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The cell of *Synura echinulata* Korshikov. Photo: Dmitry A. Kapustin.

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- Aquatic Sciences & Fisheries Abstracts Part I.
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Cryptogamie, Algologie est distribué en version électronique par / *Cryptogamie, Algologie is distributed electronically by*:

- BioOne® (<http://www.bioone.org/loi/crya>)

Cryptogamie, Algologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Algologie is a fast track journal published by the Museum Science Press, Paris

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Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

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Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*): 0181-1568 / ISSN (électronique / *electronic*): 1776-0984

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Submitted on 15 May 2020 | Accepted on 31 August 2020 | Published on 26 October 2020

Kapustin D. A., Gusev E. S., Lilitskaya G. G. & Kulikovskiy M. S. 2020. — Silica-scaled chrysophytes from the Ukrainian Polissia. *Cryptogamie, Algologie* 41 (12): 121–135. <https://doi.org/10.5252/cryptogamie-algologie2020v41a12>. <http://cryptogamie.com/algologie/41/12>

ABSTRACT

We investigated the silica-scaled chrysophyte flora from the Ukrainian Polissia by means of electron microscopy. Overall, 49 taxa were recorded, including three species each of *Chrysosphaerella* Lauterborn and *Paraphysomonas* De Saedeleer emend. Scoble & Cavalier-Smith, one unidentified *Lepidochromonas* Kristiansen taxon, two *Spiniferomonas* E. Takahashi species, 28 *Mallomonas* Perty taxa and 12 *Synura* Ehrenb. taxa. Only six species have previously been reported from this region and 29 of the taxa encountered in this study are reported for the first time from Ukraine. Two taxa, *Synura petersenii* f. *columnata* Siver and *S. korshikovii* Kapustin & Gusev were found for the second time since their original descriptions. We hypothesize that the latter species is an endemic of Polissia, however, to test this idea it would be necessary to sample the water-bodies from the adjacent territories of Belarus and Russia.

KEY WORDS

Silica-scaled
chrysophytes,
stomatocysts,
SEM,
TEM,
Ukrainian Polissia.

MOTS CLÉS
Chrysophytes à écailles
siliceuses,
stomatocystes,
SEM,
TEM,
Polésie ukrainienne.

RÉSUMÉ

Chrysophytes à écailles siliceuses de la Polésie ukrainienne.

Nous avons étudié la flore de chrysophytes à écailles siliceuses de la Polésie ukrainienne au moyen de la microscopie électronique. Au total, 49 taxons ont été enregistrés, dont trois espèces de *Chrysosphaerella* Lauterborn et *Paraphysomonas* De Saedeleer emend. Scoble & Cavalier-Smith, un taxon de *Lepidochromonas* Kristiansen non identifié, deux espèces de *Spiniferomonas* E. Takahashi, 28 taxons de *Mallomonas* Perty et 12 taxons de *Synura* Ehrenb. Seules six espèces ont été précédemment signalées dans cette région et 29 des taxons rencontrés dans cette étude sont signalés pour la première fois en Ukraine. Deux taxons, *Synura petersenii* f. *columnata* Siver et *S. korshikovii* Kapustin & Gusev ont été trouvés pour la deuxième fois depuis leur description originale. Nous supposons que cette dernière espèce est une endémique de la Polésie, cependant, pour tester cette idée, il serait nécessaire d'échantillonner les masses d'eau des territoires adjacents de la Biélorussie et de la Russie.

INTRODUCTION

The chrysophytes are unicellular or colonial algae characterized by heterokont flagella, chloroplasts with chlorophyll *a* and *c*, and by their endogenous silicified stomatocysts (Kristiansen & Škaloud 2017). The group of silica-scaled chrysophytes is additionally characterized by cells possessing an envelope of siliceous scales, sometimes with associated bristles.

In Ukraine the chrysophyte flora has been studied for over 100 years. Such prominent phycologists as A. A. Korshikov and A. M. Matvienko described many species of silica-scaled chrysophytes based on light microscopy (LM) (Korshikov 1929, 1942; Matvienko 1938, 1941, 1949). Some of these species are considered as valid taxa (e.g. *Chrysosphaerella brevispina* Korshikov, *Synura echinulata* Korshikov, *S. glabra* Korshikov, *S. spinosa* Korshikov, *S. splendida* Korshikov, *S. petersenii* Korshikov, *Mallomonopsis elliptica* Matv. (currently known as *Mallomonas matvienkoae* Asmund & Kristiansen), other taxa were reduced to synonyms (e.g. *Mallomonas mesolepis* var. *spinosa* Matv., *Mallomonas robusta* Matv.) but the scale ultrastructure of many other taxa remains unknown (e.g. *Mallomonopsis clavata* Matv., *Mallomonas bispina* Matv., etc.) and possibly dubious. Despite extensive phycological investigations in Ukraine, electron microscopy has not been used for identification of silica-scaled chrysophytes and Ukraine remains one of the largest regions in Europe without data on chrysophytes (Škaloud et al. 2013b).

Polissia (or Polesie) is a landscape province of the mixed forest zone of the East European Plain which is situated on the territory of Poland, Belarus, Ukraine and Russia. Ukrainian Polissia is situated in the northern part of Ukraine and occupies approximately 20% of its territory. The characteristic features of the Polesian landscapes are weakly differentiated relief, a significant spread of glacial water sand deposits and large areas of bogs, which reaches 6.3% (Andrienko 2006).

The chrysophytes of the Ukrainian Polissia are still poorly known. According to Dogadina & Gorbulin (2001) only 11% of the species composition of this group in Ukraine are known from Ukrainian Polissia. All previous records of silica-scaled chrysophytes have been based almost exclusively on light microscopical observations. Kapustin & Tsarenko (2013) identified only five species from Polesian Nature Reserve by means

of scanning and transmission electron microscopy (SEM and TEM respectively), but the illustrations were not given. Kapustin & Gusev (2015) described a new species, *Synura korshikovii* Kapustin & Gusev, from the waterbodies of Polesian Nature Reserve. Recently, a new species, *Mallomonas teres* Nemcova & Kapustin, has been described (Nemcova & Kapustin 2019). The distribution of this rare species is restricted to a few peat-bog localities, two in Sweden and one in Ukraine.

The aim of this study is to explore the biodiversity of silica-scaled chrysophytes in water bodies from Ukrainian Polissia by means of electron microscopy.

MATERIAL AND METHODS

Material for this study was collected from 2002 to 2015 by G. Lilitkaya and D. Kapustin. Additionally, we studied ten older samples preserved in 4% formaldehyde solution and deposited at the Phycological Herbarium of the National Herbarium of Ukraine (KW-A). A total of 52 samples were examined but silica-scaled chrysophytes were observed in 19 samples only (Table 1). Plankton samples were taken with a plankton net (mesh size 20 µm). Samples from shallow peat-bog pools were obtained by squeezing water from *Sphagnum* L. mosses. Environmental variables (temperature, pH and conductivity) were measured *in situ* using a Hanna Combo (HI 98129, Hanna Instruments, United States) device.

For electron microscopical studies, an aliquot of the sample was initially washed by repeated centrifugation in deionized water to remove fixative and digested for 4-5 minutes in sulphuric acid with potassium dichromate, followed by three washings. Subsequently, several drops were placed on aluminum stubs, coated with gold for 10 minutes and observed with a JSM-6060 LA (M. G. Kholodny Institute of Botany NANU, Kyiv, Ukraine) or a JEOL 6510 LV (Papanin Institute for Biology of Inland Waters RAS, Borok, Russia) scanning electron microscope (SEM). For transmission electron microscopy (TEM) several drops were dried onto formvar-coated grids (EMS FF200-Cu-50, Electron Microscopy Sciences) and observed with a JEM-1011 (Papanin Institute for Biology of Inland Waters RAS, Borok, Russia).

TABLE 1. — List of the investigated sampling sites and values of selected environmental parameters (when available).

No.	Name of the site	Date	Latitude	Longitude	Temp °C	pH	Cond µS·cm ⁻¹
1	Lake Svitiáz, Volyn Region, Shatsk National Nature Park	4.VIII.1976	51°29'35.2"N	23°52'43.5"E	n/a	n/a	n/a
2	Pond in Vidradnyi park, Kyiv City	28.X.2002	50°26'02.4"N	30°25'32.7"E	8	7.2	n/a
3	Lake Serednie Vyhuryvske, Kyiv City	15.VI.2003	50°30'30.54"N	30°37'30.56"E	19	7.4	n/a
4	Lake Serednie Vyhuryvske, Kyiv City	26.IV.2014	50°30'30.54"N	30°37'30.56"E	15	7.2	n/a
5	Lake Horashchykha, Pushcha-Vodytsia, Kyiv City	28.VIII.2007	50°32'05.3"N	30°21'01.4"E	17	7.6	n/a
6	Lake Horashchykha, Pushcha-Vodytsia, Kyiv City	31.V.2012	50°32'05.3"N	30°21'01.4"E	n/a	n/a	n/a
7	Lake Holube near Oleshnia, Chernihiv Region	26.VI.2013	51°57'51.0"N	31°09'54.3"E	n/a	n/a	n/a
8	Ditch in block 47 of Selezivka forestry in Polessian Nature Reserve	01.VIII.2008	51°29'38.3"N	28°03'48.7"E	n/a	n/a	n/a
9	Pond in block 50 of Selezivka forestry in Polessian Nature Reserve	15.VIII.2009	51°29'09.9"N	28°03'20.7"E	22	7.5	n/a
10	Pond "Lake Hrybove", buffer zone of Polessian Nature Reserve	13.IX.2008	51°30'25.2"N	28°37'33.6"E	n/a	n/a	n/a
11	Pond "Lake Hrybove", buffer zone of Polessian Nature Reserve	25.III.2015	51°30'03.1"N	28°06'23.5"E	9	6.67	64
12	Pond on Bolotnytsia river, Polessian Nature Reserve	25.III.2015	51°32'09.9"N	28°06'11.2"E	11	6.12	59
13	Zholobnytsia river, Polessian Nature Reserve	31.VII.2008	51°32'52.9"N	28°04'20.7"E	n/a	n/a	n/a
14	Zholobnytsia river, Polessian Nature Reserve	11.V.2011	51°32'15.5"N	28°03'46.5"E	21	5.7	10
15	Peat-bog pool in block 32 of Selezivka forestry in Polessian Nature Reserve	27.IX.2011	51°30'25.2"N	28°37'33.6"E	n/a	n/a	n/a
16	Oster river, Nizhyn, Chernihiv Region	19.V.2013	51°3'24.14"N	31°51'7.06"E	18	8.4	220
17	Oster river, Nizhyn, Chernihiv Region	27.IV.2014	51°03'01.6"N	31°52'52.3"E	n/a	n/a	n/a
18	Oster river, Nizhyn, Chernihiv Region	21.III.2015	51°03'01.6"N	31°52'52.3"E	n/a	n/a	n/a
19	Lake, Trukhaniv Island, Kyiv City	09.IX.2014	50°28'17.0"N	30°32'29.0"E	19	7.2	n/a

RESULTS

A total of 49 taxa of silica-scaled chrysophytes were recorded in the water bodies of Ukrainian Polissia, including three *Chrysosphaerella* Lauterborn, three *Paraphysomonas* De Saedeleer emend. Scoble & Cavalier-Smith, one *Lepidochromonas* Kristiansen, two *Spiniferomonas* E.Takahashi, 28 *Mallomonas* Perty and 12 *Synura* Ehrenb. (Table 2). Among them, only six species (*Mallomonas acaroides* Perty emend. Iwanoff, *M. caudata* Iwanoff, *M. tonsurata* Teiling, *Synura spinosa*, *S. petersenii* and *S. uvella* Ehrenb. emend. Korshikov) have previously been reported in the region (Dogadina 2006; Scherbak *et al.* 2011; Burova & Zhezhera 2013). Twenty-nine taxa are reported for the first time in Ukraine (Table 2).

Most taxa occurred in a single or a few locations (Table 2). None of the taxa were found in all localities and the average number was five per site. The most species-rich site was the peat-bog pool in Polessian Nature Reserve (site 12). Sometimes in early spring silica-scaled chrysophytes developed in mass quantities (sites 11, 12 and 18).

New and noteworthy taxa for the Ukrainian flora are commented upon below.

Family CHRYSOSPHAERELLACEAE Kapustin nom. prov.
Genus *Chrysosphaerella* Lauterborn

Chrysosphaerella coronacircumspina Wujek & Kristiansen
(Fig. 1B)

Chrysosphaerella solitaria Preisig & D.J.Hibberd, *Plant Systematics and Evolution* 129: 136 (1978).

DISTRIBUTION. — Widely distributed (Kristiansen 2000).

REMARKS

This species is easily distinguishable from other *Chrysosphaerella* species by its spine-scales in which the secondary base-plate is attached directly to the primary base-plate.

We observed *C. coronacircumspina* during encystment. The stomatocyst was spherical (diameter 11.6 µm) with psilate surface. The collar is cylindrical (diameter 4.19 µm, height 0.8 µm). The pore morphology is unknown.

Preisig & Takahashi (1978) illustrated the stomatocyst of *C. solitaria* Preisig & E.Takahashi but the pore and collar remained not visible. According to these authors the dimensions of stomatocysts were 13–14.7 µm. Balonov (1980) also observed spherical stomatocysts (diameter 12.3–14.8 µm) but they lacked the collar. Recently, Firsova *et al.* (2017) revealed that stomatocyst 156 Zeeb & Smol 1993 is produced by *C. coronacircumspina*.

Family PARAPHYSOMONADACEAE Preisig & D.J.Hibberd
Genus *Paraphysomonas* De Saedeleer
emend. Scoble & Cavalier-Smith

Paraphysomonas acuminata Scoble & Cavalier-Smith
(Fig. 1C)

Paraphysomonas imperforata Lucas *pro parte*, *Journal of the Marine Biological Association of the United Kingdom* 47: 330 (1967).

DISTRIBUTION. — Probably widely distributed; all previous freshwater records of *P. imperforata* should be revised.

TABLE 2. — Occurrence of silica-scaled chrysophytes found in the Ukrainian Polissia. Species in **bold** are new for Ukraine.

No. Taxon	Site number																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 <i>Chrysosphaerella brevispina</i> Korshikov (Fig. 1A)									+		+	+			+				
2 <i>Chrysosphaerella coronacircumspina</i> Wujek & Kristiansen (Fig. 1B)																			+
3 <i>Chrysosphaerella longispina</i> Lauterborn (Fig. 1I)								+		+									
4 <i>Paraphysomonas acuminata</i> Scoble & Cavalier-Smith (Fig. 1C)											+								
5 <i>Paraphysomonas truncata</i> (Preisig & D.J.Hibberd) Scoble & Cavalier-Smith (Fig. 1D)															+				
6 <i>Paraphysomonas</i> De Saedeleer emend. Scoble & Cavalier-Smith sp. (Fig. 1E)							+			+					+				
7 <i>Lepidochromonas</i> Kristiansen sp. (Fig. 1F)												+							
8 <i>Spiniferomonas bourrellyi</i> E.Takahashi (Fig. 1G)							+												
9 <i>Spiniferomonas</i> cf. <i>trioralis</i> E.Takahashi (Fig. 1H)							+												
10 <i>Mallomonas acaroides</i> Perty emend. Iwanoff (Fig. 2A)	+									+									
11 <i>Mallomonas</i> cf. <i>akrokomos</i> Ruttner (Fig. 2B)				+			+												
12 <i>Mallomonas annulata</i> (D.E.Bradley) K.Harris (Fig. 2C)				+															
13 <i>Mallomonas asmundiae</i> (Wujek & van der Veer) K.H.Nicholls (Fig. 2D)											+	+							
14 <i>Mallomonas calceolus</i> D.E.Bradley (Fig. 2E, F)									+				+						
15 <i>Mallomonas canina</i> Kristiansen (Fig. 2G)								+							+				
16 <i>Mallomonas caudata</i> Iwanoff emend. Willi Krieg. (Fig. 2H)	+		+		+	+									+		+		
17 <i>Mallomonas corcontica</i> (Kalina) L.Ş.Péterfi & Momeu (Fig. 2I)															+				
18 <i>Mallomonas costata</i> Dürschmidt (Fig. 2J)									+	+				+					
19 <i>Mallomonas crassisquama</i> (Asmund) Fott (Fig. 2K)							+												
20 <i>Mallomonas cratis</i> K.Harris & D.E.Bradley (Fig. 2L)			+														+		
21 <i>Mallomonas elongata</i> Reverdin (Fig. 2M)						+		+	+						+				
22 <i>Mallomonas heterospina</i> J.W.G.Lund (Fig. 2N)				+															
23 <i>Mallomonas mangofera</i> var. <i>foveata</i> (Dürschmidt) Kristiansen (Fig. 2O)													+						
24 <i>Mallomonas matvienkoeae</i> Asmund & Kristiansen (Fig. 3A)														+					
25 <i>Mallomonas ouradion</i> K.Harris & D.E.Bradley (Fig. 3B)									+										
26 <i>Mallomonas</i> cf. <i>pseudomatvienkoeae</i> B.YJo, W.Shin, H.S.Kim, Siver & R.A.Andersen (Fig. 3C)									+										
27 <i>Mallomonas paludosa</i> Fott (Fig. 3D)															+				
28 <i>Mallomonas papillosa</i> K.Harris & D.E.Bradley emend. K.Harris (Fig. 3E, F)															+				
29 <i>Mallomonas pillula</i> f. <i>valdiviana</i> Dürschmidt (Fig. 3G)														+					
30 <i>Mallomonas punctifera</i> Korshikov (Fig. 3H)										+									
31 <i>Mallomonas pugio</i> D.E.Bradley (Fig. 3I)									+						+				
32 <i>Mallomonas rasilis</i> Dürschmidt (Fig. 3J)																+			
33 <i>Mallomonas schwemmlei</i> Glenk emend. Glenk & Fott (Fig. 3K, L)												+	+						
34 <i>Mallomonas striata</i> Asmund (Fig. 3M)				+															
35 <i>Mallomonas teilingii</i> W.Conrad (Fig. 3N)																		+	
36 <i>Mallomonas teres</i> Nemcova & Kapustin (Fig. 3O)															+				
37 <i>Mallomonas tonsurata</i> Teiling (Fig. 3P)				+	+											+			
38 <i>Synura conopea</i> Kynčlová & Škaloud (Fig. 4A)																		+	
39 <i>Synura echinulata</i> Korshikov (Fig. 4B)								+		+			+						
40 <i>Synura glabra</i> Korshikov (Fig. 4C)		+			+														
41 <i>Synura heteropora</i> Škaloud, Škaloudová & Procházková (Fig. 4D)												+							
42 <i>Synura korshikovii</i> D.Kapustin & E.S.Gusev (Fig. 4E)					+						+	+							
43 <i>Synura macropora</i> Škaloud & Kynčlová (Fig. 4F)																		+	
44 <i>Synura petersenii</i> f. <i>petersenii</i> Korshikov (Fig. 4G)			+		+						+	+		+		+	+		
45 <i>Synura petersenii</i> f. <i>columnata</i> Siver (Fig. 4H)											+	+							
46 <i>Synura sphagnicola</i> (Korshikov) Korshikov (Fig. 4I)								+	+					+					
47 <i>Synura spinosa</i> f. <i>spinosa</i> Korshikov (Fig. 4J)						+	+			+					+	+			
48 <i>Synura spinosa</i> f. <i>longispina</i> J.B.Petersen & J.B.Hansen (Fig. 4K)												+							
49 <i>Synura uvella</i> Ehrenb. emend. Korshikov (Fig. 4L)		+		+			+									+		+	

REMARKS

This species has oval basal plate of scales ($1.7 \times 1.3 \mu\text{m}$) with annulus and long spine ($4.95 \mu\text{m}$) with acutely pointed tip.

Our specimens could be identified as *P. imperforata* Lucas *sensu lato*. Scoble & Cavalier-Smith (2014) pointed out that the spine length of the marine species *P. imperforata* is $\frac{1}{10}$ the spine length of *P. acuminata* which occurs in freshwaters.

Paraphysomonas truncata (Preisig & D.J.Hibberd)
Scoble & Cavalier-Smith
(Fig. 1D)

DISTRIBUTION. — Great Britain (Preisig & Hibberd 1982), Denmark (Vørs *et al.* 1990), Finland (Ikävalko 1994); rare species.

REMARKS

This species differs from other *Paraphysomonas* taxa in having truncate and tapering spine tip.

Paraphysomonas De Saedeleer sp.
(Fig. 1E)

REMARKS

Several scales with broken spines were observed but it is impossible to identify them since the spine length and the shape of a tip are important taxonomic features (Scoble & Cavalier-Smith 2013, 2014).

In Ukraine only *Paraphysomonas vestita* (A.C.Stokes) De Saedeleer has previously been recorded (Korshikov 1929 as *Physomonas vestita* A.C.Stokes; Shevchuk 2007a, b). More than 20 taxa described by Scoble & Cavalier-Smith (2014) were previously lumped together as *Paraphysomonas vestita*. So, the identity of this species is unclear and a neotypification is required.

Family LEPIDOCROMONADACEAE Kapustin & Guiry
Genus *Lepidochromonas* Kristiansen

Lepidochromonas Kristiansen sp.
(Fig. 1F)

REMARKS

Scoble & Cavalier-Smith (2014) removed *Paraphysomonas* species with meshed scales into a new genus *Clathromonas* Scoble & Cavalier-Smith based on scale morphology and phylogenetic analyses of 18S rDNA sequences. However, this name is illegitimate under the rules of the *International Code of Nomenclature for algae, fungi and plants*, so Kapustin & Guiry (2019) reinstated the genus *Lepidochromonas* Kristiansen.

We could not identify this species based on the single mesh scale observed in this study. The outer ring of the mesh scale bears holes of different diameters, the larger holes separated by 4-5 smaller ones. It is very likely that this scale belongs to an undescribed *Lepidochromonas* species.

Family *incertae sedis*
Genus *Spiniferomonas* E.Takahashi

Spiniferomonas bourrellyi E.Takahashi
(Fig. 1G)

DISTRIBUTION. — Widely distributed (Kristiansen 2000).

REMARKS

The plate scales of this species are circular to elliptical with weakly developed lacuna. The spine scales have conical bases and each tapers to a pointed apex.

Spiniferomonas cf. *trioralis* E.Takahashi
(Fig. 1H)

DISTRIBUTION. — Cosmopolitan (Kristiansen 2000).

REMARKS

As we found only isolated spine-scales that had spines that were triangular in cross section, exact identification is impossible.

Family MALLOMONADACEAE Diesing
Genus *Mallomonas* Perty

Mallomonas cf. *akrokomos* Ruttner
(Fig. 2B)

DISTRIBUTION. — Cosmopolitan (Kristiansen 2000).

REMARKS

We did not observe the scales of *M. akrokomos* but we found its characteristic stomatocyst (Cronberg 1980). The stomatocyst was oval ($9.45\text{--}10.85 \times 5.75\text{--}8.68 \mu\text{m}$) with a smooth surface. The collar is cylindrical, may be situated centrally or acentrically on the posterior hemisphere and often has a fluted outer margin (collar diameter $2.97\text{--}3.19 \mu\text{m}$; height $0.9\text{--}1.0 \mu\text{m}$). The pore was not observed.

Mallomonas annulata (D.E.Bradley) K.Harris
(Fig. 2C)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007).

REMARKS

A single domeless body scale was observed. The anterior flanges and shield of the scale are covered with papillae and some of them are joined so as to form a reticulate pattern.

Mallomonas asmundiae (Wujek & van der Veer)
K.H.Nicholls
(Fig. 2D)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007).

REMARKS

Initially this taxon was described as a variety of *Mallomonas cratis* K.Harris & D.E.Bradley, *M. cratis* var. *asmundiae* Wujek & van der Veer, and later it was raised to the rank of species. In *Mallomonas asmundiae* the dome is ornamented by the parallel ribs whereas in *M. cratis* the ribs are U-shaped. Additionally,

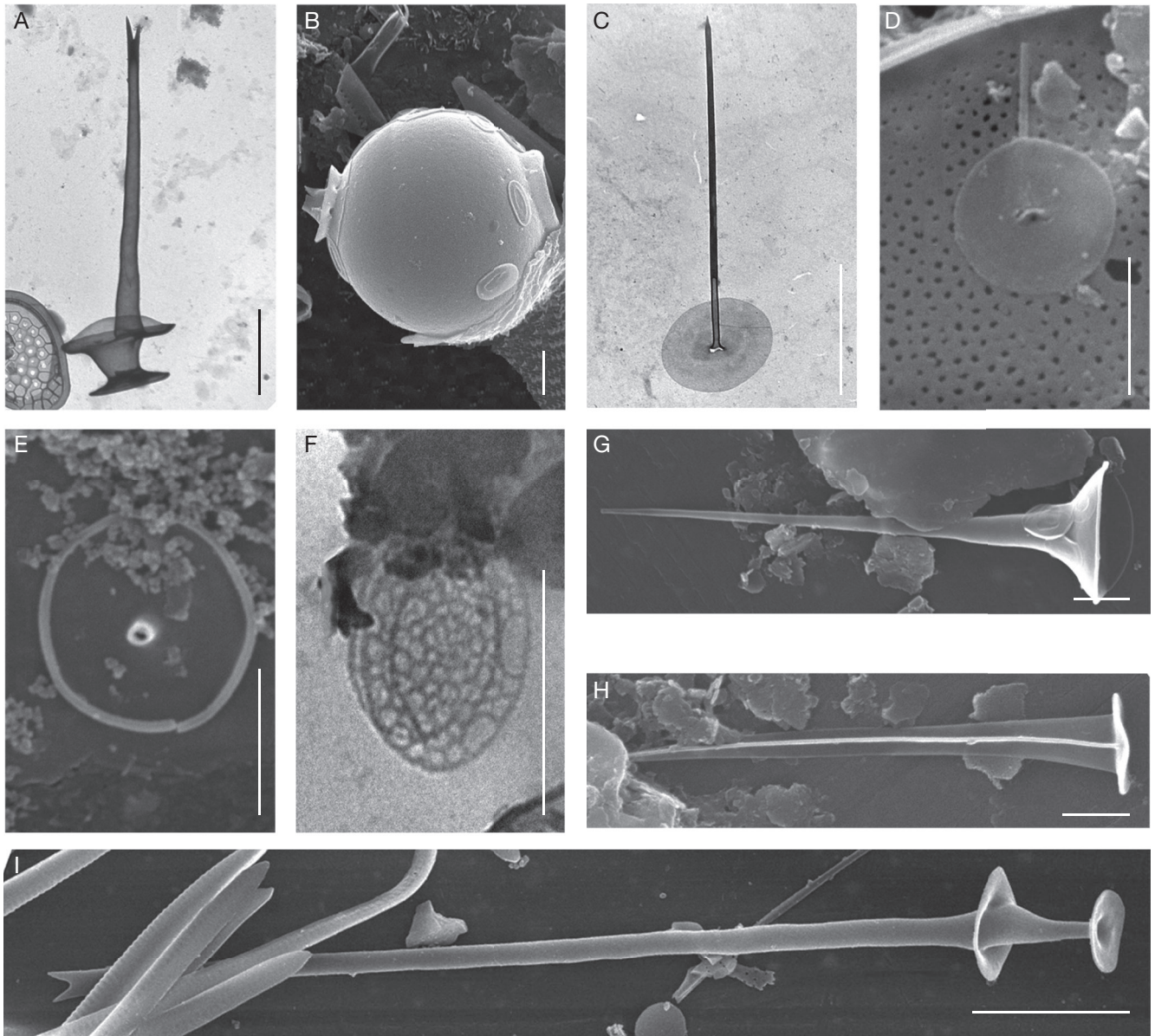


FIG. 1. — *Chrysosphaerella* Lauterborn, *Paraphysomonas* De Saedeleer emend. Scoble & Cavalier-Smith, *Lepidochromonas* Kristiansen and *Spiniferomonas* E.Takahashi species from the Ukrainian Polissia: **A**, *Chrysosphaerella brevispina* Korshikov, spine scale, TEM; **B**, Stomatocyst of *Chrysosphaerella coronacircumspina* Wujek & Kristiansen with broken spine scale and plate scales, SEM; **C**, *Paraphysomonas acuminata* Scoble & Cavalier-Smith, TEM; **D**, *Paraphysomonas truncata* (Preisig & D.J.Hibberd) Scoble & Cavalier-Smith, TEM; **E**, *Paraphysomonas* sp., scale with broken spine, SEM; **F**, *Lepidochromonas* sp., TEM; **G**, *Spiniferomonas bourrellyi* E.Takahashi, spine scale with plate scales attached to it, SEM; **H**, *Spiniferomonas* cf. *trioralis* E.Takahashi, spine scale, SEM; **I**, *Chrysosphaerella longispina* J.B.Petersen & J.B.Hansen, SEM. Scale bars: A, D, E, G, H, 1 µm; B, C, 2 µm; F, 0.5 µm; I, 5 µm.

the scales of *M. asmundiae* have pronounced lateral incurvings and a more densely striated posterior flange (Siver 1991).

Mallomonas calceolus D.E.Bradley
(Fig. 2E, F)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007; Řezáčová & Neustupa 2007).

REMARKS

We found two scales which look quite different. The first one was recorded from site 9. It represents an anterior scale.

The scale shield and a dome are covered with widely-spaced papillae. The one of the anterior submarginal ribs terminates in a short projection (Fig. 2E). Another scale was recorded from site 13. Its shield is covered with papillae regularly-spaced and arranged in rows and the dome is smooth. A distinct base plate pore is visible at the base of the V-rib (Fig. 2F). The similar scale was depicted by Bradley (1964, pl. 1, fig. 3). Although the number of papillae may significantly vary (Kristiansen 2002), the presence of the base plate pore was not mentioned in the protologue (Bradley 1964). Probably, the scale in Figure 2F belongs to another *Mallomonas* species but more scales are needed to confirm this suggestion.

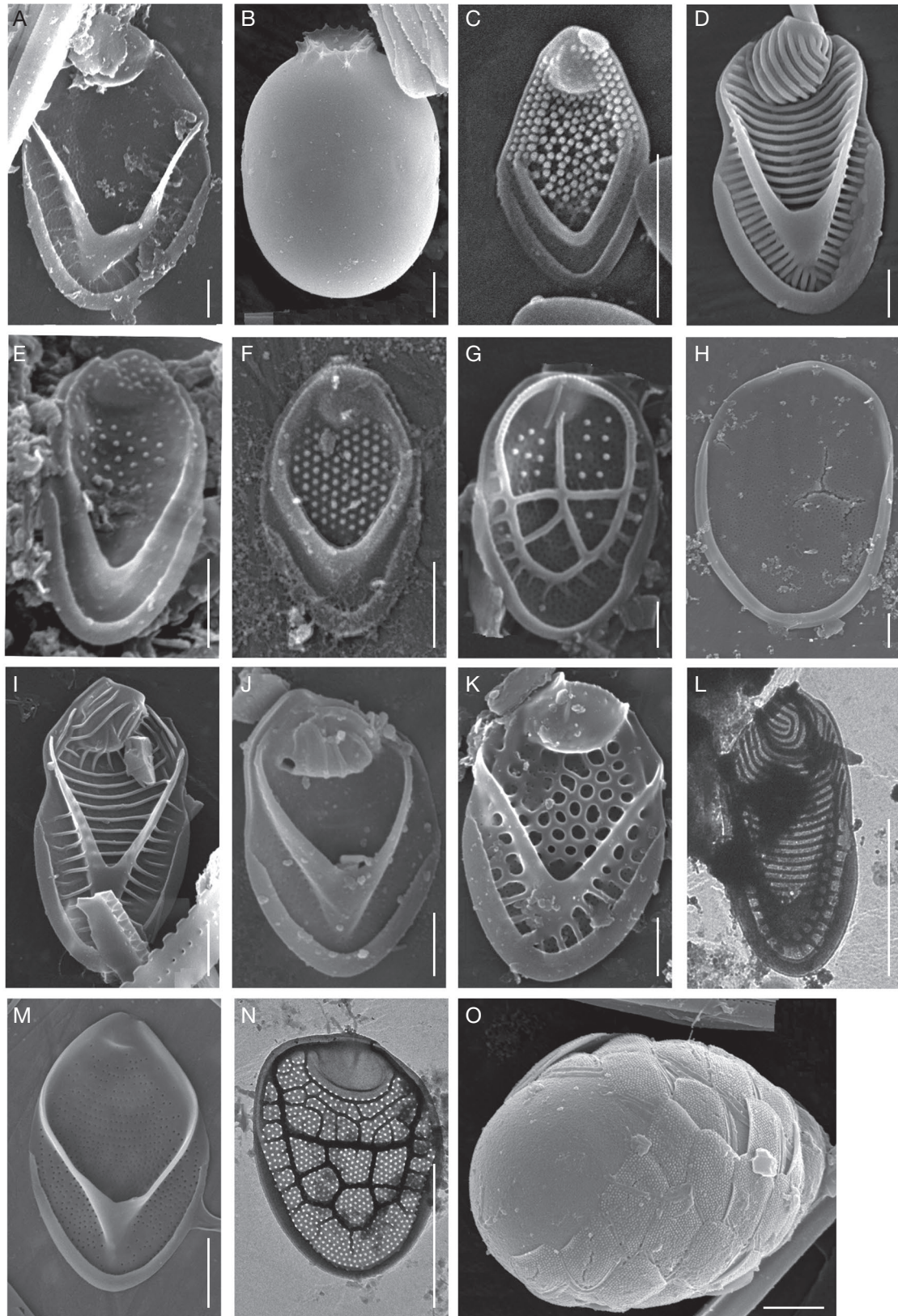


FIG. 2. — *Mallomonas* Perty taxa from the Ukrainian Polissia: **A**, *Mallomonas acaroides* Perty emend. Iwanoff, SEM; **B**, Stomatocyst of *Mallomonas* cf. *akrokomos* Ruttner, SEM; **C**, *Mallomonas annulata* (D.E.Bradley) K.Harris, SEM; **D**, *Mallomonas asmundiae* (Wujek & van der Veer) K.H.Nicholls, SEM; **E**, **F**, *Mallomonas calceolus* D.E.Bradley, SEM; **G**, *Mallomonas canina* Kristiansen, SEM; **H**, *Mallomonas caudata* Iwanoff emend. Willi Krieger, SEM; **I**, *Mallomonas corcontica* (Karlina) L.Ş.Péterfi & Momeu, SEM; **J**, *Mallomonas costata* Dürschmidt, SEM; **K**, *Mallomonas crassisquama* (Asmund) Fott, SEM; **L**, *Mallomonas cratis* K.Harris & D.E.Bradley, TEM; **M**, *Mallomonas elongata* Reverdin, SEM; **N**, *Mallomonas heterospina* J.W.G.Lund, SEM; **O**, Stomatocyst of *Mallomonas mangofera* var. *foveata* (Dürschmidt) covered with scales, SEM. Scale bars: A, D-F, H-K, 1 µm; B, C, L-O, 2 µm; G, 0.5 µm.

Mallomonas canina Kristiansen
(Fig. 2G)

DISTRIBUTION. — Bipolar (Kristiansen & Preisig 2007).

REMARKS

The scale shield of this species is divided by ribs into five meshes and covered with scattered papillae.

Mallomonas corcontica (Kalina) L.Ş.Péterfi & Momeu
(Fig. 2I)

DISTRIBUTION. — Restricted to northern temperate regions (Kristiansen & Preisig 2007; Řezáčová & Neustupa 2007).

REMARKS

The scales of this species are characterized by the struts radiating from the proximal border of the dome (Kristiansen & Preisig 2007).

Mallomonas costata Dürschmidt
(Fig. 2J)

DISTRIBUTION. — Widely distributed (Kristiansen 2000).

REMARKS

Typically, the scale shield has 6-12 curved transversal ribs with one to three rows of pores between them (Kristiansen & Preisig 2007). However, in our material the number of transverse ribs was 2-6 or sometimes they were weakly developed. There is a hole on the posterior border of the dome. Although this feature is clearly visible in published micrographs of *M. costata* (e.g. Dürschmidt 1984; Asmund & Kristiansen 1986) it was not mentioned in the original diagnosis. It is likely that this hole is homologous with the opening of the dome in *M. paludosa* Fott and *M. aperturæ* Siver (Siver 2018). Siver (2018) proposed that the opening on the dome may provide a means for securing bristles to the scales and aiding in bristle rotation.

M. costata has an interesting taxonomic history. Péterfi & Momeu (1981) re-described the species which they identified as *Mallomonopsis robusta* Matv. using transmission electron microscopy and transferred it into the genus *Mallomonas* under the name *Mallomonas robusta* (Matv.) L.Ş.Péterfi & Momeu. Later Dürschmidt (1984) pointed out that material of Péterfi & Momeu was not identical to Matvienko's taxon in several key characters. Moreover, this combination is illegitimate because of a later homonym of *Mallomonas robusta* Matv. Thus, Dürschmidt decided to describe a new species, *M. costata* (Dürschmidt 1984).

Mallomonas crasssquama (Asmund) Fott
(Fig. 2K)

DISTRIBUTION. — Widely distributed (Kristiansen 2000).

REMARKS

This species is closely related to *M. acaroides* (initially it was described as *M. acaroides* var. *crasssquama* Asmund) but the shield of its scales is ornamented with a secondary layer of ribs that form a reticulum (Siver 1991). The most reliable, distinctive character between these two species is the presence of spine-bearing rear scales in *M. crasssquama*; such scales are not present in *M. acaroides* (Kristiansen 2002).

Mallomonas cratis K.Harris & D.E.Bradley
(Fig. 2L)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007).

REMARKS

The scales of this species have the dome ornamented with U-shaped ribs (Kristiansen & Preisig 2007).

Mallomonas heterospina J.W.G.Lund
(Fig. 2N)

DISTRIBUTION. — Widely distributed (Kristiansen 2000).

REMARKS

We observed this species during encystment in late April at 15°C. Interestingly, Cronberg (1989) observed encystment in this species in April-May at 4.2-11°C.

Mallomonas mangofera var. *foveata* (Dürschmidt)
Kristiansen
(Fig. 2O)

DISTRIBUTION. — Cosmopolitan (Kristiansen 2002).

REMARKS

The scales of *M. mangofera* var. *foveata* differ from those of the type variety in having a characteristically arranged row of circular pits with a bordered pore at the bottom (Kristiansen 2002). We found this species during encystment.

Mallomonas matvienkoae Asmund & Kristiansen
(Fig. 3A)

Mallomonopsis elliptica Matv., *Trudy Naukovo-doslidnogo Instytutu Botaniky* 4: 41 (1941).

DISTRIBUTION. — Cosmopolitan (Kristiansen 2002).

REMARKS

This species has been described from Ukraine under the name *Mallomonopsis elliptica* Matv. (Matvienko 1941) and later re-described and transferred to the genus *Mallomonas* (Asmund & Kristiansen 1986).

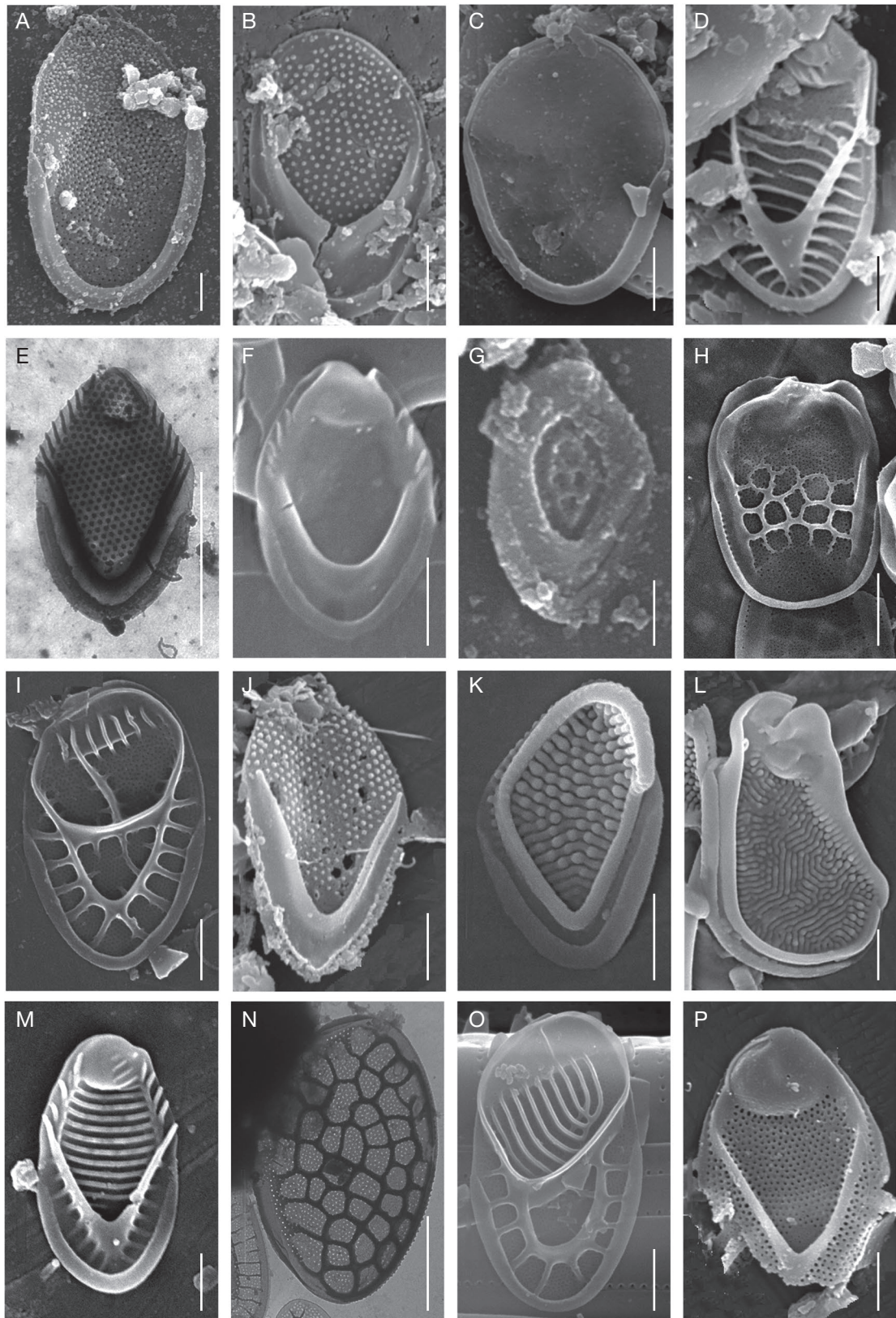


FIG. 3. — *Mallomonas* Perty taxa from the Ukrainian Polissia: **A**, *Mallomonas matvienkoae* Asmund & Kristiansen, SEM; **B**, *Mallomonas ouradion* K.Harris & D.E.Bradley, SEM; **C**, *Mallomonas cf. pseudomatvienkoae* B.Y.Jo, W.Shin, H.S.Kim, Siver & R.A.Andersen, SEM; **D**, *Mallomonas paludosa* Fott; **E**, **F**, *Mallomonas papillosa* K.Harris & D.E.Bradley emend. K.Harris, TEM (E) and SEM (F); **G**, *Mallomonas pillula* f. *valdiviana* Dürschmidt, SEM; **H**, *Mallomonas punctifera* Korshikov, SEM; **I**, *Mallomonas pugio* D.E.Bradley, SEM; **J**, *Mallomonas rasilis* Dürschmidt, SEM; **K**, **L**, *Mallomonas schwemmlei* Glenk emend. Glenk & Fott, body (K) and apical (L) scales, SEM; **M**, *Mallomonas striata* Asmund, SEM; **N**, *Mallomonas teilingii* W.Conrad, SEM; **O**, *Mallomonas teres* Nemcova & Kapustin, SEM; **P**, *Mallomonas cf. tonsurata* Teiling, SEM. Scale bars: A-F, I-M, O, P, 1 μ m; G, 0.5 μ m; H, N, 2 μ m.

The *Mallomonas matvienkoae* species complex is a rather diverse group of pseudocryptic taxa and several new species, namely *M. lacuna* B.Y.Jo, W.Shin, H.S.Kim, Siver & R.A.Andersen, *M. hexareticulata* B.Y.Jo, W.Shin, H.S.Kim, Siver & R.A.Andersen, *M. pseudomatvienkoae* B.Y.Jo, W.Shin, H.S.Kim, Siver & R.A.Andersen, *M. sorohexareticulata* B.Y.Jo, W.Shin, H.S.Kim, Siver & R.A.Andersen, *M. pleuriformis* Siver, Lott, B.Y.Jo, W.Shin, H.S.Kim & R.A.Andersen (Jo *et al.* 2013), *M. paragrandidis* Gusev (2015) and *M. lamii* Gusev *et al.* (2019a). Both recent and fossil taxa have been described from this group.

Mallomonas ouradion K.Harris & D.E.Bradley
(Fig. 3B)

DISTRIBUTION. — This species has scattered distribution (Kristiansen & Preisig 2007).

REMARKS

Except for the absence of a dome the scales of *Mallomonas ouradion* are virtually identical to those of *M. calceolus* (Siver 1991).

Mallomonas paludosa Fott
(Fig. 3D)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007).

REMARKS

The scales of *M. paludosa* have a large dome with a prominent hole along the proximal border. The shield has parallel transverse ribs which are aligned with those on the posterior flange (Siver 1991).

Mallomonas papillosa K.Harris & D.E.Bradley
emend. K.Harris
(Fig. 3E, F)

DISTRIBUTION. — Cosmopolitan (Kristiansen 2000).

REMARKS

Besides typical scales with a shield densely covered with papillae (Fig. 3E), we observed scales with nearly smooth shields (Fig. 3F). Similar nearly smooth scales were observed by Balonov (1978) from rivers in the Yaroslavl Region in Russia, Péterfi *et al.* (1998) from the bog-lake Baláta-tó in Hungary, and Gusev *et al.* (2019b) from rivers in Nizhniy Novgorod in Russia. Since we recorded the different scales from the different samples they may represent two separate taxa.

Mallomonas pillula f. *valdiviana* Dürschmidt
(Fig. 3G)

DISTRIBUTION. — Bipolar (Kristiansen & Vigna 1996; Kristiansen & Preisig 2007).

REMARKS

The scales of *M. pillula* f. *valdiviana* differ from the type form in having strong ribs forming a reticulum of irregularly-shaped meshes in the central area of the shield (Kristiansen 2002).

Mallomonas cf. *pseudomatvienkoae* B.Y.Jo, W.Shin,
H.S.Kim, Siver & R.A.Andersen
(Fig. 3C)

DISTRIBUTION. — South Korea (Jo *et al.* 2013); Russia (Gusev *et al.* 2019b); probably a widely distributed taxon but often erroneously identified as *M. matvienkoae*.

REMARKS

The scales of this species have base-plate pores restricted to the distal part and a thick secondary layer that covers the distal one-half to two-thirds of the scale. A single scale observed by us was entirely covered by the secondary layer of silica.

Mallomonas pugio D.E.Bradley
(Fig. 3I)

DISTRIBUTION. — Restricted to northern temperate regions (Kristiansen & Preisig 2007; Řezáčová & Neustupa 2007).

REMARKS

The dome of the scales is marked with five to eight evenly spaced parallel ribs. The longitudinal apical rib of the shield is continuous with ribs on the dome (Siver 1991).

Mallomonas rasilis Dürschmidt
(Fig. 3J)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007).

REMARKS

The scales of this species lack an anterior submarginal rib. The scale shield, anterior flanges and dome are covered with papillae.

Mallomonas schwemmlei Glenk emend. Glenk & Fott
(Fig. 3K, L)

DISTRIBUTION. — Restricted to northern temperate regions (Kristiansen & Preisig 2007; Řezáčová & Neustupa 2007). Our record of *M. schwemmlei* represents the eastern boundary of its distribution, based on current information.

REMARKS

This species has three types of scales with a fingerprint-like rib pattern which consists of semicircular ribs and straight or irregularly-curved parallel ribs (Kristiansen 2002).

Earlier authors synonymized *M. schwemmlei* with *M. coronifera* Matv. (Fott & Ettl 1959) but Glenk & Fott (1971)

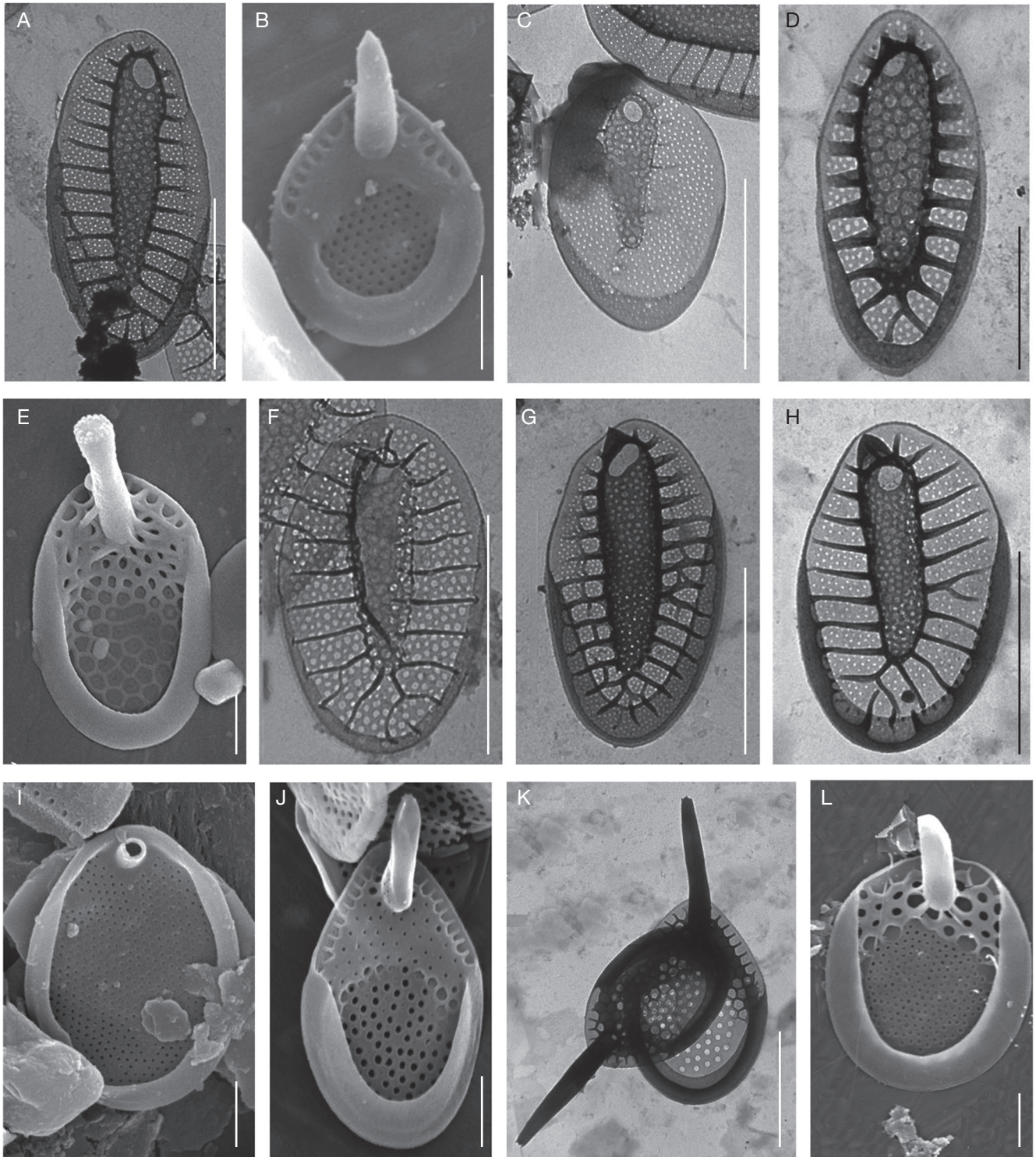


FIG. 4. — *Synura* Ehrenb. taxa from the Ukrainian Polissia: **A**, *Synura conopea* Kynčlová & Škaloud, TEM; **B**, *Synura echinulata* Korshikov, SEM; **C**, *Synura glabra*, TEM; **D**, *Synura heteropora* Škaloud, Škaloudová & Procházková, TEM; **E**, *Synura korshikovii* Kapustin & Gusev, SEM; **F**, *Synura macropora* Škaloud & Kynčlová, TEM; **G**, *Synura petersenii* Korshikov, TEM; **H**, *Synura petersenii* f. *columnata* Siver, TEM; **I**, *Synura sphagnicola* (Korshikov) Korshikov, SEM; **J**, *Synura spinosa* f. *spinosa* Korshikov, SEM; **K**, *Synura spinosa* f. *longispina* J.B.Petersen & J.B.Hansen, TEM; **L**, *Synura uvella* Ehrenb. emend. Korshikov, SEM. Scale bars: A, C, D, F–H, K, 2 μ m; B, E, I, J, L, 1 μ m.

re-evaluated earlier observations and revealed that both species are independent. Unfortunately, the scales ultrastructure of *M. coronifera* is still unknown and it has been considered as a dubious species (Kristiansen & Preisig 2007).

Mallomonas striata Asmund
(Fig. 3M)

DISTRIBUTION. — Widely distributed (Řezáčová & Neustupa 2007) or cosmopolitan (Kristiansen & Preisig 2007).

REMARKS

In this species the scale shield is marked with about 12 parallel, equally spaced, transverse ribs (Siver 1991).

Mallomonas teilingii W.Conrad
(Fig. 3N)

DISTRIBUTION. — The species restricted to northern temperate regions (Kristiansen & Preisig 2007; Řezáčová & Neustupa 2007).

REMARKS

The scales of this species are suboval or somewhat irregular, domeless, almost completely surrounded by the proximal border. Base plate has small irregular pores and an irregular secondary meshwork (Kristiansen & Preisig 2007). This species could be easily recognized with a light microscope (Kristiansen 1989).

Mallomonas teres Nemcova & Kapustin
(Fig. 3O)

DISTRIBUTION. — Sweden and Ukraine (Nemcova & Kapustin 2019).

REMARKS

This recently described species is similar to *M. pugio* but its scales have a smooth dome and a distal part with 8-12 parallel curved ribs.

Family SYNURACEAE Lemmerm. emend. B.Y.Jo,
J.I.Kim, W.Shin, Škaloud & Siver
Genus *Synura* Ehrenb.

Synura conopea Kynčlová & Škaloud
(Fig. 4A)

DISTRIBUTION. — Probably widely distributed; so far this species is recorded from Czech Republic (Škaloud *et al.* 2012), Russia (Gusev *et al.* 2016, 2017) and Korea (Jo & Kim 2017).

REMARKS

In contrast to *S. petersenii sensu stricto* (Fig. 4G), which has a nearly cylindrical keel, *S. conopea* has a keel that is much more broadened apically. The struts which extend from the

keel to the edge of the scale are not interconnected by transverse folds whereas in *S. petersenii sensu stricto* the struts are interconnected. Additionally, *S. conopea* differs in having somewhat smaller scale dimensions and large and closely arranged keel pores (Škaloud *et al.* 2012).

Synura heteropora Škaloud, Škaloudová & Procházková
(Fig. 4D)

DISTRIBUTION. — Austria, Czech Republic, Estonia, Ireland, Norway, Sweden and the United Kingdom (Škaloud *et al.* 2014).

REMARKS

The scales of this species have 22-28 struts. The keel pores (these are actually not pores, but rather reticulations [P.A.Siver, pers. comm.]) are significantly larger than base plate pores (Škaloud *et al.* 2014).

Synura korshikovii Kapustin & Gusev
(Fig. 4E)

DISTRIBUTION. — In the present study this species has been recorded for the second time since its description (Kapustin & Gusev 2015); this species restricted to Polissia so far.

REMARKS

This recently-described species has scales which are covered with a hexagonal reticulum and spine with a flat apex terminating in a few rows of papillae-like teeth.

Synura macropora Škaloud & Kynčlová
(Fig. 4F)

DISTRIBUTION. — Probably widely distributed; many previous records have been attributed to *Synura petersenii sensu lato* (Škaloud *et al.* 2012; Gusev *et al.* 2016).

REMARKS

This species can easily be distinguished from the other taxa of the *Synura petersenii*-complex by its rounded scales with large keel and large base plate pores (Škaloud *et al.* 2012).

Synura petersenii f. *columnata* Siver
(Fig. 4H)

DISTRIBUTION. — United States (Siver 1988).

REMARKS

Differs from the other taxa of *Synura petersenii*-complex in that the inner portion of the rim is ornamented with row of posts (in SEM) or dots (in TEM) (Siver 1988; Škaloud *et al.* 2012). Škaloud *et al.* (2012) believe that this forma does not belong to *S. petersenii sensu stricto* but it is premature to raise this forma to the rank of species.

Synura spinosa f. *longispina* J.B.Petersen & J.B.Hansen
(Fig. 4K)

DISTRIBUTION. — Widely distributed (Kristiansen & Preisig 2007).

REMARKS

The scales of this form differ from *S. spinosa* f. *spinosa* in having very long spine being longer than the plate (Kristiansen & Preisig 2007).

DISCUSSION

There are 61 taxa of silica-scaled chrysophytes recorded from Ukraine (Dogadina 2006; Gusev *et al.* 2016; Kapustin & Gusev 2015, 2016; Siver *et al.* 2018; Nemcova & Kapustin 2019). Scale ultrastructure is known for only 32 of them. Unfortunately, many taxon identifications were made with a light microscopy only, so their correct identifications are dubious and their records require confirmation. In our study, 49 taxa of silica-scaled chrysophytes were recorded from Ukrainian Polissia, including 29 taxa which are new records for the Ukrainian algal flora.

Most of the taxa found in this study are widely distributed and cosmopolitan. They have been reported from adjacent countries and they were not found earlier in Ukraine, mainly due to the lack of electron microscope observations as Ukrainian chrysophytes were identified for many years only by means of LM. Some taxa are interesting in terms of biogeography. *Mallomonas schwemmlei* is a northern temperate species and our record represents the eastern boundary of its distribution. *Mallomonas teres*, a newly-described species, is characterized by having a disjunct distribution. Two of the three known localities are in Northern Sweden and one is in Polessian Nature Reserve. A new record of *Synura korshikovii* in Kyiv (site 5) may suggest that it is restricted to Polissia. To test this hypothesis it would be necessary to sample the water-bodies from the adjacent territories of Belarus and Russia.

Our records of *Synura petersenii* f. *columnata* from two closely-spaced waterbodies are the first ones since the taxon was described from the United States (Siver 1988). For many years *Synura petersenii* has been treated as a polymorphic species with numerous intraspecific taxa described (Kristiansen & Preisig 2007). Molecular phylogenetic studies showed that *Synura petersenii* represents a diverse complex of pseudo-cryptic species (Boo *et al.* 2010; Kynčlová *et al.* 2010). Subsequently, more than ten species have been described and a species-level status has been proposed for many taxa previously recognized as intraspecific taxa of *Synura petersenii* (Škaloud *et al.* 2012, 2013a, 2014, 2020; Jo *et al.* 2016). Probably, *Synura petersenii* f. *columnata* will be raised to a species rank in the future. Each species from the *Synura petersenii* complex is clearly defined by a combination of several morphological and morphometric features (e.g. scale shape and dimensions, number of struts, presence or absence of interconnections between them, etc.), so identification of the field material is possible.

For instance, we identified six taxa from the *Synura petersenii* complex (Table 2). Previously, we isolated several *Synura* colonies from the site 12 and studied them using an integrative approach (Gusev *et al.* 2016). All established strains represented *Synura petersenii sensu stricto*.

A case of *Paraphysomonas* is another example of a recent revision using an integrative approach. Previously, almost all freshwater *Paraphysomonas* species with nail-like spine scales were identified either as *P. vestita* or as *P. imperforata* (Preisig & Hibberd 1982; Scoble & Cavalier-Smith 2013). The detailed molecular phylogenetic and morphological investigations by Scoble & Cavalier-Smith (2014) showed strong congruence between variations in scale morphology and rDNA sequences. They described 23 new taxa of *Paraphysomonas sensu stricto*, however, since none of the established strains correspond the original description of *P. vestita*, the generitype, Scoble & Cavalier-Smith (2014) did not propose a neotype. For identification of *Paraphysomonas* species a combination of such features as base-plate shape, presence or absence of the annulus, spine length, degree of tapering, tip shape etc. is used (Scoble & Cavalier-Smith 2013, 2014). In our study only two species of *Paraphysomonas sensu stricto*, namely *P. acuminata* and *P. truncata*, were identified (Table 2).

Ukrainian Polissia has a rather diverse silica-scaled chrysophyte flora, however, it remains far from being completely known. For instance, there is a group of more than 30 lakes (Shatsk lakes) of different origin in the western part of the Ukrainian Polissia. We could identify only two widely distributed species, *Mallomonas acaroides* and *M. caudata*, from Lake Svitiaz, the largest lake of that group. We believe many more chrysophytes will be documented from the Shatsk lakes, as well as other regions of the Ukrainian Polissia with further study.

Acknowledgements

This study was carried out within the framework of the state assignment (AAAA-A19-119041190086-6).

The authors are grateful to Pr Petro M. Tsarenko (M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine) for permission to use the fixed samples from the Phycological Herbarium of the National Herbarium of Ukraine (KW-A), to Dr Jørgen Kristiansen (Biological Institute, University of Copenhagen) for reprints of his papers, to Dr Pavel Škaloud (Department of Botany, Charles University in Prague), to Dr Olga V. Burova (M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine) and to Dr Marina D. Zhezhera (Department of Botany, V. N. Karazin Kharkiv National University) for help with the literature. We are also very appreciative to Pr John P. Kocielek (University of Colorado, United States) for improving English, to Dr Peter A. Siver (Connecticut College, United States) and an anonymous reviewer for their valuable comments and suggestions, and to the associate editor Dr Jana Kulichova (Department of Botany, Charles University in Prague) for the careful editing and criticism.

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Submitted on 15 May 2020,
accepted on 31 August 2020,
published on 26 October 2020.