

Article

Diversity of Silica-Scaled Chrysophytes in Central Vietnam

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Abstract: This paper focuses on the flora of scale-bearing chrysophytes from eight provinces located in the central part of Vietnam. Khanh Hoa, Phu Yen, Binh Dinh, Thua Thien Hue, Quang Tri, and Quang Binh provinces are located in the coastal area of Vietnam. Lam Dong and Dak Lak provinces represent mountain territories with an elevation of 500–2000 metres above sea level. In total, 212 water bodies of different origins were studied. Samples were obtained from swamp areas, lakes, rivers, reservoirs, ponds, and small temporary water bodies. In total, 76 taxa were identified by electron microscopic observations of samples. A total of 54 taxa were found in the mountainous provinces, while 73 were found in the coastal provinces. Of these, 51 species are common for both areas. The most diverse was the genus *Mallomonas* with 66 species, varieties, and forms; followed by *Synura* with 7 taxa; *Chryso-sphaerella* with 2; and *Spiniferomonas* with 1. Seven taxa of the genus *Mallomonas* were not identified to the lower rank. All these unidentified specimens may potentially represent new species for science. Ten taxa are reported for the first time in Vietnam.

Keywords: Central Vietnam; tropics; freshwaters; flora; silica-scaled chrysophytes; *Mallomonas*; *Synura*; *Chryso-sphaerella*; *Spiniferomonas*



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1. Introduction

Tropical Asia has a rich flora and fauna; however, compared with the Neotropics and Africa, it has been studied less, especially regarding the biodiversity of freshwater ecosystems [1]. Algae are often omitted from total biodiversity estimations due to their microscopic size, the time-consuming methods for identification, and insufficiently developed species concepts for many groups [2,3]. The rates of human population growth are among the highest in the tropics, which leads to rapid rates of land conversion of tropical landscapes and biodiversity loss [4]. Vietnam belongs to the Indo-Burma biodiversity hotspot, one of the 35 areas on Earth that have exceptionally high concentrations of endemic species and the greatest risk of them disappearing because of heavy human impact [5]. It is estimated that there are about 13,500 vascular plant species in the Indo-Burma hotspot, of which about 52% are endemic [6]. Unfortunately, the algal diversity of Indo-Burma is still poorly known [7].

The total area of inland waters of Vietnam is about 6% of the country's territory. For comparison, the relative size of the freshwater area of neighbouring Cambodia and Laos is two and a half times smaller, and that of Thailand is twelve times smaller [8]. It is not surprising that various freshwater and brackish water habitats play an important role for the biodiversity of Vietnam, the entire Indo-China Peninsula, and even more broadly, the Indo-Burma biogeographic region as a whole [9]. The climatic, geographical, and natural diversity of these habitats determines its unique richness and the significance of biodiversity that characterises this region of Southeast Asia. Recently, there has been a significant increase in interest in the study of protists in Vietnam [10–14]. In the last decade, many new and endemic taxa of algae and heterotrophic protists have been described from freshwaters of the country, including diatoms [15–21], cryptomonads [22,23], heterotrophic flagellates [24,25], centrohelid heliozoans [26], and testate amoebae [27].

Chrysophyte algae (class Chrysophyceae) represent an extensive but rather poorly studied group of algae with underestimated diversity, a complex evolutionary history, and many unresolved problems in their phylogeny [28–30]. The study of the diversity and taxonomy of chrysophytes is complicated by the fact that they are hard-to-cultivate organisms, which hampers their molecular study. As a consequence, there are only a small number of cultures, and for most of the species described on the basis of morphological characteristics, cultures and sequence data are absent. However, among this large group, there are species with siliceous covers (scales, spines, and bristles), which have a complex ultrastructure and provide reliable characteristics for morphological species differentiation [29]. Moreover, the developed system of morphological criteria for distinguishing taxa (morphological species concept) is considered one of the best among the protists and, in general, has been confirmed with molecular data [29,31–35]. Hence, the majority of the known species of silica-scaled chrysophytes can be identified correctly. It also allows researchers to use previously accumulated information for generalisations and comparison with modern data. Morphological studies are based on the use of transmission or scanning electron microscopy (TEM or SEM, respectively) to reveal the ultrastructure of siliceous elements of cell covers [29]. Electron microscopic studies of silica-scaled chrysophytes began in the 1950s [36–40]. Since then, confirmation of their findings by electron micrographs has become mandatory, making this a group of model protists for studying biogeographic issues [41–44]. Silica-scaled chrysophytes are used widely in water monitoring and palaeoecological studies as indicator species [45,46].

The distribution of silica-scaled chrysophytes has been studied unevenly. Most of the studies have been carried out in the temperate zone, from which most species have been described [47]. An extensive database of diversity and the distribution of silica-scaled chrysophytes has been developed for Europe [48]. The data on the diversity, distribution, and ecology of this group in North America have been presented in numerous works, [49–53], etc.

At the same time, the tropical region is still poorly studied [47]. For a long time, scale-bearing chrysophytes have been thought to be restricted to temperate waters; however, studies of the region using electron microscopy, which began in the late 1970s, revealed an interesting flora [44,54]. Data on the diversity and distribution of silica-scaled chrysophytes from the tropical region is highly fragmented. Several regions have been explored in tropical Asia. One of the first studies of the tropics was conducted in Bangladesh in the 1970s [55]. Extensive research has been carried out in India [56,57]. Sporadic studies have been carried out in Malaysia, Sri Lanka, and Papua New Guinea [41,58–60]. Studies of tropical Australia have revealed many interesting taxa [58,61–64]. Indonesia has also attracted the attention of researchers on several occasions [41,65–67]. Several works are devoted to the study of the tropics and subtropics of China [68,69]. The result of these studies has been the identification of a fairly rich flora of the tropical region and the description of several species new to science, many of which are still considered endemic to the tropical region and, most often, are found in a limited area. However, it is still too early to speak about the completeness of the study of this region. Silica-scaled chrysophytes in Vietnam have also been studied unevenly. The first paper based on SEM of silica-scaled chrysophytes included the results of investigations of eight reservoirs and was published in 2011 [70]. Subsequently, the main research attention has been focused on special habitats, such as swamps in Cam Ranh Peninsula [71,72], wetlands of Cat Tien National Park [73], the Mekong Delta [74], and a reservoir in mountains [75]. Information about diversity of algae from the order Synurales in the Northern Vietnam has also been published recently, including the description of two new species [76–78]. In addition, a number of new species for science have been described from individual regions of the country [71,76–91]. However, Central Vietnam, except for certain areas of the Khanh Hoa province, has not yet been studied. In this work, we fill this gap. We studied the diversity of silica-scaled chrysophytes in both mountainous and lowland territories of Central Vietnam, covering eight provinces

and 212 localities of different origins, to identify the most characteristic species for the studied area and to describe the distribution of rare and endemic species of the region.

2. Materials and Methods

Water samples from 212 localities in 8 provinces of Vietnam are included in this study (Figure 1, Table S1). Khanh Hoa, Phu Yen, Binh Dinh, Thua Thien Hue, Quang Tri, and Quang Binh provinces are located in the coastal area of Vietnam. Lam Dong and Dak Lak provinces represent mountain territories with an elevation of 500–2000 m above sea level. Samples were taken during an expedition of the Russian–Vietnamese Tropical Centre (Ecolan 3.2 project) in 2010–2019. The studied area has a monsoon tropical climate. More detailed data about climate characteristics are presented by Schmidt-Thomé et al. [92] and Pavlov and Zvorykin [10].

Samples were collected from the surface water layer by using a plankton net (mesh size = 20 μm). When using a mesh with such size, some small species can be overlooked in the study. However, our experience shows that organisms larger than 7 μm are present in samples. After sampling, the material was prepared for further investigation. For electron microscopy, an aliquot of each sample was washed by repeated centrifugation in deionised water. Drops of the washed sample were dried or digested for 4–5 min in sulfuric acid with potassium dichromate. For SEM, samples were placed on aluminium stubs and coated with gold for 10 min. Observations were carried out with a JEOL 6510 LV scanning electron microscope. For TEM, formvar-coated grids (EMS FF200–Cu-50, Electron Microscopy Sciences) were used, and observations were made on a JEM–1011 transmission electron microscope. Specific conductance, pH, and temperature measurements were measured with a Hanna HI 9828 device (Hanna Instruments, Inc., Smithfield, RI, USA). The chlorophyll *a* concentrations were determined using a previously described methodology [93,94]. Water was concentrated on membrane filters with a pore diameter of 1.2 μm and then placed in a container with 90% ethanol. The chlorophyll extraction was carried out for at least 24 h. Spectrophotometric analysis of the extracts for their optical density at three wavelengths in the red spectral region was performed and optical density reading at 750 nm was subtracted from these readings to correct for “background” interferences. To calculate the concentration of chlorophyll *a*, we used the formula given in [94]. The classification of Nurnberg and Shaw [95] was used to assess the trophic state based on the concentration of chlorophyll *a* in water. The taxonomic identification was based on many works cited and discussed later in this article.

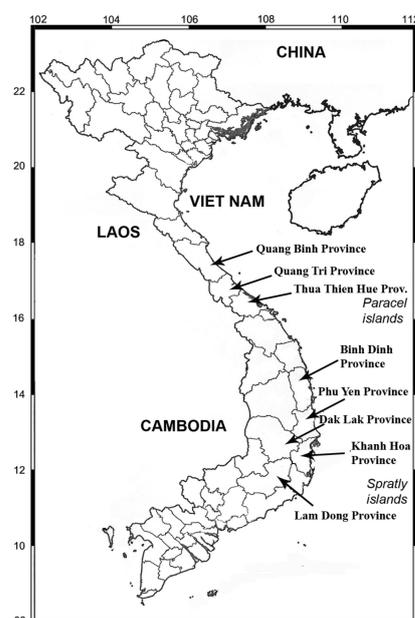


Figure 1. Geographical position of the studied area.

3. Results

A total of 76 taxa were identified at the 212 localities in Central Vietnam (Tables 1 and S3–S10 and Figures 2–5). Sixty-six taxa belonged to the genus *Mallomonas*, seven taxa belonged to the genus *Synura*, two taxa were from the genus *Chryso-sphaerella*, and one was from *Spiniferomonas*. We excluded from the analysis numerous morphotypes of the heterotrophic genus *Paraphysomonas*. Seven taxa of the genus *Mallomonas* were not identified to the lower rank. All these taxa are potentially new species for science.

Table 1. List of silica-scaled chrysophytes found in eight provinces of Central Vietnam. New taxa for Vietnam are given in bold, “+” indicates the presence of taxon.

Taxon	Provinces							
	Lam Dong	Dak Lak	Khanh Hoa	Phu Yen	Binh Dinh	Thua Thien Hue	Quang Tri	Quang Binh
<i>Mallomonas acaroides</i> Perty emend. Iwanoff	+							
<i>M. akrokomos</i> Ruttner	+			+		+		
<i>M. adamas</i> Harris & Bradley	+		+	+	+	+		
<i>M. bangladeshica</i> (E. Takahashi & T. Hayakawa) Siver & A.P. Wolfe		+	+	+		+		
<i>M. binocularis</i> Siver			+			+		
<i>M. bronchartiana</i> Compère		+	+	+	+		+	
<i>M. cattiensis</i> Gusev, Doan-Nhu & Nguyen-Ngoc		+	+	+	+	+		
<i>M. caudata</i> Iwanoff	+	+	+	+	+	+	+	+
<i>M. ceylanica</i> Dürschmidt & Cronberg		+	+		+	+	+	+
<i>M. crassisquama</i> (Asmund) Fott	+	+	+	+	+	+	+	+
<i>M. crassisquama</i> var. <i>papillosa</i> Siver & Skogstad	+							+
<i>M. cf. cristata</i> Dürschmidt		+		+		+		+
<i>M. distinguenda</i> Gusev, Doan-Nhu, Nguyen-Ngoc & Kapustin						+		
<i>M. elevata</i> Han Soon Kim	+		+	+	+	+		
<i>M. elongata</i> Reverdin				+				+
<i>M. favosa</i> f. <i>favosa</i> K.H. Nicholls	+	+	+	+	+	+		
<i>M. favosa</i> f. <i>gemina</i> Dürschmidt & Croome		+	+	+	+	+	+	
<i>M. fimbriata</i> Gusev			+					
<i>M. furtiva</i> Gusev, Certnerová, Škaloudová & Škaloud	+		+	+	+	+		
<i>M. harrisiae</i> E. Takahashi						+		
<i>M. hexareticulata</i> Jo, Shin, Kim, Siver & Andersen		+	+		+	+		+
<i>M. grata</i> E. Takahashi	+	+	+		+			
<i>M. guttata</i> var. <i>guttata</i> Wujek	+	+	+	+	+	+	+	+
<i>M. guttata</i> var. <i>simplex</i> Nicholls	+	+	+	+	+	+	+	
<i>M. kenyana</i> (Wujek & Asmund) Kapustin & Gusev	+	+	+	+	+	+	+	+
<i>M. korshikovii</i> Gusev			+	+	+			
<i>M. lamii</i> Gusev, Kulizin, Guseva, Shkurina & Kulikovskiy		+	+	+	+	+	+	
<i>M. loricata</i> Gusev, Shkurina & Kulikovskiy		+	+	+	+	+	+	
<i>M. lusca</i> Gusev & Kezlya			+					
<i>M. mangofera</i> Harris & Bradley var. <i>mangofera</i> apud Dürschmidt (1983)	+	+	+		+			
<i>M. mangofera</i> var. <i>foveata</i> (Dürschmidt) Kristiansen	+	+	+	+	+	+	+	
<i>M. cf. mangofera</i> var. <i>reticulata</i> (Cronberg) Kristiansen		+	+	+	+	+	+	
<i>M. mangofera</i> var. <i>sulcata</i> Dürschmidt				+	+	+	+	
<i>M. mangofera</i> var. <i>gracilis</i> (Dürschmidt) Kristiansen						+		

Table 1. Cont.

Taxon	Provinces							
	Lam Dong	Dak Lak	Khanh Hoa	Phu Yen	Binh Dinh	Thua Thien Hue	Quang Tri	Quang Binh
<i>M. minuscula</i> Gusev, Guseva, Kezlya & Kulikovskiy	+		+	+	+	+		
<i>M. morrisonensis</i> Croome & P.A. Tyler	+	+	+	+	+	+	+	
<i>M. multisetigera</i> Dürschmidt			+		+	+		
<i>M. neoampla</i> Gusev & Siver			+			+		
<i>M. ocellata</i> Dürschmidt & Croome	+	+	+	+	+	+		+
<i>Mallomonas</i> cf. <i>ouradion</i> Harris & Bradley				+		+		
<i>M. papillosa</i> Harris & Bradley						+		
<i>M. paragrandsis</i> Gusev		+	+	+	+	+	+	
<i>M. peronoides</i> (K. Harris) Momeu & Péterfi		+	+	+	+	+	+	
<i>M. plumosa</i> Croome & Tyler	+	+	+	+		+	+	
<i>M. portae-ferreae</i> Péterfi & Asmund		+	+		+			
<i>M. pseudobronchartiana</i> Gusev, Siver & Shin		+						
<i>M. pseudomatvienkoae</i> Jo, Shin, Kim, Siver & Andersen	+	+	+	+	+	+	+	
<i>M. pseudocratis</i> Dürschmidt								+
<i>M. punctifera</i> Korshikov	+							
<i>M. punctostriata</i> Gusev & Kulikovskiy			+					
<i>M. rasilis</i> Dürschmidt	+	+	+	+	+	+		
<i>M. siderea</i> Gusev & Kulikovskiy				+	+	+	+	+
<i>M. cf. skvoortsovii</i> Gusev, Doan-Nhu, Nguyen-Ngoc & Kapustin				+		+		
<i>M. sorohexareticulata</i> Jo, Shin, Kim, Siver & Andersen	+	+	+		+	+	+	+
<i>M. spinosa</i> Gusev emend. Wei & Kristiansen		+	+	+	+	+	+	
<i>M. splendens</i> (G.S. West) Playfair	+		+	+		+	+	
<i>M. striata</i> var. <i>serrata</i> Harris & Bradley	+					+		
<i>M. tonsurata</i> Teiling	+	+	+	+	+	+	+	+
<i>M. tropica</i> Dürschmidt & Croome			+		+	+		
<i>Mallomonas</i> sp. 1	+	+	+	+	+		+	+
<i>Mallomonas</i> sp. 2	+	+	+	+	+		+	+
<i>Mallomonas</i> sp. 3			+					
<i>Mallomonas</i> sp. 4				+	+	+	+	
<i>Mallomonas</i> sp. 5		+		+	+	+	+	
<i>Mallomonas</i> sp. 6			+					
<i>Mallomonas</i> sp. 7						+		
<i>Synura australiensis</i> Playfair	+	+	+			+		
<i>S. echinulata</i> Korshikov	+	+	+	+		+		
<i>S. mammillosa</i> E. Takahashi	+			+	+	+		+
<i>S. papillosa</i> Kapustin, Gusev & Siver		+	+	+	+	+	+	
<i>S. sphagnicola</i> (Korshikov) Korshikov	+					+	+	
<i>Synura</i> sp. 1 (<i>S. longitubularis</i> / <i>S. curtispina</i> group)	+	+	+	+	+	+	+	+
<i>Synura</i> sp. 2 (<i>S. petersenii</i> sensu lato group)	+		+					
<i>Spiniferomonas trioralis</i> E. Takahashi	+	+	+	+	+			+
<i>Chrysosphaerella annulata</i> Kristiansen & Tong		+		+		+		
<i>Ch. nichollsii</i> Kapustin & Gusev	+	+	+	+	+	+	+	+
Total	36	41	53	47	45	56	31	20

Ten taxa were reported for the first time in Vietnam: *Mallomonas bangladeshica* (Figure 2D), *M. elongata* (Figure 2P), *M. harrisiae* (Figure 3A), *M. mangofera* var. *gracilis* (Figure 3O), *M. mangofera* var. *sulcata* (Figure 3N), *M. papillosa* (Figure 4B), *M. punctifera* (Figure 4J), *M. striata* var. *serrata* (Figure 4R–S), *Synura mammillosa* (Figure 5L), and *S. sphagnicola* (Figure 5N). New species for the flora of Vietnam were found to be quite rare in the samples (Tables S3–S10). *Synura sphagnicola* was found in 11 localities of 3 provinces and *S. mammillosa* in 10 localities of 5 provinces. *Mallomonas bangladeshica* was found in

7 localities of 4 provinces, *M. mangofera* var. *sulcata* was found in 6 localities of 3 provinces, *M. harrisiae* in 4 localities, and *M. mangofera* var. *gracilis* in 3 localities in only Thua Thien Hue province. Other *Mallomonas* taxa, new to the Vietnamese flora, were found only twice: *M. elongata* in Quang Binh and Phu Yen provinces, *M. striata* var. *serrata* in Lam Dong and Thua Thien Hue provinces, *M. punctifera* only in Lam Dong province, and *Mallomonas papillosa* only in Thua Thien Hue province.

Thua Thien Hue (56 taxa) and Khanh Hoa (53 taxa) provinces had the most taxa of silica-scaled chrysophytes, followed by Phu Yen (47 taxa), Binh Dinh (45 taxa), Dak Lak (41 taxa), Lam Dong (36 taxa), and Quang Tri (31 taxa) provinces. The number of taxa found in Quang Binh province is much smaller (only 20), but this is primarily due to the small number of studied reservoirs, which, moreover, had similar abiotic parameters. A total of 54 taxa were found in the mountainous provinces, while 73 were found in the coastal provinces. Of these, 51 species are common for both areas. The high number of common taxa between mountain and lowland territories is not surprising because the reservoirs in coastal areas of Central Vietnam are fed mostly by tributaries from the mountains. However, three species, *Mallomonas pseudobronchartiana* (Dak Lak Province), *M. acaroides*, and *M. punctifera* (Lam Dong Province), were found only in mountainous areas. Interestingly, that last two species, found >1000 m above sea level, are common in temperate latitudes and rare in the tropics.

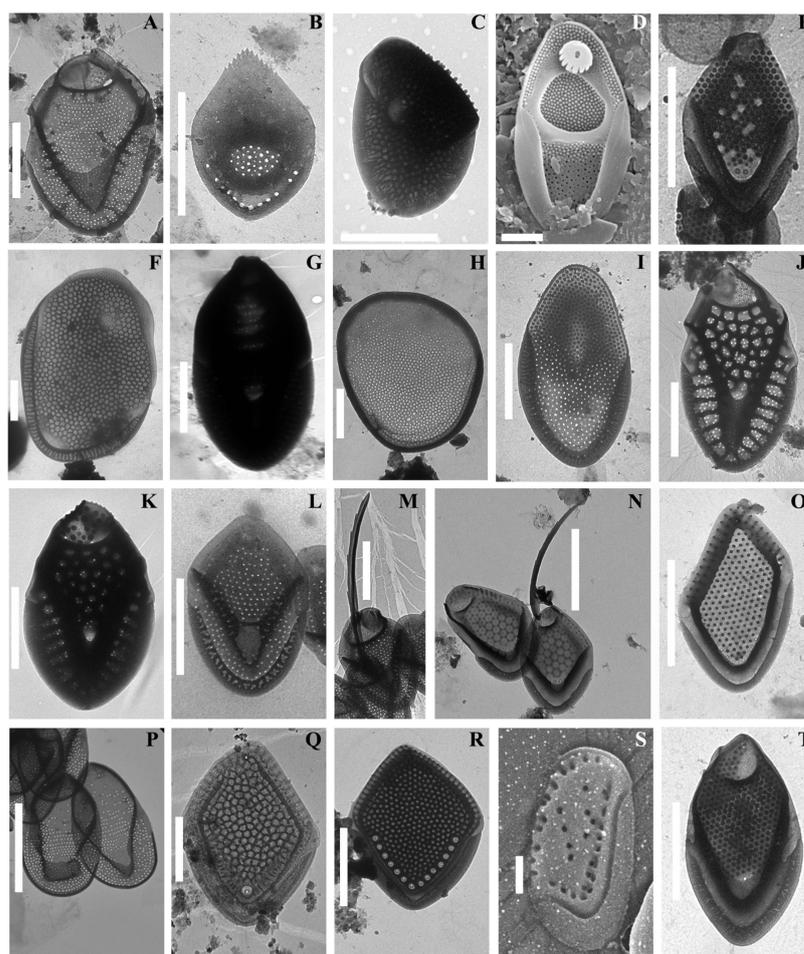


Figure 2. Scales and bristles of *Mallomonas*. (A) *M. acaroides*. (B) *M. akrokomos*. (C) *M. adamas*. (D) *M. bangladeshica*. (E) *M. binocularis*. (F) *M. bronchartiana*. (G) *M. cattiensis*. (H) *M. caudata*. (I) *M. ceylanica*. (J) *M. crassisquama*. (K) *M. crassisquama* var. *papillosa*. (L,M) *M. cf. cristata*. (N) *M. distinguenda*. (O) *M. elevata*. (P) *M. elongata*. (Q) *M. favosa* f. *favosa*. (R) *M. favosa* f. *gemina*. (S) *M. fimbriata*. (T) *M. furtiva*. Scale bars: (P): 5 μ m; (A–C,E–N,R): 2 μ m; (D,O,Q,S): 1 μ m. TEM: (A–C,E–R,T); SEM: (D,S).

Between 1 and 19 taxa were found per collection site (Tables S3–S10). The most chrysophytes taxa were found in swamp areas in Thua Thien Hue and Khanh Hoa provinces. *Synura* sp. 1 (*S. curtispina*/*S. longitubularis* morphotype) was the most frequently observed taxon (102 localities, frequency of occurrence is 48%). Among frequently found taxa were also *Mallomonas tonsurata* (35%), *M. paragrandsis* (27%), *M. crassisquama* and *M. kenya* (25% each), *M. pseudomatvienkoae* (23%), *M. guttata* var. *guttata* (18%), *M. caudata* (16%), *M. sp. 1* (15%), *M. morrisonensis* (13%), *Chrysosphaerella nichollsii* (13%), *Synura papillosa* and *M. favosa* f. *gemina* (12% each), and *M. sorohexareticulata* and *M. loricata* (10% each).

The trophic state of water bodies, assessed on the basis of chlorophyll *a* values, varied from oligotrophic to hypereutrophic (Tables S1 and S2). Most of the studied localities were eutrophic (76), followed by mesotrophic and hypereutrophic (50 and 47, respectively). Only 15 water bodies were oligotrophic. The number of species found in each type of water body was: 1–16 in eutrophic water bodies, 1–13 in oligotrophic water bodies, 1–14 in mesotrophic water bodies, and 1–18 in hypereutrophic water bodies. In total, 61 species were found in eutrophic water bodies, 64 in hypereutrophic water bodies, 44 in mesotrophic water bodies, and 30 in oligotrophic ones.

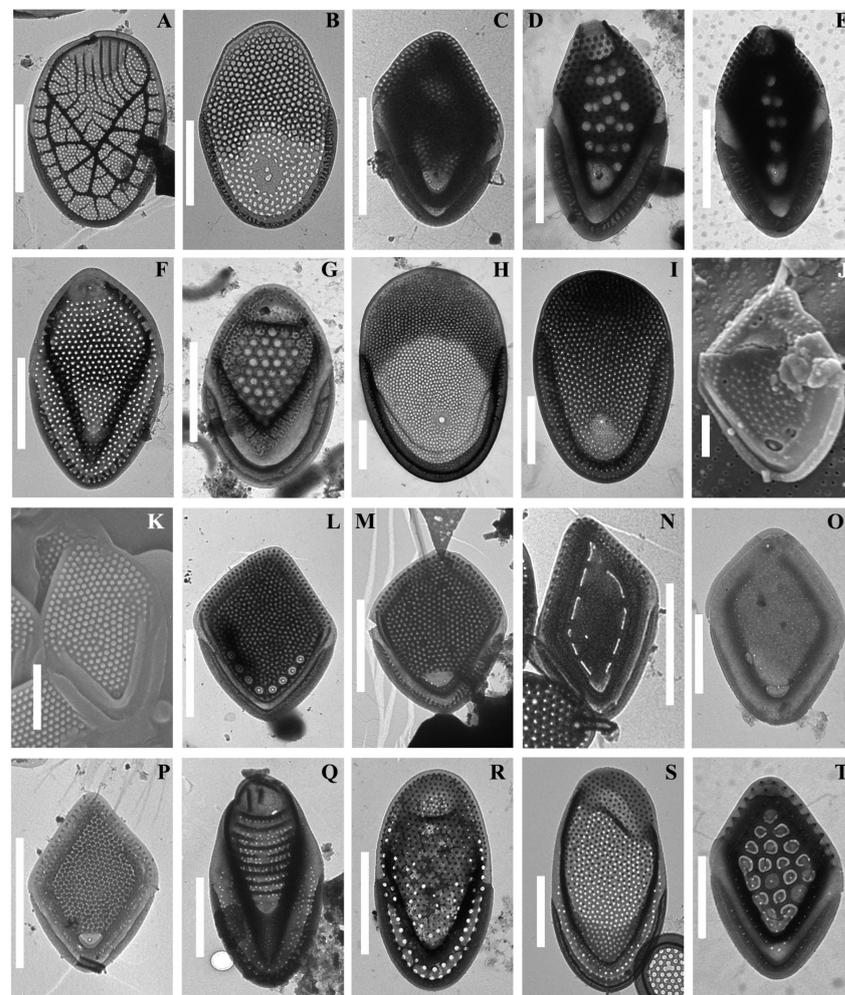


Figure 3. Scales of *Mallomonas*. (A) *M. harrisiae*. (B) *M. hexareticulata*. (C) *M. grata*. (D) *M. guttata* var. *guttata*. (E) *M. guttata* var. *simplex*. (F) *M. kenya*. (G) *M. korshikovii*. (H) *M. lamii*. (I) *M. loricata*. (J) *M. lusca*. (K) *M. mangofera* var. *mangofera*. (L) *M. mangofera* var. *foveata*. (M) *M. cf. mangofera* var. *reticulata*. (N) *M. mangofera* var. *sulcata*. (O) *M. mangofera* var. *gracilis*. (P) *M. minuscula*. (Q) *M. morrisonensis*. (R) *M. multisetigera*. (S) *M. neoampla*. (T) *M. ocellata*. Scale bars: (P): 5 μm ; (A–I, L–N, P, M–S): 2 μm ; (K, O, T): 1 μm ; (J): 0.5 μm . TEM: (A–I, L–T); SEM: (J, K).

Several morphotypes were discovered that had not previously been described in the literature or had been cited as taxa of unclear systematic position. Some of these morphotypes were found singularly or were rare. Below, we provide a brief description of such scales, such that in the future, with the accumulation of sufficient data to describe these types of data, it would be possible to include our findings in the analysis.

Mallomonas sp. 1 (Figure 5B,C) belongs in the *Mallomonas* section. It has quite large oval tripartite scales, $6.6\text{--}7.6 \times 4.0\text{--}4.5 \mu\text{m}$. A shield and flanges are lacking a secondary siliceous layer. The V-rib is large, acute and hooded, usually symmetrical, continuous with the arms of the anterior submarginal ribs. Numerous base-plate pores are placed irregularly or in regular transverse rows. A dome is large, rounded, or asymmetrical, with few ribs at the base. Such scale morphotypes were frequently found in Central Vietnam, in a total of 33 localities (15% of all studied localities).

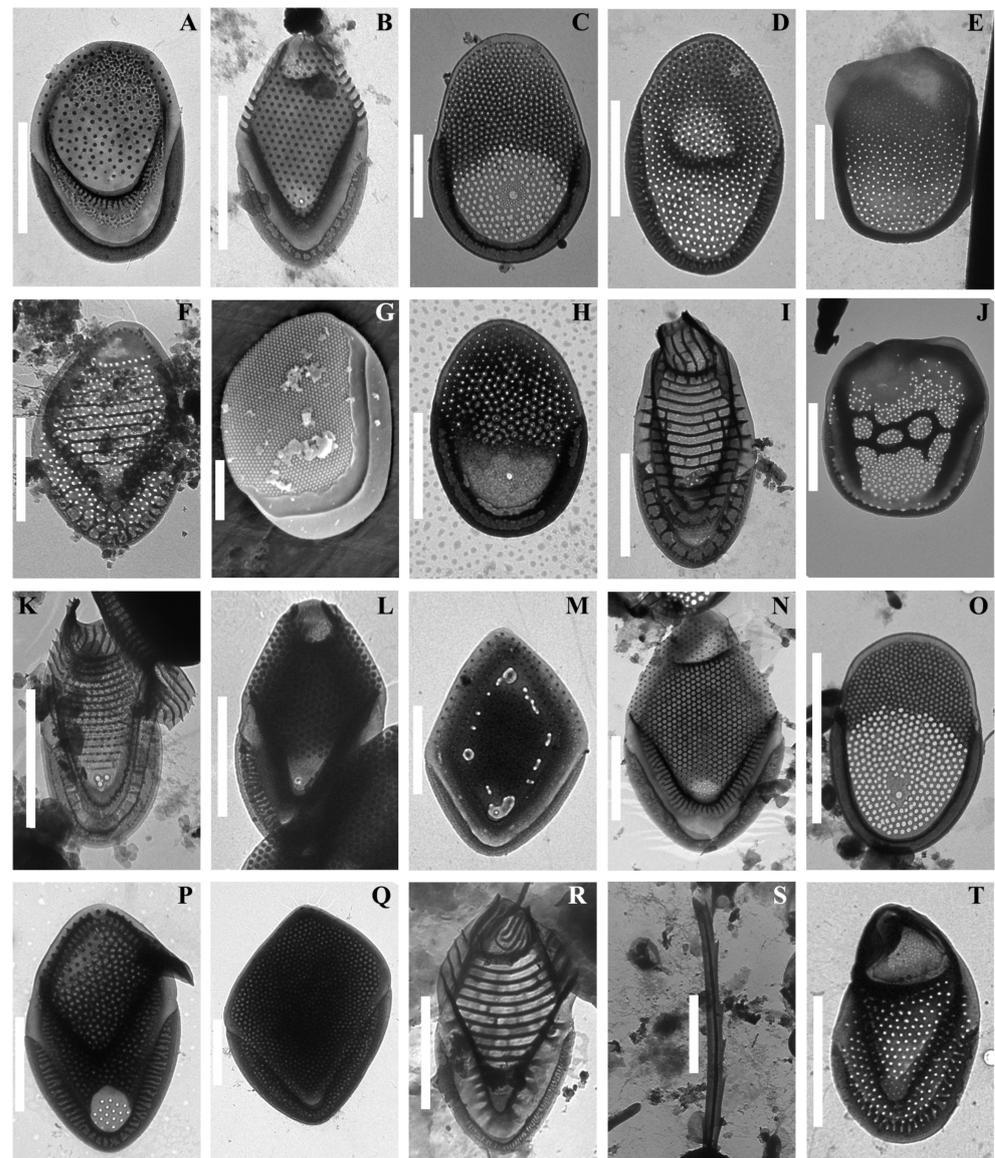


Figure 4. Scales and bristles of *Mallomonas*. (A) *M. cf. ouradion*. (B) *M. papillosa*. (C) *M. paragrandidis*. (D) *M. peronoides*. (E) *M. plumosa*. (F) *M. portae-ferreae*. (G) *M. pseudobronchartiana*. (H) *M. pseudomatvienkoae*. (I) *M. pseudocratis*. (J) *M. punctifera*. (K) *M. punctostriata*. (L) *M. rasilis*. (M) *M. siderea*. (N) *M. cf. skvortsovii*. (O) *M. sorohexareticulata*. (P) *M. spinosa*. (Q) *M. splendens*. (R,S) *M. striata* var. *serrata*. (T) *M. tonsurata*. Scale bars: 0: $5 \mu\text{m}$; (A–L,N,P–T): $2 \mu\text{m}$; (M): $1 \mu\text{m}$. TEM: (A–F,H–T); SEM: (G).

Mallomonas sp. 2 (Figure 5D) also belongs in the *Mallomonas* section. Scales are oval, tripartite, $4.9\text{--}5.8 \times 3.3\text{--}4.0 \mu\text{m}$. The dome is large, rounded, oval and asymmetrical. The V-rib is acute and slightly hooded, continuous with the arms of the anterior submarginal ribs. Anterior flanges are wide. The shield has a secondary siliceous layer forming circular or elongated oval meshes, unevenly distributed on the surface. Numerous base-plate pores are placed irregularly. The posterior rim is narrow, and the posterior flange is wide. Such scale morphotypes were found in Central Vietnam in 12 localities.

Mallomonas sp. 3 (Figure 5E) belongs in the *Torquatae* section. Body scales are rhombic, $3.4\text{--}4.5 \times 2.1\text{--}3.1 \mu\text{m}$. The shield is delimited by submarginal ribs (anterior and posterior) with arms of unequal length. The shield has a polygonal meshwork with papillae. Large pits are arranged along the arms of the posterior submarginal rib. Each pit contains a pore with the thickened surrounding ring. Pits are placed in chambers, formed by struts, perpendicular to the arms of posterior submarginal rib. Scales of *Mallomonas* sp. 3 were found only in one locality in Khanh Hoa Province.

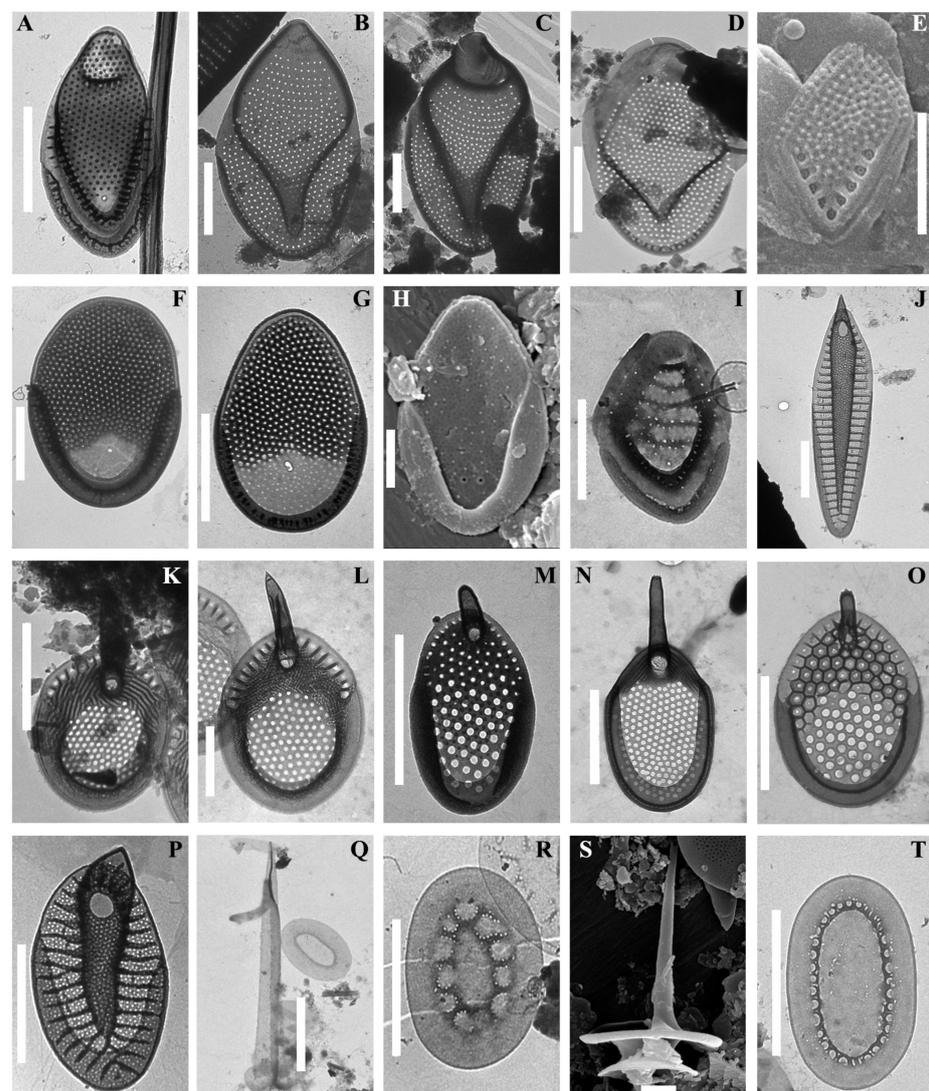


Figure 5. Scales of *Mallomonas*, *Synura*, *Spiniferomonas* and *Chrysosphaerella*. (A) *Mallomonas tropica*. (B,C) *M.* sp. 1. (D) *M.* sp. 2. (E) *M.* sp. 3. (F) *M.* sp. 4. (G) *M.* sp. 5. (H) *M.* sp. 6. (I) *M.* sp. 7. (J) *Synura australiensis*. (K) *S. echinulata*. (L) *S. mammillosa*. (M) *Synura papillosa*. (N) *Synura sphagnicola*. (O) *S.* sp. 1. (P) *S.* sp. 2. (Q) *Spiniferomonas trioralis*. (R) *Chrysosphaerella annulata*. (S,T) *C. nichollsii*. Scale bars: (A–G,J,K,M–R,T): 2 μm ; (H,I,L,S): 1 μm . TEM: (A–D,F,G,I–R,T); SEM: (E,H,S).

Mallomonas sp. 4 (Figure 5F) belongs in the Planae section. Scales are oval, $5.5\text{--}6.9 \times 4.3\text{--}4.6 \mu\text{m}$. A wide posterior rim encircles about half of the perimeter of the scale. A thick secondary meshwork covers more than the distal two thirds of the scale. Evenly spaced base-plate pores are restricted to the distal half of the scale and lacking in the proximal part without secondary reticulation where only a large pore is present at the centre. *Mallomonas* sp. 4 was found in Central Vietnam in 15 localities.

Mallomonas sp. 5 (Figure 5G) belongs in the Planae section. It has ovoid scales, $4.0\text{--}4.9 \times 2.4\text{--}3.0 \mu\text{m}$. Numerous small base-plate pores are distributed evenly on the distal two thirds of the scale. A secondary reticulation with small rounded meshes covers the distal two thirds of the scales. A large proximal pore is in the posterior portion of the scale without secondary reticulation. This morphotype was found in Central Vietnam in 16 localities.

Mallomonas sp. 6 (Figure 5H) belongs in the Planae section. The scale is oval, $4.0 \times 2.5 \mu\text{m}$. A wide posterior rim encircles more than half of the scale perimeter. A secondary siliceous layer covers almost the entire surface of the scale, except a small area in the proximal part, adjacent to the posterior rim. There are two distinct rimmed pores in the proximal part of the scale. Only one scale was found in Khanh Hoa province.

Mallomonas sp. 7 (Figure 5I) belongs in the Marsupiales section. The scale is rounded rhombic, small, $2.0 \times 1.4 \mu\text{m}$, with a small rounded dome. Posterior and anterior submarginal ribs are continuous, connected with four transverse ribs. There is a row of delicate papillae on both arms of the anterior submarginal rib and on the dome. Anterior flanges are wide and smooth. There is a base-plate with pores, proximally on the shield, and there is one distinct rimmed pore. The posterior rim is narrow and encircles about one third of the scale perimeter. Only one scale was found in Thua Thien Hue province.

4. Discussion

Expansion of agriculture, infrastructure development, and timber extraction are the major current threats to the biodiversity of Vietnam. Most of the territory of North Vietnam is under serious anthropogenic pressure. For example, most of Vietnam's rivers are currently regulated. There are about 4000 reservoirs, of which 460 are medium (1000–10,000 ha) or large (>10,000 ha) in size [96]. Modern reservoirs are often characterised by complex purposes and are used in hydropower programmes, for flood protection, navigation, irrigation, fishing, and other purposes. Most of the freshwater is used for irrigation in agriculture. The high population density of the country, rapidly developing industry, and agriculture lead to a significant anthropogenic load on the aquatic ecosystems of Vietnam. Currently, hydropower engineering and aquaculture are transforming these ecosystems at such an intensity that the nature of such transformations requires a special, well-balanced assessment [9]. In this situation, a thorough study of the processes occurring in freshwater ecosystems, the development of water quality criteria, and the principles of habitat protection for rare and important species of aquatic organisms are required. However, the first necessary step is to assess the existing diversity in the region.

Our investigations have revealed an exceptionally high diversity of silica-scaled chrysophytes, especially in the genus *Mallomonas*, for such a small area. This taxonomic diversity (76 taxa) exceeds values for all other studied tropical countries. For example, 58 species of scale-bearing chrysophytes were recorded in India [56,57], 49 taxa were recorded in tropical regions of China [68,69], and 40 species were recorded in Malaysia. In other tropical countries, the number of recorded taxa is <30.

Alongside the previous findings [72–75,97], there are now sixty-five *Mallomonas* taxa and seven *Synura* taxa that have been reported from Vietnam. With the representatives of *Spiniferomonas*, *Chryso-sphaerella*, and *Paraphysomonas*, there have been 83 taxa of silica-scaled chrysophytes recorded in the country. Thirteen unidentified morphotypes of *Mallomonas* scales and two of *Synura* have also been reported in freshwaters of the country.

Mallomonas is the most diverse genus in the order Synurales and among all chrysophytes. It includes more than 200 species [47,98]. About one-third of the known species of

the genus have now been found in Vietnam. Many *Mallomonas* species found in the country are known only from Vietnam or have a limited distribution in Southeast Asia. The most interesting finds in the studied region are discussed below.

Among eight taxa of *Mallomonas* that are new for the flora of Vietnam, four are widely distributed taxa, two can be considered endemic for Asia, and two are insufficiently studied taxa with a scattered distribution. All new taxa for the country from the genus *Mallomonas* were found only in a limited number of localities (from two to seven).

Mallomonas papillosa is a common taxon in temperate latitudes [47]. In warmer areas, it occurs rarely and has been reported from Malaysia [58], the tropics and subtropics of China [68,69], mountain areas of Papua New Guinea [60] and Indonesian Papua [99], India [57], Madagascar [100], Brazil [101], Ecuador [102], and the highlands of Colombia [54].

Mallomonas elongata, is a widely distributed species in temperate latitudes [47]. It has been reported in Vietnam from Khanh Hoa Province [70] (p. 196, Figures 5 and 6); however, this morphotype corresponds to *Mallomonas* sp. 1 in our study. *Mallomonas elongata* is characterised by the acute or rounded V-rib, which is hooded and continuous with the short anterior submarginal rib [103]. Scales and V-rib outlines are often asymmetrical. Some previous findings of *M. elongata* from Asia correspond to *Mallomonas* sp. 1 [58,68,69].

Mallomonas punctifera is a common species in northern temperate latitudes [47]. In the tropics, it has been reported only from Malaysia [58] and China [68,69].

Mallomonas striata var. *serrata* is considered a cosmopolitan taxon [47]. Most of the finds in the tropical region are from South America and Africa [100–102,104]. In Asia, this taxon has been reported from Malaysia [58], Papua New Guinea [60], and Indonesian Papua [99].

Mallomonas bangladeshica was initially described from Bangladesh [55]. It is a widely distributed species in the tropics and subtropics of Asia, namely Bangladesh [55], Sri Lanka [59], tropical and subtropical areas of China [68,69], Papua New Guinea [60], Indonesia [66], India [57], and South Korea [105].

Mallomonas harrisiae is a rare taxon that was first described from Japan [106] and was recently found in China [107]. It is reported here for the third time after its initial description.

Scales identified as *Mallomonas mangofera* var. *gracilis* were observed in three localities in Vietnam in Thua Thien province. Initially, *M. mangofera* var. *gracilis* was described from Chile [108]; subsequently, single finds were noted in Denmark [109], Finland [110], Malaysia [58], and China [69]. However, the diagnostic characters of this variety are rather dubious, and the illustrations in the original description are not clear enough. This variety differs from the type variety of *M. mangofera* by the shield with a weakly developed pattern of papillae, which are fused together to some extent, and with a pit-like depression with a pore at the base of the posterior submarginal rib. These characteristics can also be possessed by weakly silicified scales of other species of this complex. It is unclear whether scales identified as *Mallomonas mangofera* var. *gracilis* from such distant areas represent one species.

Mallomonas mangofera var. *sulcata* is the other rare and not fully described variety from the *M. mangofera* complex. After description in a Chilean water body [108], it has also been found in one locality in Singapore [41]. *Mallomonas mangofera* var. *sulcata* differs from other taxa of the *M. mangofera* complex by the presence of grooves (narrow long depressions) along the submarginal ribs. Despite the fact that only two long depressions are indicated in the diagnosis of the species, in the accompanying illustrations, there are more of them on some scales, and they can have different shapes [108] (p. 189, Figure 37). In Vietnam and Singapore, similar morphotypes have been found with numerous depressions, narrower than illustrated for organisms from the type habitat. Perhaps these are scales of a different taxon than the one described from Chile. Further research is needed to clarify this issue.

The use of molecular methods and approaches of geometric morphometry to study the diversity of silica-scaled chrysophytes has made it possible to re-evaluate morphological criteria to distinguish among species [32,35,111–114]. Studies of synuralean algae that combine morphological and molecular data clearly show that even slight differences in

scale/bristle morphology are sufficient for species delimitation [115]. Such features as the location and size of pores on the basal plate, features of the reticulation of the secondary silica layer, the arrangement of papillae on the shield, the structure of bristles, and other features previously attributed to intraspecific variability can serve as reliable characteristics to distinguish among species. Consequently, it is necessary to take these conclusions into account when identifying taxa and to illustrate all “deviating” morphotypes. Therefore, we have carefully cited those morphotypes that do not correspond to the description of closely related species, we have provided their description, and we have pointed out differences from the descriptions in the diagnosis. The illustration of new morphotypes is an important step for further revision of the diversity and study of the biogeography of silica-scaled chrysophytes. Recently, several taxa have been described, which had been illustrated earlier as single scales of unidentified taxa. Examples include taxa such as *Mallomonas spinosa* [79], *M. fimbriata* [81], *M. pseudobronchartiana* [86], and *M. lusca* [116]. Analysis of images illustrated earlier under the epithets of other species (“deviating” morphotypes or misidentified taxa) from different regions of the world [41,58,60,100] have helped clarify the distribution features of some recently described taxa, such as *Mallomonas cattiensis* [84], *M. neoampla* [82], *M. furtiva* [87], *M. loricata* [77], and *M. siderea* [78].

In this study, we found seven morphotypes of *Mallomonas* scales that could not be attributed to known taxa. However, it is not yet possible to describe them as new species. The first group consisted of well-distinguishable but rare morphotypes, represented by single scales. They require additional material for morphological description.

The scale of *Mallomonas* sp. 6 is similar to the body scales of *M. ceylanica* (Figure 2I). However, it is clearly distinguished by the long and wide posterior rim that encircles more than half of the scale perimeter and by the distinct rimmed pores in the proximal part of the scale. Scales of *M. ceylanica* have numerous simple pores in the proximal part, a narrower posterior rim, and an elliptical depression in the centre of the shield. The scale of *Mallomonas* sp. 6 represents a transitional type between the *M. peronoides*/*M. ceylanica* group and the *M. matvienkoae* group.

The scale of *Mallomonas* sp. 7 is similar to *M. perpusilla* Dürschmidt and *M. marsupialis* Kristiansen & Tyler, the only two species known in the Marsupiales section. Both species are rare and have restricted distribution. *M. perpusilla* was first described from New Zealand [117] and was found later in Australia [64]. *M. marsupialis* has only been described and known from Australia [64]. The found scales are similar to *M. marsupialis* in having transverse ribs. However, *M. marsupialis* has one stout and two weaker transverse ribs and narrow anterior flanges. *M. perpusilla*, unlike *Mallomonas* sp. 7, has three to four transverse ribs, connected by a few longitudinal ribs to form an open reticulum with few meshes. The anterior flanges of *M. perpusilla* have irregularly developed struts radiating from the anterior submarginal ribs. However, on some illustrations of specimens from the type habitats, there are images of scales with only transverse ribs and without longitudinal ones [117] (p. 95, Figures 14 and 15). It remains unclear whether the scale found in one habitat in Thua Thien Hue Province is a new species to science or a weakly silicified scale of a rare species, namely *M. perpusilla*.

Another group of unidentified taxa is represented by morphotypes that are part of complex groups of closely related species, such as *Mallomonas elongata*, *M. corymbosa*, *M. matvienkoae*, and *M. favosa*, and have morphological differences from the described taxa, but the species rank must be confirmed by molecular studies.

Mallomonas sp. 1 has a similar scale ultrastructure to the widely distributed *M. elongata*, also reported in our study. Both taxa lack a secondary siliceous layer on the shield and flanges and have a large V-rib and quite large scales. *Mallomonas* sp. 1, unlike *M. elongata*, has a symmetric outline of scales and a different V-rib shape, usually long arms of the anterior submarginal rib, and distinct rows of base-plate pores on the shield and flanges. More data on the bristle structure and molecular data of *Mallomonas* sp. 1 is needed to clarify its taxonomic status. A similar morphotype has also been reported in Malaysia [58]

and Korea [118]. In Vietnam, this morphotype has also been reported from Northern Vietnam [97].

Mallomonas sp. 2 is similar to *M. corymbosa* Asmund & Hilliard. Scales under the name *M. corymbosa* have often been documented from the tropical region [55,68,69]. However, *M. corymbosa* was first described from a northern area (Alaska) [119] and is now believed to have a bipolar distribution [47]. Scales of *Mallomonas* sp. 2 differ from scales of *M. corymbosa* (based on the original description) in size ($4.9\text{--}5.8 \times 3.3\text{--}4.0 \mu\text{m}$ versus $5.8\text{--}7.2 \times 3.4\text{--}5 \mu\text{m}$), features of the development of the secondary silica layer on the shield, and wide anterior margins, especially on scales without a dome. Scales similar to ones of *Mallomonas* sp. 2 have been well illustrated in studies of silica-scaled chrysophytes in Bangladesh [55] and China [69]. In Vietnam, this morphotype has been reported in Northern Vietnam [97] and in the Mekong Delta under the name *Mallomonas* cf. *corymbosa* [74].

Scales of *Mallomonas* sp. 3 are similar to *M. favosa* f. *favosa* and *M. favosa* f. *gemina*. These taxa all have rhomboidal and slightly asymmetrical body scales. The shield of scales of these species has a reticulated meshwork. Well-developed anterior submarginal ribs on the scales of all three taxa have a number of transverse struts. These three taxa differ from each other in the form, structure, and position of pits, located near the posterior submarginal rib. *Mallomonas* sp. 3 differs from *M. favosa* f. *favosa* by the presence of a distinct row of pits located on the shield along the posterior submarginal rib. *Mallomonas favosa* f. *gemina* also has such a row of pits. The differences between *Mallomonas* sp. 3 and *M. favosa* f. *gemina* include the size, shape, and number of pits. *M. favosa* f. *gemina* has numerous (>10) small pits located on the shield along the arms of posterior submarginal rib. Pits (<10) on the scales of *Mallomonas* sp. 3 represent quite large rectangular chambers, each containing a rimmed pore. Scales similar to *Mallomonas* sp. 3 have been reported from a single locality in Malaysia and one in Australia under the name *Mallomonas favosa* forma 2 [58].

Mallomonas sp. 4 and *Mallomonas* sp. 5 are representatives of the Planae section. Species without a V-rib, which are grouped in the Planae section, have a simpler scale structure and, accordingly, fewer potential diagnostic features to distinguish among species. However, molecular data have shown high diversity in this clade, resulting in the description of several new taxa in the *Mallomonas matvienkoae* and *M. caudata* species complexes [113]. For the delimitation of taxa, authors have used features such as the perforations on the scale's basal plate, the structure of the secondary silica layer, the ornamentation formed by papillae, and the structure of bristles. Molecular data have confirmed the importance of these structures to delimit taxa at the species level [113]. Our detailed studies of silica-scaled chrysophytes in Central Vietnam have revealed new morphotypes in the *M. matvienkoae* group. In general, the *Mallomonas matvienkoae* complex is a complicated group, which first needs typification of *Mallomonas matvienkoae* Asmund & Kristiansen with molecular methods for its revision and further description of new species [77,113]. *Mallomonas* sp. 4 and *Mallomonas* sp. 5 are similar to *M. pseudomatvienkoae* (Figure 4H). *Mallomonas* sp. 4 differs from it by larger scales ($5.5\text{--}6.9 \times 4.3\text{--}4.6 \mu\text{m}$ versus $3\text{--}5 \times 2\text{--}3 \mu\text{m}$ in *M. pseudomatvienkoae*), the shape of the reticulation of the secondary silica layer in the distal part of the scales, and the presence of papillae on the shield of the scales. Additional research is required to describe this organism. This morphotype is fairly common in Vietnam, where it has been reported from the Cat Tien National Park, swamp water bodies of the Cam Ranh Peninsula, Northern Vietnam, and the Mekong Delta [72–74,97]. Scales of *Mallomonas* sp. 5 are in size range of *M. pseudomatvienkoae*; however, they are clearly differentiated by the ovoid shape with a narrower distal part in contrast to the broadly oval and obovate scales of *M. pseudomatvienkoae*.

Some of the rare species we found, such as *Mallomonas* cf. *cristata* (Figure 2L,M), *M.* cf. *ouradion* (Figure 4A), and *M.* cf. *skvortsovii* (Figure 4N), we could not reliably identify, although morphologically they are similar to known taxa. With a high degree of probability, these are new species for science that are part of the complex of already described morphologically similar species. To clarify their status and description, additional

molecular studies and/or additional material are required for a more thorough study of the scale ultrastructure. *Mallomonas cristata* was first described from Chile [120] and later found in many habitats throughout the world [47]. Specimens from Vietnam differ mainly by serrated bristles, while only 1–2 small teeth on distal portion of bristles originally were described for *M. cristata*. *Mallomonas ouradion* was described from the United Kingdom [121] and has a scattered distribution [47]. In contrast to the original description of *M. ouradion*, scales from Central Vietnam are wide-oval, with a wide posterior flange, with a V-rib shifted toward the centre of the scale, a weakly developed anterior rib, and well-developed anterior flanges. *Mallomonas skvortsovii* is a recently described species from Vietnam, known from only one locality in Cat Tien National Park [85]. In contrast to the original description of *M. skvortsovii*, scales from Central Vietnam do not have ribs on the dome and struts in the posterior rim, have numerous pores in the angle of the V-rib, and have raised anterior flanges.

We also observed a number of rare *Mallomonas* species. *Mallomonas binocularis* was found the third time in Vietnam. This rare taxon has been reported in a few localities in North America [122,123]. *Mallomonas distinguenda* was originally described in Cat Tien National Park, located in the Southern Vietnam [85], and found only for the second time after its description. *Mallomonas korshikovii* (Figure 3G) and *M. neoampla* (Figure 3S) are species, described from Khanh Hoa Province of Vietnam [71,82], and were also found in Thanh Hoa province in Northern Vietnam [97]. We have provided a few more localities where we observed these taxa. *Mallomonas pseudobronchartiana* (Figure 4G) was recently described from Vietnam and is also known from several localities in South Korea and the United States [86]. Here, we reported this taxon for second time in Vietnam. *Mallomonas tropica* (Figure 5A) is a rare taxon, previously reported only from the type locality in Malaysia [58] and one locality in Vietnam [71]. In our studies, it was reported from six more localities in two provinces.

Synura represents another species-rich genus of the order Synurales and includes more than 50 species [35]. We discovered two new species for the flora of Vietnam in our research.

Synura mammillosa is a widely distributed taxon [47]. In tropical Asia, this morphotype is known from China [68] and Indonesian Papua [99]. *Synura sphagnicola* is also a widely distributed taxon, which prefers humic acid waters [47]. In tropical Asia, it has been found in Malaysia [58] and China [68]. Scales of *Synura sphagnicola* from central provinces in Vietnam are characterised by the presence of several rows of ribs at the distal part.

By contrast, *Synura* sp. 1 (Figure 5O) is one of the most widespread species of synurophytes algae in Vietnam, as shown both in this study and earlier works [72,73,97]. It represents the *S. curtispina*/*S. longitubularis* morphotype. The identification of this taxon based on morphological data is problematic [35]. Both *Synura curtispina* (Petersen & Hansen) Asmund and *S. longitubularis* Jo, Shin, Kim & Siver, are almost indistinguishable from each other in terms of the morphological scale structure [114]. Our unpublished molecular data indicate that only *S. longitubularis* was found in water bodies of Vietnam. However, additional studies are needed regarding the distribution of this taxon.

Synura papillosa (Figure 5M) has recently been described from Vietnam [91]. Our research showed that it is widely distributed throughout Vietnam.

Among the two observed species of *Chryso-sphaerella*, *C. nichollsii* (Figure 5S,T) was quite common, observed in 28 localities in Vietnam, and *Chryso-sphaerella annulata* (Figure 5R) was found rarely—only in six sites. *C. nichollsii* has been described from Indonesia [66] and is now known only in Indonesia and Vietnam. However, based on the wide distribution of this species in Vietnam, it can be assumed that it is a common species for tropical Asia.

Chryso-sphaerella annulata has been found in Vietnam, in Dong Nai province [124]. It is a widespread species in the tropical region [54,55,57,59,68,69,100,125] and has been noted in the temperate zone [126].

Most of the species found in our study have restricted distribution patterns within regions with a warmer climate. The endemics of Vietnam and neighbouring countries are

M. cattiensis, *M. distinguenda*, *M. lusca*, *M. fimbriata*, *M. korshikovii*, *M. lamii*, *M. loricata*, *M. minuscula*, *M. neoampla*, *M. ocellata*, *M. paragrandsis*, *M. punctostriata*, *M. siderea*, *M. spinosa*, *M. tropica*, *M. sp. 3*, *M. sp. 5*, and *Chryso-sphaerella nichollsii*.

The endemics of a wider area, including tropical and subtropical Asia, found in our studies include the following species: *M. bangladeshica*, *M. elevata*, *M. favosa* f. *gemina*, *M. harrisiae*, *M. hexareticulata*, *M. ceylanica*, *M. grata*, *M. sorohexareticulata*, *M. sp. 1*, and *M. sp. 4*.

Mallomonas bronchartiana, *M. kenyana*, *M. morrisonensis*, *M. splendens*, *Synura australiensis*, and *S. papillosa* are pantropic species and are sometimes found in the subtropics. *Mallomonas plumosa* is restricted in distribution to South Asia, Australia, and New Zealand [47].

Widely distributed taxa in our study are *Mallomonas acaroides*, *M. akrokomos*, *M. adamas*, *M. caudata*, *M. crassisquama*, *M. elongata*, *M. favosa* f. *favosa*, *M. guttata* var. *guttata*, *M. multisetigera*, *M. papillosa*, *M. peronoides*, *M. portae-ferreae*, *M. pseudocratis*, *M. punctifera*, *M. rasilis*, *M. striata* var. *serrata*, *M. tonsurata*, *Synura echinulata*, *S. mammillosa*, *S. sphagnicola*, and *Spiniferomonas trioralis* [43,47]. However, molecular studies are needed to confirm that these morphotypes are indeed widespread species and not cryptic taxa. Examples of cryptic/pseudo-cryptic species have been found—for example, in the *M. furtiva*/*M. kalinae* Rezáčova [87] and *S. curtispina*/*S. longitubularis* [114] complexes.

These data confirm the inconsistency of the concept of cosmopolitan distribution of microorganisms [127–129] and are consistent with the data of a moderate endemic model, namely that some species have a cosmopolitan distribution and many others have limited habitats [35,130,131]. Our data show that the study and revision of the tropical flora of microalgae should lead to a revision of the widely discussed theory of cosmopolitan distribution of protists.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w14010065/s1>, Table S1. Basic characteristics of the localities (pH, temperature, specific conductance, chlorophyll *a* concentrations, elevation, and tropic state of analysed water bodies). Table S2. Distribution of the studied waterbodies in Central Vietnam by trophic categories based on the concentration of chlorophyll *a* in the surface layer. Tables S3–S10. Distribution of *Mallomonas*, *Synura*, *Spiniferomonas*, and *Chryso-sphaerella* species in water bodies of eight studied provinces.

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