diversity

MDPI

Article

Diversity of Silica-Scaled Chrysophytes (Stramenopiles: Chrysophyceae) from Indonesian Papua

Evgeniy Gusev [1,*], Dmitry Kapustin [2], Nikita Martynenko [1] and Maxim Kulikovskiy [2]

[1] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, 119071 Moscow, Russia
[2] K.A. Timiryazev Institute of Plant Physiology, Russian Academy of Sciences, Botanical Street 35, 127276 Moscow, Russia
* Correspondence: evsergus@yahoo.com

Abstract: The silica-scaled chrysophyte flora from Indonesian Papua was investigated by means of electron microscopy. A total of twenty-four taxa were recorded, including five belonging to *Paraphysomonas*, one to *Chrysosphaerella*, one to *Spiniferomonas*, fifteen to *Mallomonas* and two to *Synura*. Thirteen taxa were recorded for the first time in Indonesia. Comparison of the species composition of silica-scaled chrysophytes from different parts of the Island of New Guinea shows significant differences. A "living fossil" was discovered, *Mallomonas preisigii*, which was described previously from Eocene deposits in Northern Canada. Although the scales from Papua slightly differ from those of the fossil one, we believe they belong to the same morphospecies. *Mallomonas preisigii* can be considered as a paleoendemic species.

Keywords: chrysophytes; siliceous scales; morphology; taxonomy; distribution; paleoendemic; New Guinea

check for updates

Citation: Gusev, E.; Kapustin, D.; Martynenko, N.; Kulikovskiy, M. Diversity of Silica-Scaled Chrysophytes (Stramenopiles: Chrysophyceae) from Indonesian Papua. *Diversity* **2022**, *14*, 726. https://doi.org/10.3390/d14090726

Academic Editors: Małgorzata Poniewozik and Glenn B. McGregor

Received: 8 August 2022
Accepted: 30 August 2022
Published: 2 September 2022

1. Introduction

Silica-scaled chrysophytes comprise heterokont protists from different evolutionary lineages belonging to three orders (Paraphysomonadales, Chromulinales and Synurales) within a single class Chrysophyceae. The scale ultrastructure is species-specific. Therefore, there is a well-developed morphological species concept for several chrysophyte genera (e.g., *Synura*, *Mallomonas* and *Paraphysomonas*) that is congruent with molecular phylogenetic data [1,2]. Electron micrographs, published in the last 70 years, can be used for floristic and biogeographic analysis. Thus, chrysophytes can be considered as a model group for biogeographical studies [3–5].

Despite numerous floristic and taxonomic studies of silica-scaled chrysophytes performed all over the world, there is a predominance of such studies in the temperate zone, mainly in Europe and Northern America [6]. In particular, there are numerous unstudied areas exist in tropical regions. During the last two decades, diverse tropical flora has been documented [4,7–16], and our knowledge on the biodiversity of silica-scaled chrysophytes in tropical regions has been significantly expanded. Every additional investigation from tropical zones results in discoveries of new species to science, e.g., from Africa [17–19] and Asia [11,12,20–28].

Numerous Indonesian islands belong to the Indo-Malaysian-North-Australian phycogeographical region—one of ten regions defined by Krieger [29] based on the composition of desmid floras. The study on Indonesian algal flora has been performed for a long time and made it possible to identify diverse floras of desmids [29–31], euglenoids [30,32] and diatoms [33–35]. Many generic (e.g., *Ichthyodontum*, *Tetralunata*, *Celebesia* and *Alveocymba*) and species endemics among desmids [36] and diatoms [37–42] have been described in these studies. Therefore, algal floristic studies of this region are essential for the understanding of the biodiversity and biogeography of different algal groups in the Asian tropics.

2. Materials and Methods

Samples for this study were collected in November 2015 by E. Gusev and M. Kulikovskiy in Indonesian Papua (Table 1, Figure 1). Two areas were studied in Papua province (Jayapura and Jayawijaya Regency), Indonesia. Lake Sentani and the surrounding water bodies are located in Jayapura Regency. This territory is adjacent to the sea coast and has an elevation of 81–119 m a.s.l. In Jayawijaya Regency two highland areas were studied: Lake Habbema and surrounding swamps and streams at elevation 3328–3337 m a.s.l. and water bodies in Baliem Valley in the suburbs of Wamena City at elevation 1654–1730 m a.s.l.

Table 1. List of the sampling sites with environmental variables (T—temperature, SC—specific conductance and n/a—no parameters were measured).

	Locality Name	Sample Type	Date	Coordinates	Elevation, m a.s.l.	T, °C	pH	SC, μS·cm^{-1}
1	Lake Sentani	Plankton	14 September 2015	2°38′23.7″ S 140°34′04.3″ E	81	29.7	7.6	230
2	Lake Sentani	Periphyton	14 September 2015	2°38′23.7″ S 140°34′04.3″ E	81	30	7.6	240
3	Water body along the road 1	Plankton	14 September 2015	2°39′54.72″ S 140°32′51.47″ E	119	n/a	n/a	n/a
4	Lake Habbema	Plankton	15 September 2015	4°07′49.5″ S 138°40′22.9″ E	3331	17	7.33	22
5	Lake Habbema	Squeeze from moss	15 September 2015	4°07′49.5″ S 138°40′22.9″ E	3331	17	7.33	n/a
6	Peat-bog pool	Plankton	15 September 2015	4°7′40.02″ S 138°40′3.90″ E	3333	16.7	4.75	8
7	Stream in a bog	Plankton	15 September 2015	4°7′36.30″ S 138°39′55.56″ E	3327	n/a	4.78	n/a
8	Puddle near the stream	Plankton	15 September 2015	4°7′34.68″ S 138°39′53.34″ E	3330	n/a	n/a	n/a
9	Peat-bog pool	Benthos	15 September 2015	4°7′36.60″ S 138°39′53.58″ E	3328	n/a	n/a	n/a
10	Small puddle in a bog	Plankton	15 September 2015	4°7′30.96″ S 138°39′53.88″ E	3337	n/a	n/a	n/a
11	Lake Anagera	Plankton	16 September 2015	3°57′07.4″ S 138°52′27.6″ E	1656	25	7.3	229
12	Water body along the road 2	Plankton	16 September 2015	3°54′33.4″ S 138°50′15.1″ E	1661	25	7.06	234
13	Small ephemeral pond	Plankton	16 September 2015	3°54′09.9″ S 138°50′17.1″ E	1730	27	6.99	162
14	Water body along the road 3	Plankton	16 September 2015	3°54′49.6″ S 138°51′27.4″ E	1654	30	7.05	47

Plankton samples were taken with a plankton net (mesh size 20 μm). Samples from shallow peat-bog pools were obtained by squeezing the water from mosses. All samples were immediately fixed with Lugol's solution.

Water specific conductance, pH and temperature measurements were performed using the Hanna Combo (Hanna HI 9828) device (Hanna Instruments, Inc., Ann Arbor, MI, USA). For electron microscopy studies, an aliquot of each sample was rinsed in deionized water in a centrifuge. Drops of the rinsed sample were dried or digested in sulfuric acid with potassium dichromate. For scanning electron microscope (SEM) studies, the samples were placed on the SEM stub and coated with gold for 10 min. Observations were performed with JEOL 6510 LV. For transmission electron microscope (TEM) studies formvar-coated grids (EMS FF200-Cu-50, Electron Microscopy Sciences, Hatfield, PA, USA) were used, and observations were made on a JEM-1011 (Papanin Institute for Biology of Inland Waters RAS, Borok, Russia).

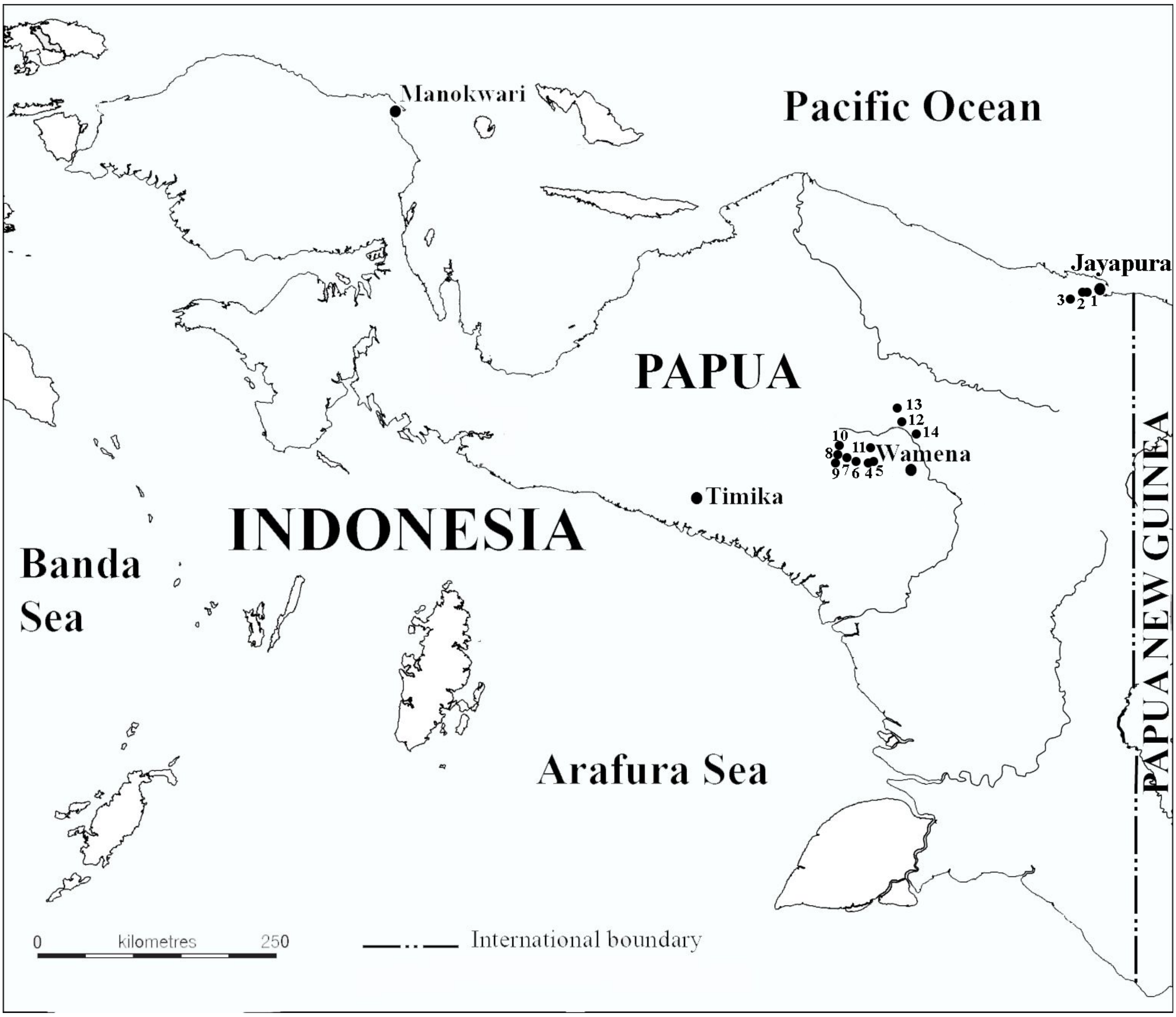

Figure 1. Map of the study area (dots indicate sampling sites).

3. Results

A total of twenty-four taxa of silica-scaled chrysophytes were recorded in the water bodies of Indonesian Papua (Table 2), including five belonging to *Paraphysomonas* De Saedeleer emend. Scoble and Cavalier-Smith (Figure 2A–D,F,G), one to *Chrysosphaerella* Lauterborn (Figures 2H and 3A), one to *Spiniferomonas* E. Takahashi (Figure 2E), fifteen to *Mallomonas* Perty (Figures 3B–L and 4A–J) and two to *Synura* Ehrenberg (Figure 4K,L). Thirteen taxa were recorded for the first time in Indonesia. Several noteworthy taxa are characterized below.

Table 2. List of taxa observed at the investigated waterbodies (new taxa for Indonesia are in bold).

Taxon	**Site Number**													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Paraphysomonadales														
Paraphysomonas cf. *segmenta* Scoble and Cavalier-Smith	×													
Paraphysomonas sp.														×
Paraphysomonas uniformis Scoble and Cavalier-Smith			×											
Paraphysomonas vulgaris subsp. *vulgaris* Scoble and Cavalier-Smith	×													
Paraphysomonas vulgaris subsp. *brevispina* Scoble and Cavalier-Smith	×		×											
Chromulinales														
Chrysosphaerella annulata Kristiansen and Tong	×										×			
Spiniferomonas sp.					×									×
Synurales														
Mallomonas cratis K. Harris and D.E. Bradley														×
Mallomonas cyathellata Wujek and Asmund	×	×												
Mallomonas cf. *elongata* Reverdin														×
Mallomonas furtiva Gusev, Čertnerová, Škaloudová and Škaloud														×
Mallomonas mangofera var. *foveata* (Dürrschmidt) Kristiansen					×								×	
Mallomonas cf. *mangofera* var. *reticulata* (Cronberg) Kristiansen											×	×		×
Mallomonas multisetigera Dürrschmidt					×	×			×					
Mallomonas papillosa K. Harris and D.E. Bradley emend. K. Harris							×							
Mallomonas papuensis Kapustin, Gusev and Kulikovskiy									×	×				
Mallomonas cf. *portae-ferreae* L.S. Péterfi and Asmund												×		×
Mallomonas preisigii Siver						×								×
Mallomonas solea-ferrea var. *irregularis* Němcová, Kreidlova, Pusztai and Neustupa						×								
Mallomonas striata var. *serrata* K. Harris and D.E. Bradley							×					×		×
Mallomonas sp. 1												×	×	
Mallomonas sp. 2					×		×					×		
Synura cf. longitubularis Jo, Shin, Kim and Siver												×	×	×
Synura mammillosa E. Takahashi				×	×	×	×	×						×

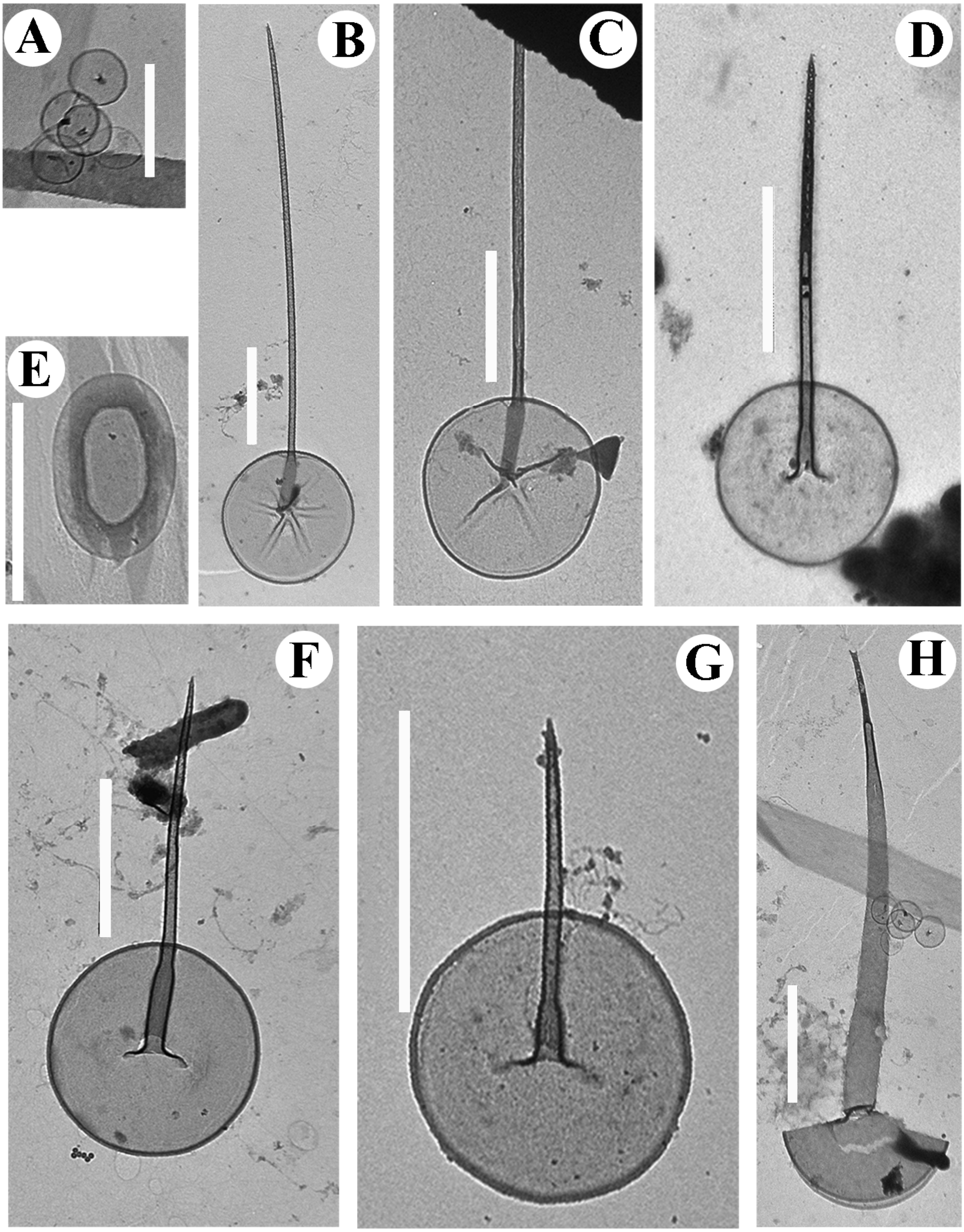

Figure 2. (**A**–**H**) *Paraphysomonas*, *Spiniferomonas* and *Chrysosphaerella* taxa from Indonesian Papua, TEM. (**A**) *Paraphysomonas* cf. *segmenta*; (**B**,**C**) *Paraphysomonas* sp. (**D**) *Paraphysomonas uniformis*. (**E**) *Spiniferomonas* sp., a plate-like scale. (**F**) *Paraphysomonas vulgaris* subsp. *vulgaris*. (**G**) *Paraphysomonas vulgaris* subsp. *brevispina*. (**H**) *Chrysosphaerella annulata*, spine scale. Scale bars: (**A**): 1 µm, (**B**–**H**): 2 µm.

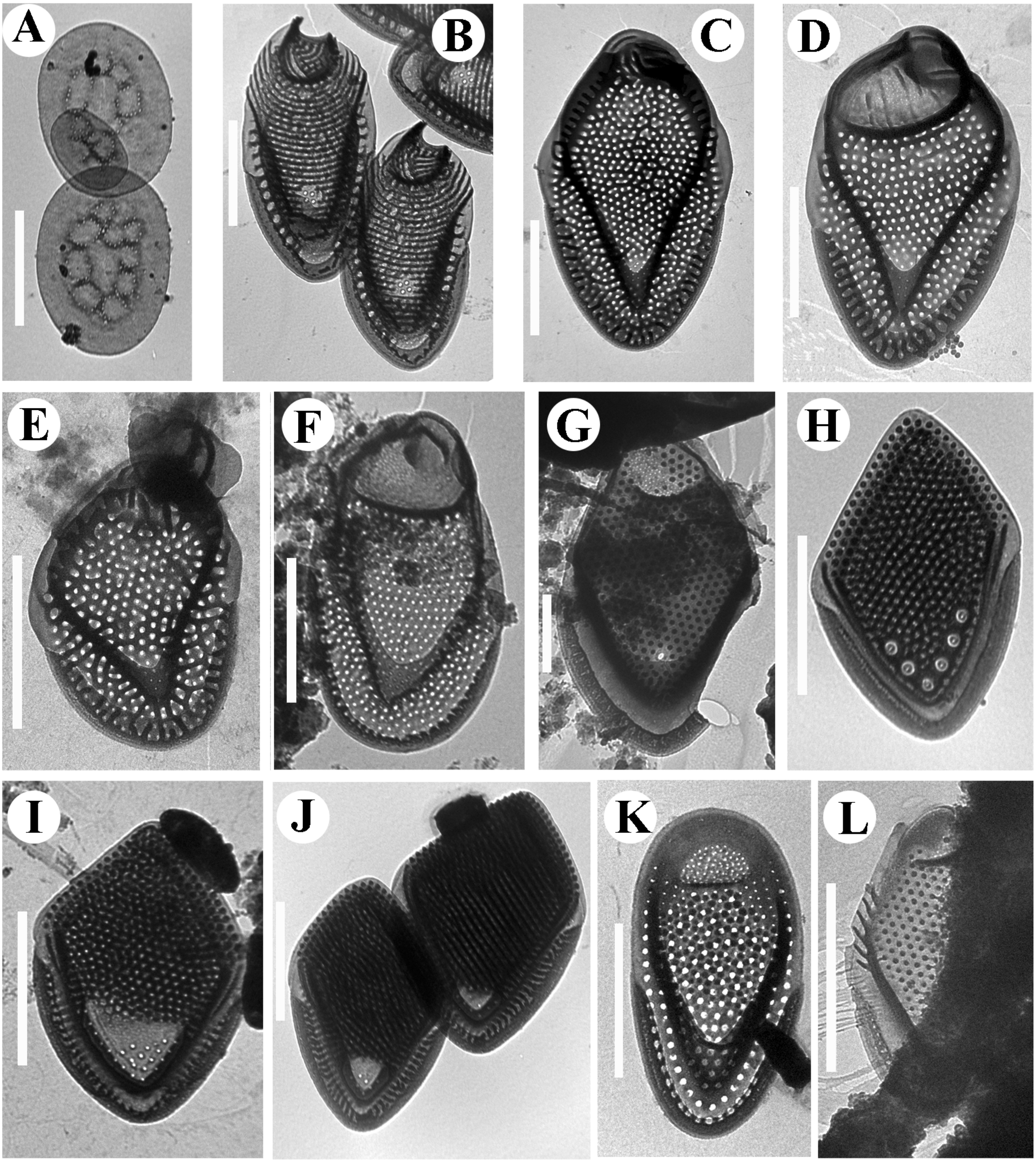

Figure 3. (**A**–**L**) *Chrysosphaerella* and *Mallomonas* taxa from Indonesian Papua, TEM. (**A**) *Chrysosphaerella annulata*, plate-like scales. (**B**) *Mallomonas cratis*, a group of scales. (**C**–**E**) *Mallomonas cyathellata*, domeless scale (**C**), domed scale (**D**) and rear scale (**E**) with cyathus (arrow). (**F**) *Mallomonas* cf. *elongate*. (**G**) *Mallomonas furtiva*. (**H**) *Mallomonas mangofera* var. *foveata*. (**I**,**J**) *Mallomonas mangofera* var. *reticulata*. (**K**) *Mallomonas multisetigera*. (**L**) *Mallomonas papillosa*. Scale bars: (**A**–**F**,**H**–**L**): 2 μm, (**G**): 1 μm.

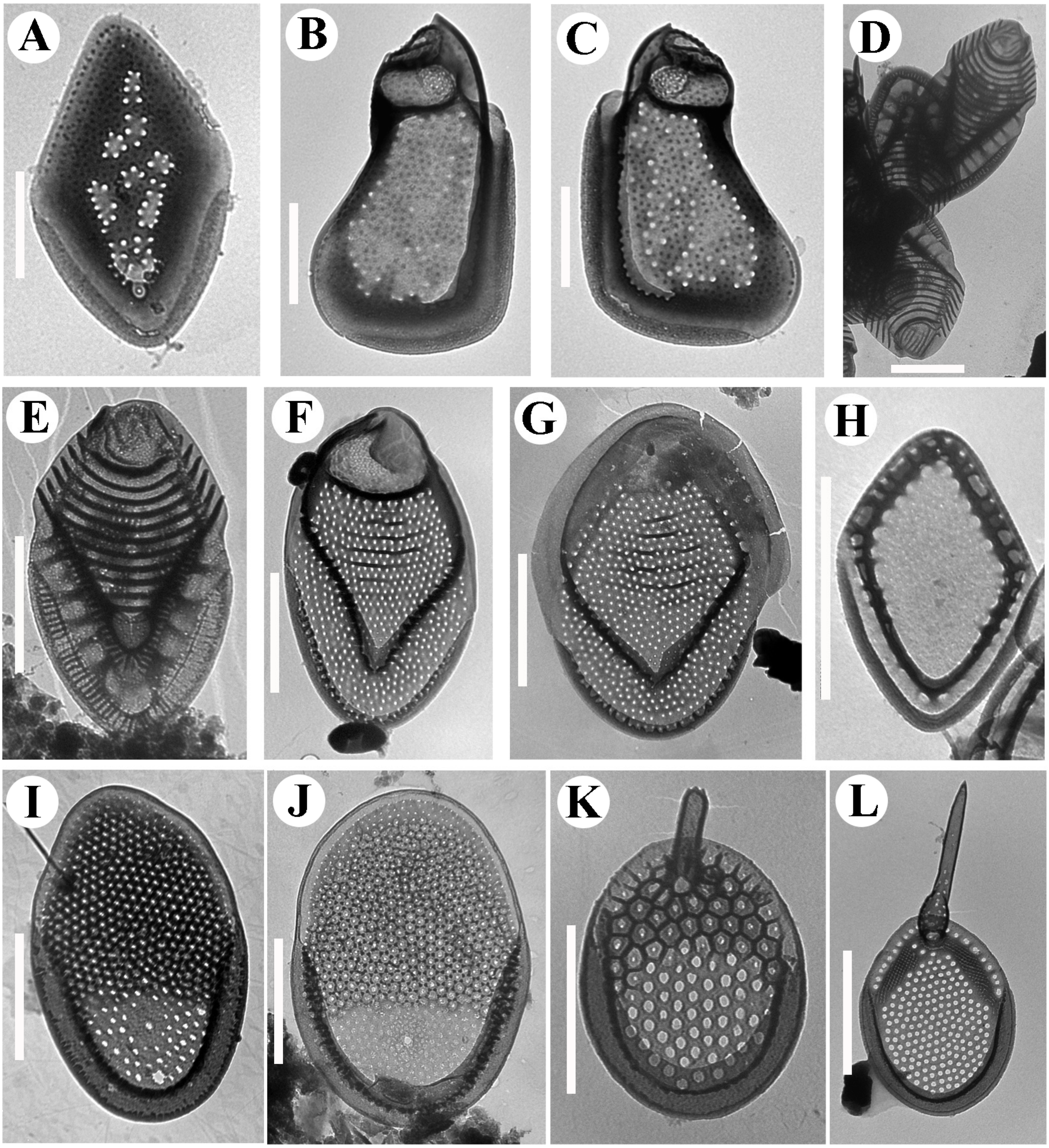

Figure 4. (**A**–**L**) *Mallomonas* and *Synura* taxa from Indonesian Papua, TEM. (**A**–**C**) *Mallomonas solea-ferrea* var. *irregularis*, body (**A**) and apical (**B**,**C**) scales. (**D**,**E**) *Mallomonas striata* var. *serrata*. (**F**,**G**) *Mallomonas* cf. *portae-ferreae*. (**H**) *Mallomonas papuensis*, a body scales. (**I**) *Mallomonas* sp. 1. (**J**) *Mallomonas* sp. 2. (**K**) *Synura* cf. *longitubularis*. (**L**) *Synura mammillosa*. Scale bars: (**D**–**L**): 2 µm, (**A**–**C**): 1 µm.

Several new records of *Paraphysomonas* in the Indonesian flora were observed in our investigations.

Paraphysomonas cf. ***segmenta*** (Figure 2A) was identified on the basis of a group of five scales; however, only a single scale had a well-developed spine. The base-plate is round (diameter 0.41–0.47 µm) with a thickened rim; the spine is two-segmented, 0.47 µm in length; S/P ratio of 1. According to Scoble and Cavalier-Smith [2], this species has a base-plate that is 0.40–0.53 μm in diameter, a spine length of 0.52–0.73 μm and a spine length to base-plate diameter ratio (S/P ratio) of 1.3–1.7. Therefore, our specimen has a slightly shorter spine. Additional material is needed for accurate identification. This species has previously been recorded from the United Kingdom [2].

One unidentified taxon from this genus was observed. ***Paraphysomonas*** sp. (Figure 2B,C) is similar to *Paraphysomonas uniformis* subsp. *hemiradia*, described by Scoble and Cavalier-Smith [2], in which they have four to six radial ribs on the basal plate of the scales. However, *Paraphysomonas* sp. significantly differs from *P. uniformis* subsp. *hemiradia* by its scale dimensions. Scales have a spine length of 8.93 μm, a spine base width of 0.25 μm, a base-plate diameter of 2.50–2.54 μm and an S/P ratio of 3.57. Furthermore, the spine length and base-plate diameter in our species are significantly larger than in *P. longispina* Scoble and Cavalier-Smith. It is likely that these scales belong to a yet undescribed species; however, more material is needed for a formal description.

Paraphysomonas uniformis subsp. ***uniformis*** (Figure 2D) is characterized by scales with a round to oval base-plate, 1.71–2.02 μm in diameter. The spine is straight, gently tapered with small oblique blunt point, 4.62–4.8 μm in length and with an S/P ratio of 2.3–2.8. The species has previously been recorded from Austria [2].

Paraphysomonas vulgaris subsp. ***vulgaris*** (Figure 2F) has a round base-plate (2.0–2.5 μm in diameter) with a dense rim. The spine is 3.3–4.3 μm in length with a bulbous base and oblique dull-pointed tip; S/P ratio of 1.6–1.8. This taxon has previously been recorded from the United Kingdom, Switzerland [2] and Vietnam [43].

Paraphysomonas vulgaris subsp. ***brevispina*** (Figure 2G) differs from *P. vulgaris* subsp. *vulgaris* in having shorter spines (1.8–3.1 μm). The scales in our finding have the following dimensions: a base-plate with a diameter of 1.63–1.76 μm, a spine length of 2.06–2.39 μm and an S/P ratio of 1.17–1.47. This taxon has previously been recorded from the United Kingdom, India [2], Austria [44] and Vietnam [43].

Mallomonas furtiva (Figure 3G) is a recently described taxon from Vietnam [45], which is morphologically similar to *M. kalinae* Řezáčová. Both species differ in nucleotide sequences of the SSU rDNA, LSU rDNA and *rbc*L genes, as well as by minute, but statistically significant, morphological differences in the structure of the silica scales. These differences were prominent in the number of papillae on the shield, the presence of papillae on the dome and the scale length.

Mallomonas cf. ***mangofera*** var. ***reticulata*** (Figure 3I,J) belongs to the complex and ambiguous group of taxa from the section *Torquatae* series *Mangoferae*, which include many morphospecies. Some of them were described from the tropics as *M. crocodilorum*, *M. lemuriocellata*, *M. madagascariensis* [46], *M. minuscula* [26] and *Mallomonas mangofera* var. *reticulata* [47]. Several characteristics that were used for distinguishing taxa have unclear taxonomic significance. In particular, this applies to the presence or absence of reticulation and its form (triangular, polygonal and circular). Originally, scales of *Mallomonas mangofera* f. *reticulata*, according to the original description and holotype given by Cronberg [47], were considered to have a network of triangular meshes. Later, many authors identified this variety based on scales with polygonal or circular reticulation similar to our scales from Indonesia [11,48,49]. Further investigations including molecular studies are needed to clarify the taxonomic status of this organism and taxonomic significance of such character as reticulation on the shield.

Mallomonas preisigii (Figures 5 and 6) is the most intriguing species in our study. This species was described from Eocene deposits in the Northwest Territories of Canada [50], and it was considered to be extinct. Our finding suggests that *M. preisigii* is a paleo-endemic and relict species. Two populations were found in highlands at different elevations (3300 and 1650 m a.s.l). Both sites are located in the Baliem River basin. The scales of our specimens slightly differ from those described by Siver [50]. Scales from Papua are larger than fossil scales (4.7–5.2 × 2.8–3.2 μm vs. 3.5–4 × 2.2 μm). The shield of fossil scales is smooth, whereas some Papuan scales have scattered papillae on the shield in one population from site 14. Fossil and modern scales have shallow domes, expanded laterally and recessed from the distal margin (domeless scales also existed in fossil material). In the *M. preisigii* formal description, the information on bristle structure is lacking.

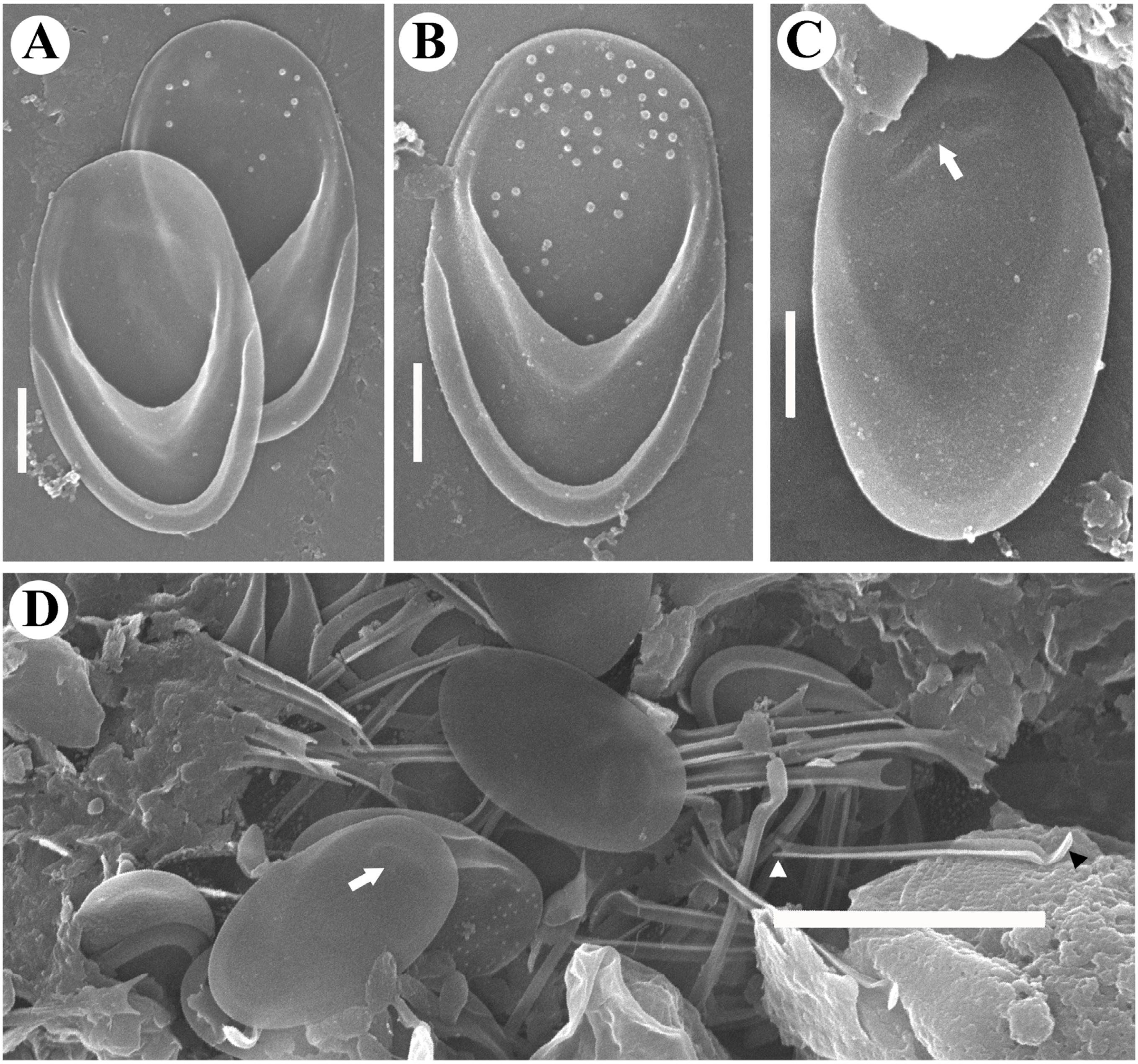

Figure 5. (**A**–**D**) Scales and bristles of *Mallomonas preisigii*, SEM. (**A**) Two scales with (in the background) or without (in the foreground) papillae. (**B**) A scale covered with papillae. (**C**) Undersurface of the scale illustrating the shallow concavity (arrow). (**D**) A group of scales and bristles (an arrow indicates the shallow concavity on the scale, a white arrowhead indicates the bristle tip and a black arrowhead indicates the bristle foot). Scale bars: (**D**): 5 μm, (**A**–**C**): 1 μm.

In our material, the bristle shafts were gutter-shaped with a flattened and usually bifurcated apical tip and a hooked-shaped foot. P. Siver (pers. com.) observed similar shaped bristles in the fossil samples containing *M. preisigii* scales; however, because the samples contained numerous scale types, he was not able to definitively link them to *M. preisigii*.

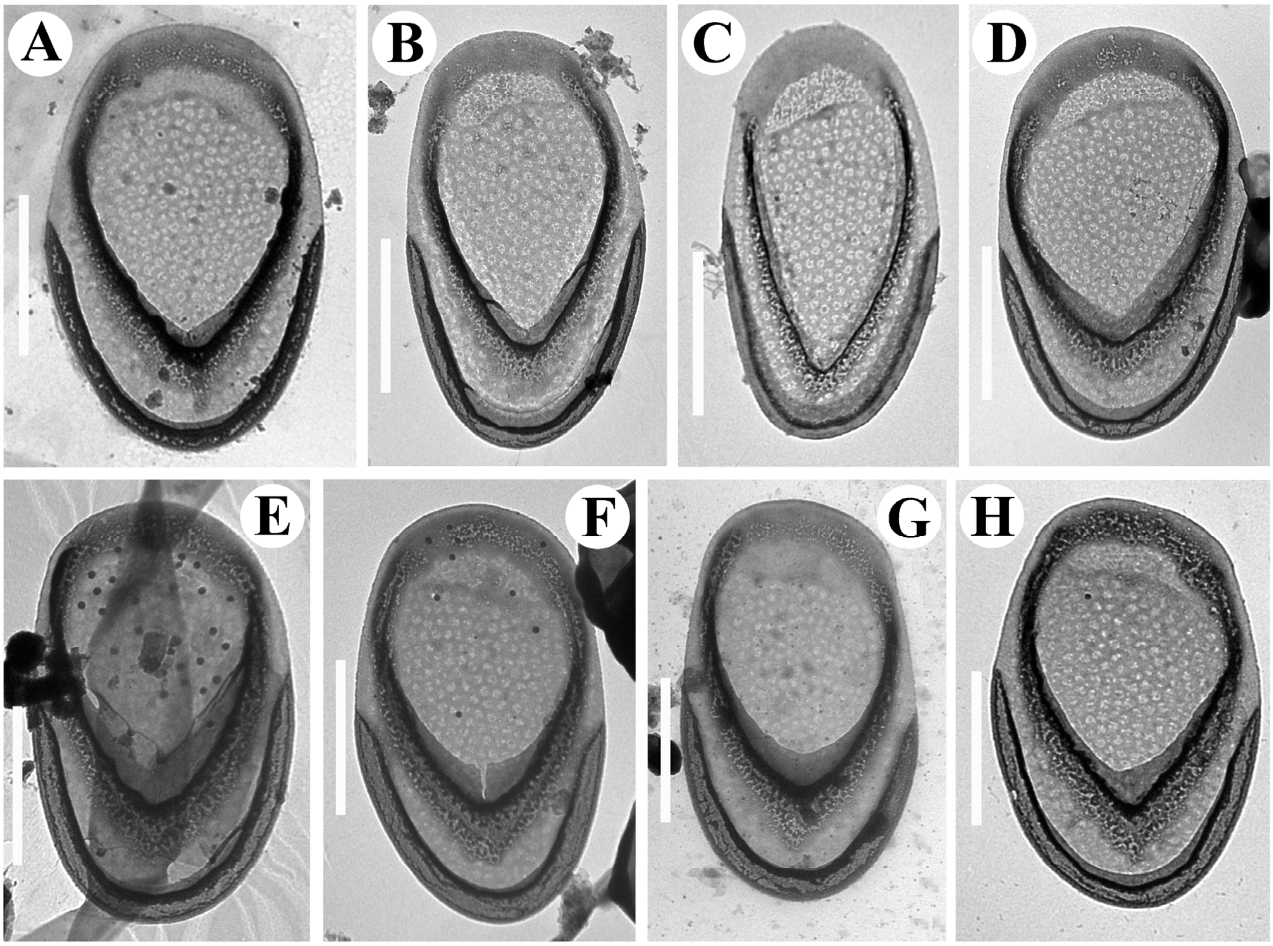

Figure 6. (**A**–**H**) Scales of *Mallomonas preisigii*, TEM. (**A**–**D**) Scales from site 6. (**E**–**H**) Scales from site 14. Note the presence of scattered papillae on some scales. (**E**,**F**) Scale bars: 2 µm.

Mallomonas solea-ferrea var. ***irregularis*** (Figure 4A–C) is a recently described taxon [51], which differs from the type variety in having a less distinctive shield pattern and a more prominent (higher) peak of the dome in collar scales. The body scales differ significantly from the type variety in shape and in the more irregular pattern of the shield where the meshes of the reticulum enclose various numbers of pores. *Mallomonas solea-ferrea* var. *irregularis* was described from the Czech Republic, where it was found only at two sites. Our finding is the first observation of this species outside Europe.

Scales of ***Mallomonas* sp. 2** (Figure 4J) resemble those of *Mallomonas pseudomatvienkoae* Jo, Shin, Kim, Siver and Andersen, but differ in the form of reticulation in the distal part and by the presence of papillae on the shield. They are similar to scales found in Vietnam [12,13]. Scales from Indonesia and Vietnam are larger than in *Mallomonas pseudomatvienkoae* (5.3–5.9 × 3.7–4.2 µm instead of 3–5 × 2–3 µm in type specimens). Our unpublished data, based on collection of images and molecular studies of cultures, indicate that it is a common organism in tropical Asia.

Synura* cf. *longitubularis (Figure 4K). *Synura longitubularis* was described recently from South Korea based on data obtained from molecular analysis [52]. It resembles *S. curtispina* (Petersen and Hansen) Asmund by the morphological structure of scales. Although *S. longitubularis* has a slightly larger mesh diameter of the secondary silica layer and longer tubular caudal scales, their values overlap with other species, which prevents them from being distinguished morphologically. A reliable identification of the species is possible using molecular data. Studies of strains from this complex, isolated from water bodies of Vietnam, demonstrate that only *S. longitubularis* is present in this tropical country (our unpublished data). Therefore, we can suggest that Indonesian scales belong to *Synura longitubularis* but this assumption must be confirmed by molecular methods.

Among other *Mallomonas* and *Synura* taxa *M. cratis*, *M. cyathellata*, *M.* cf. *elongata*, *M. mangofera* var. *foveata*, *M. multisetigera*, *M. papillosa*, *M. portae-ferreae*, *M. striata* var. *serrata* and *S. mammillosa* are widely distributed [53], and *M. papuensis* is endemic for Indonesian Papua [54].

4. Discussion

4.1. Comparison of Silica-Scaled Chrysophyte Floras of Indonesian Papua and Papua New Guinea

Previously, Vyverman [55] reported twelve taxa (including two unidentified *Mallomonas* species) of silica-scaled chrysophytes from lakes and swamps in Wasur National Park and Yos Sudarso Island (formerly Frederik Hendrik Island). Surprisingly, there is no common taxa between our findings and those of Vyverman's. Nevertheless, the species composition of silica-scaled chrysophytes from Wasur National Park and Yos Sudarso island is extremely similar to the species composition found in Australia [56]. Indeed, among the twelve taxa listed by Vyverman [55], nine taxa were recorded from Australia (although taxonomic inconsistencies are likely) and only *Mallomonas bangladeshica* is not known there.

It is common to compare the composition of silica-scaled chrysophyte floras of Indonesian Papua and Papua New Guinea. The study performed by Vyverman and Cronberg [57] is the only work published on silica-scaled chrysophytes from Papua New Guinea. The authors identified 20 taxa of scale-bearing chrysophytes and therefore the two floras are comparable. Although their list requires taxonomic revision, a comparison is possible. In freshwaters of Papua New Guinea as well as of Indonesian Papua most taxa, predictably, belong to *Mallomonas* because it is the largest genus of chrysophytes.

The only common taxon that existed is *M. striata* var. *serrata*, which is considered to be a cosmopolitan [51]. In Papua New Guinea, five *Synura* species were recorded while only two species were found in Indonesian Papua. One taxon, each of *Chrysosphaerella* and *Spiniferomonas,* was recorded from both countries. However, we could not identify our *Spiniferomonas* species based on isolated plate scales only.

It is likely that those isolated plate scales might belong to a cosmopolitan species, *S. trioralis,* which has previously been reported from Indonesian Papua [55]. Vyverman and Cronberg [57] reported a single *Paraphysomonas* species, *P. vestita*. However, the identity of this species is currently unclear [2,58]. In the current study, we identified six *Paraphysomonas* taxa based on the revision by Scoble and Cavalier-Smith [2]. Vyverman and Cronberg [57] observed scales of *P. vestita* from five sites therefore it is likely that more than one species existed in those regions.

However, the only micrograph in Vyverman and Cronberg [57] with close-up base-plate scale and cropped spine restricted the re-identification of that specimen. Thus, both floras contain only one common species, *M. striata* var. *serrata*. Unexpectedly, they look completely different. Interestingly, silica-scaled chrysophytes from Wasur National Park, Yos Sudarso island and Papua New Guinea are much more similar to each other (i.e., all ten identified taxa recorded from Wasur National Park and Yos Sudarso island were also reported from Papua New Guinea) than to those from the central part of the Papua province. The taxonomic inconsistencies could be an explanation for this observation; however, it is obvious that biogeographical reasons may also exist.

4.2. Endemism in Silica-Scaled Chrysophytes from Indonesian Papua

Kristiansen and Lind [59] (p. 73) stated that "neither have Indonesia and Papua-New Guinea with their ancient lakes yielded chrysophyte endemics". This statement was valid in 2005. However, including our recent findings, 46 taxa of silica-scaled chrysophytes were reported from Indonesia. Several of them are endemics or taxa with restricted distribution. Recently Kapustin and Gusev [60] recognized, among Javanese chrysophytes, a group of Indochinese-Sundaic endemics, which are restricted to Southeast Asia. Later, Kapustin et al. [52] discovered a first local endemic, *Mallomonas papuensis*. It was discovered in a bog pool at the altitude more than 3000 m above sea level. This species is similar to *Mallomonas newfoundlandicus* Siver, which was described from a small bog in Newfoundland, Canada [61].

In the present study we discovered a "living fossil", *Mallomonas preisigii*. It was originally described from a 40-Ma Eocene maar lake, referred to as Giraffe Pipe, situated near the Arctic Circle in Northern Canada [43]. Despite the geographic location, there were warm conditions where ice was lacking, winter temperatures were above freezing, and the mean annual temperature of this location estimated to be 17 °C—much warmer than today [62,63].

Records of silica-scaled chrysophytes from Giraffe Pipe fossil locality are important for understanding the biogeography of this group because it contains siliceous scales morphologically identical to those of modern taxa [1,64]. For instance, *Mallomonas bangladeshica*, which is now restricted to the tropics, occurred in these Eocene sediments [64]. *Mallomonas preisigii* was discovered in two bog pools in highlands of Indonesian Papua (3300 and 1650 m a.s.l).

Although the scales from Papua are slightly larger than those of fossil ones and sometimes have scattered papillae on the scale shield, they belong to the same morphospecies. Thus, both findings, fossil and modern, indicate that this taxon prefers warm climate conditions. Since we found the scales of this species in modern samples, it allowed us to consider *M. preisigii* as a paleoendemic, which was widely distributed in the past.

This finding of a relict species related to the genus *Mallomonas* is not the first observation in a tropical region. The recent discovery of *M. vietnamica* and *M. neoampla*, which have ultrastructural elements similar to fossil scales, shows that tropical flora includes a number of relict taxa [22,65]. Therefore, several evidences are identified to conclude that the tropical areas can be refugia for ancient microorganisms.

Olefeld et al. [66] studied centres of endemism of freshwater protists (including chrysophytes) in Europe using SSU-V9- and ITS1-region of the rDNA. They revealed that protist diversity of high mountain lakes, as azonal habitats, deviated from surrounding lowlands and many taxa were found exclusively in high mountain lakes.

The cases of endemism of silica-scaled chrysophytes from Indonesian Papua also confirm this observation. Both *Mallomonas papuensis* and *M. preisigii* were found in high mountain habitats. Our unidentified *Paraphysomonas* sp. could also represent an undescribed new species and a putative endemic.

5. Conclusions

The study of the silica-scaled chrysophyte flora from Indonesian Papua revealed great differences from the flora of adjacent territories studied earlier. Rare, regionally and locally endemic taxa were found. The most interesting finding is *Mallomonas preisigii*, a paleoendemic species, which was known previously only from Eocene deposits in Northern Canada. Thus, New Guinea is an important area for further floristic, taxonomic and biogeographical studies.

Author Contributions: E.G., samples, wrote and drafted the manuscript, TEM observations and identification; D.K., SEM observations, identification and wrote and drafted the manuscript; N.M., sample preparation, measurements and editing of manuscript; M.K. field expeditions and sampling. All authors contributed to the drafts and gave final approval for publication. All authors have read and agreed to the published version of the manuscript.

Funding: This work was performed with financial support from the Russian Science Foundation (20–14–00211) for the SEM and TEM studies. The analysis of environmental parameters was performed within the state assignment of Ministry of Science and Higher Education of the Russian Federation (theme No. 122042700045-3).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The authors are grateful to the staff of the Interlaboratory Centre of Electron Microscopy of the Papanin Institute for Biology of Inland Waters, RAS for the technical assistance. We especially thank Peter A. Siver (Connecticut College, United States) for the helpful discussion on the identity of *Mallomonas preisigii* and Yvonne Němcová (Department of Botany, Charles University in Prague) for confirming the identification of *Mallomonas solea-ferrea* var. *irregularis*. The authors are grateful to anonymous reviewers for their remarks that improved the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Siver, P.A.; Jo, B.Y.; Kim, J.I.; Shin, W.; Lott, A.M.; Wolfe, A.P. Assessing the evolutionary history of the class Synurophyceae (Heterokonta) using molecular, morphometric, and paleobiological approaches. *Am. J. Bot.* **2015**, *102*, 921–941. [CrossRef] [PubMed]
2. Scoble, J.M.; Cavalier-Smith, T. Scale evolution in Paraphysomonadida (Chrysophyceae): Sequence phylogeny and revised taxonomy of *Paraphysomonas*, new genus *Clathromonas*, and 25 new species. *Eur. J. Protistol.* **2014**, *50*, 551–592. [CrossRef] [PubMed]
3. Kristiansen, J. Biogeography of silica-scaled chrysophytes. *Nova Hedw. Beih.* **2001**, *122*, 23–39.
4. Řezáčová, M.; Neustupa, J. Distribution of the genus *Mallomonas* (Synurophyceae)–ubiquitous dispersal in microorganisms evaluated. *Protist* **2007**, *158*, 29–37. [CrossRef]
5. Siver, P.A.; Lott, A.M. Biogeographic patterns in scaled chrysophytes from the east coast of North America. *Freshw. Biol.* **2012**, *57*, 451–466. [CrossRef]
6. Kristiansen, J. Dispersal and biogeography of silica-scaled chrysophytes. *Biodivers. Conserv.* **2008**, *17*, 419–426. [CrossRef]
7. Compère, P. *Mallomonas bronchartiana*, Chrysophyceé nouvelle du lac Tchad. *Bull. Jard. Bot. Nat. Belg.* **1974**, *44*, 61–63. [CrossRef]
8. Wei, Y.-X.; Yuan, X.-P. Studies on silica-scaled chrysophytes from the tropics and subtropics of China. *Nova Hedw. Beih.* **2001**, *122*, 169–187.
9. Gusev, E.S.; Nguyen, T.H.T. Silica-scaled chrysophytes (Chrysophyceae and Synurophyceae) from Vietnam (Khanh Hoa and Quang Nam provinces). *Nova Hedw.* **2011**, *93*, 191–199. [CrossRef]
10. Gusev, E.S. Studies on synurophycean algae from mangrove wetlands (Vietnam). *Nova Hedw. Beih.* **2013**, *142*, 87–98.
11. Wei, Y.-X.; Yuan, X.-P.; Kristiansen, J. Silica-scaled chrysophytes from Hainan, Guangdong Provinces and Hong Kong Special Administrative Region, China. *Nord. J. Bot.* **2014**, *32*, 881–896. [CrossRef]
12. Gusev, E.S.; Doan-Nhu, H.; Nguyen-Ngoc, L. Silica-scaled chrysophytes from Cat Tien National Park (Dong Nai Province, Viet Nam). *Nova Hedw.* **2017**, *105*, 347–364. [CrossRef]
13. Gusev, E.S.; Doan-Nhu, H.; Nguyen-Ngoc, L.; Guseva, E.E.; Luom, P.T. Silica-scaled chrysophytes from Cam Ranh Peninsula (Khanh Hoa Province, Vietnam). *Nova Hedw. Beih.* **2019**, *148*, 63–76. [CrossRef]
14. Gusev, E.; Martynenko, N.; Tran, H. Studies on Algae from the Order Synurales (Chrysophyceae) in Northern Vietnam. *Diversity* **2021**, *13*, 602. [CrossRef]
15. Doan-Nhu, H.; Tinh, T.T.; Gusev, E.S.; Kulikovskiy, M.S.; Phan-Tan, L.; Nguyen-Ngoc, L. Taxonomic composition of silica-scaled chrysophytes in a tropical mountain reservoir. *Inl. Wat. Biol.* **2021**, *14*, 490–499. [CrossRef]
16. Gusev, E.; Martynenko, N. Diversity of Silica-Scaled Chrysophytes in Central Vietnam. *Water* **2022**, *14*, 65. [CrossRef]
17. Němcová, Y.; Bulant, P.; Kristiansen, J. *Mallomonas solea-ferrea* and *Mallomonas siveri* (Chrysophyceae/Synurophyceae): Two new taxa from the Western Cape (South Africa). *Nova Hedw.* **2011**, *93*, 375–384. [CrossRef]
18. Němcová, Y.; Kreidlová, J. Two new species of *Mallomonas* (Chrysophyceae: Synurales): *Mallomonas temonis* and *Mallomonas divida*. *Phytotaxa* **2013**, *87*, 11–18. [CrossRef]
19. Piątek, J. *Mallomonas camerunensis* sp. nov. (Chrysophyceae, Stramenopiles) from a shallow puddle in the Guineo-Congolian rainforest (Cameroon). *Pol. Bot. J.* **2015**, *60*, 119–126. [CrossRef]
20. Gusev, E.S. A new species of the genus *Mallomonas* (Synurophyceae), *Mallomonas spinosa* sp. nov., from Vietnam. *Phytotaxa* **2012**, *66*, 1–5. [CrossRef]
21. Gusev, E.S. A new species of the genus *Mallomonas* (Synurales, Chrysophyceae), *Mallomonas fimbriata* sp. nov. *Phytotaxa* **2015**, *195*, 291–296. [CrossRef]
22. Gusev, E.; Siver, P.A. *Mallomonas neoampla* sp. nov. from Vietnam, a new species that bridges the gap between fossil and modern taxa. *Nova Hedw.* **2017**, *104*, 521–528. [CrossRef]
23. Gusev, E.S.; Kulikovskiy, M.S. Two new species of genus *Mallomonas* from swamp localities in Vietnam. *Phytotaxa* **2020**, *468*, 121–129. [CrossRef]
24. Gusev, E.S.; Siver, P.A.; Shin, W. *Mallomonas bronchartiana* Compère revisited: Two new species described from Asia. *Cryptogam. Algol.* **2017**, *38*, 3–16. [CrossRef]
25. Gusev, E.S.; Kapustin, D.A.; Martynenko, N.A.; Guseva, E.E.; Kulikovskiy, M.S. *Mallomonas gusakovii* sp. nov. (Chrysophyceae, Synurales), a new species from Phu Quoc Island, Vietnam. *Phytotaxa* **2019**, *406*, 199–205. [CrossRef]

26. Gusev, E.; Guseva, E.; Kezlya, E.; Kulikovskiy, M. *Mallomonas minuscula* sp. nov. (Synurales, Chrysophyceae), a new member in the section *Torquatae* from Vietnam. *Fottea* **2019**, *19*, 132–137. [CrossRef]
27. Gusev, E.; Kezlya, E. *Mallomonas lusca* sp. nov.—A rare species from Southeast Asia. *Phytotaxa* **2021**, *529*, 105–112. [CrossRef]
28. Gusev, E.S.; Kulikovskiy, M.S. *Mallomonas siderea* sp. nov. (Synurales, Chrysophyceae), a new tropical species from the section *Torquatae*. *Nova Hedw.* **2021**, *113*, 291–301. [CrossRef]
29. Krieger, W. Die Desmidiaceen der Deutschen limnologischen Sunda-Expedition. *Arch. Hydrobiol. Suppl.* **1932**, *11*, 129–230.
30. Behre, K. Die Süsswasseralgaen der Wallacea-Expedition (ohne die Diatomeen und Peridineen). *Arch. Hydrobiol. Suppl.* **1956**, *23*, 1–104.
31. Scott, A.M.; Prescott, G.W. Indonesian desmids. *Hydrobiologia* **1961**, *17*, 1–132. [CrossRef]
32. Conrad, W. Flagellates des Iles de la Sonde (*Euglénacées*). *Bull. Mus. R. Hist. Nat. Belg.* **1938**, *14*, 1–20.
33. Hustedt, F. Die fossile Diatomeenfl ora in den Ablagerungen des Tobasees auf Sumatra. *Arch. Hydrobiol. Suppl.* **1935**, *14*, 143–192.
34. Hustedt, F. Systematische und ökologische Untersuchungen über die Diatomeenflora von Java, Bali und Sumatra nach dem Material der Deutschen Limnologischen Sunda-Expedition. Teil, I. Systematischer Teil. *Arch. Hydrobiol. Suppl.* **1938**, *15*, 393–506.
35. Hustedt, F. Süßwasser-Diatomeen des indomalayischen Archipels und der Hawaii-Inseln. *Int. Rev. ges. Hydrobiol. Hydrogr.* **1942**, *42*, 1–252. [CrossRef]
36. Scott, A.M.; Prescott, G.W. Notes on Indonesian freshwater algae II. *Ichthyodontum*, a new desmid genus from Sumatra. *Reinwardtia* **1956**, *3*, 351–362.
37. Hamsher, S.E.; Graeff, C.L.; Stepanek, J.G.; Kociolek, J.P. Frustular morphology and polyphyly in freshwater *Denticula* (Bacillariophyceae) species, and the description of *Tetralunata* gen. nov. (Epithemiaceae, Rhopalodiales). *Pl. Ecol. Evol.* **2014**, *147*, 346–365. [CrossRef]
38. Kapustin, D.A.; Kulikovskiy, M.S.; Kociolek, J.P. *Celebesia* gen. nov., a new cymbelloid diatom genus from the ancient Lake Matano (Sulawesi Island, Indonesia). *Nova Hedw. Beih.* **2017**, *146*, 147–155. [CrossRef]
39. Kapustin, D.A.; Kociolek, J.P.; Glushchenko, A.M.; Kulikovskiy, M.S. Four new species of *Cymbella* (Bacillariophyta) from the ancient Malili Lakes (Sulawesi Island, Indonesia). *Bot. Zhurn.* **2019**, *104*, 766–780. [CrossRef]
40. Kapustin, D.A.; Kociolek, J.P.; Glushchenko, A.M.; Kulikovskiy, M.S. A rediscovery of *Cymbella mirabilis* Hustedt, a rare endemic diatom, and description of *Alveocymba* gen. nov. *Diat. Res.* **2020**, *35*, 281–287. [CrossRef]
41. Kapustin, D.A.; Glushchenko, A.M.; Kociolek, J.P.; Kulikovskiy, M.S. *Encyonopsis indonesica* sp. nov., a new diatom from the ancient lake Matano (Sulawesi, Indonesia). *PhytoKeys* **2021**, *175*, 1–11. [CrossRef] [PubMed]
42. Kapustin, D.A.; Glushchenko, A.M.; Kulikovskiy, M.S. *Achnanthidium bratanense* sp. nov. (Bacillariophyceae, Achnanthidiaceae), a new diatom from the Lake Bratan (Bali, Indonesia). *PhytoKeys* **2022**, *188*, 167–175. [CrossRef] [PubMed]
43. Gusev, E.S.; Gusakov, V.A.; Guseva, E.E.; Kulikovskiy, M.S.; Tsvetkov, A.I.; Định, C.N. Flora of Silica-Scaled Chrysophytes (Chrysophyceae: Synurales, Paraphysomonadales) of the Mekong Delta. *Inl. Wat. Biol.* **2020**, *13*, 349–357. [CrossRef]
44. Němcová, Y.; Rott, E. Diversity of silica-scaled chrysophytes in high-altitude Alpine sites (North Tyrol, Austria) including a description of *Mallomonas pechlaneri* sp. nov. *Cryptogam., Algol.* **2018**, *39*, 63–83. [CrossRef]
45. Gusev, E.S.; Čertnerová, D.; Škaloudová, M.; Škaloud, P. Exploring cryptic diversity and distribution patterns in the *Mallomonas kalinae/rasilis* species complex with a description of a new taxon — *Mallomonas furtiva* sp. nov. *J. Euk. Microbiol.* **2018**, *65*, 38–47. [CrossRef] [PubMed]
46. Hansen, P.; Kristiansen, J. *Mallomonas madagascariensis*, *M. lemuriocellata* and *M. crocodilorum* (Synurophyceae), three new species from Madagascar. *Nord. J. Bot.* **1995**, *15*, 215–223. [CrossRef]
47. Cronberg, G. Scaled chrysophytes from the tropics. *Nova Hedw. Beih.* **1989**, *95*, 191–232.
48. Neustupa, J.; Řezáčová, M. The genus *Mallomonas* (Mallomonadales, Synurophyceae) in several Southeast Asian urban water bodies — the biogeographic implications. *Nova Hedw.* **2007**, *84*, 249–259. [CrossRef]
49. Němcová, Y.; Kreidlová, J.; Kosová, A.; Neustupa, J. Lakes and pools of Aquitaine region (France)—A biodiversity hotspot of Synurales in Europe. *Nova Hedw.* **2012**, *95*, 1–24. [CrossRef]
50. Siver, P.A.; Lott, A.M. Fossil species of *Mallomonas* from an Eocene Maar Lake with recessed dome structures: Early attempts securing bristles to the cell covering? *Nova Hedw.* **2012**, *95*, 517–529. [CrossRef]
51. Němcová, Y.; Kreidlová, J.; Pusztai, M.; Neustupa, J. *Mallomonas pumilio* group (Chrysophyceae/Stramenopiles) – a revision based on the scale/scale-case morphology and analysis of scale shape. *Nova Hedw. Beih.* **2013**, *142*, 27–49.
52. Jo, B.Y.; Kim, J.I.; Škaloud, P.; Siver, P.A.; Shin, W. Multigene phylogeny of *Synura* (Synurophyceae) and descriptions of four new species based on morphological and DNA evidence. *Eur. J. Phycol.* **2016**, *51*, 413–430. [CrossRef]
53. Kristiansen, J.; Preisig, H.R. Chrysophyte and haptophyte algae. Part 2: Synurophyceae. In *Süsswasserflora von Mitteleuropa*, 2nd ed.; Büdel, B., Gärtner, G., Krienitz, L., Preisig, H.R., Schagerl, M., Eds.; Spektrum Akademischer Verlag: Berlin–Heidelberg, Germany, 2007; Volume 1, pp. 1–252.
54. Kapustin, D.A.; Gusev, E.S.; Kulikovskiy, M.S. *Mallomonas papuensis* sp. nov. (Chrysophyceae, Synurales), a new species from the high mountain bog pool in Papua province, Indonesia. *Phytotaxa* **2019**, *402*, 281–287. [CrossRef]
55. Vyverman, W. A systematic account of the algal flora of the seasonal swamps in the southern part of Irian Jaya (Indonesia). In *Recent Trends in Algal Taxonomy*; Vidyavati, Mahato, A.K., Eds.; Associated Publishing Co.: New Delhi, India, 2006; Volume 2, pp. 3–19.

56. Croome, R.L.; Tyler, P.A. Distribution of silica-scaled Chrysophyceae (Paraphysomonadaceae and Mallomonadaceae) in Australian inland waters. *Aust. J. Mar. Freshw. Res.* **1985**, *36*, 839–853. [CrossRef]
57. Vyverman, W.; Cronberg, G. Scale bearing chrysophytes from Papua New Guinea. *Nord. J. Bot.* **1993**, *13*, 111–120. [CrossRef]
58. Kapustin, D.A.; Gusev, E.S.; Lilitskaya, G.G.; Kulikovskiy, M.S. Silica-scaled chrysophytes from the Ukrainian Polissia. *Cryptogam., Algol.* **2020**, *41*, 121–135. [CrossRef]
59. Kristiansen, J.; Lind, J.F. Endemicity in silica-scaled chrysophytes. *Nova Hedw. Beih.* **2005**, *128*, 65–83.
60. Kapustin, D.A.; Gusev, E.S. Silica-scaled chrysophytes from West Java (Indonesia) including description of a new *Chrysosphaerella* species. *Nova Hedw. Beih.* **2019**, *148*, 11–20. [CrossRef]
61. Siver, P.A.; Lott, A.M. The scaled chrysophyte flora in freshwater ponds and lakes from Newfoundland, Canada, and their relationship to environmental variables. *Cryptogam. Algol.* **2017**, *38*, 325–347. [CrossRef]
62. Zachos, J.C.; Dickens, G.R.; Zeebe, R.E. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **2008**, *451*, 279–283. [CrossRef]
63. Wolfe, A.P.; Reyes, A.V.; Royer, D.L.; Greenwood, D.R.; Doria, G.; Gagen, M.H.; Siver, P.A.; Westgate, J.A. Middle Eocene CO_2 and climate reconstructed from the sediment fill of a subarctic kimberlite maar. *Geology* **2017**, *45*, 619–622. [CrossRef]
64. Siver, P.A.; Wolfe, A.P. Tropical ochrophyte algae from the Eocene of Northern Canada: A biogeographic response to past global warming. *Palaios* **2009**, *24*, 192–198. [CrossRef]
65. Gusev, E.; Kezlya, E.; Tran, H.; Kulikovskiy, M. *Mallomonas vietnamica* sp. nov. (Synurales, Chrysophyceae), a new species, that shares some features with fossil taxa. *Cryptogam. Algol.* **2021**, *42*, 39–46. [CrossRef]
66. Olefeld, J.L.; Bock, C.; Jensen, M.; Vogt, J.C.; Sieber, G.; Albach, D.; Boenigk, J. Centers of endemism of freshwater protists deviate from pattern of taxon richness on a continental scale. *Sci. Rep.* **2020**, *10*, 14431. [CrossRef] [PubMed]