



## Mallomonas solea-ferrea and Mallomonas siveri (Chrysophyceae/Synurophyceae): two new taxa from the Western Cape (South Africa)

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With 30 figures and 1 table

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**Abstract:** Two new species, *Mallomonas solea-ferrea* and *M. siveri*, are described based on both transmission and scanning electron microscopy from the Western Cape (South Africa). *Mallomonas solea-ferrea* is located in the section Torquatae, with typical collar scales bearing a smooth, curved bristle, rhomboid body scales, and rear scales with a diminutive spine. The shield of the body scales is covered with delicate papillae and a secondary reticulum where each mesh encloses approximately six pores. The proximal-most reticulation forms a depression in the shape of a horseshoe. The most similar taxon to *M. solea-ferrea* is the nominal variety of *M. pumilio*. *Mallomonas siveri* belongs to the section Striatae. All scales of the cell coat have a smooth dome and possess a sharply terminated, slightly curved bristle. The scales of *M. siveri* are most similar to those of *M. striata* since they possess the special groups of pores posteriorly on the shield. However, in *M. siveri*, the V-rib arms are continuous with the anterior submarginal ribs, and both flanges are smooth.

**Key words:** Chrysophyceae; *Mallomonas solea-ferrea*; *Mallomonas siveri*; new species; scale morphology; South Africa; Synurophyceae.

### Introduction

The genus *Mallomonas* Perty (Chrysophyceae/Synurophyceae clade, Stramenopiles) currently comprises about 160 species and infraspecific taxa. In recent molecular phylogenetic analyses the former class Synurophyceae is placed within members of Chrysophyceae (e.g. Grant et al. 2009). The presence of more or less bilaterally

symmetrical silica scales precisely arranged over the cell is characteristic of the genus. In *Mallomonas*, some or all of the scales may be associated with a bristle, an elongated siliceous structure the base of which is fitted under the anterior end of the scale. Silica scale morphology, examined by electron microscopy, is used as the primary, and often only, character for taxa determination. More recently, molecular systematic techniques have been applied to test the validity of scale-based taxonomy (Andersen 2004, 2007, Jo et al. 2009). Although Kristiansen & Preisig (2007) reported that taxonomy based on scale morphology may be artificial, preliminary results revealed that most of the morphologically defined sections were supported by molecular analyses (Jo et al. 2009). Despite numerous floristic and ecological studies of silica scaled chrysophytes from different geographical areas and habitats, there are still large unexplored territories, including South Africa. About 50 scaled chrysophytes have been found in the southern African region, including Madagascar (Cronberg 1989, 1996, Hansen 1996). Three new species, *Mallomonas madagascariensis* P.Hansen, *M. lemuriocellata* P.Hansen and *M. crocodilorum* P.Hansen, were described from subtropical Africa (southern part of Madagascar, Hansen & Kristiansen 1995).

The purpose of this paper is to describe two additional species of *Mallomonas* from South Africa.

### Materials and methods

Both of the stations investigated are situated on Table Mountain, Western Cape, Republic of South Africa, and were sampled only once in January 2009. Station 1 comprised a small, shallow, unnamed pool with a sandy bottom and dark water rich in humic acids (33.97157S 18.4087E, 846 m asl). Woodhead Reservoir (station 2) was built in 1897 on the Disa River and it supplies water to Cape Town. The reservoir has a capacity of 927,000 m<sup>3</sup> and a surface area of 13 ha (33.9766S 18.4052E, 732 m asl). A Mediterranean-like climate, with warm, dry summers and mild, moist winters, is typical for this area. The long-term monthly precipitation in January is 15 mm (World Meteorological Organization; WMO). Most of the area comprises the Fynbos Biome, with various Fynbos vegetation types (Cowling & Richardson 1995).

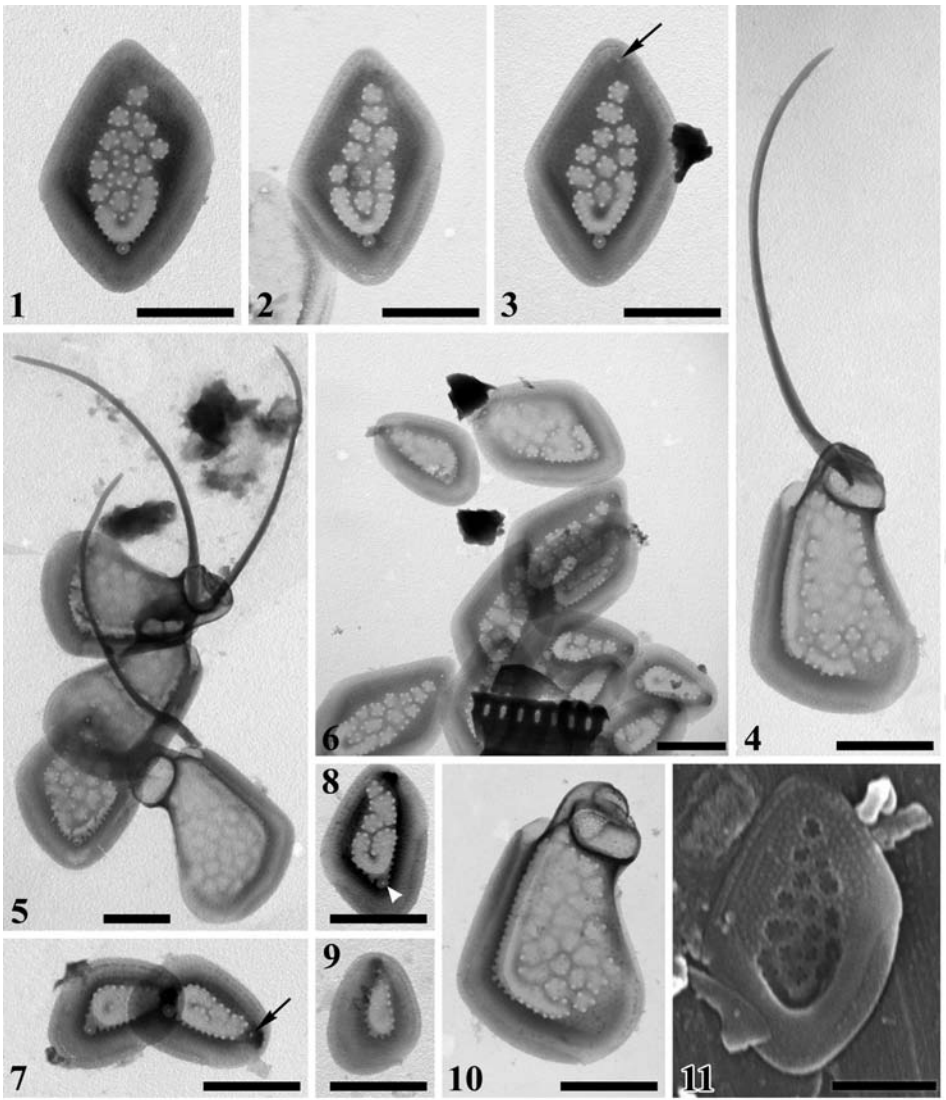
This paper is based on surface sediment samples fixed with Lugol's solution. A 5 ml sample was obtained by syringe suction from the upper sediment layers. The samples were washed by repeated centrifugation in deionized water. Drops of the washed sample were dried either onto Formvar-coated transmission electron microscopy (TEM) grids or onto a piece of aluminium foil for scanning electron microscopy (SEM). The aluminium foil was mounted onto an SEM stub with double-sided adhesive carbon tape, coated with gold for 5 min (3 nm layer) with a Bal-Tec SCD 050 sputter coater and observed with a JEOL 6380 LV scanning electron microscope. The TEM grids were examined with a JEOL 1011 transmission electron microscope. Descriptions of the new species were based on iconotypes, as it was impossible to preserve a specimen showing the features attributed to the taxon.

### Results

#### *Mallomonas solea-ferrea* Němcová & Kristiansen sp. nov.

Figs 1–11

Cellula tribus typis squamarum obiecta: squamis collaribus, mediis et posticis. Squamae collares subtriangulae, cupula rotunda laevi, a scuto costa dentata limitata. Limbi dorsales et posteriores lati laevesque, limbus dorsalis distale indentus. Pars posterior et pars dorsalis costae submarginalis valde conspicuae, in parte posteriori dentata. Scutum reticulo regulari, quaque macula 5–6 poros cingenta, et maculis juxta partem proximalem costae submarginalis in depressionem manifestam u-formem



Figs 1–11. *Mallomonas solea-ferrea* Němcová & Kristiansen sp. nov. Figs 1–3. Body scales, note the anterior pore (arrow). Figs 4–5. Collar scales with smooth, curved and attenuated bristles attached to the dome. Fig. 6. Scales from the posterior part of the cell. Figs 7–9. Rear scales with more or less confluent reticulation, note the anterior pore next to the diminutive spine (arrow) and the rimmed pore situated posteriorly (arrowhead). Fig. 10. A collar scale with a smooth flange intended distally at a dome. Fig. 11. A body scale observed by scanning electron microscopy, note the horseshoe-shaped depression posteriorly on the shield, and the papillae arranged in rows oriented longitudinally with the scale border on the anterior part of the scale. Scale bar = 1  $\mu$ m. Remark: Figs 1–4 and 7–10 are shown in the same magnification.

confluentibus. Squamae mediae et posticae rhombicae, sine cupula. Limbi lati laevique, circum scutum continuantes. Porus conspicuus in angulo v-formi, alius porus minor prope apicem. Squamae posticae reticulo tenui, nonnumquam dente minuto instructa.

Setae curvatae, laeves, obtuse attenuatae.

Cysta ignota.

Dimensiones: Squamae collares  $2.5\text{--}2.9 \times 1.7\text{--}1.9 \mu\text{m}$ , squamae corporis  $2.2\text{--}2.6 \times 1.3\text{--}1.9 \mu\text{m}$ , squamae posticae  $1.4\text{--}1.8 \times 0.9\text{--}1.2 \mu\text{m}$ ; setae  $1.4\text{--}1.8 \times 0.9\text{--}1.2 \mu\text{m}$ .

Typus (iconotypus) Fig. nostra 1. 15.1.2009 inventus, in stagno (sine nomine), Table Mountain, Western Cape, Republic of South Africa (33.97157S, 18.4087E, 846 m asl).

Three types of scale are discerned, including collar, body and rear scales. The collar scales ( $2.5\text{--}2.9 \times 1.7\text{--}1.9 \mu\text{m}$ ) are trapezoid-shaped (Figs 4–5) with a well-developed, circular dome partly ornamented with small papillae (Fig. 10). The dome is proximally delimited by a strong dentate rib. The submarginal rib is well developed at the dorsal edge, but less prominent along the ventral edge. The flange is smooth, forming a prominent rounded protrusion on the dorsal edge just below the dome (Fig. 10). The proximal border encompasses the posterior and dorsal parts of the collar scale. The whole shield is covered with regularly spaced papillae. The meshes of the reticulum are irregularly arranged and each encloses five to six pores and forms a slight depression. Meshes along the dorsal and proximal parts of the submarginal rib fuse to form a single long depression surrounded by pores. Body scales ( $2.2\text{--}2.6 \times 1.3\text{--}1.9 \mu\text{m}$ ) are rhombic, domeless, and with no apparent submarginal rib (Figs 1–3). The shield is covered with delicate papillae. At the anterior end of each scale, the papillae are arranged in rows oriented longitudinally with the scale border (Fig. 11). The posterior flange is smooth, and the proximal border is considerably attenuated at the posterior end of the scale. The meshes of the reticulum form distinct depressions, each enclosing approximately six pores. Reticulation is proximally confluent, forming a horseshoe-shaped depression with a denticulate proximal edge (Fig. 11). There are two distinct pores on the base plate not visible on the SEM image; one is placed anteriorly (Fig. 3, arrow) and the second one, a rimmed pore, is situated inside the posterior flange just behind the horseshoe-shaped depression. The rear scales ( $1.4\text{--}1.8 \times 0.9\text{--}1.2 \mu\text{m}$ ) are asymmetric with a smooth, broad flange surrounding the whole scale (Figs 7–9), in some cases bearing a diminutive spine at the anterior end (Fig. 7, arrow). The reticulation of the shield is more or less confluent (Fig. 6), both types of infra-scale pores are present and the proximal border surrounds less than half of the perimeter.

Bristles ( $3.9\text{--}4.6 \mu\text{m}$ ) are smooth, curved and attenuated, with a blunt tip (Figs 4–5).

Cyst unkn. Cell shape and dimensions unknown.

ICONOTYPE: Figure 1.

TYPE LOCALITY: unnamed pool, Table Mountain, Western Cape, Republic of South Africa (33.97157S 18.4087E, 846 m asl), sampled on 15.1.2009.

ETYMOLOGY: The epithet "iron shoe" is based on the horseshoe-shaped depression on the scale.

DISTRIBUTION: The species was only found in the type locality (station 1).

Squamae ovals, lateraliter exigue incurvatae, cupula laevi. Costa v-formis et costae submarginales anteriores conjunctae. Limbus laevis, cupulam circumveniens. Scutum 8 costis transversis regulariter interjectis instructum, in angulo costae v-formis grece 4–10 pororum ornatum. Setae exigue curvatae, convolutae, acutae, raro cum dentibus subapicularibus.

Cysta ignota.

Dimensiones: Squamae 2.7–3.3 × 1.3–2.0 µm, setae 3.5–6.2 µm longae.

Typus (iconotypus) Fig. nostra 12 depictus, 15.1.2009, in stagno Woodhead Reservoir inventus, Western Cape, Republic of South Africa. (33.9766S 18.4052E, 732 m asl)

The scales (2.7–3.3 × 1.3–2.0 µm) are oval with slight lateral incurvings. All scales possess a rounded smooth dome (Figs 12–20). The pores of the base plate are minute and only visible in the less silicified scales; in mature scales they are covered by secondary material (Figs 17, 18). The V-rib is rounded, not acutely angled. The distal ends of the arms of the V-rib curve and become continuous with the anterior submarginal ribs, the latter of which are only weakly developed, and sometimes not discernable from the rest of the anterior flange (Figs 27–30). The anterior and posterior flanges are smooth, rather narrow, and the boundary between them not strictly delimited. The shield is marked with about eight regularly spaced transverse ribs. Scales with aberrant or deviating rib patterns were also observed (Figs 15, 16). A group of 6–10 pores is located on the posterior part of the shield (e.g. Fig. 20). The proximal border is smooth. Elongated, slightly asymmetric scales were observed (Fig. 17).

Bristles (3.5–6.2 µm) are delicate, slightly curved with a longitudinal incision (Figs 21–23), and with an acute tip (Fig. 26) formed as an extension of the rolled-up sheet. Subapical teeth were present on some bristles, but rarely observed (Figs 24, 25).

Cyst unknown. Cell shape and dimensions unknown.

ICONOTYPE: Figure 12.

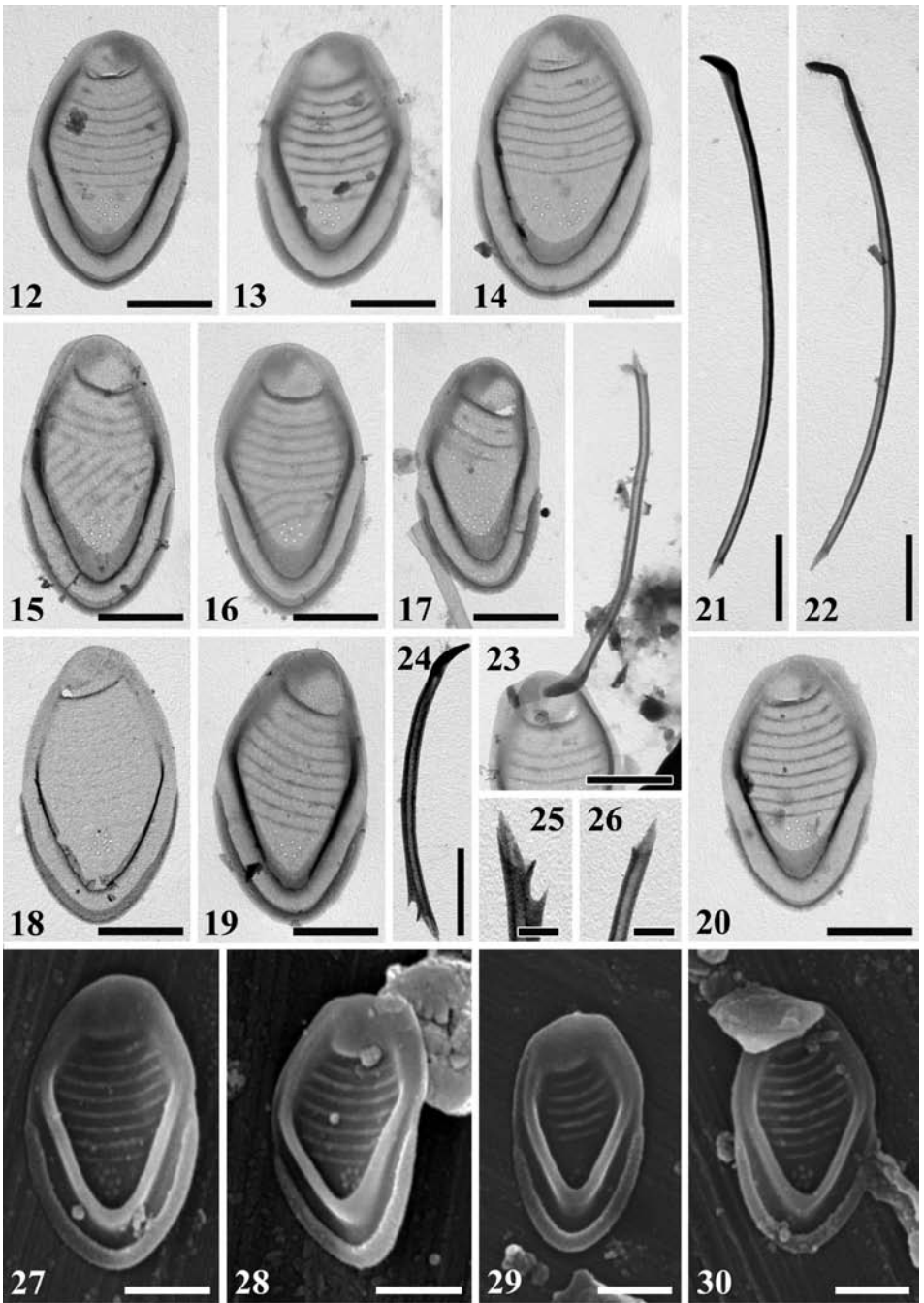
TYPE LOCALITY: Woodhead Reservoir, Western Cape, Republic of South Africa (33.9766S 18.4052E, 732 m asl), sampled on 15.1.2009

ETYMOLOGY: The epithet is in honour of the chrysophyte specialist Peter A.Siver, USA.

DISTRIBUTION: This species was found in the type locality (station 2) and in station 1.

## Discussion

*Mallomonas solea-ferrea* belongs to the section Torquatae Momeu & Péterfi, series Pumilae. The most similar taxon to *M. solea-ferrea* is the nominal variety of *Mallomonas pumilio* Harris & Bradley emend. Asmund, Cronberg & Dürschmidt. The scales of both species are similar in having smooth posterior flanges, lacking distinctly delimited submarginal ribs and having anterior flanges covered with regularly spaced longitudinal rows of papillae. However, in *Mallomonas pumilio* var. *pumilio*, the papillae of the anterior flanges are mostly arranged simultaneously in transverse rows and sometimes the rows of papillae may merge to form incon-



Figs 12–30. *Mallomonas siveri* Němcová & Kristiansen sp. nov. Figs 12–13. Body scales. Fig. 14. A body scale with a doubled group of pores. Figs 15–16. Scales with an aberrant rib pattern. Fig. 17. An asymmetric scale, note the minute pores on the base. Fig. 18. A weakly silicified scale. Fig. 19. An

spicuous transverse ribs. The body scales of *M. pumilio* var. *pumilio* are distinguishable from those of *M. solea-ferrea* in that the reticulum of the shield comprised fewer pores (3–4) at the bottom of each mesh (compared to six pores in *M. solea-ferrea*) and in lacking the conspicuous horseshoe-like depression proximally on the shield. Moreover, the dome of a collar scale in *Mallomonas pumilio* var. *pumilio* is provided with a forward-pointing short peak (Asmund et al. 1982), whereas in *M. solea-ferrea* the dome is rounded without a peak. Scales of *Mallomonas pumilio* var. *munda* Asmund, Cronberg & Dürschmidt, *M. pumilio* var. *silvicola* Harris & Bradley and *M. clavus* Bradley possess well-developed struts on the anterior flanges which clearly separate them from those of *M. solea-ferrea*. Moreover, the extreme rear scales of *Mallomonas clavus* bear long, tapering spines (Bradley 1964). The scales and bristles of all *Mallomonas pumilio* varieties are larger than those of *M. solea-ferrea* (Kristiansen 2002). *Mallomonas lanalhuensis* Dürschmidt is similar to *M. solea-ferrea* in possessing the V-shaped window (depression) where the secondary layer is absent or weakly developed; however, *M. lanalhuensis* differs from *M. solea-ferrea* by the presence of regularly spaced struts radiating from a conspicuous anterior submarginal rib, and in the elaboration of the shield (Dürschmidt 1983). *Mallomonas lanalhuensis* also lacks a posteriorly situated rimmed pore. Scales of *Mallomonas alata* Asmund, Cronberg & Dürschmidt are distinguishable from those of *M. solea-ferrea* by strongly asymmetric (wing-like) anterior flanges.

*Mallomonas solea-ferrea* also closely resembles *Mallomonas scrobiculata* Nicholls from the series Eoae. Both species have poorly developed or missing anterior submarginal ribs, shield and anterior flanges marked with papillae, a window (a horseshoe-shaped depression in *M. solea-ferrea*) with a missing secondary layer and smooth posterior flanges and a proximal border. However, the shield of *M. scrobiculata* scales is marked with small circular single pits and the dome of the collar scales is slightly peaked (Nicholls 1984).

*Mallomonas siveri* belongs to the section Striatae Asmund & Kristiansen, series Striata and within this series is most closely related to *Mallomonas striata* Asmund. *Mallomonas siveri* differs from the other members of this series in lacking anterior flange struts, nevertheless regarding the other characters we decided to place *M. siveri* into the series Striata. Within the series Striata, only domed scales bearing a bristle are produced. Except for *Mallomonas kristiansenii* Wujek & Bicudo, the shield of body scales is covered with evenly spaced, curved transverse ribs (Kristiansen & Preisig 2007). The scales of *Mallomonas striata* are similar to those of *M. siveri* in possessing special groups of pores posteriorly on the shield. However, several features can be used to distinguish *Mallomonas striata* from *M. siveri* (see Table 1). *Mallomonas striata* has an acutely-angled, strongly-hooded V-rib with straight arms

asymmetric body scale. Fig. 20. A scale with a reduced proximal border. Figs 21–22. Slightly curved and delicate bristles with an acute tip. Fig. 23. A bristle associated with the dome of the scale. Fig. 24. A bristle terminated with subapically located teeth. Figs 25–26. Detailed views of the bristle tips. Scale bar for Figs 25, 26 = 250 nm. Figs 27–30. Morphological plasticity of scales observed in SEM, the V-rib is distally continuous with the anterior submarginal rib. Scale bar = 1  $\mu$ m, except for Figs 25 and 26 (scale bar = 250 nm). Remark: Figs 12–24 are shown in the same magnification.

Tab. 1. A survey of diagnostic features on silicate structures in *Mallomonas siveri* and related taxa *M. striata* var. *striata* and *M. striata* var. *serrata*.

	<i>M. striata</i> var. <i>striata</i>	<i>M. striata</i> var. <i>serrata</i>	<i>M. siveri</i>
Dome	triangular or rounded with ribs or without ornamentation	triangular or rounded, ribs mostly U-shaped	rounded without ornamentation
V-rib	acutely angled, lower edge smooth	acutely angled, lower edge supported by internal radial struts in well silicified scales	with rounded base, lower edge always smooth
Hood	well developed, strongly hooded	well developed, strongly hooded	less prominent, tenuous
Anterior submarginal ribs	well developed, not continuous with V-rib	well developed, not continuous with V-rib	weakly developed or missing, continuous with V-rib
Proximal border	bearing internal struts	bearing internal struts	smooth
Number of ribs on the shield	7–12	7–12	6–9
Ribs on anterior flange	3–6	3–6, sometimes connected with net like reticulum	no ribs
Ribs on posterior flange	16–20	7–13	no ribs
Lateral incurvings	conspicuous	conspicuous	slight or absent
Bristle	with a blunt tip and a single small subapical tooth	serrated with short pointed teeth	with a sharp tip and occasionally with sub-apical tooth (teeth)

that extend almost to the margin of the scale. The distal ends of the arms of the V-rib are not continuous with the well-developed anterior submarginal ribs (Siver 1991). *Mallomonas siveri*, on the other hand, has a roundly-angled V-rib with a less prominent hood. The arms of the V-rib curve and become continuous with anterior submarginal ribs. Both flanges (anterior and posterior) and the dome of *M. striata* are all marked with ribs, unlike those of *M. siveri*, which are smooth. On average, there are more ribs (7–12) on the shield of *M. striata* scales compared to *M. siveri* (6–9). Moreover, the scales of *M. striata* differ from those of *M. siveri* by having conspicuous lateral incurvings. Finally, the scales and bristles of *M. striata* are larger than those of *Mallomonas siveri* (Kristiansen 2002). Well-silicified scales of *Mallomonas striata* var. *serrata* Harris & Bradley have the lower edge of the V-rib supported by internal radial struts visible by transmission electron microscopy, whereas in *M. siveri* the V-rib is always smooth. Bristles of *Mallomonas striata* var. *serrata* differ from those of *M. siveri* in possessing a unilateral serration along the whole convex edge (Harris & Bradley 1960). *Mallomonas striata* var. *striata* bristles have a single small subapical tooth and a slight swelling at the distal part, whereas the bristle for *Mallomonas siveri* usually has a sharp tip extended from the rolled-up sheet.



*Mallomonas siveri* also closely resembles *Mallomonas verrucosa* Vigna from the series Retiferae. Scales of both species are similar in size and lack ribs on both flanges and a dome (Vigna 1981). Scales of *Mallomonas verrucosa* possess densely spaced papillae on the dome, anterior submarginal ribs and anterior flanges which clearly separate them from those of *M. siveri*. The similar taxon to *M. siveri* is also *Mallomonas calceolus* Bradley from the sectio Papillosae. *Mallomonas calceolus* differs in having papillae on the shield instead of transverse ribs. Moreover, both anterior flanges and a dome are marked with papillae in *M. calceolus*.

Additional studies on silica scaled chrysophytes in subtropical regions may help to further evaluate the status of endemism and elucidate the ecological preferences of the newly described species *Mallomonas solea-ferrea* and *M. siveri*.

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### References

- ANDERSEN, R.A. (2004): Biology and systematics of heterokont and haptophyte algae. – *Am. J. Bot.* **91**: 1508–1522.
- ANDERSEN, R.A. (2007): Molecular systematics of the Chrysophyceae and Synurophyceae. – In: BRODIE, J. & J. LEWIS (eds): *Unravelling the algae: the past, present, and future of algal systematics*: 286–310. CRC Press.
- ASMUND, B., G. CRONBERG & M. DÜRRSCHMIDT (1982): Revision of the *Mallomonas pumilio* group (Chrysophyceae). – *Nord. J. Bot.* **2**: 383–395.
- BRADLEY, D.E. (1964): A Study of the *Mallomonas*, *Synura* and *Chryso-sphaerella* of Northern Iceland. – *J. Gen. Microbiol.* **37**: 321–333.
- COWLING, R.M. & D. RICHARDSON (1995): *Fynbos – South Africa's unique floral kingdom*. – Fernwood Press, Cape Town.
- CRONBERG, G. (1989): Scaled chrysophytes from the tropics. – *Nova Hedwigia Beih.* **95**: 191–232.
- CRONBERG, G. (1996): Scaled chrysophytes from the Okavango Delta, Botswana, Africa. – *Nova Hedwigia Beih.* **114**: 91–108.
- DÜRRSCHMIDT, M. (1983): Three new species of *Mallomonas* (Chrysophyceae, Mallomonadaceae) from Lake Lanalhue, Chile. – *Nord. J. Bot.* **3**: 423–430.
- GRANT, J., Y.I. TEKLE, O.R. ANDERSEN, D.J. PATTERSON & L.A. KATZ (2009): Multigene evidence for the placement of a heterotrophic amoeboid lineage *Leukararchnion* sp. among photosynthetic stramenopiles. – *Protist* **160**: 376–38.
- HANSEN, P. (1996): Silica-scaled Chrysophyceae and Synurophyceae from Madagascar. – *Arch. Protistenkd.* **147**: 145–172.
- HANSEN, P. & J. KRISTIANSEN (1995): *Mallomonas madagascariensis*, *M. lemuriocellata* and *M. crocodilorum* (Synurophyceae), three new species from Madagascar. – *Nord. J. Bot.* **15**: 215–223.
- HARRIS, K. & D.E. BRADLEY (1960): A taxonomic study of *Mallomonas*. – *J. Gen. Microbiol.* **22**: 750–777.

- JO, B.Y., W. SHIN & J.H. KIM (2009): Phylogeny of the genus *Mallomonas* (Synurophyceae) based on ultrastructure of silica scale and combined nuclear SSU and LSU rDNA and plastid rbcL data. – *Phycologia* **48**: 51. Meeting Abstract: 146.
- KRISTIANSEN, J. (2002): The genus *Mallomonas* (Synurophyceae). A taxonomic survey based on the ultrastructure of silica scales and bristles. – *Opera Bot.* **139**: 1–218.
- KRISTIANSEN, J. & H.R. PREISIG (2007): Chrysophyte and Haptophyte Algae, 2nd part: Synurophyceae. – In: BÜDEL, B., G. GÄRTNER, L. KRIENITZ, H.R. PREISIG & M. SCHAGERL (eds.): Süßwasserflora von Mitteleuropa, vol. 1/2, Springer-Verlag, Berlin.
- NICHOLLS, K.H. (1984): Four new *Mallomonas* species of the Torquatae series (Chrysophyceae). – *Can. J. Bot.* **62**: 1583–1591.
- SIVER, P.A. (1991): The biology of *Mallomonas*. Morphology, taxonomy, ecology. – *Dev. Hydrobiol.* **63**: 1–228. Kluwer Academic Publishers, Dordrecht.
- VIGNA, M. (1981): Estudio con microscopio electronico de barrido de nuevos taxones de la familia Synuraceae (Chrysophyceae). – *Physis, B*, **39**: 15–20.
- World Meteorological Organization: [http://www.wmo.int/pages/index\\_en.html](http://www.wmo.int/pages/index_en.html)

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