

## The effect of patterned structures on the mechanical resistance of microscopic silica scales

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**Abstract:** Surfaces of microscopic organisms are often adorned with various patterns whose putative functions are largely unexplored. In this study, we tested the hypothesis that the formation of parallel-arranged ribs improves the mechanical resistance of microscopic silica scales. Computer models of scales were constructed for chrysophyte species *Mallomonas striata* and *Synura petersenii*, varying the ribs number and orientation. The finite element method was used to evaluate the model static parameters. Our results showed a large difference in the function of ribs depending on the species studied. In *S. petersenii*, the ribs play a key role in scale stability by fixing the longitudinal tubular structure (the median keel) to the basal plate. Although a larger number of ribs increases the scale strength, in extant species the number of ribs is usually optimised to save silicate. In *M. striata*, on the other hand, ribs have a negligible effect on overall scale stability. Moreover, vertically arranged ribs that most stabilize the scales are very rarely produced in nature. This suggests that these ribs have a function other than improving the mechanical resistance of the scales.

**Key words:** Chrysophyceae, finite element method, morphological evolution, mechanical resistance, silica scales

### INTRODUCTION

Living nature takes myriad forms, whose aesthetics and complexity rightfully attract our attention. One element that often contributes to the complexity of form in living organisms is a pattern (STEVENS 1974). In general, biological patterns are visible regularities of form based on a few simple motifs. Well-known biological patterns include zebra and tiger stripes, elytral sculptures of carabid beetles, the wing patterns of butterflies, or skin pigmentation patterns in fish. Patterns, however, do not occur in the macroscopic world only. Indeed, they can be often found on the surfaces of many microscopic organisms, which use controlled crystallization to form diverse shells (BERMAN et al. 1993; DEMADIS 2018). Silica ( $\text{SiO}_2$ ), calcium carbonate ( $\text{CaCO}_3$ ), or celestine ( $\text{SrSO}_4$ ) are the materials most commonly used to form these structures (RAVEN & GIORDANO 2009). Interestingly, investigations of Neoproterozoic microfossils show the putative ability of ancient protists to form the phosphatic scales (COHEN & KNOLL 2012). Although these patterned microstructures were already highlighted in the nineteenth century by Ernst Haeckel, who was obviously fascinated by their truly amazing intricacy (HAECKEL 1904), their putative adaptive properties are largely unknown. In haptophytes,

it was hypothesised that the pattern of disc-shaped calcareous scales may have a light-scattering function to stimulate photosynthesis (MIZUKAWA et al. 2015). In addition, several experiments on diatoms and haptophytes suggested possible role of nano-patterning in reflection of UV light away from the cell (QUINTERO-TORRES et al. 2006; ELLEGAARD et al. 2016). However, the function of the great majority of microscopic structures is still far to be understood.

One of the iconic examples of microscopic pattern structures are the silica scales of chrysophyte algae. In particular, the genera *Mallomonas* Perty and *Synura* Ehrenberg are characteristic by producing a broad range of variously ornamented scales (Fig. 1). The scales are generally composed of a basal plate, on which secondary structures of various shapes are formed, including patterns of perforations, papillae, ribs, reticulations or ridges. In *Mallomonas*, the majority of species produce scales with a prominent V-shaped rib, which is considered to ensure the proper arrangement of scales on the cell surface (SIVER & GLEW 1990; Fig. 1A). In *Synura*, the scales possess either a forward projecting spine or a raised elongated ridge positioned on the middle of the scale – the median keel (Fig. 1B). In both genera, usually the posterior part of the scales is folded, forming an upturned rim.

One of the most frequent patterns occurring on the scales of both *Mallomonas* and *Synura* species are parallelly arranged, regularly spaced ribs. In *Mallomonas*, the ribs occur in more than 20 species and have evolved multiple times during the evolution of the genus (ČERTNEROVÁ et al. 2019). Depending on the species, about 5–30 ribs can be formed on the scale shield (Fig. 2A–J). Regardless of the species, the ribs are almost always slightly bent and arranged horizontally, perpendicular to the main axis of the scale, though some species are capable of forming scales with diagonally arranged ribs (Fig. 2F). In exceptional cases, some species may form vertically arranged or wavy ribs. These may be found mainly in cultured strains (Fig. 2K–O), although such scales have also been observed in natural specimens (BESSUDOVA et al. 2018). Only two species, *M. recticostata* Takahashi and *M. rhombica* Cronberg have been described to have the ribs usually arranged vertically (TAKAHASHI 1972; CRONBERG 1989). In *Synura*, the ribs are formed in all species belonging to the section Petersenianae, where they are radially arranged around the median keel (Fig. 2P–S). In addition, short ribs may be formed on the scales of some other *Synura* species, such as *S. echinulata* Korshikov (Fig. 2T).

Despite the apparently frequent occurrence of ribs on the scales of chrysophyte algae, no study has yet addressed the function of these microscopic patterns. It was only hypothesized by ČERTNEROVÁ et al. (2019) that the formation of ribs could be a response to increasing UV–B radiation in the Pleistocene, as these structures could effectively reflect light of this wavelength. However, the ribs may also increase the mechanical resistance of the silica scales. If the scales serve as a defense against predators, increasing their mechanical resistance through rib formation might represent a major evolutionary advantage that favoured survival of their carriers (SMETACEK 2001). The main objective of this study is to determine whether the formation of ribs improves the mechanical resistance of the silica scales. We also aim to assess the

role of the number of ribs and their orientation on scale strength. Single representatives of two above-mentioned genera were selected as a model: *M. striata* Asmund and *S. petersenii* Korshikov, and their computer models were used in the study.

## MATERIALS AND METHODS

The computer models of silica scales were constructed by the structural analysis software RFEM, v. 5.27.01 (Dlubal Software GmbH, Germany), based on a 3D finite element method (FEM). Finite elements of surfaces and members were used for the scale models. The members, as elements capable of transmitting all internal forces, were evaluated as the most suitable for modelling the ribs. For the purpose of static calculations, it was necessary to enlarge the scale model compared to the original at a scale of 1,000,000:1 and in some cases to slightly simplify its shape. This is primarily the case for the basal plate, which is a flat surface in the model, whereas it is probably slightly convex in the real scale (HÖRNING et al. 2020). The isotropic, linear elastic glass was selected as a scale material. Its material properties were set to follow the measurements made by TOPAL et al. (2020): modulus of elasticity 31,800 N.mm<sup>-2</sup>, shear modulus: 13,250 N.mm<sup>-2</sup>.

The model of *M. striata* was based on the scale microphotograph published in NEUSTUPA & NĚMCOVÁ (2007). The ribs had an isosceles trapezoidal cross-section, with a height of 70 nm, a long base of 50 nm, and a short base of 30 nm. The ribs beneath the V-rib were flat. In addition to the realistic model of the scale, four additional models were constructed: the model with half the number of ribs, twice the number of ribs, vertically oriented ribs, and completely missing ribs (Fig. 3A–E). The model of *S. petersenii* was based on the scale microphotograph of the strain S89.F9 (ŠKALOUD et al. 2014). The ribs had an oval cross-section, with a height of 132 nm and the width of 66 nm. In addition to the realistic model of the scale, four additional models were constructed: the model with half the number of ribs, twice the number of ribs, additional vertical connecting ribs, and completely missing ribs (Fig. 3F–J). In both *Mallomonas*

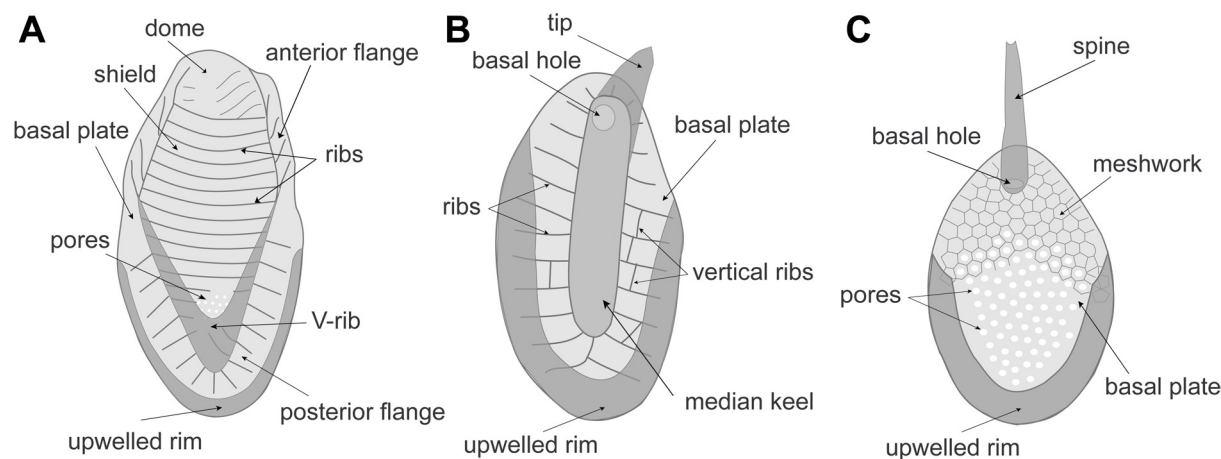


Fig. 1. Schematic representation of the major morphological features of silica scales of the genera *Mallomonas* (A) and *Synura*, in which scales with a median keel (B) and a spine (C) are presented.

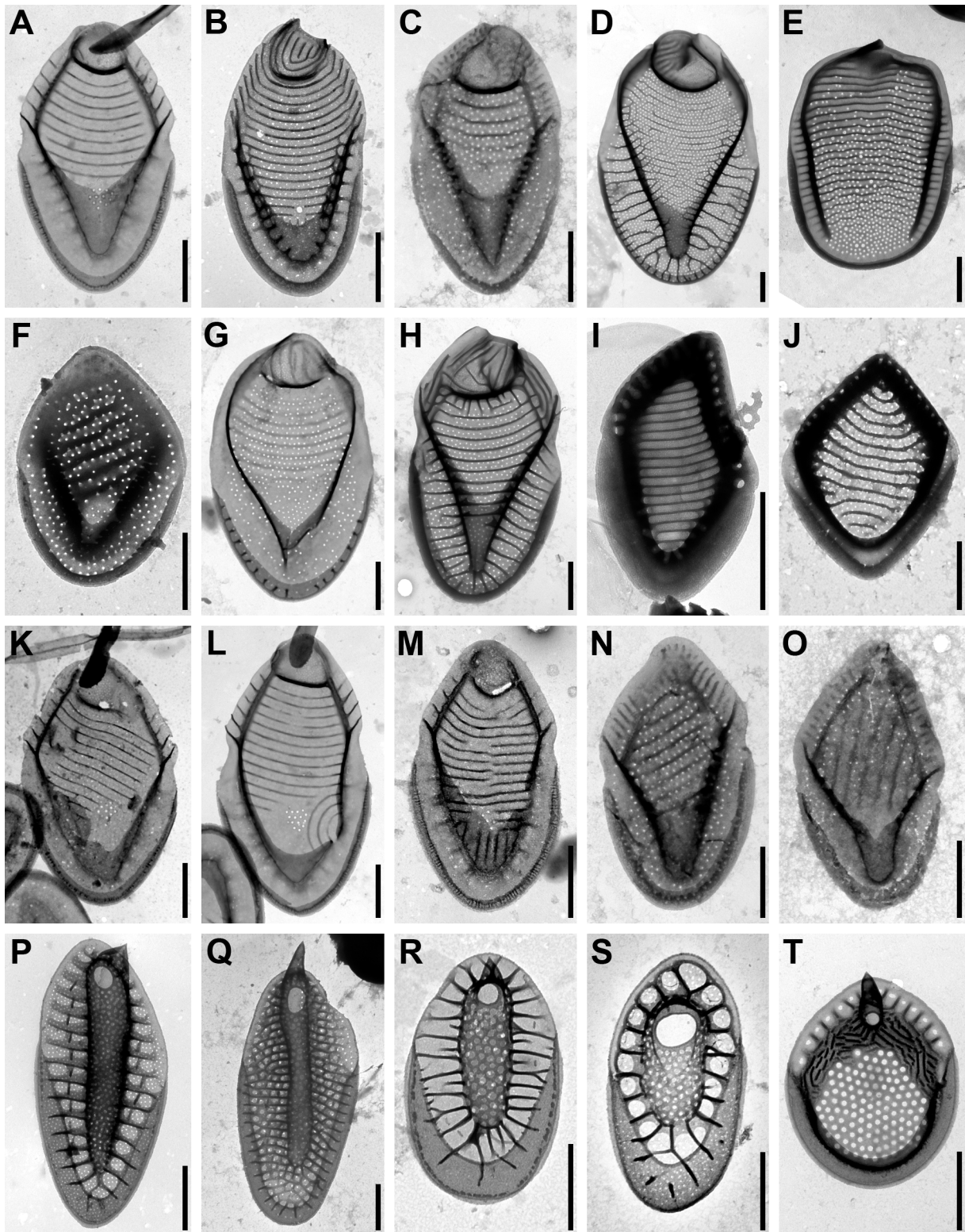


Fig. 2. Formation of regularly spaced ribs on the scales of silica-scaled chrysophytes. (A–J) A selection of *Mallomonas* species; section Striatae: (A) *M. striata*, (B) *M. cratis*, (C) *M. actinoloma* var. *maramuresensis*; section Leboimeanae: (D) *M. lebiomei*; section Punctiferae: (E) *M. transylvanica*; section *Mallomonas*: (F) *M. trummensis*, (G) *M. costata*, (H) *M. corcontica*; section Torquatae: (I) *M. dickii*, (J) *M. doignonii*. (K–O) Scales with atypically oriented ribs observed in cultured *Mallomonas* strains: (K–M) *M. striata* strain CZ\_12D, (N–O) *M. actinoloma* var. *maramuresensis* strain CZ\_105B. (P–T) A selection of *Synura* species; section Petersenianae: (P) *S. petersenii*, (Q) *S. macracantha*, (R) *S. asmundiae*, (S) *S. bjoerkii*; section Curtispinae: (T) *S. echinulata*. Scale bars represent 1 µm.

and *Synura*, the thickness of the model was set to 33 nm, based on the measurement of transverse sections of scales published by LEADBEATER (1986).

The scale models were supported by three linear supports that simulate the natural seating and attachment of the scales to form the scale case (LEADBEATER 1990; SIVER & GLEW 1990). In *Mallomonas*, one of the linear supports was located at the upper edge of the V rib, simulating attachment to the basal plates of two overlapping scales by an extracellular polymer substance. The other two linear supports were located underneath the basal plate, simulating the seating of the scale on the V ribs of the two scales underneath (Fig. 4A). In *Synura*, similar supports were used, using the upturned rim as the supporting structure instead of the V rib (Fig. 4B). In contrast to *Mallomonas striata*, the arrangement of *S. petersenii* scales is diagonally deflected. Interestingly, this deflection in both *Synura* and *Mallomonas* species is reflected in the form of the upwelled rim, which is longer on one side of the scale than the other (LEADBEATER 1986) (Fig. 1B). Due to the considerable scaling of the model, the self-weight load was not considered, and all surfaces were exposed to a constant perpendicular load of  $0.5 \text{ N}\cdot\text{mm}^{-2}$ . Global deformation and mechanical stress (von Mises equivalent stress) were chosen to evaluate overall mechanical resistance to external forces (LU et al. 2015). Thus, the scale models with the lowest values of global deformation and von Mises equivalent stress are considered as the most mechanically resistant and least prone to breakage.

## RESULTS

The final model of *Mallomonas striata* consisted of 389 nodes, 20 surfaces, and 61 members. The mesh consisted of 986 1D and 23,593 2D finite elements. The mechanical resistance analysis identified the largest structural stress to be located at the ribs of anterior flange closely related to the dome (von Mises stress 1,138 and 455 MPa, respectively), and at the ribs of posterior flange (the highest stress 450 MPa; Fig. 5A). The deformation occurred at both the anterior and posterior ends of the scale, with the maximum estimated deformation of 119 nm (Fig. 5A'). The analyses of other four scale models resulted in highly congruent findings, identifying identical ribs to be subjected to the highest stress (Fig. 5B–E). The model with completely missing ribs was determined to be structurally most vulnerable (the largest von Mises stress 1,239 MPa). Contrary, the models with twice the number of ribs and vertically oriented ribs exhibited the lowest stress values (1,118 MPa). Deformation of four additional models was similar to that of the original model, with only slight differences in maximum deformation values (Fig. 5B'–E'). The largest deformation occurred in

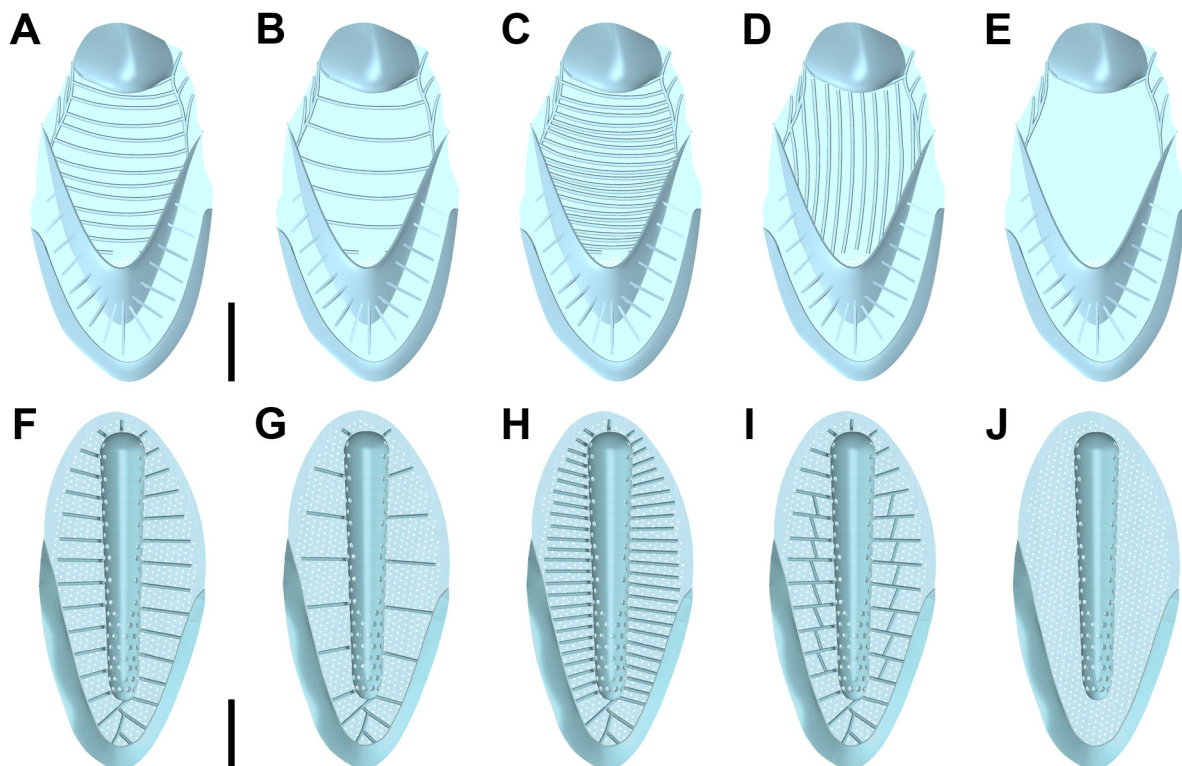


Fig. 3. Top-view computer models of silica scales used for mechanical resistance analysis: (A–E) variants of the *Mallomonas striata* scale model: (A) the original model constructed to resemble a real scale as closely as possible; (B) modified model with half the number of shield ribs; (C) modified model with twice the number of shield ribs; (D) modified model with vertically oriented shield ribs; (E) modified model with completely missing shield ribs.; (F–J) variants of the *Synura petersenii* scale model: (F) the original model constructed to resemble a real scale as closely as possible; (G) modified model with half the number of ribs; (H) modified model with twice the number of ribs; (I) modified model with additional vertical connecting ribs; (J) modified model with completely missing ribs. Scale bars represent 1  $\mu\text{m}$ .

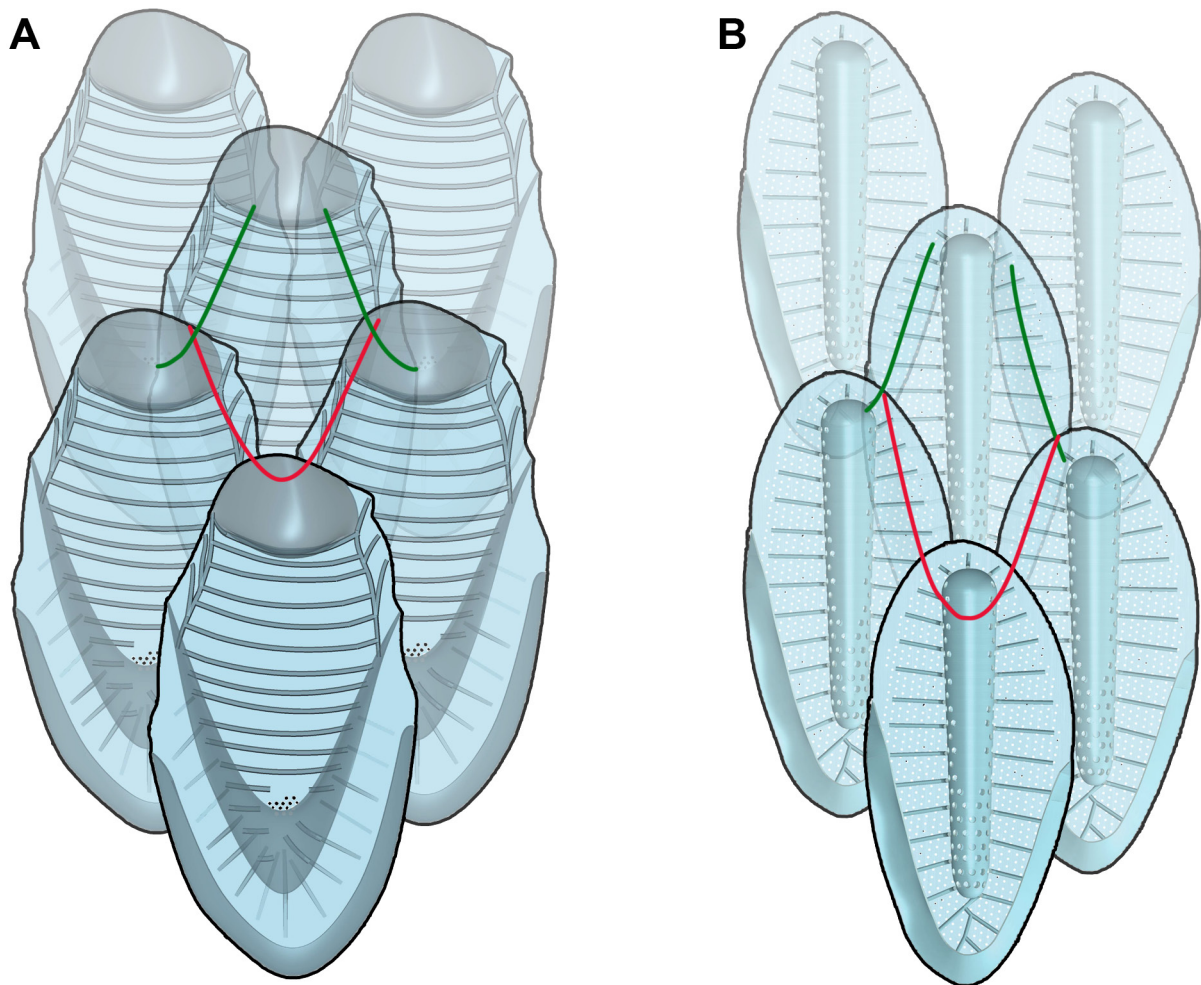


Fig. 4. Placement of linear supports depending on the position of the V-rib in case of *Mallomonas* scale model (A) and the position of the upwelled rim in case of *Synura* scale model (B). The red lines represent the attachment supporting the structure from above and the green lines supports underneath the basal plate.

the model with completely missing ribs (128 nm), whereas the lowest deformation was identified in the model with vertically arranged ribs (113 nm).

The final model of *Synura petersenii* consisted of 7,487 nodes, 809 surfaces, and 116 members. The mesh consisted of 518 1D and 37,776 2D finite elements. The mechanical resistance analysis identified the largest structural stress to be located at the posterior part of the scale, at the connection of ribs with the median keel (von Mises stress 2,321 MPa). In general, ribs represented mechanically most vulnerable parts of the scale, with the highest stress values to be identified at their ends where they are connected to the keel (Fig. 6A). The deformation occurred at the posterior part of the scale and was primarily caused by vertical shift of the posterior end of median keel by 229 nm (Fig. 6A'). The analyses of three scale models with varying rib numbers and arrangements resulted in generally congruent findings (Fig. 6B–D). In all cases, the connection of posterior ribs with the median keel obtained the highest von Mises stress

values. The model with twice the number of ribs was clearly most resistant to the mechanical stress (von Mises stress 1,489 MPa; Fig. 6D), and it also exhibited the lowest deformation shift (194 nm; Fig. 6D'). On the contrary, retaining the half number of ribs only led to the increase of both von Mises stress (2,815 MPa; Fig. 6B) and deformation (271 nm; Fig. 6B').

Interestingly, the considerable loss of mechanical resistance was identified by the analysis of the scale model with completely missing ribs. Both the basal plate and upwelled rim were subjected to a heavy mechanical stress (Fig. 6E). The maximum von Mises stress increased to 12,938 MPa, and the posterior end of the median keel was identified as the most vulnerable part of the scale. In this model, we also detected almost tenfold increase of scale deformation, leading to the vertical shift of the posterior end of the median keel by 2  $\mu\text{m}$  (Fig. 6E'). The deformation analysis even indicated that the basal plate was punctured by a median keel.

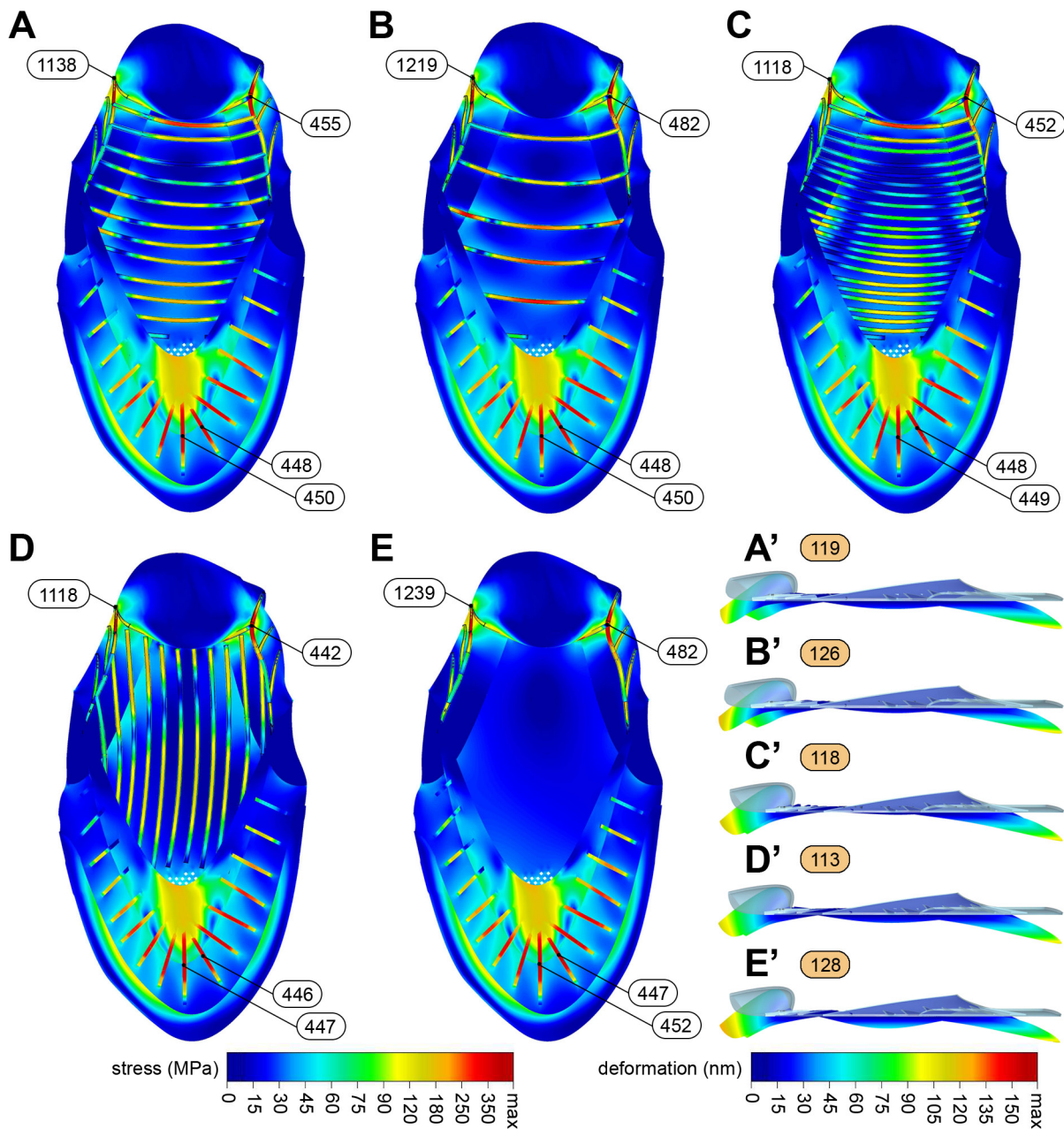


Fig. 5. Results of the mechanical resistance analysis of the model of *Mallomonas striata* silica scale represented by visualized mechanical stress: (A–E) top view of the scale model variations with displayed von Mises equivalent stresses with the highest values marked: (A) the original model constructed to resemble a real scale as closely as possible; (B) modified model with half the number of shield ribs; (C) modified model with twice the number of shield ribs; (D) modified model with vertically oriented shield ribs; (E) modified model with completely missing shield ribs. The stress colour scale is on bottom left. (A'–E') Lateral view of the scale model variations with displayed global deformation with the highest values: (A') The original model constructed to resemble a real scale as closely as possible; (B') modified model with half the number of shield ribs; (C') modified model with twice the number of shield ribs; (D') modified model with vertically oriented shield ribs; (E') modified model with completely missing shield ribs. The deformation colour scale is on bottom right.

## DISCUSSION

### The function of silica scales and their ribbed patterns

The silica scales are formed in all species of the genera *Mallomonas* and *Synura* without exception. Although it is possible to completely inhibit scale formation in growing cultures by silica deprivation (SANDGREN et al. 1996), the scale-less populations have only rarely been

observed in nature. The scales of Synurales taxa therefore clearly play an important role for their carriers. Many hypotheses have been proposed to explain the potential benefits of a silica cell covering, including conserving resources, increasing light diffraction, reducing dangerous UV radiation, or impeding grazing, parasitoid or viral attack (FINKEL & KOTRC 2010; JADRŇÁ et al. 2021 and references herein). Though a mechanical defense against predation is the most mentioned function of

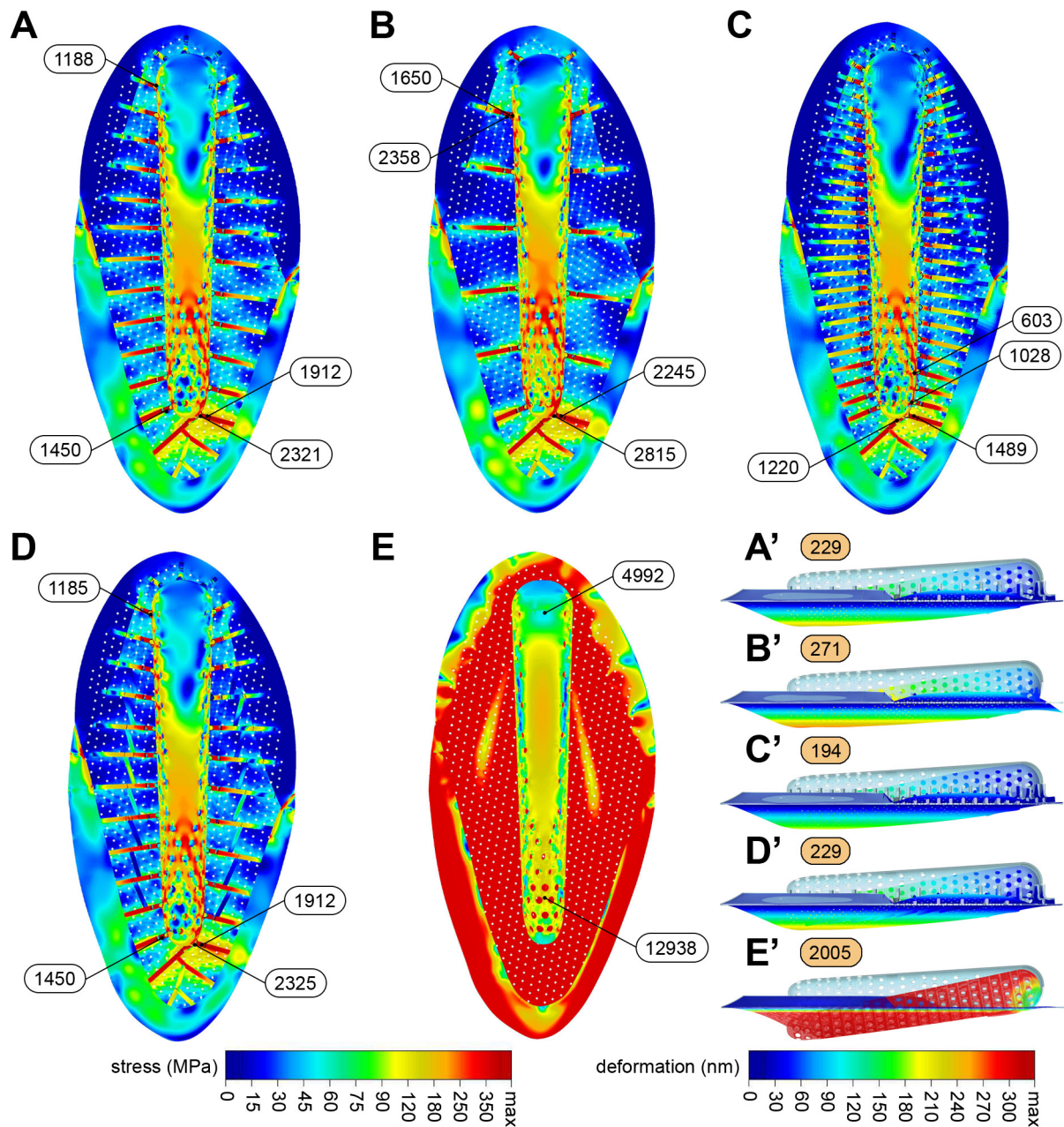


Fig. 6. Results of the mechanical resistance analysis of the model of *Synura petersenii* silica scale represented by visualized mechanical stress: (A–E) top view of the scale model variations with displayed von Mises equivalent stresses with the highest values marked: (A) the original model constructed to resemble a real scale as closely as possible; (B) modified model with half the number of ribs; (C) modified model with twice the number of ribs; (D) modified model with additional vertical connecting ribs; (E) modified model with completely missing ribs. The stress colour scale is on bottom left. (A'–E') Lateral view of the scale model variations with displayed global deformation with the highest values: (A') the original model constructed to resemble a real scale as closely as possible; (B') modified model with half the number of ribs; (C') modified model with twice the number of ribs; (D') modified model with additional vertical connecting ribs; (E') modified model with completely missing ribs. The deformation colour scale is on bottom right.

silica structures in chrysophytes, the results of laboratory experiments are quite confusing since in some cases predators preferred the scale-covered over naked cells or colonies of the same prey species (SANDGREN & WALTON 1995). Nevertheless, it is generally assumed that the various siliceous structures produced by protists on their cell surfaces, including chrysophytes, serve as an armor against attack by other organisms (HAMM & SMETACEK 2007). Recent laboratory experiments on

diatoms indicate that cells with thicker armor are actively rejected by the grazers from Copepod group (RYDERHEIM et al. 2022). It should then be evolutionarily advantageous for the protists to produce shells and scales that are as mechanically robust as possible. In *Synurales* taxa, the mechanical resistance of the scales may be increased by the formation of ribbed patterns.

Our results of the mechanical resistance analyses showed a large difference in the function of ribs on

*Mallomonas striata* and *Synura petersenii* scales. The ribs on the scales of *S. petersenii* are essential for scale stability and they apparently fix the median keel to the basal plate. If we removed all the ribs from the scale model, the scale collapsed and the keel dropped 2  $\mu\text{m}$  below the basal plate of the scale (Figs 6E, E'). We further demonstrated that increasing the number of ribs results in improved mechanical resilience of the scale through a stronger attachment of the median keel. On the other hand, species with a reduced medial keel can maintain the mechanical stability of the scale even with fewer ribs, thus saving silicate consumption. Indeed, the two *Synura* species with the smallest number of ribs have median keels either narrow and short (*S. glabra* Korshikov) or lightened by large pores (*S. macropora* Škaloud et Kynčlová; ŠKALOUD et al. 2012, 2014). In *M. striata*, on the other hand, the ribs on the basal plate have a negligible effect on the overall stability of the scale. According to our results, the mechanical stability of the scale is mainly determined by the V rib and the ribs on the posterior flange (Fig. 5). Interestingly, the V rib has in the past been attributed a key role in organizing scales into a compact silica case (SIVER & GLEW 1990; LAVAU & WETHERBEE 1994). There is, however, quite a large variation in the way the scales of *Mallomonas* species attach to each other. Although in some species the edges of the scales do indeed adhere to the V rib which then serves as a guide in the proper spacing of the scales, often the scales merely lie on the V ribs of the scales below (SIVER 1991). It is therefore possible that

originally the V rib evolved as a structure to increase the scale strength, but later during the evolution of the genus it began to serve as an organizing guide.

The above-mentioned difference in the function of ribs in *Mallomonas* and *Synura* has an interesting implication concerning the overall morphological variability of the scales. Since the ribs in *Synura* species belonging to the section Petersenianae are essential for anchoring the median keel to the basal plate and their presence on the scales is therefore essential, all species possessing a median keel are morphologically very similar. Due to this similarity, even evolutionarily distinct species such as *S. asmundiae* (Cronberg et Kristiansen) Škaloud, Kristiansen et Škaloudová and *S. bjoerkii* (Cronberg et Kristiansen) Škaloud, Kristiansen et Škaloudová were first described just as forms of *S. petersenii* (CRONBERG & KRISTIANSEN 1980). In contrast, our finding that the ribs on the scale shield do not significantly improve the mechanical resistance of silica scales may explain the enormous morphological diversity of scales in *Mallomonas* species (KRISTIANSEN & PREISIG 2007). It is the scale shield between the V rib and the dome that is typically ornamented by various secondary structures such as ribs, papillae, polygonal meshes, and labyrinths. These structures may then have a completely different purpose than the mechanical resistance of the scale.

#### The evolution of ribbed patterns

Thanks to the fossil record of silica-scaled chrysophytes and available time-calibrated phylogenetic reconstructions,

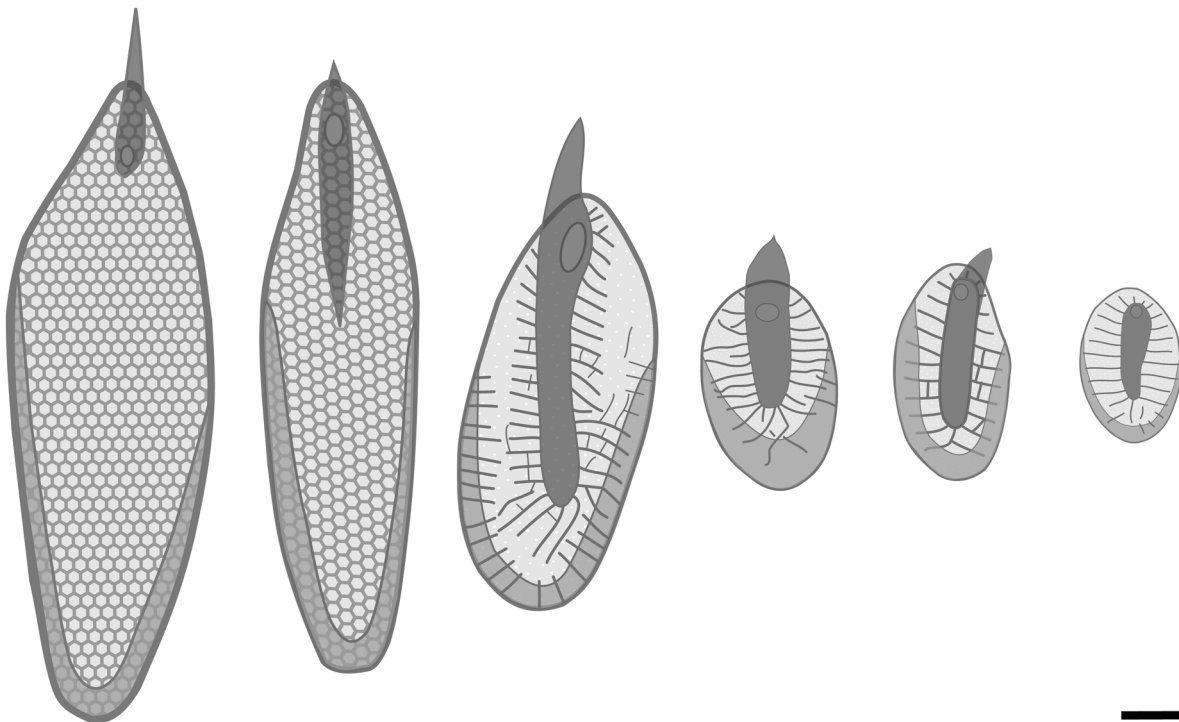


Fig. 7. Evolutionary trend in the number and arrangement of ribs on silica scales in section Petersenianae, linked with the development of the median keel and size decrease. From left to right: *Synura cronbergiae*, *S. longisquama*, *S. macracantha*, *S. asmundiae*, *S. petersenii*, and *S. glabra*. Scale bar represents 1  $\mu\text{m}$ .



we are able to outline the evolutionary history of rib formation of the scales of Synurales taxa. As mentioned above, the formation of ribs in *Synura* species belonging to the section Petersenianae is closely linked to the development of median keel. The section Petersenianae evolved in by at least the Upper Cretaceous since the ancestors of its modern species are present in the fossil record at about 83 Ma (SIVER 2023). The oldest species of this group probably include *S. cronbergiae* Siver (SIVER 2013) and *S. longisquama* Wujek et Elsner (WUJEK & ELSNER 2000), for which unfortunately we do not have molecular data; moreover, the former is known only from the fossil record. Both species are characterized by elongated scales and the presence of a secondary layer formed by hexagonal chambers. The former species has a spine, while the latter has a short median keel in addition to the spine. Interestingly, both species have no ribs, which first developed in *S. macracantha* (Petersen et Hansen) Asmund, the oldest species of the section Petersenianae for which the genetic molecular data are already available. *S. macracantha* scales are present in the fossil record at about 42–44.5 Ma and already they possess fully developed keel with several densely arranged, interconnected ribs, which probably replaced the hexagonal chambers in the role of strengthening the scale (SIVER et al. 2013). During the further evolution of the group, the number of ribs and their interconnections decreased. While in *S. asmundiae* the ribs are still closely arranged and often bifurcated, all the recently evolved Petersenianae species have a smaller number of regularly spaced ribs, often without any interconnections. Summarizing our current knowledge, we can outline the putative morphological development of silica scales during the evolution of the genus *Synura*, section Petersenianae (Fig. 7). Soon after the development of the median keel the hexagonal chambers were replaced by ribs that served to attach the keel to the basal plate of the scale. During further evolution, the number of ribs was then optimized to reach the compromise between scale mechanical resistance and silica requirements. Interestingly, the scale size also decreased significantly, as already described for the genus *Mallomonas* (SIVER

2022). The median keel itself may primarily have formed to provide better stability for the elongated shape of scales. Indeed, the presence of a keel correlates well with the development of elongated scales during the evolution of the genus *Synura*, whereas the scales without or with a poorly developed keel are mostly rounded (JADRŇÁ et al. 2021). Interestingly, similar reinforcement in the centre of the elongated plate-shaped siliceous scales occurs in the unrelated protist genus *Raphidiophrys* Archer (Centrohelida, Hacrobia) (SIEMENSMA & ROIJACKERS 1988). It is possible that the development of central scale reinforcement structures represented a crucial evolutionary step towards the ability to form elongated scales. These might fit easier around elongated cells, which may not only be beneficial in terms of nutrient competition (JADRŇÁ et al. 2021), but such cells may also form larger colonies to avoid predators.

In *Mallomonas*, ribs on the scale shield have arisen many times independently of each other and represent one of the most recently evolved structures originated approximately 60 Ma (ČERTNEROVÁ et al. 2019). This is matched by the rather poor fossil record, with *M. asmundiae* (Wujek et van der Veer) Nicholls representing the only fossil record of a species producing scales with ribs (SIVER & WOLFE 2005; SIVER et al. 2009). It is remarkable that the number and spacing of the ribs have remained virtually unchanged for over 48 Ma. It is likely that while the species of the genus *Synura* optimized the ribs on their silica scales as described above, *Mallomonas* species have not changed the number and spacing of ribs since their development. This invariability could point to a role of the ribs in light diffraction or in reducing dangerous UV radiation, as mentioned at the beginning of the discussion. Interestingly, although our analyses identified a vertical orientation of the ribs as the best technical solution for scale stability, such an arrangement is extremely rare in nature. This again suggests a specific, yet unknown function of the ribs. Clearly, further experimental studies are necessary to understand the function of ribs and other microscopic pattern structures that have evolved on the surface of *Mallomonas* scales.

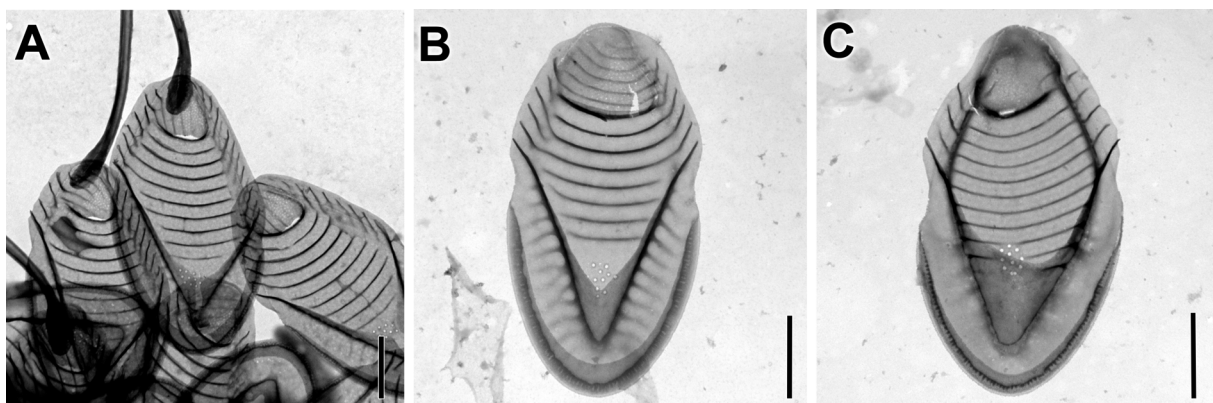


Fig. 8. Silica scales of *Mallomonas striata* damaged at the base of dome, i.e., at or near the location predicted by mechanical resistance analysis.

### The application of finite element analysis in microbial research

The finite element method (FEM) is a method based on subdivision of complex structures into a finite number of smaller and simpler parts called finite elements. The mechanical properties of the studied structure can then be determined by summing up the equations for all these elements. Although this method is predominantly used in engineering disciplines such as structural analysis, it has also become increasingly used in biology, especially in studies of the mechanical properties of macroscopic objects such as human bones (OTA et al. 1999; MOBASSERI et al. 2022). Despite its wide range of applications, this method has been used only sporadically in the case of protists, and so far, practically only for the study of silica frustules of diatoms. In these cases, the method has been used primarily to investigate mechanical resistance and several other properties important for potential applications in nanotechnology (HAMM et al. 2003; LU et al. 2015; ABDUSATOROV et al. 2020; TOPAL et al. 2020).

In this study, we did not only use the FEM to determine the overall mechanical properties of silica scales, but we also focused on how their mechanical resistance is affected by the specific structure on their surface. For this purpose, we used rather simpler models with fewer elements compared to other studies. This means a certain simplification of the structures and results, but on the other hand full control over all parts of the models, avoiding possible inaccuracies and above all the possibility to model secondary structures that cannot be identified in nature. Modelling only one of the silica scales from the complex scale case represents another significant simplification of our analyses. While this allowed us to better define physical factors such as supports and loads, it deprived us of information about how the whole silica case responds to the load. We consider this problem as one of the future challenges.

Despite all these drawbacks, we are reasonably confident that our results are relevant. This conclusion is mainly driven by two findings: (i) the analyses of scales with different numbers of ribs give the expected results; (ii) the structures revealed by our mechanical resistance analyses as the most stressed are indeed susceptible to damage in nature. For example, the largest structural stress in *Mallomonas* scales was located at the ribs of anterior flange. This is the area of the scale where we detected deformations or even small holes in the scales of *M. striata* (Fig. 8). Thanks to the possibilities provided by FEM, we were able to reveal the importance of ribbed patterns on silica scales of the genera *Synura* and *Mallomonas*. From our experience, this method can be recommended for studying the mechanical properties of other solid structures on the surface of various microorganisms.

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