present study, the first of its kind, evaluates the hypothesis that surface convolutions of the cells are actually used for allometric S:V scaling, both within and among species, in accordance with Okie's (2013) model. In total, 49 independent population samples belonging to the desmid genus *Micrasterias* were used. Members of this genus are found worldwide in oligo- and mesotrophic freshwater wetlands. About 65 *Micrasterias* species have been described (Růžička, 1981; Škaloud *et al.*, 2011). The generic name was derived from the Greek term for "little star" and, indeed, the members of this genus include possibly some of the most spectacularly shaped unicellular organisms on earth. Their species-specific shape is formed by multiple lobes and incisions. The presence of repeatedly branched cellular lobes is even considered as one of the characteristic features of the lineage (Škaloud *et al*., 2011). It includes taxa with morphologies ranging from relatively simple oval semicell shapes, without any marked incisions, to extremely complex star-like cells (Škaloud *et al.*, 2011). Cells of the *Micrasterias* species typically have flat cells and ellipsoidal outlines; thus their overall shape pattern can be represented by their front view. Therefore, microphotographs of the cells in front view, together with data on the thickness of the cells, can be used for geometric morphometric registration and subsequent estimation of the cell volume and surface area (Neustupa *et al.*, 2011, 2013). In addition, overall cell complexity can be represented by the quotient of isoperimetric inequality that evaluates the deviation of the cellular shapes from circular outlines (Osserman, 1978; Škaloud *et al.*, 2011). Using these techniques, the allometric patterns of the *Micrasterias* shape were investigated in order to evaluate the effects of cell surface elaboration on the surface-to-volume scaling strategies not only at the level of clonal strains, but also for interspecific comparison. The question, whether populations of the desmid algae inherently exhibit static morphological allometry, i.e. surface area to volume scaling following a power law with an exponent significantly different from two-thirds, has never been explicitly evaluated. Positive allometry would mean that cellular incisions and processes are relatively more pronounced in larger cells. Such a trend would decelerate the decrease in S:V ratio related to increase in cell volume. Conversely, the absence of static allometry (i.e. the surface area scaling exponent is approximately 2/3) would indicate that morphological complexity of the desmid cells does not have any immediate relation to physiology, such as nutrient or CO_2 uptake, and might be due to neutral evolution (Bonner, 2013). In addition, it is not known whether such morphological allometry might be solely resulting from the genetic variation among different populations and species, or whether allometric deviation from the two-thirds scaling rule is determined by the plastic response of a single genome. In that case, it should also be discernible within a single clonal population. Positive allometry at the interspecific level would mean that larger species typically have more elaborated cells. However, should positive allometry also be a part of the plastic response of individual genomes, the above mentioned morphological pattern should be more or less equal among natural and cultured desmid populations.

I also wanted to ascertain whether the possible deviation from the two-thirds scaling would correlate with species-specific cell morphology. Do taxa with morphologically complicated cells have a more pronounced allometric response than those with simpler shapes? Eventual higher allometric scaling of populations with larger and more elaborate cells would indicate that they have to cope with stronger evolutionary limits on their cellular S:V ratio, driving their morphological plasticity. In addition, is the pattern of the allometric response within the populations more or less uniform across the genus? Neustupa *et al.* (2008) illustrated that temperature-related plasticity of a clonal strain of *Micrasterias rotata* involved allometric changes consisting of gradual deepening of incisions with increase in semicell size. Is this pattern shared by other species of the genus? Relatively homogenous allometric patterns of the size-related shape change would suggest that variation is channelled in a single direction within the morphospace of the *Micrasterias* species. It would also mean that this allometric direction would be the most suitable dimension for an evolutionary change with the least relative constraints for morphological evolution (Klingenberg, 2010).

To evaluate the patterns of allometric shape changes, two parallel approaches were chosen. First, I compared the empirical morphospace of the investigated group, based on geometric morphometric registration of morphological data (Zelditch *et al.*, 2004; Adams *et al.*, 2013), with the allometric slopes of individual populations and species. If there is any significant relation between species-specific cellular shapes and mean allometric S:V slopes of individual populations, then it should be possible to identify the morphospace segments that are typified by higher or lower slopes. Alternatively, the absence of any relation between allometric S:V scaling and the shape characteristics of individual taxa should result in a more or less random distribution of the observed allometric slopes among populations represented in the morphospace. Second, the allometric space of the investigated populations was constructed. The concept of an allometric space – a space of the allometric trajectories – was originally introduced by Gerber *et al.* (2008). Since then, it has proven to be an invaluable tool for elucidating allometric disparity, evolution of allometries, and ecological correlates of allometric diversification (e.g. Wilson & Sánchez-Villagra, 2010; Wilson, 2013; Watanabe & Slice, 2014). Each population within an allometric space is represented by a set of allometric coefficients that are subjected to a principal component analysis. Then, a population is depicted by a point in the resulting multivariate space that illustrates the patterns of allometric diversity and differences in allometric trajectories among populations. In the present study, low-dimensional allometric diversity within the genus *Micrasterias* would probably mean that most of the populations share a few allometric trajectories. Conversely, higher diversity of the allometric trajectories, spanned by multiple PC axes of the allometric space, would indicate that allometric variation within the genus *Micrasterias* is multidimensional and possibly does not form a single constraint on its morphological evolution.

Material and Methods

Sampling and cultivation

The dataset comprised 25 natural populations and 24 clonal strains of 16 *Micrasterias* species (Fig. 1, Table S1). The natural populations originated from samples taken between 2012 and 2014 in various European temperate and boreal locations. The clonal strains were either newly isolated by single-cell pipetting, or acquired from public culture collections (Table S1). The strains were cultivated in MES-buffered DY IV liquid medium at 22°C and illuminated at 40 μmol photons m^{-2} s^{-1} with 18 W cool fluorescent tubes (Philips TLD 18W/33), at a light:dark (L:D) regime of 12:12 hours.

Data acquisition

For each population or strain, a total of 50 mature semicells were photographed. Thus, the entire dataset consisted of 2450 objects. Microphotographs were taken at 200× magnification on an Olympus BX51 light microscope with Olympus Z5060 digital photographic equipment. Then, 21 structurally corresponding landmarks were depicted along the front view outlines of the semicells (Figure S1) using TpsDig software, ver. 2.15 (Rohlf, 2013).

The area (*A*) and perimeter (*P*) of the front view outlines were calculated from the landmark coordinates. The area was computed as a two-dimensional region enclosed by a polygon, formed by the connecting line joining adjacent successive landmarks positioned along the semicell outline (Weisstein, 2014), as follows:

$$A = \frac{1}{2} \times \left| \sum_{i=0}^{n-1} \left(x_i y_{i+1} - x_{i+1} y_i \right) \right|$$

Likewise, the perimeter was computed as the sum of the Euclidean distances among the adjacent successive landmarks. The isoperimetric quotient (*Q*) was used as a measure of the deviation of the front views of cellular shapes from circularity (Osserman, 1978). The *Q* value of an outline has been defined as the ratio of its area and that of a circle with the same perimeter. It can also be depicted as follows:

$$Q = \frac{4 \cdot \pi \cdot A}{P^2}$$

where *Q* reaches values from 0 to 1, which means that an ideally circular object has $Q = 1$ and increasing deviation from circularity leads to a consequent decrease in the *Q* value.

The cell volumes and surface areas were estimated following previously described algorithms for desmids with biradial cells (Neustupa, *et al.* 2011, 2013). Briefly, the length (*a*) and width (*b*) of each cell were measured in TpsDig, ver. 2.15. The maximum thickness (*c*) was estimated on the basis of published width-to-thickness ratios of individual taxa (Růžička, 1981) and by direct measurements of the cells. The area of an ellipse ($A_{ellipse}$) with *a* and *b* axes, as well as the volume of a scalene ellipsoid ($V_{ellipsoid}$) with *a*, *b*, and *c* axes were computed by trivial formulas using values corresponding to the length, width, and thickness of each cell. Likewise, the perimeter of an ellipse with *a* and *b* axes was calculated by Muir's approximation formula as follows:

$$P_{ellipse} \approx 2 \cdot \pi \cdot \left[\left(a^{\frac{3}{2}} + b^{\frac{3}{2}} \right) \Big/ 2 \right]^{\frac{2}{3}}$$

and the surface of a scalene (general) ellipsoid with *a*, *b*, and *c* axes corresponding to length, width, and thickness values, respectively, of the cells was approximated by Knud Thomsen's formula as follows:

$$S_{ellipsoid} \approx 4 \cdot \pi \cdot \left[\left(a^p \cdot b^p + a^p \cdot c^p + b^p \cdot c^p \right) / 3 \right]^{\frac{1}{p}}$$

where $p = 1.6075$ yields the maximum error rate of the surface values at 1.061% (Michon, 2009). Then, the surface area (S_x) and volume (V_x) of a cell with a given length (a), width (b) and thickness (c) were estimated as follows:

$$S_x \approx \left(P_x \cdot S_{ellipsoid} \right) \big/ P_{ellipse}$$

and:

$$V_x \left(A_x \cdot V_{ellipsoid} \right) \big/ A_{ellipse}$$

which, after algebraic simplification of trivial geometric formulas for the scalene ellipsoid, finally gives:

$$V_x = \left(2 \cdot A_x \cdot c \right) / 3$$

Morphometric and regression analyses

For the geometric morphometric analysis, landmark configurations were superimposed by generalised Procrustes analysis (GPA) in TpsRelw, ver. 1.45 (Rohlf, 2013). In *M. ralfsii*, a species without conspicuous cell incisions, the landmarks were slid along along a curve to minimize the amount of shape change between a specimen and the Procrustes average of all the specimens (Gunz & Mitteroecker, 2013). The correlation between Procrustes and the tangent shape distances was assessed using TpsSmall, ver. 1.20, to ensure that the shape variation within the entire dataset was small enough to allow subsequent statistical analyses (Zelditch *et al.*, 2004). Indeed, this correlation proved to be very high ($r = 0.999$). Therefore, I proceeded with further geometric morphometric analysis. The configurations were made symmetrical using the standard method of Klingenberg *et al.* (2002). Multivariate regression of morphometric data on size was conducted in TpsRegr, ver. 1.31, using centroid size (CS) values of individual configurations as the independent variable. These analyses, aimed to test the shape-to-size relationship illustrating possible static morphological allometry, were conducted separately for each population. The significance of individual regression models was evaluated by permutation tests (with 999 permutations) on Wilk's λ (Zelditch *et al.*, 2004). In addition, the effect sizes were illustrated by percentages of the variation explained by individual multivariate regression models (Rohlf, 2013).

Surface area to volume scaling of cells within the populations was assessed by a set of the standardised major axis (SMA) linear regressions (Warton, 2007; Warton *et al.*, 2012). They were based on the logarithmic form of the original allometric power law function:

$$S \propto k \cdot V^{\alpha}$$

expressed as follows:

$$\log S \propto a \cdot \log V + \log k$$

Thus, the slope of the SMA regression line was used as an indicator of the scaling exponent of the allometric power law function reflecting the surface-to-volume relation within individual populations. SMA regression was preferred over least-squares regression as both variables – surface area and volume of cells – were measured with an error, i.e. they represent a typical symmetric relationship, most suitably fitted with an SMA line (Warton, 2007; Smith, 2009). The SMA analysis, as well as the 95% confidence intervals for the slope of the SMA line, was computed using the *smatr* package ver. 3.4 (Warton *et al.*, 2012) in R, ver. 2.15.3. (R Development Core Team, 2013).

Linearity of the log S vs. log V relation within the *Micrasterias* lineage was evaluated using the Rainbow test implemented by function *raintest* in package *lmtest* in R, ver. 2.15.3 (Zeileis & Hothorn, 2002). Non-linear relation would suggest possible mixed power-law relationship of the S:V scaling across the entire cell size span of the lineage. The relation of the shape variation in different populations and their allometric slopes was graphically illustrated by multiquadric spatial interpolation of the slopes values onto the two-dimensional ordination plot of the principal component analysis (PCA) of the geometric morphometric data. PCA was conducted in TpsRelw, ver. 1.52 (Rohlf, 2013). The scores of the objects on the first two axes, spanning most of the shape variation among the mean shapes of individual populations, provided a basis for the continuous spatial estimate of the changes in values of the allometric slopes within the morphospace. The analysis was conducted in PAST, ver. 2.17c (Hammer *et al.*, 2001). The deformation grids, illustrating shape changes spanned by first and second principal components, were computed using the thin-plate spline function in TpsRelw, ver. 1.52.

Phylogenetic analysis

The 18S rDNA sequences of the *Micrasterias* taxa (Table S1) were acquired from the GenBank database and manually aligned using MEGA software, ver. 6.0 (Tamura *et al.*, 2013). The total alignment, consistent with the findings of Škaloud *et al.* (2011), consisted of 1641 homologous characters with 122 variable positions (Appendix S1). The sequence of *Staurastrum margaritaceum* (GenBank accession no. AJ829649) was used as an outgroup rooting the *Micrasterias* lineage. The most appropriate evolutionary model for the maximum likelihood phylogenetic analysis was determined by the *modelTest* function of the *phangorn* package, ver. 1.7-4 (Schliep, 2011). The procedure evaluated individual models on the basis of the Bayesian information criterion (BIC) in R, ver. 2.15.3 (R Development Core Team, 2013). The lowest value for the BIC was obtained by the general-time-reversible model with invariable sites and gamma distribution (GTR+G+I) and, consequently, this model was chosen for the maximum likelihood (ML) phylogenetic analysis in the *pml* and *optim.pml* functions of the *phangorn* package. Bootstrap supports of nodes of the phylogenetic tree were calculated by non-parametric bootstrap analysis using the *bootstrap.pml* function (with 999 replicates) of the *phangorn* package.

Mapping the morphospace structure onto the phylogeny of the group was conducted by squared-change parsimony in MorphoJ, ver. 1.06b (Klingenberg, 2011). The same software was used for illustrating the evolutionary trajectories through the shape space. The phylogenetic signal in the morphometric data was evaluated by a permutation test simulating the null hypothesis of the absence of any phylogenetic signal by randomly permuting the shape data among the terminal nodes and computing the total amount of squared change summed over the branches of the phylogenetic tree (Klingenberg & Gidaszewski, 2010). The phylogenetic signal in the values of the allometric slopes was evaluated by a permutation test on the Blomberg's *K* (Blomberg *et al.*, 2003) using the *phylosig* function of the *phytools* package (Revell, 2012) in R ver. 2.15.3.

Allometric space analysis

Allometric trajectories of populations were constructed using a procedure based on the multivariate regression of shape data on CS values of the landmark configurations. The objects were first aligned by GPA. Then, the *x*- and *y*-axis of the Procrustes coordinates were subjected to least squares regression analysis. The slope values of the regression analyses for each population were used as observations in a dataset containing information on the differences in their allometric trajectories. PCA of this dataset resulted in a multivariate space with each population represented by a point summarizing its allometric patterns. A point representing a theoretical population without any allometric shape change was also included with values of the slopes $a = 0$ for all columns corresponding to the *x*- and *y*-axis of the Procrustes coordinates of the aligned landmarks.

This method is slightly different from previous studies that employed the concept of allometric space (e.g. Gerber *et al.*, 2008; Wilson & Sánchez-Villagra, 2010; Wilson, 2013). In those studies the allometric space was based on the coefficients of the first principal component acquired from PCA of the morphological data, typically encompassing both juvenile and adult specimens. In such datasets, inherently including the ontogenetic allometry, the first PC has usually been considered as the "allometric axis", closely corresponding to the growth-related morphological changes (Klingenberg, 1998; Gerber *et al.*, 2008). However, the data used in this study solely include non-growing mature semicells with a fully developed rigid secondary cell wall. Thus, any size-to-shape relation clearly corresponds to static morphological allometry (Klingenberg, 1998), which typically includes considerably lower proportions of the total shape variation. In such datasets, the first PC may not necessarily be identical with allometry. Conversely, the coefficients of the multivariate regression model explicitly describe the size-related shape variation. In the geometric morphometric framework, with the Procrustes coordinates standardised within a joint shape space, the slope values of individual least-squares linear regressions could be used as mutually corresponding descriptors of the allometric patterns of populations.

ProTest analyses

The multivariate spaces were compared using the Procrustean tests (Jackson, 1995; Peres-Neto & Jackson, 2001) implemented by the *protest* function of the *vegan* package (Oksanen *et al.*, 2013) in R, ver. 2.15.3. First, the multivariate datasets, such as the principal components of the morphometric data, the principal components of the allometric trajectories, or the phylogenetic distance matrix, were subjected to a three-dimensional non-metric multidimensional scaling (NMDS) procedure (Hammer *et al.*, 2001). The phylogenetic distance matrix, entering the

NMDS analysis, was based on the Tajima-Nei distances among the 18S rDNA sequences of taxa (Tajima & Nei, 1984). For each dataset, the NMDS resulted in a matrix of three axes spanning the variation patterns among populations. Then, pairs of these matrices were rotated to maximum similarity, minimizing the sum of squared differences (Peres-Neto & Jackson, 2001). The significance of the resulting Procrustes statistic was assessed by a permutation test with 9999 repetitions.

The partial Procrustean test was used to assess the variation in two matrices with the effects of the third matrix (or variable) partitioned out prior to the actual analysis (Peres-Neto & Jackson, 2001). Besides comparison of matrices, the effects of the univariate variables, such as the slope values of the S:V scaling, or mean isoperimetric quotient values of the populations, were also assessed using the Procrustean tests. In these cases, the three-dimensional matrices entering the ProTest procedure consisted of a first column including values of the actual variable and two all-zero columns. The Procrustean test of two univariate variables is equivalent to the Pearson's *r* of the ordinary least squares linear correlation analysis, which was evaluated in parallel in PAST, ver. 2.17c.

Results

The set of 49 investigated populations comprised cellular shapes profoundly differing in circularity of their front views (Fig. 1). This was reflected in their mean isoperimetric quotients (*Q*) ranging from 0.13 in two populations of *M. rotata* to 0.81 in one of the *M. ralfsii* populations (Table S1).

Positive allometry was detected in an analysis of the surface-to-volume scaling of the entire dataset of 2450 desmid cells ($r = 0.92$, $R^2 = 0.19$, $p = 0$, slope $a = 0.91$; 95% confidence intervals for a: 0.89–0.92). This pattern clearly showed that populations with larger cells had more complicated cellular shapes, thus compensating for a decrease of their S:V ratio. The Rainbow test did not reject the assumption of linearity of the genus-level log S vs. log V dataset ($R_{1176, 1270} = 1.067$, $p = 0.1297$). The scaling coefficients (α) of the S:V relation within individual populations ranged from 0.57 to 1.01 (Fig. 2, Table S1). The hypothesis of surface-to-volume isometry was rejected in 38 populations for which the 95% confidence interval of the scaling coefficients excluded the 0.67 value (Fig. 3, Table S1). Isometric S:V scaling could not be rejected in 11 populations, although in 7 of them the estimated slope was higher than 0.67, but the lower bound confidence interval reached below this value. There were three populations with scaling coefficients significantly lower than 0.67; thus, indicating negative allometry of the cellular S:V scaling. Notably, both studied populations of *Micrasterias ralfsii*, a species almost completely lacking cellular incisions, had negative S:V allometry. In addition, negative allometric patterns were also detected in a single strain of *M. crux-melitensis* (*MiCM5*) with a relatively high degree of cell lobulation ($Q = 0.18$). Allometric patterns were not detected in both populations of *M. denticulata* var. *angulosa*, a species with multiple incisions and intermediate *Q* values.

Populations with more lobulated shapes (i.e. with lower Q values) had steeper allometric slopes (r = -0.44, R^2 = 0.19, p = 0.0013). However, this correlation largely disappeared once two *M. ralfsii* populations with extremely compact cellular shapes were excluded (r = -0.21, R^2 = 0.04, p = 0.156). The correlation between allometric slope and Q value was highly dependent on the phylogenetic structure of the data. This was indicated by the partial ProTest analysis that compared the residual values of the slopes and isoperimetric quotients, with the variation due to phylogenetic relationships of the populations kept fixed (Table 1). The populations with larger cells tended to have steeper S:V allometric slopes (linear regression of mean surface area to allometric slopes: r = 0.38, R^2 = 0.15, p = 0.0061, mean volume to allometric slopes: r = 0.32, R^2 = 0.10, p = 0.024). Once again, this relation proved to be highly dependent on the phylogenetic structure of the populations in the partial ProTest analyses. The clonal strains (mean slope = 0.793) and natural populations (mean slope = 0.801) did not significantly differ in their slope values (permutation t-test, $t_{24,25}$ = -0.27, p = 0.773).

The maximum-likelihood tree of the investigated *Micrasterias* species (Figure S2) had a topology similar to the comprehensive phylogeny of the genus published by Škaloud *et al.* (2011). Notably, *M. truncata*, *M. ralfsii*, and *M. semiradiata* formed a tightly related lineage, which was part of the strongly supported clade including also *M. crux-melitensis*, *M. radians*, *M. pinnatifida* and *M. truncata* var. *pusilla*. This clade corresponded to lineage "A" previously illustrated by Škaloud *et al.* (2011). It was recovered in sister position to a lineage that included the species pair *M. rotata* and *M. fimbriata*. At the same time, four additional tightly supported lineages were also recovered. *M. papillifera* and *M. americana* formed two separate clades on their own. A species pair of *M. compereana* and *M. brachyptera* formed a strongly supported lineage, as well as the assemblage of *M. thomasiana*, *M. jenneri*, and *M. denticulata*.

Morphospace spanned by PCA of the geometric morphometric data primarily differentiated between cells with wide polar lobes and comparatively shallow incisions, such as populations of *M. truncata*, *M. semiradiata*, or *M. pinnatifida*, and cells characterised by narrow polar lobes and pronounced incisions, such as *M. thomasiana* or *M. rotata* (Fig. 4). The first principal component, spanning this morphological pattern, described 77.3% of the total variation. The second principal component (9.4% of the variation) differentiated between populations with convex polar lobes and very shallow incisions, typical for *M. ralfsii*, and most other populations with rather flat polar lobes and lobulated semicells. Mapping the morphospace data onto the 18S rDNA phylogeny illustrated that the members of the *M. truncata*/*M. ralfsii* lineage were positioned in the left part of the PC1 × PC2 plot (Fig. 5). Additional taxa of the lineage "A", such as *M. crux-melitensis* and *M. radians*, had intermediate positions on PC1. Most members of the *M. rotata* and *M. thomasiana* clades had positive PC1 scores and were positioned on the marginal left of the ordination plot. The morphospace structure was closely related to the phylogeny of the group as the null hypothesis, a lack of any phylogenetic signal, was rejected in the permutation test with $p = 10^{-4}$. This was also corroborated by a strong Procrustes correlation between phylospace and morphospace matrices (Procrustes SS = 0.58, r = 0.65, p = 0.0001). Likewise, the null hypothesis of no phylogenetic signal in values of the allometric slopes was rejected with p = 0.007 on Blomberg $K = 2.1 \times 10^{-6}$. In addition, the ProTest analysis, comparing the phylospace structure with values of the allometric slopes, also revealed a fairly strong correlation illustrated by Procrustes SS = 0.84, $r = 0.40$, and $p = 0.001$ (Table 1).

Values of allometric slopes were marginally related to the morphospace structure (Table 1, Fig. 4). This pattern remained virtually unchanged in a partial ProTest with the phylospace data partitioned out prior to the analysis of the relation between the allometric slopes and morphospace structure.

The allometric space was based on the PCA of the regression vectors acquired from a set of linear regressions of the Procrustes aligned landmark data on centroid size values of individual semicells. At the same time, the isometric vector, identifying the position of the theoretical population without any allometric shape variation, was also included in the PCA analysis. The resulting ordination space illustrated differences in allometric shape patterns of individual populations, as well as their distance from isometry (Fig. 6). The first two principal components of this analysis spanned 53.7% of the total variation in allometric patterns (PC1 – 29.8%, PC2 – 23.9%). A closer look at the allometric patterns of individual populations positioned in opposite marginal parts of the ordination space revealed strikingly different shape trajectories. The taxa with negative scores on PC1 (such as *MiRf1*, *MiRf2*, or *MiBr1*) displayed a variation in relative width of the apical parts of the semicells from relatively compressed in smaller specimens to stretched polar lobes in large ones. In addition, the lateral lobes were typically appressed to the polar lobe in smaller semicells, while the incisions between the polar lobe and the lateral lobes were distinctly more open in larger semicells (such as in *MiBr1* or *MiCM2*). Conversely, the opposite part of the PC1 spanned populations, such as *MiRa1*, *MiRo2*, or *MiPa3*, with wide apical parts and shallow incisions in smaller semicells, but distinctly narrower apical lobes and more pronounced incisions in larger semicells. This allometric pattern was very similar to that observed by Neustupa *et al.* (2008) in the *M. rotata* strain cultured at different temperatures. The allometric pattern of the populations with the highest scores on PC2 typically encompassed little change in the relative depth of the incisions (*MiCM2*), whereas the allometric trajectories of the opposite populations included a visible change from shallow incisions in small semicells to more pronounced lobulation in large specimens (*MiBr1*, *MiRo2*).

The structure of the allometric space proved to be significantly correlated with the morphospace structure and this relation persisted in a partial ProTest that included phylospace as a covariate (Table 1). Conversely, the ProTest also illustrated that the allometric space was unrelated to the phylogenetic structure. The lack of any significant relation between the phylogenetic relationships and allometric patterns can also be illustrated by an obvious dispersion of the populations belonging to a single species, such as *M. crux-melitensis* (*MiCM*), *M. rotata* (*MiRo*), or *M. compereana* (*MiCo*), within the allometric space (Fig. 6). Finally, the structure of the allometric space was significantly related to the allometric slopes and, taking the phylospace as a covariate did not strongly influence this pattern (Table 1).

Discussion

The surface area and volume of *Micrasterias* cells did not scale according to the two thirds scaling rule. Conversely, the data indicated that there was a significant positive allometry of the surface-to-volume scaling relation. The linearity check of the log S vs. log V relation did not reject the assumption of a linear relation of these parameters across the entire lineage. Thus, we can consider the *Micrasterias* S:V scaling relationship as probably resulting from a single power law function. The observed scaling coefficient $\alpha = 0.91$ was considerably higher than the 2/3 S:V scaling that would indicate isometry. This value was also considerably higher than the S:V scaling coefficients 0.66–0.70 reported for unicellular algae by Niklas (1994) on the basis of data from earlier studies (Williams, 1964; Eppley & Sloan, 1966; Mullin *et al.*, 1966). However, these studies were largely based on interspecific comparisons of taxa belonging to various diatom and dinoflagellate genera, characterised by relatively simple geometric shapes, such as spheres, oblate spheroids, prolate spheroids, or terete cylinders (Lewis, 1976; Niklas, 1994). None of these datasets included taxa with cells characterised by fractalized surfaces possessing successively divided lobes and incisions. Reynolds (2006) obtained an S:V scaling exponent of ~ 0.82 for a set of phytoplankton taxa spanning multiple taxonomic groups. In comparison with previously mentioned studies, his dataset included more morphologically diversified taxa, such as those with protuberances, lobes, and horns that contributed to an increased surface area but not more cellular volume (Reynolds, 2006). The even higher scaling coefficient ~ 0.91 (± 0.89–0.92), observed in the present study using a dataset from an algal lineage with variable cell compactness values (0.13–0.81) and high variability in the amount of lobulation, illustrated that morphological diversification of unicellular algae may lead to sublinear S:V scaling. This pattern generally confirmed the models presented by Okie (2013), who showed that different strategies of surface area scaling may lead to considerably different shifts in the scaling coefficients. While the classic solid-object geometric dissimilitude may elevate the scaling exponents above the 0.67 level, evolution of the fractal-like cell surface convolutions, lobes, and incisions in some taxa increases the scaling coefficients to sublinear S:V relationships.

At the species level, the allometric S:V scaling clearly proved to be evolutionarily conserved. Thus, while most of the *M. crux-melitensis*, *M. denticulata*, and *M. truncata* populations had rather low allometric slopes, other species, such as *M. americana* and *M. thomasiana*, typically had a sublinear S:V relation within their population. Average cell compactness (indicated by the *Q* value) was also significantly correlated to the allometric slope of the population. In addition, it was also closely related to the phylogenetic structure. A similar relation was already presented by Škaloud *et al.* (2011), who showed that the branching pattern of *Micrasterias* species (i.e. the degree of cellular lobulation) closely corresponded to their phylogenetic history. It can be concluded that higher cell lobulation of *Micrasterias* species usually leads to higher positive allometry of the S:V scaling within the population. Thus, these findings indicate that successive lobulation of desmid cells, a feature that has always attracted the attention of desmidiologists (Ralfs, 1848; Brook, 1981; Coesel & Meesters, 2007), may actually be considered as an evolutionary adaptation that enables these unicellular algae to increase their surface-to-volume scaling coefficients above the isometric level.

However, several populations with a relatively high degree of lobulation (and with comparatively low *Q* values), had a more or less isometric S:V scaling, which indicated a size-related decrease of their S:V ratio. Most notably, both populations of *M. denticulata* var. *angulosa*, originating from distantly located natural habitats, scaled isometrically. Whether the absence of an allometric scaling in this morphologically distinct taxon may truly be an evolutionarily conserved pattern should be evaluated by analysing more independent populations and strains. The species with weak lobulation (and with comparatively high Q values) typically had weak or no positive S:V allometric scaling, at all. Most notably, the surface area of two *M. ralfsii* populations, a species almost lacking cellular lobes, scaled negatively in relation to an increase in volume. Such taxa may use different strategies to compensate for an increase in their cellular volumes. Okie (2013) suggested that increasing the proportion of metabolically inactive vacuoles may be one of strategies frequently used by phototrophic protists to compensate for a total increase in cell volume. His meta-analysis on the proportion of the cell volume occupied by vacuoles in different groups of unicellular algae illustrated that it ranged from 2% in the smallest eukaryotic phytoplankton taxa to more than 99% in giant ulvophycean cells. Thus, the proportion of vacuoles could also change as a function of cell volume in desmids. This should especially be worth an investigation in those species that either lack any significant lobulation (such as *M. ralfsii* or most members of the genus *Cosmarium*) or that have lobulated cells, but do not exhibit any cell shape allometry, such as *M. denticulata* var. *angulosa*. Would these species have greater changes in the proportion of vacuoles in relation to taxa with significantly positive S:V allometric scaling? This question could be evaluated in a future comparative study that may shed light on the different allometric scaling strategies underlying morphological differentiation in unicellular algae.

Interestingly, the structure of the allometric space illustrated that size-related changes in cellular morphology of individual populations, such as arrangement of the lobes, were not homogenous among populations. Besides the anticipated contrast in allometric trajectories of populations with rudimentary lobulation, such as *M. ralfsii*, and those with richly lobulated cells, such as *M. radiata* or *M. rotata*, spanned by the first principal component of the allometric space, additional differences were illustrated by further PCs with a relatively high proportion of total variation. The allometric trajectory with deeper cellular incisions in larger cells, illustrated by Neustupa *et al.* (2008) as the temperature-related plastic response of a single *M. rotata* strain, was typical for populations with positive scores on PC1 of the allometric space. These populations were also characterised by relatively high slopes of S:V scaling. However, the allometric trajectory was clearly different in several strains, which was reflected by their distant position in the allometric space. For example, the strains *MiCM2* and *MiSm1* were characterised by allometric trends primarily affecting the width of the polar lobe, with little changes in the depth of the incisions. A similar pattern was also observed in the *MiBr1* population, but besides allometric changes in the shape of the polar lobe, it was also characterised by slightly deeper incisions in larger cells. This variation in allometric trajectories was often not species-specific. Conversely, the relation of the allometric space to the phylogenetic structure was very weak. Therefore, it should be assumed that this variation in allometric patterns of taxa, such as *M. crux-melitensis* or *M. rotata*, is not evolutionarily conserved, but may be the result of either random variation, or local adaptive differences among populations.

Variation in the allometric trajectories has been identified as an important factor in the morphological evolution of organisms, because individual allometric trajectories may act as constraints that canalize the evolutionary change of morphology (Klingenberg, 2010; Wilson, 2013, Pélabon *et al.*, 2014). Such constraints may have likely influenced morphological diversification of the *Micrasterias* lineage. Differences in allometric patterns among populations reflect morphological differences among taxa, such as varying depth of the incisions, degree of lobulation, or width of the polar lobe (Škaloud *et al.,* 2011). The possible relation of allometric diversity and evolutionary diversification of species could in the future be tested by comparing the relative disparity of the allometric space in species-rich desmid lineages, such as *Micrasterias* or "core" *Euastrum*, with that of less diversified desmid lineages, such as *E. verrucosum, E. pectinatum*, or *Xanthidium* clades (Gontcharov & Melkonian, 2011; Šťastný *et al.*, 2013). In addition, such analyses could also identify a possible correlation between allometric space and phylospace structure at deeper branches of the phylogenetic tree.
With their complex cellular shapes and rigid cell walls the desmids are ideally suited for the analysis of allometric scaling and shape trajectories of unicellular organisms. This study illustrated that the evolution of their complex cellular morphologies may have been driven by selective pressure for an increased surface-to-volume scaling. In addition, it has been demonstrated that variation in shape trajectories within the allometric space of the group was closely related to the S:V scaling of populations. Thus, analyses of morphological allometry in these microalgae may shed light on the principles of their morphological diversification. In this way, the desmids may be used as a suitable model group for future studies in this unexplored field of evolutionary morphology.

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Table 1 Results of Procrustean tests. Matrices representing multivariate spaces (such as morphospace, phylospace and allometric space), as well as two univariate factors (mean cell shape compactness and allometric slopes of populations) are compared. Partial Procrustean tests compared two matrices with variation accounted by a third matrix (or variable) partitioned out prior to the actual analysis. Strongly significant relations with *p*-values < 0.01 are depicted in bold.

Matrices compared	Procrustes SS (m_{12}^2)	Correlation of symmetric Procrustes rotation	*p*-value (based on 9999 permutations)
Morphospace vs. Phylospace	**0.58**	**0.65**	**0.0001**
Morphospace vs. Allometric space	**0.84**	**0.40**	**0.0004**
Allometric space vs. Phylospace	0.95	0.21	0.3290
Morphospace vs. Slopes	0.93	0.27	0.0448
Phylospace vs. Slopes	**0.84**	**0.40**	**0.0010**
Allometric space vs. Slopes	**0.88**	**0.35**	**0.0009**
Cell shape compactness vs. Slopes	**0.81**	**0.44**	**0.0017**
Morphospace vs. Allometric space | Phylospace	**0.84**	**0.39**	**0.0002**
Morphospace vs. Slopes | Phylospace	0.93	0.26	0.0504
Allometric space vs. Slopes | Phylospace	**0.91**	**0.30**	**0.0048**
Cell shape compactness vs. Slopes | Phylospace	0.95	0.22	0.1249

Figures

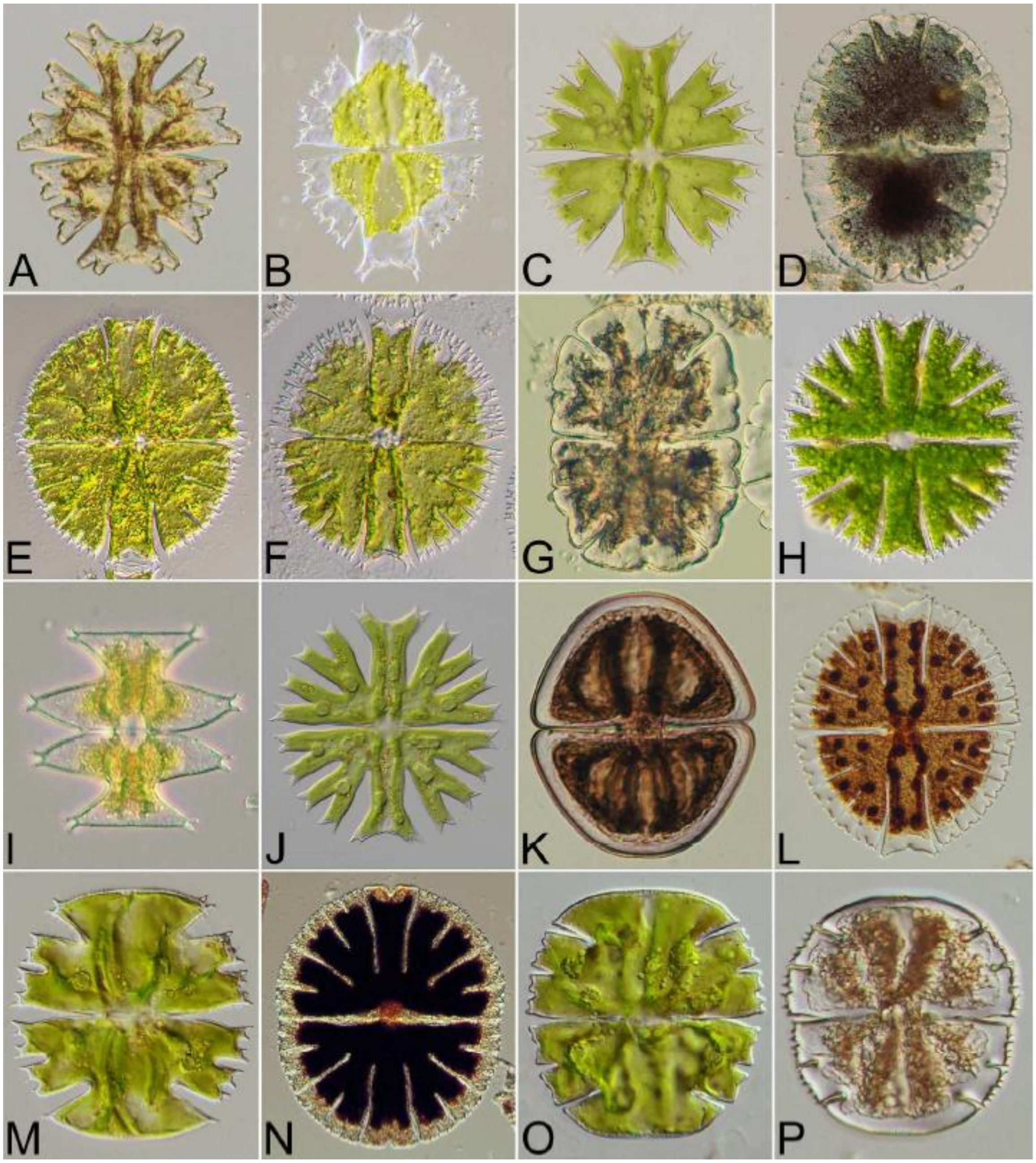

Fig. 1 Morphology of *Micrasterias* species investigated for surface-to-volume scaling and allometric patterns. (a) *M. americana*; (b) *M. brachyptera*; (c) *M. crux-melitensis*; (d) *M. denticulata* var. *angulosa*; (e) *M. fimbriata*; (f) *M. compereana*; (g) *M. jenneri*; (h) *M. papillifera*; (i) *M. pinnatifida*; (j) *M. radians* var. *evoluta*; (k) *M. ralfsii*; (l) *M. rotata*; (m) *M. semiradiata*; (n) *M. thomasiana*; (o) and (p) *M. truncata*.

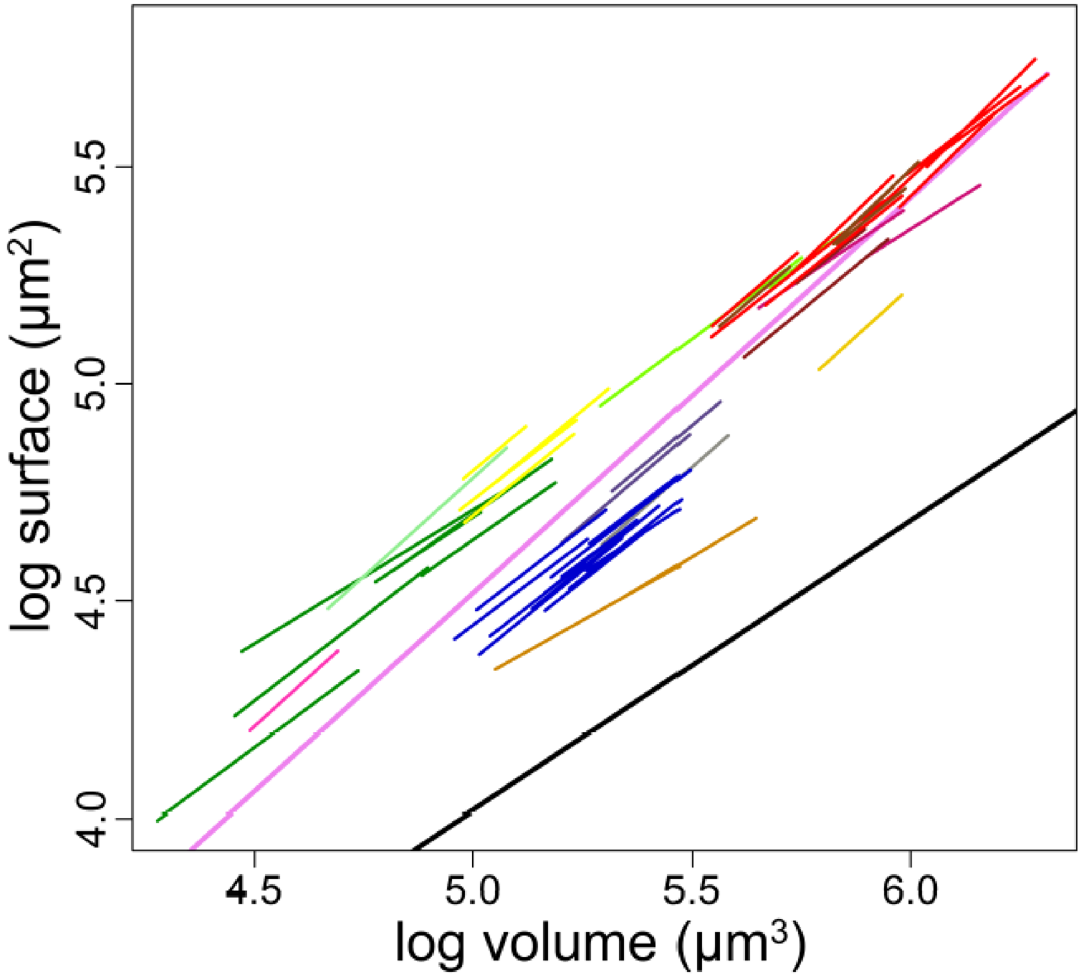

Fig. 2 The SMA regression lines of the log surface to log volume in individual populations. Colours distinguish individual species. The black line illustrates isometric log S vs. log V relationship of a sphere. Thus, the space below this line cannot be occupied. The violet line illustrates log S vs. log V relation of the entire dataset (r = 0.92, a = 0.91).

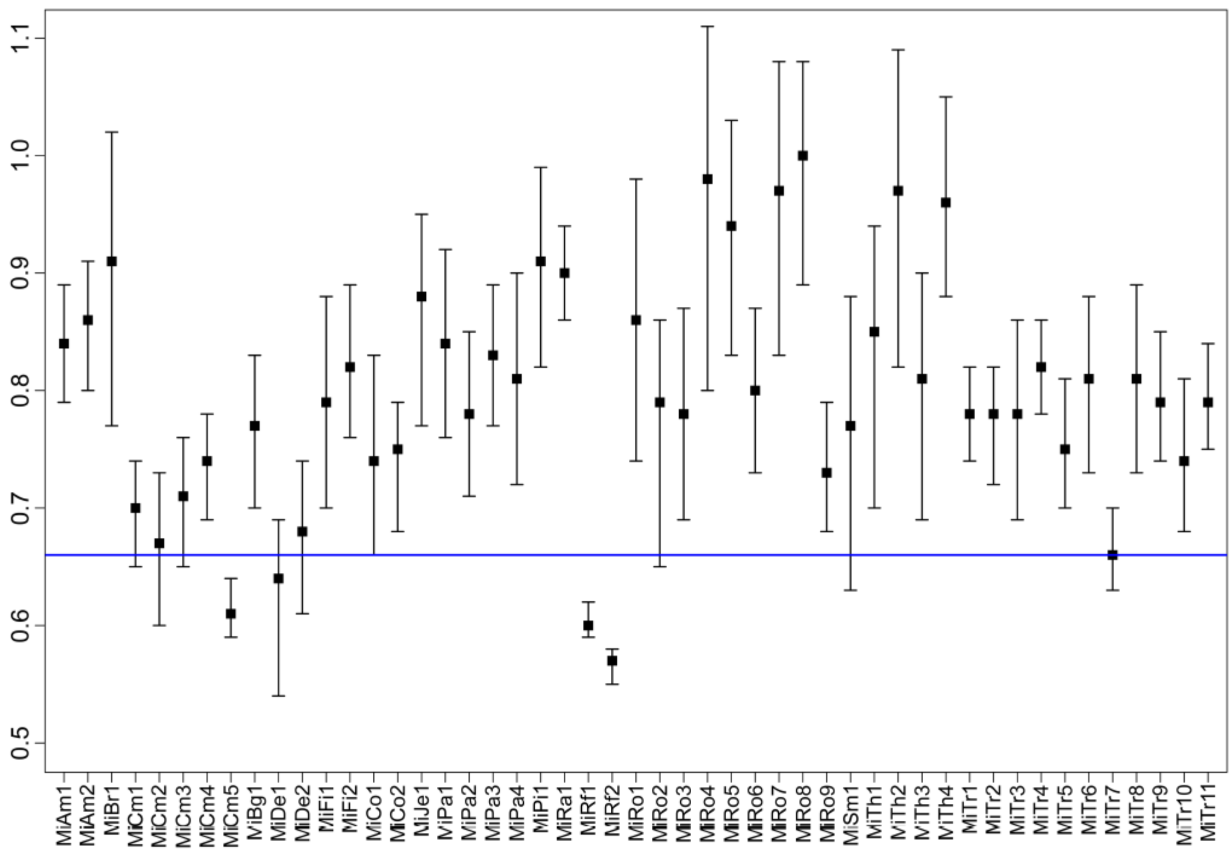

Fig. 3 Scaling exponents (α) and 95% confidence intervals of the surface-to-volume relation in individual populations. The isometric level $\alpha = 0.67$ is indicated by a horizontal line.

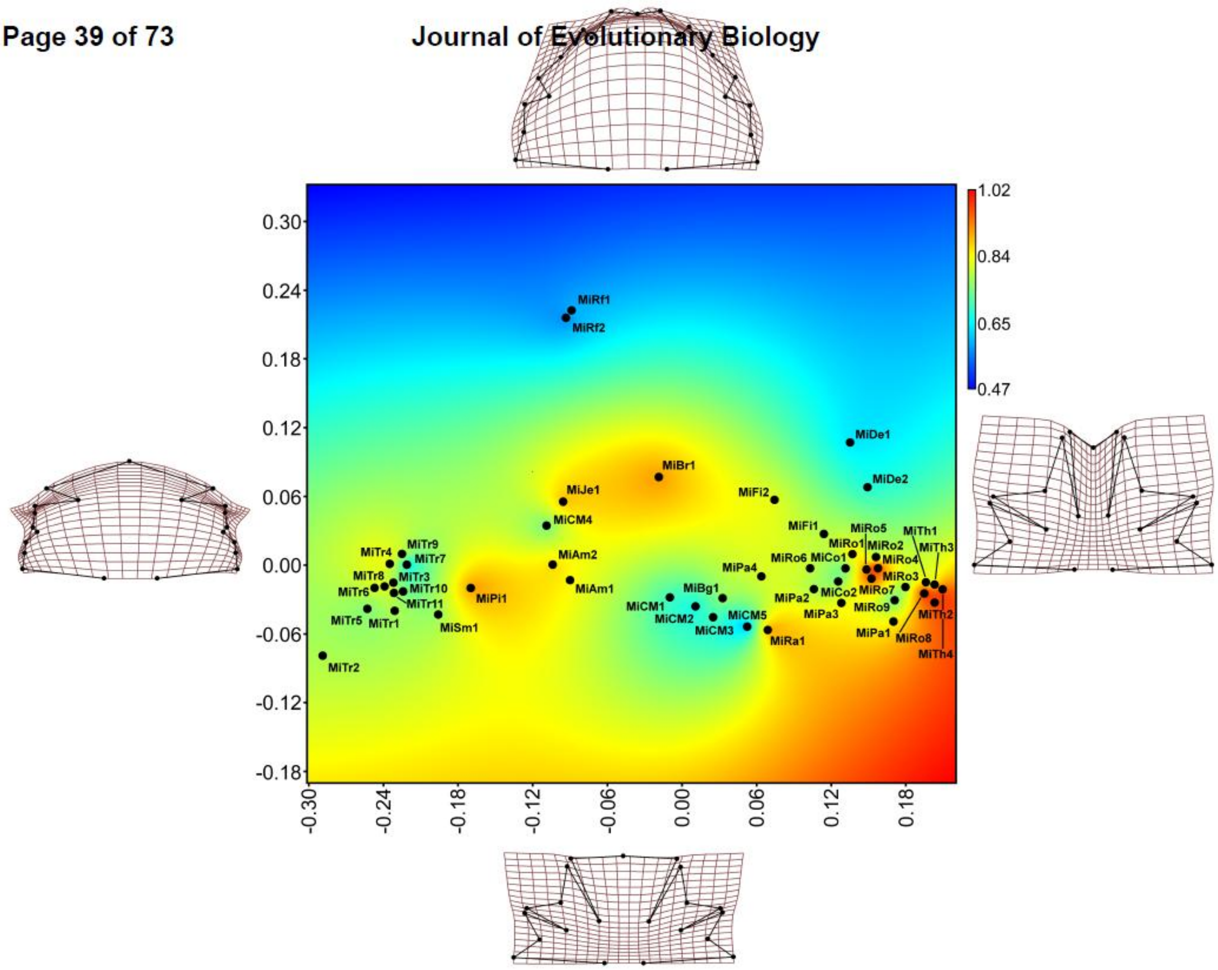

Fig. 4 Morphological space illustrated by the ordination plot of PC1 vs. PC2 that resulted from principal component analysis of geometric morphometric data. PC1 spanned 77.3% and PC2 9.4% of total variation. Semicell shapes typical for marginal positions on both axes are illustrated by deformation grids. The distribution of allometric slope values of the populations within the ordination space was illustrated by multiquadric spatial interpolation of the slope values onto the two-dimensional PC1 vs. PC2 ordination plot.

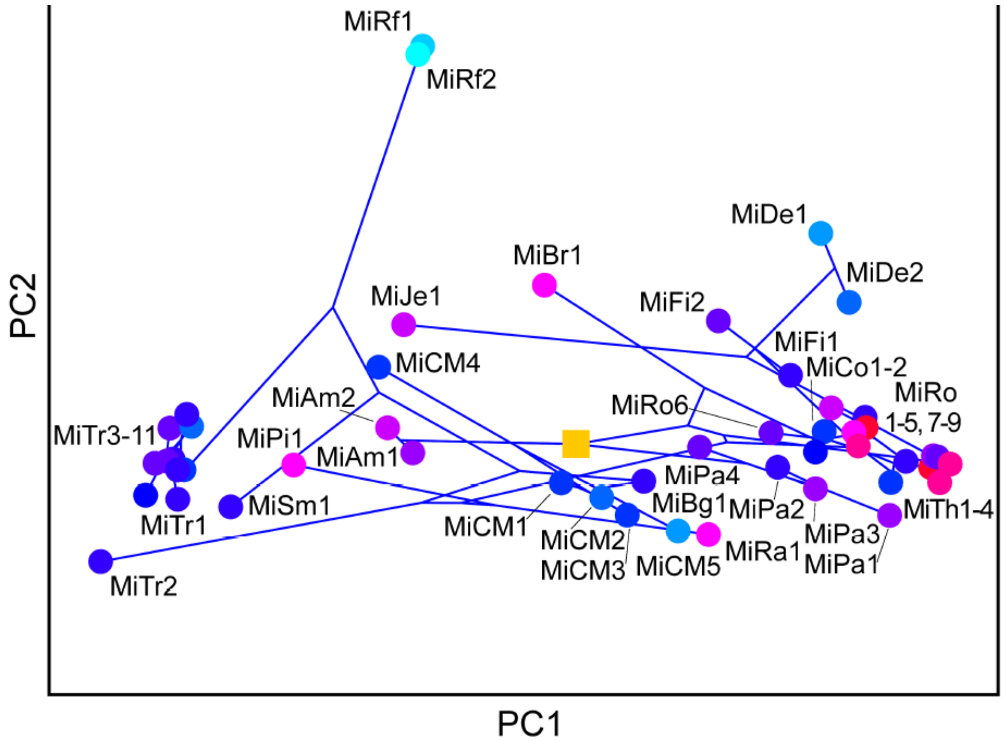

Fig. 5 *Micrasterias* phylogeny mapped onto the morphospace represented by the PC1 vs. PC2 ordination plot. The phylogenetic tree was based on the maximum likelihood analysis of the 18S rDNA sequences. Colours of points correspond to allometric slope values of populations (from bright blue representing the lowest values to dark red depicting populations with the highest values of allometric slopes).

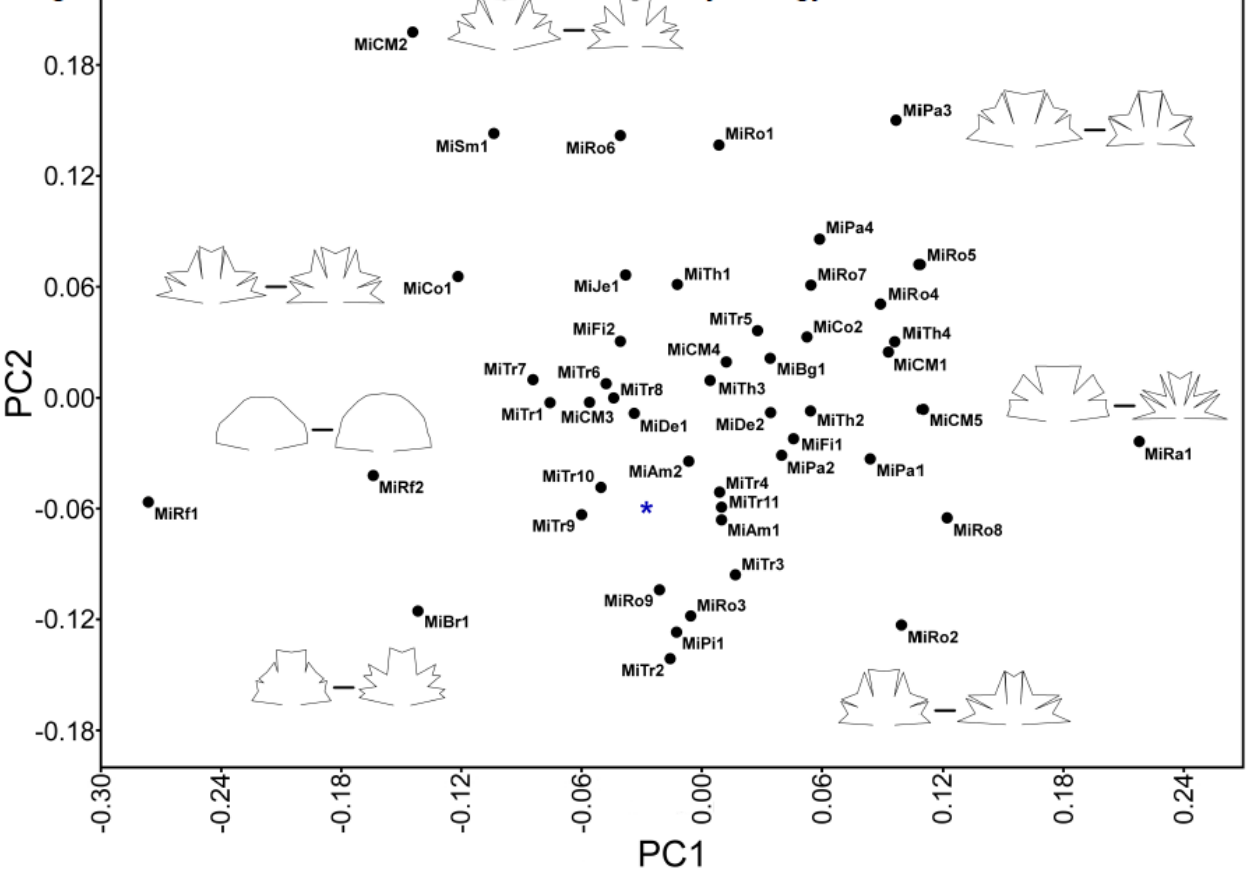

Fig. 6 Allometric space represented by the ordination plot of PC1 vs. PC2 that resulted from the principal component analysis of allometric coefficients of populations. PC1 spanned 29.8% and PC2 23.9% of total variation. Allometric trajectories of several populations occupying marginal positions are depicted. The position of the isometric vector is indicated by an asterisk.

Table S1 List of populations indicating their allometric slopes, cell surface areas, volumes, and other characteristics.

Code	Species	Strain no.	Sampling localities	Coordinates of the sampling locality	Allometric slope	95% confidence interval		Correlation coefficient, log S vs. log V (r)	Mean cell volume (μm^3)	Mean cell surface (μm^2)	Isoperimetric quotient (Q)	Multivariate allometry (% explained / Wilk's λ)
						lower bound	upper bound					
MiAm1	*M. americana*	natural population	a peat bog near Úněšov, Czech Republic	49°53'50.68"N 13°10'56.78"E	0.84	0.79	0.89	0.97	255110	66896	0.27	8.93% 0.27****
MiAm2	*M. americana*	natural population	near Dollgen, Germany	52°00'23.30"N 14°01'15.80"E	0.86	0.80	0.91	0.97	231613	59019	0.32	5.28% 0.43**
MiBr1	*M. brachyptera*	natural population	a peat bog lake in Troms county, Norway	68°51'15.64"N 18°17'35.72"E	0.91	0.77	1.02	0.90	796174	135854	0.37	10.09% 0.39***
MiCM1	*M. crux-melitensis*	natural population	peat bogs near Borkovice, Czech Republic	49°14'10.94"N 14°37'20.18"E	0.70	0.65	0.74	0.98	123259	50302	0.24	11.34% 0.21****
MiCM2*	*M. crux-melitensis*	CAUPK602 (isol.: 2004)	peat bogs near Borkovice, Czech Republic	49°14'08.19"N 14°37'23.46"E	0.67	0.60	0.73	0.96	77968	41610	0.20	10.48% 0.36***
MiCM3*	*M. crux-melitensis*	CAUPK607 (isol.: 2004)	a pool in "Březina" fen, Czech Republic	50°32'54.60"N 13°54'18.33"E	0.71	0.65	0.76	0.98	100691	50012	0.18	8.99% 0.27****

MiCM4*	*M. crux-melitensis*	SVCK98 (isol.: 1963)	peat bogs by Korvanen, Finland	not available	0.74	0.69	0.78	0.98	36227	16016	0.41	5.28% 0.36^{***}
MiCM5*	*M. crux-melitensis*	SVCK128 (isol.: 1964)	Neuried, Baden-Württemberg, Germany	not available	0.61	0.59	0.64	0.99	69286	40380	0.18	5.94% 0.48^{*}
MiBg1*	*M. crux-melitensis* var. *bogoriensis*	SVCK389 (isol.: 1993)	Kuching, Malaysia	not available	0.77	0.70	0.83	0.96	53636	27876	0.20	8.04% 0.37^{***}
MiDe1	*M. denticulata*	natural population	a pool in Nötvikmyran, Sweden	62°34'43.76"N 16°40'58.03"E	0.64	0.54	0.69	0.94	1150200	248065	0.25	1.93% $0.66^{n.s.}$
MiDe2	*M. denticulata*	natural population	near Ossling, Germany	51°22'45.30"N 14°10'15.80"E	0.68	0.61	0.74	0.93	673158	196284	0.21	1.56% $0.61^{n.s.}$
MiFi1	*M. fimbriata*	C11	bogs near Marienteich, Czech Republic	50°32'43.53"N 14°40'39.44"E	0.79	0.70	0.88	0.94	650478	195601	0.19	3.48% 0.36^{***}
MiFi2	*M. fimbriata*	I7	an unnamed pool near Lecknavarna, Ireland	53°34'10.60"N 09°48'29.57"W	0.82	0.76	0.89	0.97	645000	165085	0.26	13.64% 0.20^{****}
MiCo1*	*M. compereana*	CAUPK608	a bog near Étang Hardy, Aquitaine, France	43°43'08.60"N 01°22'09.42"W	0.74	0.67	0.83	0.88	603110	199556	0.16	2.35% $0.64^{n.s.}$

MiCo2*	*M. compereana*	SAG162.80 (isol.: 1976)	Texas, USA	not available	0.75	0.68	0.79	0.98	405780	152436	0.16	13.92% 0.23****
MiJe1	*M. jenneri*	natural population	a pool in the "Swamp" peat bog, Czech Republic	50°34'33.40"N 14°40'16.02"E	0.88	0.77	0.95	0.94	296919	60830	0.38	6.99% 0.39***
MiPa1*	*M. papillifera*	CAUPK603 (isol.: 2004)	peat bogs near Borkovice, Czech Republic	49°14'15.32"N 14°37'54.76"E	0.84	0.76	0.92	0.93	115335	70947	0.14	5.24% 0.45**
MiPa2	*M. papillifera*	natural population	a peat bog near Úněšov, Czech Republic	49°53'50.68"N 13°10'56.78"E	0.78	0.71	0.85	0.92	130886	66343	0.19	4.47% 0.48*
MiPa3	*M. papillifera*	natural population	near Jamlitz, Germany	51°57'44.50"N 14°20'03.00"E	0.83	0.77	0.89	0.94	159639	79054	0.17	9.64% 0.40***
MiPa4	*M. papillifera*	natural population	a peat bog pool near Hubenov, Czech Republic	49°53'55.62"N 13°13'10.48"E	0.81	0.72	0.90	0.92	128985	60887	0.23	7.34% 0.44**
MiPi1	*M. pinnatifida*	natural population	near Zeissholz, Germany	51°23'08.90"N 14°08'41.80"E	0.91	0.82	0.99	0.94	36990	18730	0.32	7.08% 0.28****
MiRa1*	*M. radians* var. *evoluta*	SVCK518 (isol.: 2001)	Lake Ol Bolossat, Kenya	not available	0.90	0.86	0.94	0.98	79543	49161	0.15	12.9% 0.32****
MiRf1	*M. ralfsii*	natural population	"Rybí Loučky" peat bog, Czech Republic	50°50'45.53"N 15°20'26.67"E	0.60	0.59	0.62	0.99	320510	40180	0.80	4.43% 0.50*

MiRf2	*M. ralfsii*	natural population	a pool in the "Swamp" peat bog, Czech Republic	50°34'33.40"N 14°40'16.02"E	0.57	0.55	0.58	0.99	199969	30249	0.81	1.42% $0.66^{\text{n.s.}}$
MiRo1	*M. rotata*	C8	a mountain fen near Nové Hamry, Czech Republic	50°21'50.46"N 12°39'21.90"E	0.86	0.74	0.98	0.87	453691	169522	0.16	3.37% $0.66^{\text{n.s.}}$
MiRo2*	*M. rotata*	CAUP K604 (isol.: 2005)	pools by Cep, Czech Republic	48°55'23.65"N 14°50'23.96"E	0.79	0.65	0.86	0.95	706812	223363	0.16	12.39% 0.10^{****}
MiRo3	*M. rotata*	natural population	a pool close to Navarn lake, Sweden	62°35'48.25"N 16°42'37.83"E	0.78	0.69	0.87	0.94	1401903	400878	0.13	7.16% 0.42^{**}
MiRo4	*M. rotata*	natural population	"U Polínek" peat bog, Czech Republic	49°56'19.15"N 13°04'22.73"E	0.98	0.80	1.11	0.88	1219732	329003	0.16	7.43% 0.44^{**}
MiRo5*	*M. rotata*	SVCK1 (isol.: 1952)	near Potsdam, Germany	not available	0.94	0.83	1.03	0.91	968583	289459	0.15	3.73% $0.64^{\text{n.s.}}$
MiRo6*	*M. rotata*	SVCK26 (isol.: 1962)	Wildes Moor, Schwabstedt, Germany	not available	0.80	0.73	0.87	0.97	747277	221840	0.18	11.88% 0.34^{***}
MiRo7*	*M. rotata*	SVCK78 (isol.: 1963)	peat bogs by Korvanen, Finland	not available	0.97	0.83	1.08	0.93	710900	236890	0.15	4.64% 0.38^{***}
MiRo8	*M. rotata*	natural population	near Dollgen, Germany	52°00'23.30"N 14°01'15.80"E	1.00	0.89	1.08	0.92	1453660	421753	0.13	13.14% 0.46^{**}

MiRo9	*M. rotata*	natural population	a pool near Svanatjärnen lake, Sweden	62°33'34.50"N 16°42'08.03"E	0.73	0.68	0.79	0.92	1574181	422927	0.14	1.33% $0.54^{n.s.}$
MiSm1*	*M. semiradiata*	CAUP K606 (isol.: 2006)	peat bogs near Borkovice, Czech Republic	49°14'12.58"N 14°37'18.83"E	0.77	0.63	0.88	0.83	237506	51803	0.32	6.47% 0.42^{**}
MiTh1*	*M. thomasiana*	CAUP K605 (isol.: 2005)	pools by Cep, Czech Republic	48°55'23.65"N 14°50'23.96"E	0.85	0.70	0.94	0.87	419611	152823	0.15	2.86% $0.51^{n.s.}$
MiTh2	*M. thomasiana*	natural population	a peat bog near Úněšov, Czech Republic	49°53'50.68"N 13°10'56.78"E	0.97	0.82	1.09	0.82	854568	268044	0.14	5.05% $0.51^{n.s.}$
MiTh3	*M. thomasiana*	natural population	near Dollgen, Germany	52°00'23.30"N 14°01'15.80"E	0.81	0.69	0.90	0.88	824019	246460	0.15	0.94% $0.77^{n.s.}$
MiTh4	*M. thomasiana*	natural population	a peat bog near Polínka, Czech Republic	49°56'19.15"N 13°04'22.73"E	0.96	0.88	1.05	0.94	793053	248480	0.14	6.94% 0.35^{***}
MiTr1	*M. truncata*	C3	Kateřina bog, Czech Republic	50°09'16.23"N 12°24'28.13"E	0.78	0.74	0.82	0.98	238919	51081	0.35	15.43% 0.25^{****}
MiTr2*	*M. truncata* var. *pusilla*	NIES784 (isol.: 1988)	near Cairns, Queensland, Australia	not available	0.78	0.72	0.82	0.98	143508	39128	0.31	9.65% 0.25^{****}
MiTr3*	*M. truncata*	SVCK18 (isol.: 1962)	Wildes Moor, Schwabstedt, Germany	not available	0.78	0.69	0.86	0.96	147061	32984	0.45	4.88% 0.34^{***}

MiTr4*	*M. truncata*	SVCK248 (isol.: 1970)	bogs near Pfronten im Allgäu, Germany	not available	0.82	0.78	0.86	0.98	155030	33047	0.50	8.14% 0.24^{****}
MiTr5*	*M. truncata*	SVCK359 (isol.: 1952)	United Kingdom	not available	0.75	0.70	0.81	0.97	135178	34759	0.37	7.47% 0.30^{****}
MiTr6*	*M. truncata*	SVCK412 (isol.: 1995)	Laguna de Mucubaji, Merida, Venezuela	not available	0.81	0.73	0.88	0.94	230712	43830	0.49	3.59% 0.32^{***}
MiTr7	*M. truncata*	natural population	near Zeissholz, Germany	51°23'16.40"N 14°08'55.20"E	0.66	0.63	0.70	0.97	227305	42971	0.46	5.56% 0.43^{**}
MiTr8	*M. truncata*	natural population	near Jamlitz, Germany	51°57'44.50"N 14°20'03.00"E	0.81	0.73	0.89	0.95	201421	41469	0.44	5.82% 0.31^{****}
MiTr9	*M. truncata*	natural population	a pool in the "Swamp" peat bog, Czech Republic	50°34'33.40"N 14°40'16.02"E	0.79	0.74	0.85	0.97	197611	38026	0.50	4.04% 0.39^{***}
MiTr10	*M. truncata*	natural population	a pool near Zahrádka, Czech Republic	49°53'35.94"N 13°12'24.83"E	0.74	0.68	0.81	0.94	204347	43075	0.41	4.69% $0.55^{n.s.}$
MiTr11	*M. truncata*	natural population	a peat bog pool near Hubenov, Czech Republic	49°53'55.62"N 13°13'10.48"E	0.79	0.75	0.84	0.97	193371	41089	0.42	7.27% 0.31^{****}

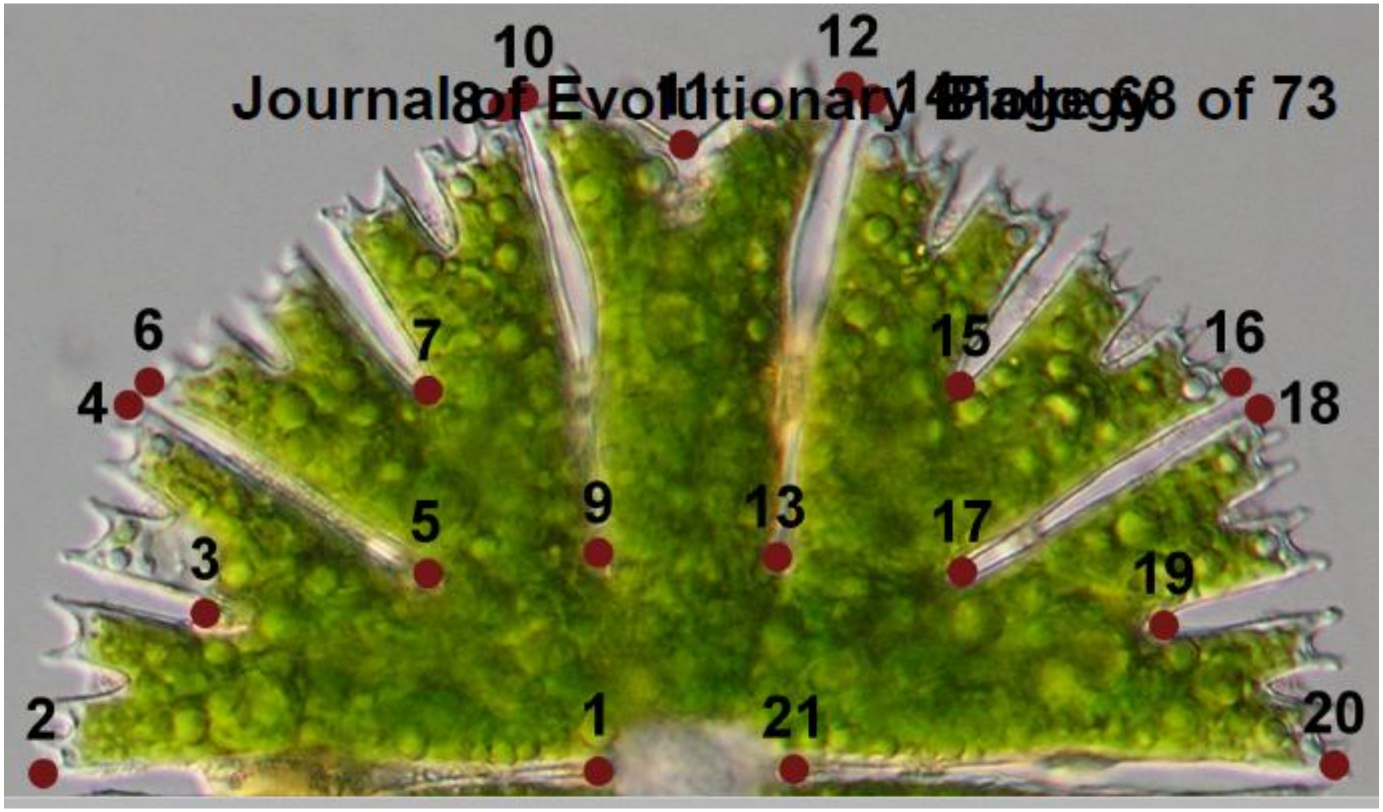

Figure S1 Position of landmarks on the *Micrasterias* semicell.

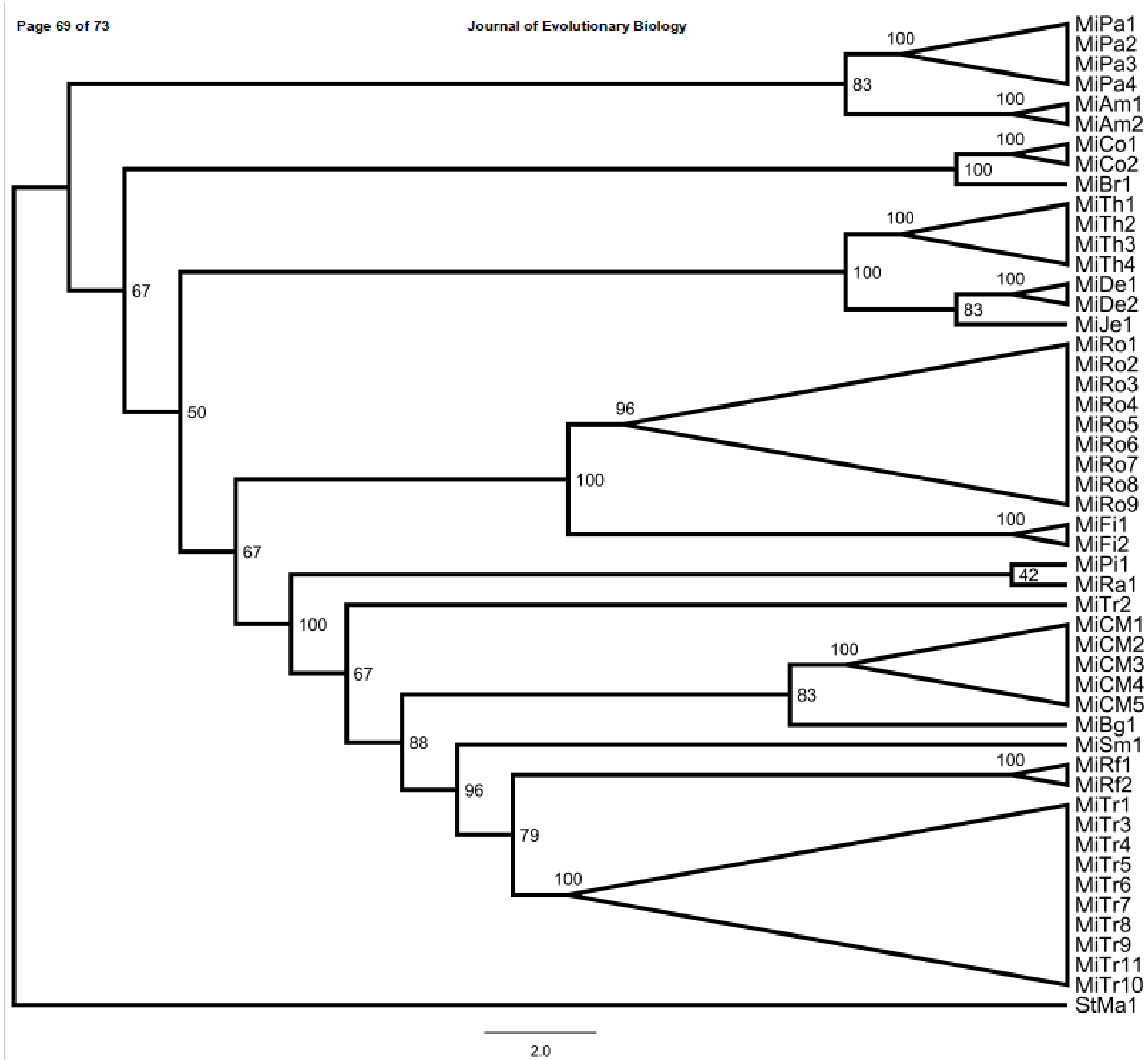

Figure S2 Maximum likelihood phylogenetic tree based on the 18S rDNA data.

Appendix S1 Alignment of the 18S rDNA sequences.

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