



Mallomonas alpestrina sp. nov. (Synurales, Chrysophyceae, Stramenopiles) and its spineless relatives—*Mallomonas alata* group

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Abstract

In this paper, we define the *Mallomonas alata* group and describe *M. alpestrina* sp. nov. from an oligotrophic high mountain glacial lake on the slopes of Haba Xue Shan (Haba Snow Mountain), China. The *Mallomonas alata* group is excluded from the *M. pumilio* group primarily based on the approximately triangular shape of the collar scales, the small hook-like protruded dome, and one considerably broader anterior flange of the body scale. We extend previous research on small species from the section Torquatae with reticulated scale-shield pattern. Molecular genetic data for the *Mallomonas alata* group species are not currently available; therefore, we provide detailed information on scale and scale-case morphology, environmental requirements, and geographical distribution of these species.

Introduction

The genus *Mallomonas* Perty (1852: 170) includes heterokont photosynthetic flagellates covered by overlapping silica scales. A cell contains a single, golden brown, deeply divided plastid. Pigment composition is dominated by the brown pigment fucoxanthin, chlorophyll *a*, and chlorophyll *c*₂. Currently, ca. 180 taxa have been described within the genus *Mallomonas* (Siver 1991, Kristiansen & Preisig 2007) based primarily on the silica scale morphology. However, recently descriptions based on both molecular data and scale morphology have been published (Jo *et al.* 2013, Kim *et al.* 2014). The term *Mallomonas pumilio* group [including *M. alata* Asmund *et al.* (1982: 391) f. *alata*] was introduced by Asmund *et al.* (1982). The group included species with small (7–20 µm) ovoid to ellipsoidal cells from the section Torquatae, which exhibited a reticulated scale-shield pattern with the reticulum meshes enclosing one to several pores at the bottom. Asmund *et al.* (1982) reported that the *Mallomonas pumilio* type [Harris & Bradley (1957: 45)] included two different species. They designated one species (their fig. 4 in Asmund *et al.* 1982) as a lectotype of *Mallomonas pumilio* Harris & Bradley (1957) *emend.* Asmund *et al.* (1982: 387) var. *pumilio*, and described the other as the new species *Mallomonas alata* f. *alata* (their Fig. 3). A new form from a paludal forest in southern Chile, *M. alata* f. *hualvensis* Asmund *et al.* (1982: 394), also was introduced in that paper. Subsequently, *M. alata* f. *hualvensis* was reported from Ontario, Canada (Nicholls 1988) and the Aquitaine Region, France (Němcová *et al.* 2012), which placed its endemic status in dispute.

Detailed revision and elaborate definition of the *Mallomonas pumilio* group based on scale morphology and scale shape analysis was provided by Němcová *et al.* (2013). To evaluate slight differences in scale morphology, landmark-based geometric morphometrics analysis was used. Two new species [*Mallomonas jubata* Němcová *et al.* (2013: 36) and *M. directa* Němcová *et al.* (2013: 40)] and two new varieties [*M. pumilio* var. *dispersa* Němcová *et al.* (2013: 42) and *M. solea-ferrea* var. *irregularis* Němcová *et al.* (2013: 40)] were introduced, and the emended definition of *M. pumilio* var. *pumilio* *emend.* Němcová *et al.* (2013: 44) was provided. The varieties *Mallomonas pumilio* var. *silvicola* Asmund *et al.* (1982: 391) and *M. pumilio* var. *munda* Asmund *et al.* (1982: 391) were erected to the species level *M. silvicola* Němcová *et al.* (2013: 38) and *M. munda* Němcová *et al.* (2013: 36), respectively. Only species exhibiting collar scales with a well-developed circular to oval dome, harboring smooth curved bristle, were retained in the *M. pumilio* group. Species exhibiting approximately triangular collar scales with a small hook-like protruded dome and body scales with one considerably broader anterior flange (*M. alata* f. *alata* and *M. alata* f. *hualvensis*) were not

included in the analyses. Recently, the new species *Mallomonas tirolensis* Pichrtová *et al.* (2013: 79), which exhibits similar collar and body-scale morphology, was identified in the eastern Alpine region of North Tyrol, Austria.

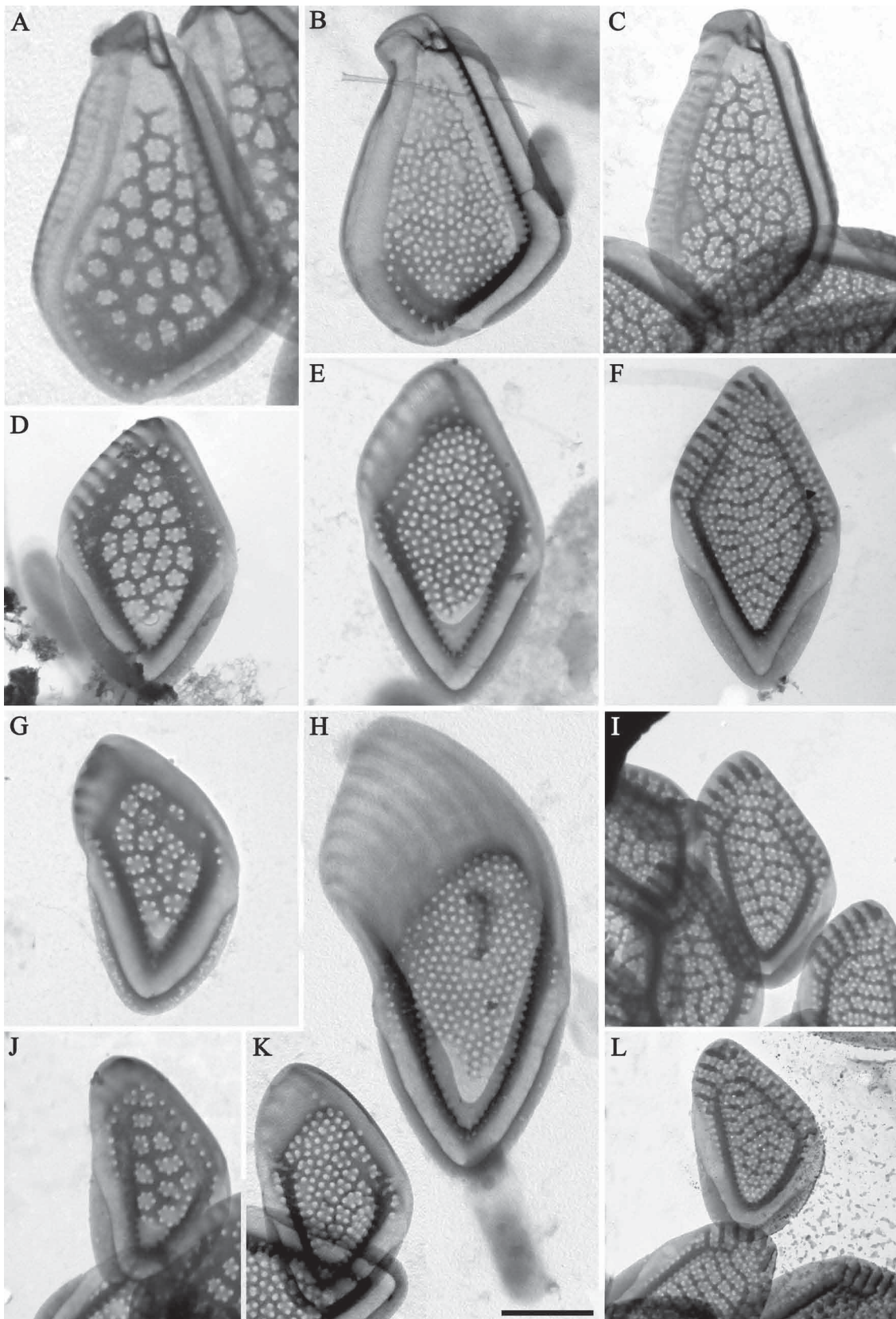


FIGURE 1. A–C. Collar scales in: A. *Mallomonas alata* f. *alata*. B. *Mallomonas alata* f. *hualvensis*. C. *Mallomonas tirolensis*. D–F. Body scales in: D. *Mallomonas alata* f. *alata*. E. *Mallomonas alata* f. *hualvensis*. F. *Mallomonas tirolensis*. G–I. Transitional scales between the rear and the body scales in: G. *Mallomonas alata* f. *alata*. H. *Mallomonas alata* f. *hualvensis* (note the considerably broad anterior flange). I. *Mallomonas tirolensis*. J–L. Rear scales in: J. *Mallomonas alata* f. *alata*. K. *Mallomonas alata* f. *hualvensis*. L. *Mallomonas tirolensis*. Scale bar = 1µm. A–L are shown at the same magnification.

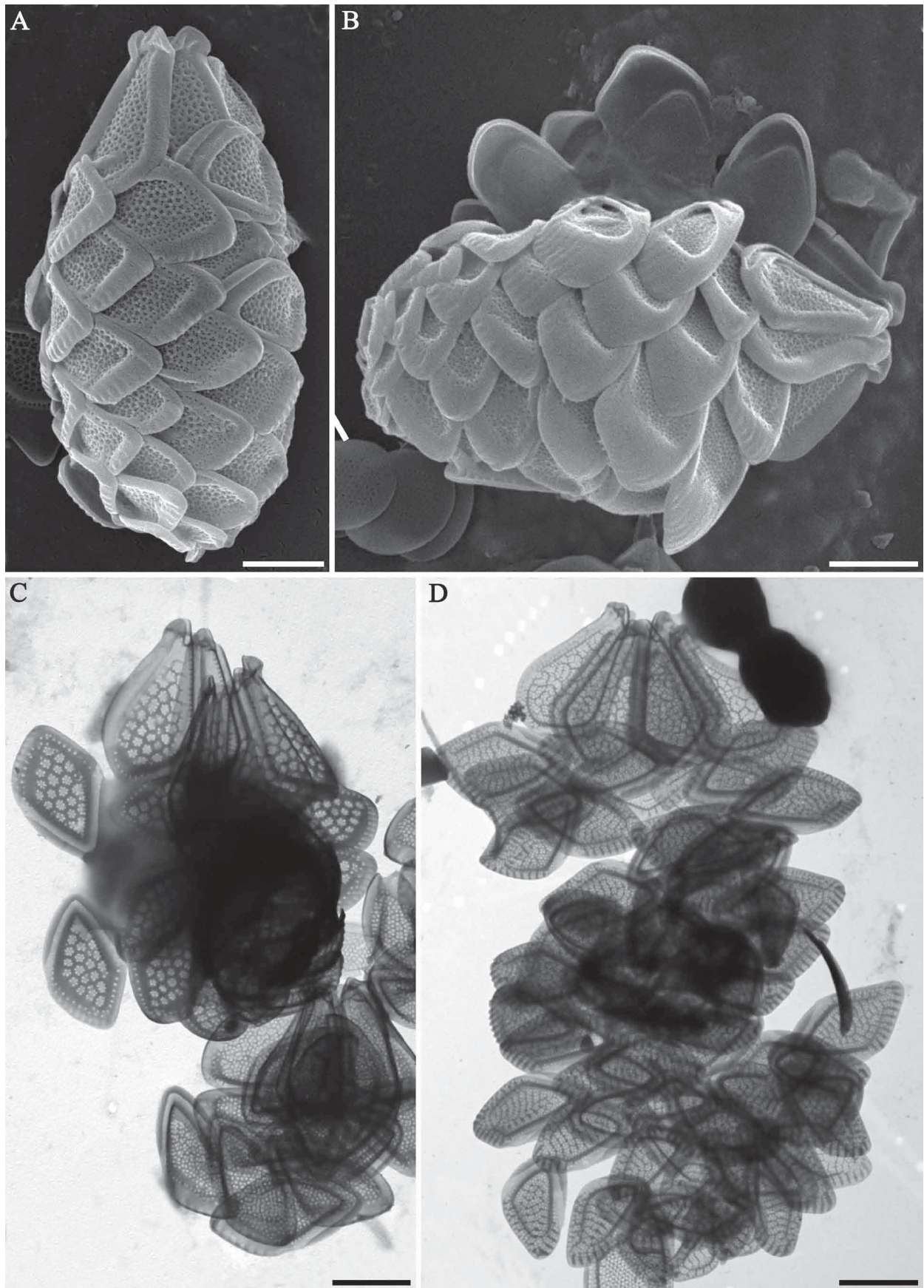


FIGURE 2. A. Whole-cell armor of *Mallomonas alata* f. *alata* in a scanning electron microscope (SEM) micrograph. B. *Mallomonas alata* f. *hualvensis*, whole cell in SEM. C. A combined micrograph of whole-cell armors of *M. alata* f. *alata* (upper part) and *M. alata* f. *hualvensis* (lower part) in a transmission electron microscope (TEM) micrograph. D. Whole-cell armor of *M. tirolensis* in TEM. Scale bar = 2 μm .

The purpose of this paper is to define the *Mallomonas alata* group and describe *M. alpestrina* sp. nov. We extend previous research on small species from the section Torquatae with reticulated scale-shield pattern. Molecular genetic data are not currently available; therefore, we provide detailed information on scale and scale-case morphology, environmental requirements, and geographical distribution of the *Mallomonas alata* group species.

Materials and Methods

The new species *Mallomonas alpestrina* was identified in one of many glacial lakes (4192 m a.s.l.) on the slopes of Haba Xue Shan (Haba Snow Mountain), Zhongdian (Shangri-La County, Deqen Tibetan Autonomous Prefecture, Northwestern Yunnan), China. The lake is located in a long narrow valley and it follows the shape of the valley; the lake length from SE to NW is ca. 225 m and it reaches ca. 73 m at the widest point. The lake depth is not known. However, as this glacial lake lies in a deep valley, it may be tens of meters deep. The lake is surrounded by steep subalpine rocky slopes dominated by various grasses and shrubs (mostly *Rhododendron* spp.). The species description is based on surface sediment samples obtained by syringe suction from the upper sediment layers, which were fixed with Lugol's solution.

Samples containing other species were collected using a plankton net (20 µm mesh). *Mallomonas alata* f. *alata* was sampled in Zeller Loch, Germany (Fig. 1A), Basco Pantano near Policoro, Italy (Fig. 1D), Aquitaine, France (Figs 1G, J; Figs 2A, C). *M. alata* f. *hualvensis* was sampled in Aquitaine, France. *Mallomonas tirolensis* samples were from North Tyrol, Austria.

The Lugol-fixed samples were washed by repeated centrifugation in deionized water. Drops of fresh or washed samples were dried onto Formvar-coated transmission electron microscopy (TEM) grids (Nováková *et al.* 2004). The TEM grids were examined with a JEOL 1011 transmission electron microscope. Photomicrographs were obtained using a Veleta CCD camera equipped with image analysis software (Olympus Soft Imaging Solution GmbH). For scanning electron microscopy (SEM), the Formvar-coated grid (already observed in TEM) was mounted onto an SEM stub with double-sided adhesive carbon tape, coated with gold for 5 min with a Bal-Tec SCD 050 sputter coater (which formed a 3-nm thick gold layer), and observed with a JEOL 6380 LV scanning electron microscope. Typification of the new species is based on the illustrations published in this study, because it was impossible to preserve specimens showing the features attributed to the taxon (ICN art. 40.5).

Results

Description of the Mallomonas alata group

The *Mallomonas alata* group includes small species (approximately 10 µm) with ovoid to ellipsoid cells prolonged in the anterior part, which is formed primarily by six collar scales. The collar scales are approximately triangular with a small hook-like protruded dome. The proximal border (rim) and the submarginal rib serve as a track to position the overlapping collar scale. No group members were observed to have bristles attached to the dome. There is one considerably broader anterior flange in the body scale. The body scales form a precisely organized scale-case; the broader flanges are exposed to the surface, whereas the shorter flanges are more or less overlapped by adjacent body scales. The rear scales are asymmetrical; the side bearing a broad flange extension is always shorter than the other side. No spines on the rear scales were observed, except for the newly described *Mallomonas alpestrina*, in which diminutive spines were occasionally found. The shield of all scale types is covered by a regularly arranged reticulum with different numbers of pores (1–25) surrounded by short ridges of reticulum. Four taxa have met the description criteria and have been included in the *Mallomonas alata* group: *M. alata* f. *alata*, *M. alata* f. *hualvensis*, *M. tirolensis*, and *M. alpestrina* sp. nov. The diagnostic features of these species are summarized in Table 1.

TABLE 1. Diagnostic features of *Mallomonas alata* species group.

| | Collar scale | | | | Body scale | | | |
|--------------------------------------|--|----------------|---|--|---|----------------------------------|---------------------|------------------|
| | Size (μm) | Ventral flange | Shield pattern /No. of pores at the bottom of each mesh | Shield pattern / no. of pores at the bottom of each mesh | Broader anterior flange | Shorter anterior flange | Posterior subm. rib | Posterior flange |
| <i>M. alpestrina</i> | 4.5×2.9 | smooth | rosette-like with central papilla / 20–25 | rosette-like with central papilla / 20–25 | ca. 5 ridges, wavy appearance, 2–3 pores | several groups of 2–3 pores | internal struts | smooth |
| <i>M. alata</i> f. <i>alata</i> | $3.9\text{--}4.5 \times 2.5\text{--}3.0$ | wavy | annular groups / 5–8 | annular groups / 5–8 | 6–8 ridges, wavy appearance, one row of large pores | one row of large pores | smooth | smooth |
| <i>M. alata</i> f. <i>hualvensis</i> | $3.5\text{--}4.0 \times 2.1\text{--}2.7$ | smooth | usually single pores / 1–(3) | single pores | 8–10 ridges, wavy appearance, no pores | smooth | smooth | smooth |
| <i>M. tirolensis</i> | $3.4\text{--}4.0 \times 2.1\text{--}2.6$ | wavy | irregularly shaped mash / (4)–8–(20) | two rows of pores / often 4 | 8–10 pronounced ridges, continuous to the shield | similar pattern as on the shield | smooth | smooth |

Mallomonas alata f. *alata* (Figs 1A, D, G, J; Fig. 2A, C; upper part of the micrograph) is widely distributed with numerous records all over the world (Kristiansen 2002), including New Zealand (Dürschmidt 1986). The species is tolerant to a wide range of ecological conditions (Němcová *et al.* 2003). In Europe, the frequency of occurrence is highest in water bodies with pH 6.5–7.0 (46% of all records, 31 in total) and conductivity 60–260 $\mu\text{S}\cdot\text{cm}^{-1}$ (60% of all records, 42 in total; Škaloud *et al.* 2013). *Mallomonas alata* f. *hualvensis* (Figs 1B, E, H, K; Figs 2B, C; lower part of the micrograph) was described from Chile, with subsequent descriptions in North America (Nicholls 1988) and Europe (Péterfi *et al.* 1998, Barreto 2005, Siver *et al.* 2005, Němcová *et al.* 2012). There are no records from subtropical and tropical regions. We may consider a bipolar distribution of the species in temperate regions of both hemispheres. Water conductivity and pH ranged from 19–240 $\mu\text{S}\cdot\text{cm}^{-1}$ and 5.5–7.1, respectively (50% of all records, 4 in total; were from pH 6.5–6.8; Škaloud *et al.* 2013). *Mallomonas tirolensis* (Figs 1C, F, I, L; Fig. 2D) was identified in two lakes in North Tyrol, Austria (pH 8.2 and 8.1, and conductivity 371 and 414 $\mu\text{S}\cdot\text{cm}^{-1}$; Pichrtová *et al.* 2013). *Mallomonas alpestrina* (Figs 3A–I) is known only from the type locality, the oligotrophic high mountain glacial lake, Haba Xue Shan (Snow Mountain), China (this article). Records of *Mallomonas alpestrina*, *M. alata* f. *hualvensis* and *M. tirolensis* accompanied by environmental conditions are summarized in Table 2.

TABLE 2. Records of *Mallomonas alpestrina*, *M. alata* f. *hualvensis* and *M. tirolensis*.

| | Records | Sampling year | pH | Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) | Temp. ($^{\circ}\text{C}$) | Coordinates | References |
|--------------------------------------|---|---------------|-----|---|------------------------------|--------------------------------|------------------------------|
| <i>M. alpestrina</i> | Asia, China unnamed lake between villages Haba and Haba Xue Shan | 2012 | - | - | - | 27° 20.798' N 100° 4.582' E | This paper |
| <i>M. alata</i> f. <i>hualvensis</i> | South America, Chile pond near the town Villarrica | 1979 | 6.5 | 39 | 12 | - | Asmund <i>et al.</i> (1982) |
| | North America, Canada Pond 1, Galway Twp. | 1988 | - | - | - | 44° 48.033' N 78° 29' W | Nicholls (1988) |
| | Europe, Hungary bog-lake Baláta-tó | 1998 | - | - | - | - | Péterfi <i>et al.</i> (1998) |
| | Europe, Hungary pond in Visegrád mountains | 1999 | 6.8 | 240 | 10.5 | - | Barreto (2005) |
| | Europe, Russia Vorkuta tundra, pond Vorgashor | 2002 | 5.5 | - | 8.0 | 67° 35' N 63.47' E | Siver <i>et al.</i> (2005) |
| | Europe, Russia Kharbey, small pond | 2003 | - | 19 | 19.7 | 67° 32.437' N 62° 58.78' E | Siver <i>et al.</i> (2005) |
| | Europe, Russia Vash.-Kharbey, small pond | 2003 | - | 39 | 14.9 | 67° 53.208' N 62° 11.802' E | Siver <i>et al.</i> (2005) |
| | Europe, France pool close to Lac du Bousquet | 2010 | 7.1 | 178 | - | 44° 30.032' N 0° 37.853' W | Němcová <i>et al.</i> (2012) |
| | Europe, France enclosed bay of Étang de Cazaux | 2010 | 6.8 | 236 | - | 44° 26.456' N 1° 11.299' W | Němcová <i>et al.</i> (2012) |

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TABLE 2. (Continued)

| Records | Sampling year | pH | Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) | Temp. ($^{\circ}\text{C}$) | Coordinates | References |
|---|---------------|-----|---|------------------------------|--------------------------------|--------------------------------|
| Europe, Czech Republic Velke Darko Pond | | | | | | Škaloud <i>et al.</i> (2013) |
| Europe, Germany Reeckkanal | 2011 | 7.9 | 511 | 11.5 | 53° 30.385' N 12° 38.043' E | Škaloud <i>et al.</i> (2013) |
| <i>M. tirolensis</i> Europe, Austria Möserer See | 2012 | 8.2 | 371 | 5.8 | 47° 18.864' N 11° 8.652' E | Pichrtová <i>et al.</i> (2013) |
| Europe, Austria Seefeldler See (Wildsee) | 2012 | 8.1 | 414 | 7.1 | 47° 19.344' N 11° 11.52' E | Pichrtová <i>et al.</i> (2013) |

Taxonomy

Mallomonas alpestrina Němcová & Zeisek, *sp. nov.* (Fig. 3A–I)

Three types of scale are discerned, including collar, body, and rear scales; however, a continuous transition between body and rear scales is evident. Collar scales ($4.5 \times 2.9 \mu\text{m}$) are approximately triangular with rounded distal part. The submarginal rib is well developed at the dorsal and posterior ends of the scale, but totally reduced along the ventral edge. The submarginal rib is reinforced by internal struts, which appear striated in TEM images. The ventral flange is broad and smooth. The triangular hook-like dome is small, and protrudes above the surface of the other scales. The proximal border (rim) encircles only the dorsal part of the collar scale; together with the submarginal rib, they serve as tracks to fit the neighbouring collar scale in place. The scale shield is covered by a regularly arranged reticulum, large groups of pores (up to 20–25) are surrounded by short ridges of reticulum, and there is a thickened part (papilla) in the middle of each pore group (Fig. 3A). Domeless body scales ($3.5\text{--}3.9 \times 1.9\text{--}2.1 \mu\text{m}$) are rhombic and extremely asymmetrical (Figs 3C, F). There is a smooth transition between posterior submarginal ribs and anterior flanges/submarginal ribs. Posterior submarginal ribs are striated (or bear internal struts, see Fig. 3D for detail). One of the anterior flanges is considerably broader and shorter, strengthened by ribs providing a wavy appearance. The other flange is penetrated by several groups of pores positioned along the anterior submarginal rib, but it lacks cross ribs (Figs 3B, E). The posterior flange is narrow and smooth. The proximal border (rim) encircles approximately one-third of the scale. Reticulation of the shield is similar to that of the collar scales. The rear scales ($2.4\text{--}2.7 \times 1.5\text{--}1.6 \mu\text{m}$) are asymmetric, with one anterior flange considerably longer than the other, and the longer one bears 2–3 ribs (Figs 3G–I). The distal rear scales are almost rounded and bear a diminutive spine (Fig. 3I). Bristles are not observed; the species probably does not produce bristles. The cyst is unknown. The cell dimensions are unknown.

Type:—CHINA. Northern Yunnan: Diqin county, Zhongdian, unnamed lake on the slopes of Haba Xue Shan (Haba Snow Mountain), close to Haba village, 27° 20.798' N 100° 4.582' E, 4192 m a.s.l., *V. Zeisek*, 8 September 2012 (holotype: Fig. 3B).

Etymology:—The epithet refers to the occurrence of the species in a glacial lake at high elevation.

Habitat:—Oligotrophic high mountain lake.

Distribution:—China, the species was only found in the type locality.

Discussion

The *Mallomonas alata* group is excluded from the *M. pumilio* group primarily based on the approximately triangular shape of the collar scales and the small hook-like protruded dome without attached bristles. One anterior flange of the body scale is considerably broader. Harris (1970) considered *M. alata* collar scales to be an immature form of *M. pumilio* collar scales. Asmund *et al.* (1982) disputed this “immature scales” theory, and delimited *M. alata* f. *alata* as a separate species. A scale is formed endogenously within a silicon deposition vesicle (SDV); its shape cannot be changed after silicification and extrusion to the cell surface (Leadbeater 1990). However, slight changes in scale shape and proportions during scale biogenesis inside the SDV are inducible by shifts in environmental conditions such as temperature (Řezáčová-Škaloudová *et al.* 2010, Pichrtová & Němcová 2011) and pH (Němcová & Pichrtová 2012). Insufficiently silicified scales are often reported in dense cultures where a deficiency of diluted SiO_2 may occur (Němcová *et al.* 2010). In natural populations, insufficiently silicified scales may be released after cell death if the process of silicification has not been completed. However, complete alteration of the dome after scale release to the

cell surface would be inconsistent with the scale construction principles. All *Mallomonas alata* group members share the same dome structure. Based on the dome shape (no cavity develops on the inner scale surface), we presume an absence of bristles in the *Mallomonas alata* group. Harris (1970) reported a single, short, delicate bristle (see p. 77, Plate 1, Fig. 3 in Harris 1970). However, after close inspection of the image, we conclude that this structure likely represents a dorsal submarginal rib.

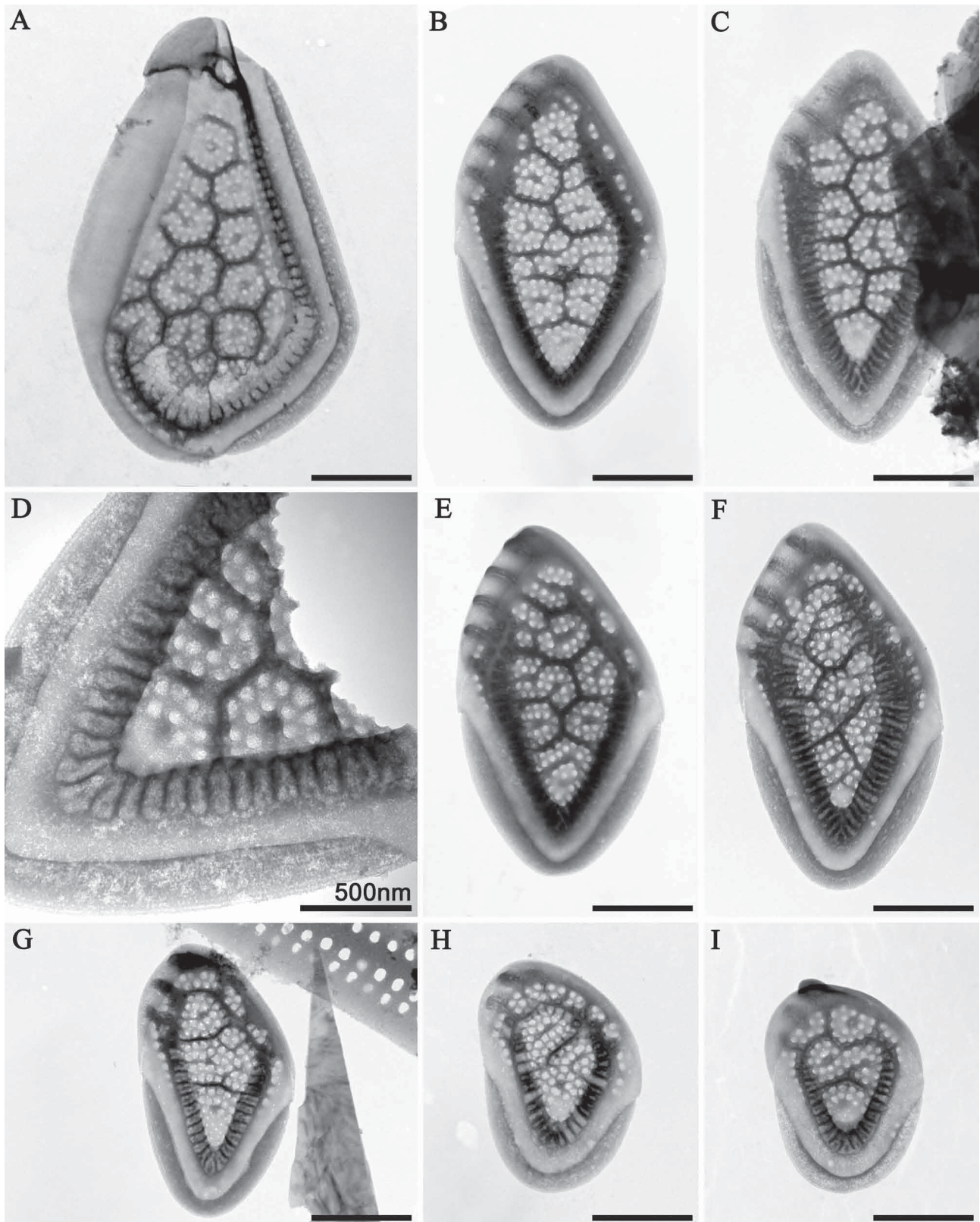


FIGURE 3. *Mallomonas alpestrina* sp. nov. A. A collar scale. B–C. Body scales. D. Detail of body scale; note short ridges of reticulum surrounding large groups of pores. E–F. Asymmetrical body scales with one anterior flange considerably broader and shorter than the other. G–I. Rear scales. I. A rear scale bearing a diminutive spine. Scale bars = 1 μm , if not stated otherwise.

All described species of the *Mallomonas alata* group have small cells (ca. 10 µm). The length and width of the collar scales are very similar in all investigated species. It is not sufficient to measure the length of a body scale for morphological characterization, because the length is influenced by the broadness of the anterior flange. Broadness of the anterior flange differs according to the scale position within the scale-case, which is most pronounced in *Mallomonas alata* f. *hualvensis* (Fig. 2B). In the *Mallomonas pumilio* group, differences in body-scale shape were captured using landmark-based geometric morphometrics (GM) analysis (Němcová *et al.* 2013). However, GM methods are not applicable in the *M. alata* group because of the extremely variable body-scale shape. By contrast, the scale-shield pattern on both collar and body scales embodies a stable character that can be used to distinguish the taxa. The shield pattern (Table 1) varies from single pores (*M. alata* f. *hualvensis*) to groups of 20–25 pores surrounded by short ridges of reticulum (*M. alpestrina*). We considered raising *M. alata* f. *hualvensis* to the species level. However, there is a weak glimpse of reticulation on the shield of some body scales and samples from various geographical locations differ by the broadness of the anterior flange [e.g. *M. alata* f. *hualvensis* from Chile, their fig. 29 in Asmund *et al.* (1982), has got narrower anterior flange compared to the *M. alata* f. *hualvensis* from Aquitaine, France]. That is why we finally decided to keep the taxon as a forma. More information is needed on the scale structure from different populations.

The taxon that is most similar to *M. alpestrina* (in addition to other species from the *M. alata* group) is *M. roscida*, which was described from New Zealand (Dürschmidt 1986: 104). Scales of both taxa have the shield similarly ornamented by a regularly arranged reticulum. Large groups of pores (up to 20–25) are surrounded by short ridges of reticulum with a thickened papilla in the middle of each pore group. The anterior flanges in *M. roscida* are equally broad. Numerous and regularly spaced transverse struts radiate bilaterally from the anterior submarginal rib. By contrast, one of the anterior flanges in *M. alpestrina* is considerably broader than the other, and there is not a distinct anterior submarginal rib. Moreover, *M. roscida* exhibits *M. pumilio*-group-type collar scales with distinctly ornamented domes.

Although *M. alata* f. *alata* is widely distributed, *M. alata* f. *hualvensis* could be considered as a bipolar species that occurs in temperate regions of both hemispheres. The biogeography and ecology of *M. tirolensis* and *M. alpestrina* are unknown. *Mallomonas alpestrina* sp. nov. is described from an oligotrophic high mountain glacial lake (4192 m a.s.l.). It was associated with a rich community of widely distributed silica-scaled chrysophytes, including *Synura conopea* Škaloud *et al.* (2012: 325), *Mallomonas annulata* (Harris & Bradley 1960: 764) Harris (1967: 187), and *M. papillosa* Harris & Bradley (1957: 44). This result indicated that the environmental conditions in the lake were not extreme.

Although all described species of the *Mallomonas alata* group have the same cell size and shape, there are great differences in the record frequencies. We may consider the growth rate, number of propagules (stomatocysts), ecological amplitude, dispersal ability, and biogeographical pattern (Siver & Lott 2012) of the species as factors that drive its abundance in natural localities.

Acknowledgements

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