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Photobiont composition of some taxa of the genera *Micarea* and *Placynthiella* (Lecanoromycetes, lichenized Ascomycota) from Ukraine

Anna Voytsekhovich, Lyudmila Dymytrova & Olga Nadyeina

M. H. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv 01601, Ukraine.
E-mail: trebouxia@gmail.com

Abstract: The photobionts of 22 specimens of *Placynthiella* and *Micarea* genera were identified. The photobionts of *Placynthiella dasaea* (Stirt.) Khodosovtsev, *P. icmalea* (Ach.) Coppins & P. James, *Micarea melanobola* (Nyl.) Coppins and *M. misella* (Nyl.) Hedl. are reported for the first time. This is also the first report about *Elliptochloris reniformis* (Watanabe) Ettl & Gärtner, *E. subsphaerica* (Reisigl) Ettl & Gärtner, *Interfilum* spp. and *Neocystis* sp. as the photobionts of lichens. The mycobiont of some taxa of *Micarea* and *Placynthiella* can be associated with several algae at the same time. In this case, one is the primary photobiont (common for all lichen specimens of a certain lichen species) while the others are additional algae which vary depending on the substratum or the habitat. *Elliptochloris* and *Pseudococcomyxa* species are primary photobionts for the studied taxa of the genus *Micarea*. The species of *Radiococcus* and *Pseudochlorella* are primary photobionts of the studied species of *Placynthiella*. For all investigated lichens the low selectivity level of the mycobiont is assumed.

Kokkuvõte: Perekondade *Micarea* ja *Placynthiella* (Lecanoromycetes, lihheniseerunud kottseened) mõnede taksonite fotobiondi liigiline koosseis Ukrainas

Määrati lihheniseerunud seente *Micarea* ja *Placynthiella* 22 eksemplari fotobiondid. Liikide *Placynthiella dasaea* (Stirt.) Khodosovtsev, *P. icmalea* (Ach.) Coppins & P. James, *Micarea melanobola* (Nyl.) Coppins ja *M. misella* (Nyl.) Hedl. fotobiondid identifitseeriti esmakordselt. Samuti on see esimene teade vetikate *Elliptochloris reniformis* (Watanabe) Ettl & Gärtner, *E. subsphaerica* (Reisigl) Ettl & Gärtner, *Interfilum* spp. and *Neocystis* sp. esinemisest samblike fotobiondina. Perekondade *Micarea* ja *Placynthiella* mõned taksonid võivad samaaegselt assotsieeruda mitme vetikaga. Sellisel juhul on üks fotobiont esmane (ühine sama liigi kõigil eksemplaridel), samas kui teised on täiendavad vetikad, mis eksemplariti erinevad, sõltuvalt substraadist ja kasvukohast. *Elliptochloris* ja *Pseudococcomyxa* liigid on esmased fotobiondid perekonna *Micarea* uuritud liikides ning *Radiococcus* ja *Pseudochlorella* liigid – perekonna *Placynthiella* uuritud liikides. Kõikide uuritud samblike puhul täheldati mükobiondi madalat selektiivsust.

INTRODUCTION

For a long time it was considered that the photobiont composition of lichens was constant. Questions concerning the origin and constancy of a photobiont within different lichens appeared about twenty years ago (Friedl, 1987; Ott, 1987; Ihda et al., 1993; Beck et al., 1998; Helms, 2003). According to the latest data (Kirk et al., 2008) the number of lichen-forming fungi average 17 500 to 20 000 species, while the number of known photobionts does not exceed 148 species (Voytsekhovich et al., 2011). Several levels of mycobiont selectivity have been established (Beck et al., 2002). Thus, majority of lichen-forming fungi (approximately 40%) is specific to their photobiont and form lichen association with only one algal strain (very high level of selectivity) or a certain species (high level of selectivity). For instance, *Xanthoria parietina* (L.) Th. Fr. forms its thallus with either *Trebouxia arboricola* Puymaly, or with the species which are closely related to this alga (*T. arboricola* subclade) (Nyati, 2006); investigated species of the genus *Pertusaria* are associated mainly with *Trebouxia potteri* Ahmadjian ex Gärtner (Ahmadjian, 1993), whereas *Umbilicaria* species associate mainly with *Trebouxia simplex* Tscherm.-Woess (Beck, 2002; Romeike et al., 2002).

Some lichen-forming fungi show a middle-level of selectivity. They form permanent associations with the different species of the same photobiont genus. This level is known for *Cladonia* species (which form the association with *Asterochloris* Tscherm.-Woess only – Ahmadjian, 1993; Piercey-Normore & De Priest, 2001; Yahr et al., 2004), *Megalospora* (with *Dictyochloropsis* Geitler em. Tscherm.-Woess – Tschermak-Woess, 1984), and *Collema* (with *Nostoc* Vauch.

ex Born. & Flah. – Degelius, 1954). The same selectivity level is probably common within cephalodial lichens, for instance, *Peltigera aphtosa* (L.) Willd. which forms symbiodemes with *Nostoc* and *Coccomyxa* Schmidle (O'Brien et al., 2005).

The lichen-forming fungi that form their thalli with the photobionts from the same families or orders (low selectivity), or even from the groupings of higher taxonomic levels (very low selectivity), are characterized by "non-specific" relations between the lichen bionts. Thus, the common examples of low selectivity are the following: *Stereocaulon ramulosum* Räuschel, which associates with cyanobionts *Gloeocapsa* Kütz., *Nostoc*, *Scytonema* C. Agardh ex Bornet & Flahault and *Stigonema* C. Agardh ex Bornet & Flahault (Lamb, 1951: cit. Tschermak-Woess, 1989), and lichen-forming fungi of *Coenogoniaceae, Graphidaceae* and *Roccellaceae* families that form their thalli with the representatives of *Trentepohliaceae* family (Rands, 1933, Santesson, 1952, Uyenko, 1965: cit. Tschermak-Woess, 1989; Meier & Chapman, 1983). The very low selectivity level is common for *Verrucaria* Schrad. species that form associations with *Dilabifilum prostratum* Broady & Ingerfeld (Ettl & Gärtner, 1995), *Diplosphaera chodatii* Bial. (Geitler, 1960: cit. Tschermak-Woess, 1989), *Heterococcus caespitosus* Vischer (Tschermak, 1941; Zeitler, 1954; Sanders, 2004), *Petroderma maculiforme* (Wollny) Kuckuck (Wynne, 1969; Moe, 1997; Sanders, 2004), etc. Some of lichenized basidiomycetes can be associated with several photobionts at the same time. For instance, *Multiclavula mucida* (Pers.) R.H. Petersen was associated with *Mesotaenium* Nägeli, *Coccomyxa* and *Gloeocystis* Nägeli (Geitler, 1955).

However, the selectivity levels were ascertained only for 3% of the world lichen diversity (Voytsekhovich et al., 2011), while the photobionts of remaining 97% of lichen species are still unknown. Most of the latest publications on selectivity of the mycobionts deal with the representatives of certain families of lichens. It was established that the families *Physciaceae* (Bhattacharya et al., 1996; Friedl et al., 2000; Dahlkild et al, 2001; Helms et al., 2001), *Cladoniaceae* (Piercey-Normore & DePriest, 2001; Yahr et al., 2004), *Teloschistaceae* (Beck, 2002; Honegger et al., 2004; Nyati, 2006), *Graphidaceae* (Nakano, 1988) etc., and genera – *Letharia* (Th. Fr.) Zahlbr. (Kroken & Taylor, 2000), *Lecanora* Ach. (Blaha et al., 2006) and *Umbilicaria* (Romeike et al., 2002) have high and middle levels of selectivity.

Although, for many lichen species, like e.g., *Placynthiella* Elenkin or *Micarea* Fr., the data on photobiont composition are discrepant and still in need of further investigations. Several photobionts for the representatives of *Placynthiella* have been recorded. For instance, *Stigonema* was isolated from *Placynthiella arenicola* Elenkin (= *P. hyporhoda* (Th. Fr.) Coppins & P. James) (Elenkin, 1912); *Gloeocystis* sp. (probably, = *Radiococcus* Schmidle) (Oxner, 1974) and *Coccobotrys lecideae* Warén (Ettl & Gärtner, 1995) – from *Placynthiella uliginosa* (Schrad.) Coppins & P. James; *Chlorella lichina* Chod. (= *Chloroidium ellipsoideum* (Gerneck) Darienko et al.) and *Nostoc* sp. – from *Placynthiella* sp. (Coppins & James, 1984); *Chlorella* sp. was reported for *Placynthiella uliginosa, P. icmalea* (Ach.) Coppins & P. James and *P. oligotropha* (J.R. Laundon) Coppins & P. James (Rosentreter et al., 2007). Besides, Tønsberg (1992) reported several algal species for the lichen *P. dasaea,* but did not indicate their names: the green coccoid photobiont up to 12 μm in diameter and additional algae, which were "2–4-celled, globose or broadly ellipsoid or more or less cubic, surrounded by a thick, (3–4 μm wide) gelatinous cap, up to 15(–17.5) μm in diameter".

There are various data concerning the photobionts of the genus *Micarea*. According to Coppins (1983), the photobionts of 45 species of *Micarea* were presented with "three types" of green algae: "micareoid", "protococcoid" and chlorococcoid. Unfortunately, the author gave only descriptions but no species names for these algae. The photobiont *Pseudochlorella pyrenoidosa* (Zeitler) Lund was isolated from *Micarea assimilata* (Nyl.) Coppins (Zeitler, 1954); *Elliptochloris* sp. – from *M. prasina* Fr. (Brunner, 1985). The cyanobionts *Nostoc* and *Stigonema* were also discovered in cephalodia of some *Micarea* species (*M. assimilata*, *M. incrassata* Hedl., *M. subviolascens* (Magnusson) Coppins) (Coppins, 1983).

The data on photobiont composition often play a valuable role in lichen identification. Certain keys for lichen identification (e.g. Coppins, 1983; Ahti et al., 1999) require the information about the type of the photobiont (i.e. trebouxioid, chlorococcoid or micareoid). Thereby, considering the gap in data concerning the photobionts of lichen species of *Micarea* and *Placynthiella*, which are often inconsistent, the investigation of algal components of these two lichen genera as well as the analysis of the correlation of their ecological characters with photobiont composition would be topical and essential, and might be helpful in clarifying of the problems in biont interactions.

The aim of the present investigation was the exploration of algal component of the representatives of two lichen genera – *Micarea* (which mainly consists of epiphytic bark-growing species) and *Placynthiella* (terricolous and lignicolous species), as well as a comparison and analysis of obtained data in respect to the ecological peculiarities of these lichen species.

MATERIAL AND METHODS

Lichen samples

Total 22 specimens belonging to 8 species of *Placynthiella* and *Micarea* lichen-forming fungi were used in the present investigation. Lichen specimens were collected during 2005–2009 in five different districts of Ukraine (Donetsk, Kherson, Kyiv, Luhansk, and Transcarpathian). The further information on lichen specimens is given in Table 1. All lichen specimens are deposited in lichen herbarium of National Academy of Sciences of Ukraine (KW-L).

Photobionts

Small pieces of lichen thalli were washed in distilled water. After that the cortical layer of the thallus was cut out with a sterile razor blade. Photobionts were isolated directly from the photobiont layer according to the micropipette method (Ahmadjian, 1993) and grown on agarized Bold's medium (3N BBM) in standard conditions (Friedl & Büdel, 2008): the intensity of illumination was 10–30 μmol $m^{-2} s^{-1}$ PPFD, at 12:12 – light/dark cycle and the temperature +15±2 °C. After several weeks of cultivation, the algal strains were investigated in all stages of the life cycle with the help of the light microscopy techniques using the microscope Mikmed-2 (LOMO, Russia). The photobionts were examined both in the lichenized and cultured state by standard light microscopic techniques. Thus, the primary identification of the photobionts on the generic level and their percentage in lichen thalli was conducted in lichenized state using light microscopy; five slices from each lichen thallus were studied. Primary photobiont was identified by the fact of its presence in all investigated specimens of certain lichen species. For identification, isolated strains of *Trebouxia* and *Asterochloris* were compared with cultures of all known species of these genera, obtained from culture collections (SAG and CCAP). Culture strains of the isolated photobionts are maintained in the algal collection of Department of Lichenology and Bryology of M.G. Kholodnyi Institute of Botany (K).

Epiphytes

Epiphytic algae were scrapped from lichen surface on agarized medium in Petri dishes with the help of sterile preparation needle. After several weeks of cultivation on agarized Bold's medium (3N BBM) in standard conditions (Friedl & Büdel, 2008), the isolated strains of epiphytic algae were investigated in all stages of the life cycle using light microscopy techniques and compared with photobiont composition of investigated lichens.

RESULTS

Photobionts

The microscopic study revealed that the specimens of *Placynthiella dasaea*, *Micarea prasina* (No. 19, 20) and *M. subnigrata* contained only one photobiont, while the other investigated lichen species, *Placynthiella icmalea, P. uliginosa, Micarea melanobola, M. misella, M. peliocarpa* and *M. prasina*, contained several photobionts at the same time (Fig. 1a). Later the presence of additional photobionts was confirmed with the help of the cultural methods. The detailed data concerning photobiont composition of investigated lichen specimens are given in Table 2.

In seven specimens of *Placynthiella uliginosa,* as well as in two specimens of *P. icmalea,* the photobiont *Radiococcus signiensis* was discovered (Fig. 2c). The abundance of this alga in lichen thalli differed in different specimens. The cells of *Radiococcus signiensis* in the specimen of *Placynthiella uliginosa* (No. 10) visually presented more than 80% from a total photobiontal mass, while in the specimen of *P. uliginosa* (No. 6) – it was approximately 50%, and in *P. uliginosa* (No. 9) – less than 20%. However, the mycobiont of some of the investigated thalli of *Placynthiella icmalea* and *P. uliginosa* was associated with other algal species, which usually were presented in photobiont layer in

Table 1. Original data of investigated lichen specimens

No.	Lichen species	Locality in Ukraine, date of specimen collection, and the collector(s)
1	*Placynthiella dasaea* (Stirt.) Khodosovtsev	Transcarpathian District, Tiachivsky region, Carpathian Biosphere Reserve, Shyrokoluzhansky massif, near Posich village, *Abies+Fagus* woodland, 48°21.091'N 23°43.924'E, 770 m alt., 05.10.2009, leg. O. Nadyeina, L. Dymytrova, S. Postoyalkin & A. Naumovich, det. L. Dymytrova (KW).
2	*P. dasaea*	Transcarpathian District, Tiachivsky region, Carpathian Biosphere Reserve, in the vicinity of Mala Uhol'ka, 48°16.623'N 23°37.221'E, 812 m alt., 9.10.2009, leg. & det. L. Dymytrova (KW).
3	*P. icmalea* (Ach.) Coppins & P. James	Kherson District, Tsuryupynsky region, "Oleshkivski pisky" National Nature Park, 46°38.549'N 33°01.185'E, 3 m alt., 01.10.2009, leg. & det. A. Khodosovtsev (KW).
4	*P. icmalea*	Transcarpathian District, Tiachivsky region, Carpathian Biosphere Reserve, in the vicinity of Mala Uhol'ka, 48°16.623'N 23°37.221'E, 812 m alt., 9.10.2009, leg. & det. L. Dymytrova (KW).
5	*P. uliginosa* (Schrad.) Coppins & P. James	Luhansk District, Lutugynsky region, in the vicinity of Karl Libkneht's village, sandstone outcrops, 03.05.2005, leg. & det. O. Nadyeina (KW45506).
6	*P. uliginosa*	Luhansk District, Lutugynsky region, in the vicinity of Verhnya Horikhivka village, steppe hills near "Pershozvanivs'ke" water storage, leg. & det. O. Nadyeina (KW45507).
7	*P. uliginosa*	Luhansk District, Lutugynsky region, between Myrne village and Uspenka town, southern slope of "Kryven'ky Yar" gully, 05.05.2005, leg. & det. O. Nadyeina (KW45508).
8	*P. uliginosa*	Luhansk District, Lutugynsky region, between Myrne village and Uspenka town, friable sandstones of "Kryven'ky Yar" gully, 05.05.2005, leg. & det. O. Nadyeina (KW45509).
9	*P. uliginosa*	Luhansk District, Sverdlovsky region, in the vicinity of Provallya village, pasture land, on soil among mosses, 18.07.2005, leg. & det. O. Nadyeina (KW63536).
10	*P. uliginosa*	Luhansk District, Sverdlovsky region, in the vicinity of Provallya village, steppe slopes, 22.07.2005, leg. & det. O. Nadyeina (KW45510).
11	*P. uliginosa*	Kherson District, Tsuryupynsky region, "Oleshkivski pisky" National Nature Park, 46°38.549'N 33°01.185'E, 3 m alt., 01.10.2009, leg. & det. L. Dymytrova (KW).
12	*Micarea melanobola* (Nyl.) Coppins	Transcarpathian District, Tiachivsky region, Carpathian Biosphere Reserve, Shyrokoluzhansky massif, near Posich village, 48°21.058'N 23°43.955'E, 728 m alt., 05.10.2009, leg. & det. L. Dymytrova (KW).
13	*M. misella* (Nyl.) Hedl.	In the vicinity of Kyiv, "Lisnyky" State Botanical Rreserve, 50°17.53'N 30°32.35'E, *Quercus* forest, 02.04.2009, leg. & det. L. Dymytrova (KW).
14	*M. peliocarpa* (Anzi) Coppins & R. Sant.	Transcarpathian District, Tiachivsky region, Carpathian Biosphere Reserve, Shyrokoluzhansky massif, near Posich village, *Abies-Fagus* woodland, 48°21.091'N 23°43.924'E, 770 m alt., 05.10.2009, leg. O. Nadyeina, L. Dymytrova, S. Postoyalkin & A. Naumovich, det. L. Dymytrova (KW).
15	*M. prasina* Fr.	Donetsk District, Shakhtars'ky region, in the vicinity of Saurovka village, the dell near Saur-Mohyla, "Donetsky Kryazh" Regional Landscape Park, 17.04.2006, leg. & det. O. Nadyeina (KW63549).
16	*M. prasina*	Donetsk District, Shakhtars'ky region, in the vicinity of Petrivs'ke village, steppe slopes above the dell near tributary of Sevost'yanivka river, 18.04.2006, leg. & det. O. Nadyeina (KW63539).
17	*M. prasina*	Donetsk District, Shakhtars'ky region, in the vicinity of Petrivs'ke village, along the dell near tributary of Sevost'yanivka river, solitary *Quercus* trees, 18.04.2006, leg. & det. O. Nadyeina (KW63544).
18	*M. prasina*	Donetsk District, Shakhtars'ky region, in the vicinity of Saurivka village, SW direction from Saur-Mohyla, *Pinus* plantation, 19.04.2006, leg. & det. O. Nadyeina (KW63550).
19	*M. prasina*	Donetsk District, Shakhtars'ky region, in the vicinity of Saurivka village, SW direction from Saur-Mohyla, *Populus+Betula* plantation, 19.04.2006, leg. & det. O. Nadyeina (KW63545).
20	*M. prasina*	Donetsk District, Shakhtars'ky region, the dell "Urochysche Hrabove", 20.04.2006, leg. & det. O. Nadyeina (KW63543).
21	*M. prasina*	Luhansk District, Krasnoluchsky region, the dell along Mius river, 19.07.2006, leg. & det. O. Nadyeina (KW63547).
22	*M. subnigrata* (Nyl.) Coppins & H. Kilias	Luhansk District, Sverdlovsky region, sandstone between Dar'yino-Yermakovo and Astakhovo villages, 22.07.2006, leg. & det. O. Nadyeina (KW 45511).

smaller quantity, rather than with the primary photobiont *Radiococcus signiensis*. The number of these algae and their species composition varied. In most cases, additionally to *Radiococcus signiensis* the thalli of *Placynthiella uliginosa* also contained *Elliptochloris subsphaerica* (Fig. 3c, d) and *Interfilum massjukiae* (Fig. 2b). Rarely the members of *Asterochloris* and *Trebouxia* genera were found. One specimen (No. 10) contained *Leptosira* cf. *thrombii*. However, not all of the investigated species of *Placynthiella* were associated with *Radiococcus*. Both specimens of *P. dasaea* were associated with the photobiont *Pseudochlorella* sp. (Fig. 1c, 2e).

The majority of the investigated specimens of the genus *Micarea* contained several photobionts as well. The exceptions were *M. prasina* (No. 19, 20) and *M. subnigrata,* which were associated with one photobiont only. Nine out of ten investigated specimens of *Micarea* contained the photobionts from the genus *Elliptochloris.* Thus, the photobiont *Elliptochloris subsphaerica* was found in thalli of *Micarea melanobola, M. prasina* (No. 16) and *M. subnigrata*. The thalli of *Micarea misella,* and *M. prasina* (specimens No. 15, 17, 18, 19, 21) were associated with *Elliptochloris bilobata* (Fig. 3a, b), while *M. peliocarpa* contained *Elliptochloris reniformis* (Fig. 3e, f). Furthermore,

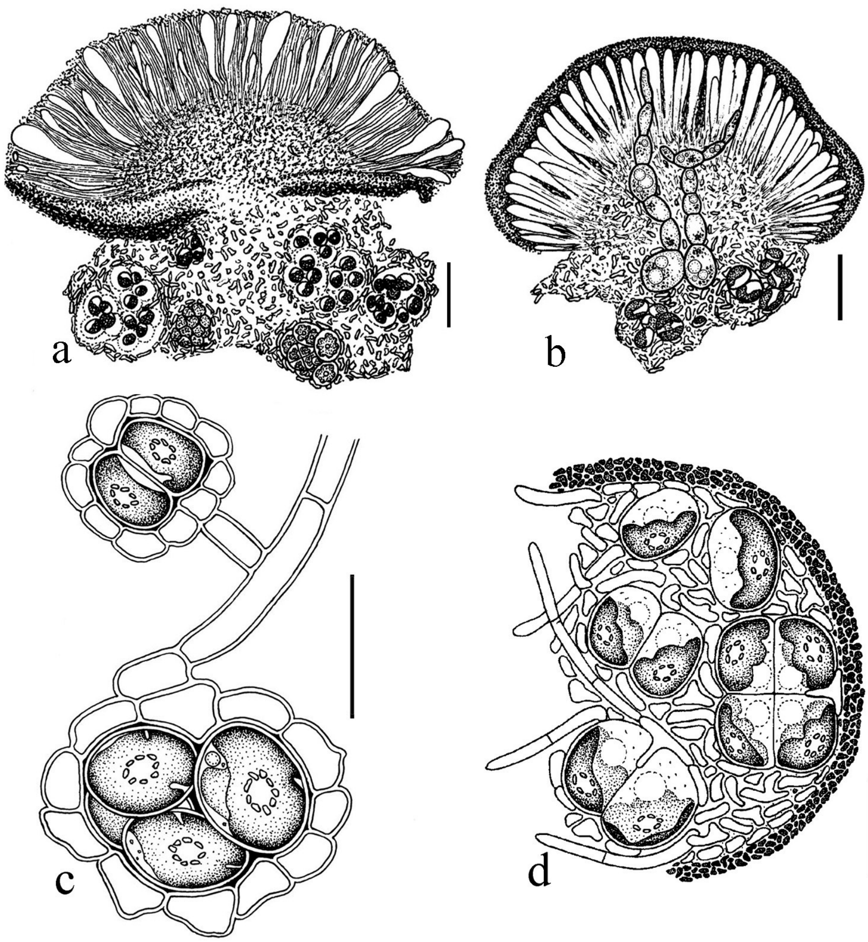

Fig. 1. Schematical drawings of cuts of *Micarea* and *Placynthiella* thalli: (a) photobiont location in the thallus of *Placynthiella uliginosa* (scale = 40 µm); (b) *Trentepohlia annulata* in apothecium of *Micarea misella* (scale = 40 µm); (c) lichenized cells of *Pseudochlorella* sp., surrounded by fungal hyphae (scale = 10 µm); (d) lichenized *Interfilum* sp. in *Micarea* thallus (scale = 10 µm).

Table 2. The photobiont composition of investigated lichen specimens of *Micarea* and *Placynthiella* genera compared with literature data.

Lichen (specimen No.)	Substratum	Photobiont		Epiphytes
		Original data	Literature data	
Placynthiella dasaea (No. 1)	decomposed wood of *Abies,* covered with mosses	***Pseudochlorella* sp.**[11]	Green coccoid photobiont and sometimes additional algae (Tønsberg, 1992)	*Bracteacoccus giganteus* Bisch. & Bold *Chlamydomonas* sp. *Elliptochloris bilobata* Tscherm.-Woess *Radiococcus signiensis* (Broady) Kostikov et al. *Trentepohlia annulata* Brand
P. dasaea (No. 2)	decomposed wood of *Abies,* covered with mosses	***Pseudochlorella* sp.**		*Diplosphaera chodatii* Bial. *Interfilum terricola* (J.B.Petersen) Mikhailyuk et al. *Elliptochloris bilobata* *Elliptochloris subsphaerica* (Reisigl) Ettl & Gärtner *Pseudococcomyxa* sp.
P. icmalea (No. 3)	sand	***Radiococcus signiensis*** *Elliptochloris subsphaerica*	*Chlorella* sp. (Rosentreter et al., 2007)	
P. icmalea (No. 4)	dead wood of *Pinus* tree (in vicinity of *Trapeliopsis flexulosa*)	***Radiococcus signiensis*** *Elliptochloris subsphaerica* *Interfilum massjukiae* Mikhailyuk et al.		
P. uliginosa (No. 5)	mosses (near *Amandinea punctata*)	***Radiococcus signiensis*** *Interfilum massjukiae*	*Gloeocystis* sp. (Oxner, 1974); *Coccobotrys lecideae* Warén (Ettl & Gärtner, 1995); *Chlorella* sp. (Rosentreter et al., 2007)	*Klebsormidium* cf. *flaccidum* (Kütz.) Silva et al. *Leptosira* cf. *thrombii* Tscherm.-Woess *Trebouxia* sp.
P. uliginosa (No. 6)	soil with crushed rock	*Radiococcus signiensis* *Elliptochloris subsphaerica*		*Asterochloris* sp.
P. uliginosa (No. 7)	mosses	***Radiococcus signiensis*** *Elliptochloris subsphaerica*		*Interfilum massjukiae* *Trebouxia* sp.
P. uliginosa (No. 8)	mosses (near *Cladonia fimbriata*)	*Radiococcus signiensis* *Elliptochloris subsphaerica* *Interfilum massjukiae* *Asterochloris* sp.		*Asterochloris* sp.
P. uliginosa (No. 9)	mosses (near *Cladonia foliacea*, and *Neofuscelia pokornyi*)	*Radiococcus signiensis* *Asterochloris* cf. *excentrica* (Archibald) Skaloud & Peksa *Elliptochloris subsphaerica* *Interfilum massjukiae* *Trebouxia* cf. *incrustata* Ahmadjian & Gärtner		*Diplosphaera chodatii* *Parietochloris* cf. *ovoideus* Mikhailyuk et al.
P. uliginosa (No. 10)	thalli of *Cladonia coniocraea* (near *C. foliacea*)	*Radiococcus signiensis* *Asterochloris* sp. *Elliptochloris subsphaerica* *Interfilum massjukiae* *Leptosira* cf. *thrombii*		*Interfilum massjukiae* *Leptosira* cf. *thrombii*
P. uliginosa (No. 11)	sand	*Radiococcus signiensis* *Interfilum massjukiae* *Trebouxia* sp.		*Klebsormidium* cf. *flaccidum*

Micarea melanobola (No. 12)	bark of *Abies* tree	*Elliptochloris subsphaerica* *Pseudococcomyxa* sp.	«micareoid» type of photobiont (Hedlund, 1882, 1895: cit. Coppins, 1983)	*Apatococcus lobatus* (Chodat) J.B. Petersen *Trentepohlia* cf. *umbrina* (Kütz.) Bornet
M. misella (No.13)	decomposed stub	***Elliptochloris bilobata*** *Pseudococcomyxa* sp *Neocystis* sp.		*Trentepohlia annulata*
M. peliocarpa (No. 14)	decomposed wood of *Abies*	***Elliptochloris reniformis*** (Watanabe) Ettl & Gärtner *Elliptochloris subsphaerica*	«micareoid» type of photobiont (Hedlund, 1882, 1895: cit. Coppins, 1983)	
M. prasina (No. 15)	bark of *Fraxinus* tree	*Elliptochloris bilobata* *Elliptochloris subsphaerica* *Interfilum* sp.	*Elliptochloris* sp. (Brunner, 1985)	*Trebouxia* sp.
M. prasina (No. 16)	bark of *Fraxinus* tree	***Elliptochloris subsphaerica*** *Interfilum* sp.		
M. prasina (No. 17)	bark of *Quercus* tree	***Elliptochloris bilobata*** *Elliptochloris subsphaerica* *Interfilum* sp.		
M. prasina (No. 18)	bark of *Betula* tree	***Elliptochloris bilobata*** *Interfilum* sp.		
M. prasina (No. 19)	bark of *Betula* tree	***Elliptochloris bilobata***		
M. prasina (No. 20)	bark of *Fraxinus* tree	***Pseudococcomyxa* sp.**		
M. prasina (No. 21)	bark of *Betula* tree (near *Lecanora hagenii*, *Melanelia* sp., and *Scoliciosporum chlorococcum*)	***Elliptochloris bilobata*** *Interfilum* sp.		*Apatococcus lobatus*
M. subnigrata (No. 22)	on *Candelariella vitellina* (near *Rhizocarpon distinctum*, *Bellemerea cupreoatra*, *Acarospora fuscata*, *Sarcogyne regularis*)	***Elliptochloris subsphaerica***	«micareoid» type of photobiont (Hedlund, 1882, 1895: cit. Coppins, 1983)	

The main photobiont of lichen is in bold.

in the thalli of *Micarea melanobola, M. misella* and *M. prasina* (No. 15, 16, 17, 18, 21) several additional photobionts were discovered (see Table 2). For instance, *Neocystis* sp. was found and recognized as an additional photobiont of *M. misella*; *Pseudococcomyxa* sp. (Fig. 2f) – as additional photobiont of *Micarea melanobola, M. misella* and *M. prasina* (No. 20). The majority of the specimens also contained *Interfilum sp.* (Fig. 2a), which differs from *Interfilum massjukiae* by the absence of distinct filaments in culture conditions.

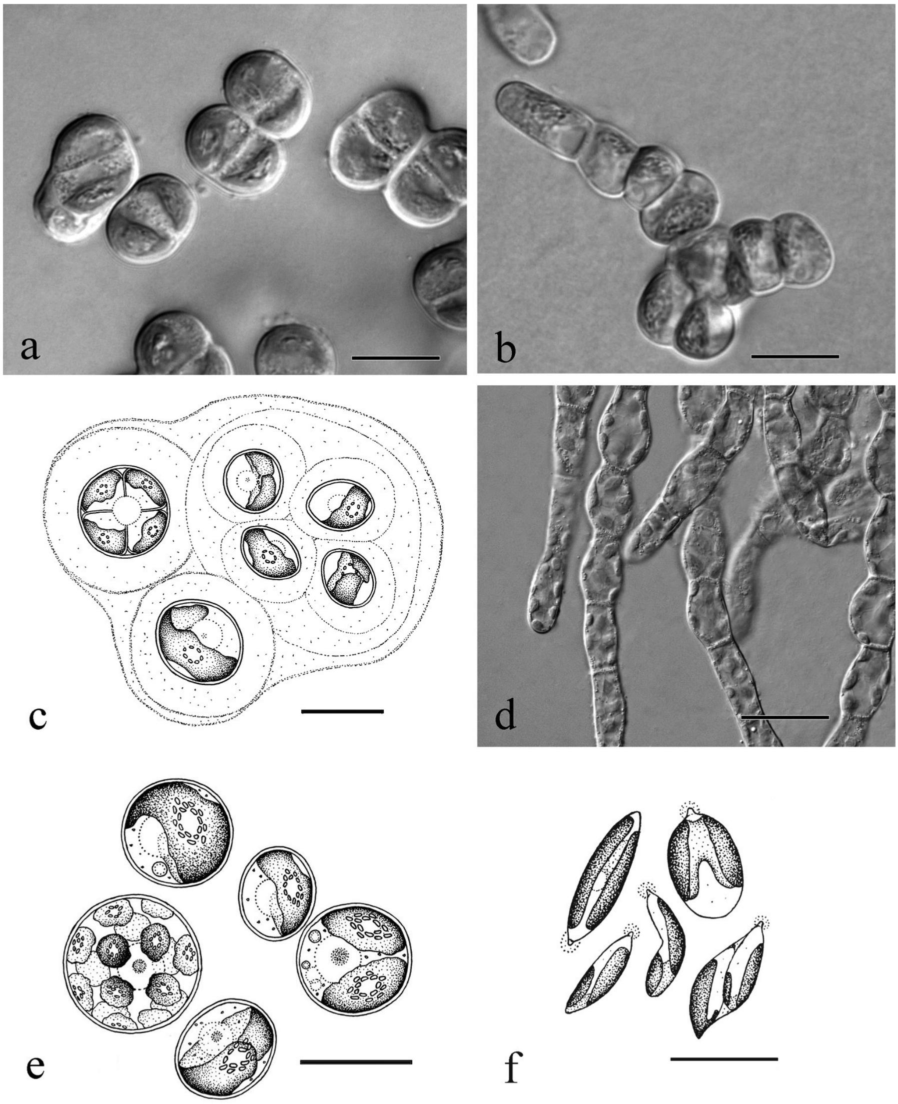

Fig. 2. Photobionts and epiphytes of *Micarea* and *Placynthiella* species in 4-weeks-old cultures: (a) cell packages of *Interfilum* sp.; (b) the filament of *Interfilum massjukiae*; (c) schematical drawing of *Radiococcus signiensis* (the cells are covered with mucilage), the primary photobiont of *Placynthiella icmalea* and *P. uliginosa*; (d) the fragment of filaments of epiphytic alga *Trentepohlia umbrina*; (e) schematical drawing of *Pseudochlorella* sp., the primary photobiont of *Placynthiella dasaea*; (f) schematical drawing of *Pseudococcomyxa* sp., the primary photobiont of *Micarea prasina.* Scale = 20 µm.

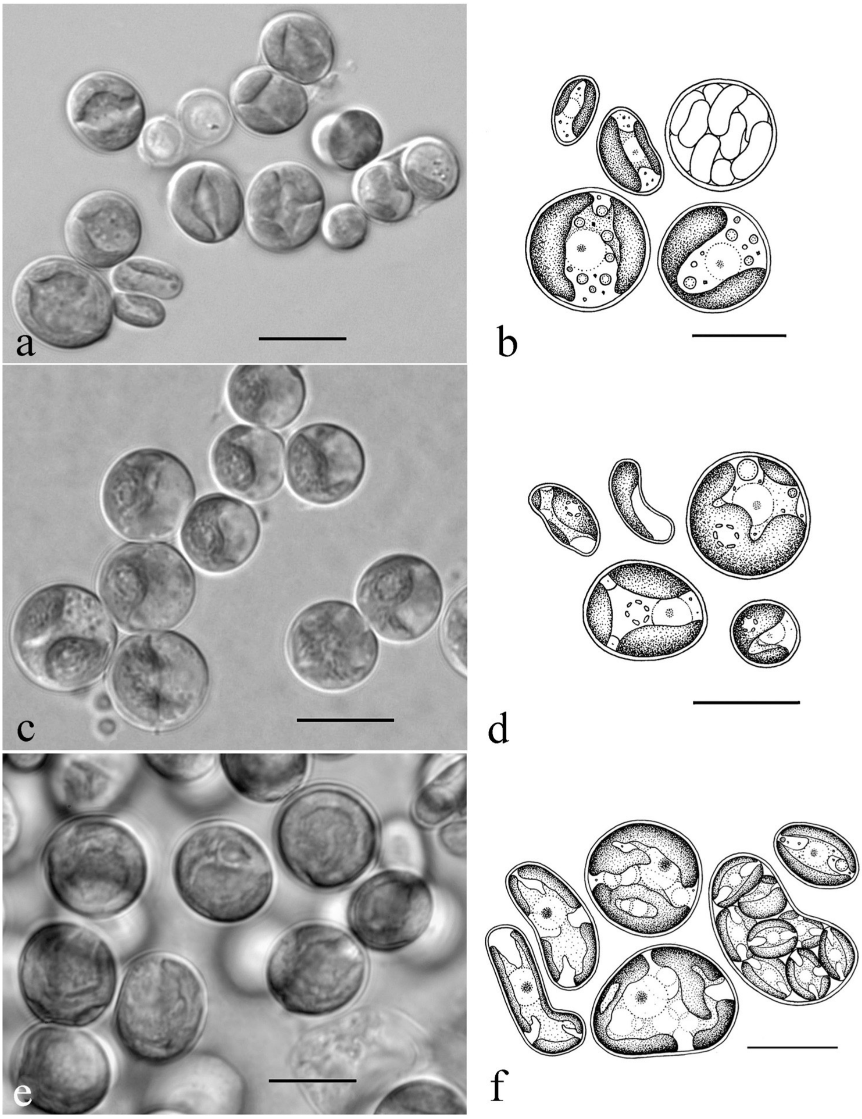

Fig. 3. Micrographs and schematical drawings of primary photobionts of *Micarea* species in 4-weeks-old cultures: (a, b) *Elliptochloris bilobata*, photobiont of *Micarea misella* and *M. prasina*; (c, d) *E. subsphaerica*, photobiont of *M. melanobola*, *M. prasina* and *M. subnigrata*; (e, f) *E. reniformis*, photobiont of *M. peliocarpa*. Scale = 10 µm.

Epiphytes

A total of 17 species out of 14 genera from two divisions Chlorophyta and Streptophyta were identified as epiphytes of investigated lichens (see Table 2). The most frequent of them was *Trebouxia* sp., which was found on the surface of three lichen specimens. The highest number of epiphytic algae, five species, was found on the surface of *Placynthiella dasaea* which grew on decomposed wood (No. 1, 2). In general, the specimens of *Placynthiella* had more epiphytes than *Micarea*. *Trentepohlia annulata,* which was discovered on the surface of the thallus of *M. misella* as an epiphyte at first, was later found in the apothecia of the same lichen (Fig 1b).

DISCUSSION

Primary photobiont

The alga, which was registered in all specimens of a certain lichen species, and associated with fungal hyphae, is called here the primary photobiont. We declare that the primary photobiont of *Placynthiella icmalea* and *P. uliginosa* is *Radiococcus signiensis*; the primary photobiont of *P. dasaea* is *Pseudochlorella* sp. The obtained data clarify and add new information to previously known photobiont diversity for investigated species. Earlier *Gloeocystis* sp. (probably, = *Radiococcus* Schmidle) (Oxner, 1974), *Coccobotrys lecideae* Warén (Ettl & Gärtner, 1995) and *Chlorella* sp. (Rosentreter et al., 2007) have been reported for *Placynthiella uliginosa. Chlorella* sp. was discovered in *P. icmalea* (Rosentreter et al., 2007). Unknown green coccoid photobiont up to 12 µm in diameter was reported for *P. dasaea* (Tønsberg, 1992).

In *Micarea*, ten out of eleven investigated specimens were associated with the primary photobiont from the genus *Elliptochloris*. One specimen of *M. prasina* contained *Pseudococcomyxa* sp. as the primary photobiont. According to the results of molecular phylogenetic studies (Beck, 2002), some species of *Pseudococcomyxa* are closely related to *Elliptochloris bilobata*. Our results partly confirm the data of Brunner (1985), who reported *Elliptochloris* sp. as the photobiont of *M. prasina*. This is the first report of *Elliptochloris reniformis* and *E. subsphaerica* as lichen photobionts. Earlier these two species were known as free-living terrestrial algae (Ettl & Gärtner, 1995; Kostikov et al., 2001). The photobionts of *Micarea* species were described as three types of green algae by Coppins (1983): micareoid, chlorococcoid and "with protococcoid type of division". The most frequent type of photobiont of *Micarea* species is micareoid, which is most likely, according to its description (Coppins, 1983), referring to *Diplosphaera chodatii*. Description of the second type, chlorococcoid, corresponds to the members of *Elliptochloris* genus. The third type of *Micarea* photobiont having a "protococcoid type of division", corresponds to the photobiont of *Scoliciosporum umbrinum*, which is known as *Apatococcus lobatus* (Beck, 2002). However, these are only our assumptions that require further confirmation. Thus, despite the fact that Coppins (1983) reported "micareoid" photobiont for *Micarea prasina*, which according to its description cannot be *Elliptochloris* or *Pseudococcomyxa*, we revealed just these algae as the primary photobionts of this lichen species.

Due to relatively high species diversity of the photobionts among *Micarea* and *Placynthiella* species, we assume a low selectivity of their mycobiont toward the algal partner. However, this issue requires further study using lichen samples from a wider geographic area.

Additional photobionts

In addition to the primary photobiont, several non-specific photobionts were found in thalli of investigated *Micarea* and *Placynthiella* species (see Table 2). The number and species composition of these algae varied. These algae were revealed to be associated with fungal hyphae directly inside the lichen thalli, but not on its surface, therefore, they are considered as the additional photobionts but not as the epiphytes. Consequently, our results support the observations of Tønsberg (1992), who distinguished such additional algae from the specimens of *Placynthiella dasaea*. Unfortunately, the algal species which Tønsberg (1992) mentioned was not identified; according to his description, it could be a member of *Radiococcaceae* (e.g. *Radiococcus signiensis*).

Some of additional algae presented in this article are the common lichen photobionts. For instance, the species of *Asterochloris* and *Trebouxia* are well known as obligate photobionts and are associated with more than 55% of all known lichen species (Voytsekhovich et al., 2011). In our opinion, *Asterochloris* cf. *excentrica* and *Trebouxia* cf. *incrustata* that were discovered in *Placynthiella uliginosa* (No. 9) possibly got there from the thalli of neighbouring *Cladonia foliacea* (Huds.) Willd. and *Neofuscelia pokornyi* (Zahlbr.) Essl., respectively (see Table 2). It is known that *Neofuscelia* species form their thalli with *Trebouxia gigantea* (Hildreth & Ahmadjian) Gärtner (Ahmadjian, 1993) and *Trebouxia incrustata* (Beck, 2002), which are closely related species according to the molecular phylogenetic studies (Friedl & Büdel, 2008). The species of *Cladonia* are associated with *Asterochloris* species (Piercey-Normore & De Priest, 2001). At the same time, there is at least one report about *Placynthiella icmalea* being a parasite of other lichens (Fedorenko et al., 2006). Unfortunately, the authors did not indicate the species of lichen hosts on which *P. icmalea* parasitized. Therefore, the presence of *Asterochloris* sp. inside the thallus of *P. uliginosa* (No. 10) can be explained by the nearby growth of *Cladonia coniocraea* (Flörke) Vainio and *C. foliacea*. However, the specimens of *Micarea* (*Micarea prasina* No. 21 and *M. subnigrata*), were not associated with the photobionts of neighbouring lichens (see Table 2). It seems that the entry of the photobiont from the environment into the thallus has a casual character.

Elliptochloris bilobata, Leptosira thrombi and *Pseudococcomyxa* sp. are the facultative photobionts. It means that these algae exist in both lichenized and free-living stage. *Elliptochloris bilobata* has been reported as the photobiont of *Baeomyces rufus, Catolechia wahlenbergii, Protothelenella corrosa* and *P. sphinctrioides* (Tschermak-Woess, 1980, 1985); *Leptosira thrombii* is known as the photobiont of *Thrombium epigaeum* (Pers.) Wallr. (Tschermak-Woess, 1953, Schiman, 1961: cit. Tschermak-Woess, 1989), and *Pseudococcomyxa* is known as the photobiont of *Baeomyces* (Pott, 1972, Peveling, Galun, 1976: cit. Tschermak-Woess, 1989), *Lichenomphalia* (Jaag, 1933; Oberwinkler, 1984), *Peltigera* (Jaag, 1933), *Solorina* and *Icmadophila* (Jaag, 1933).

Alternatively *Interfilum* spp., *Elliptochloris subsphaerica* and *Neocystis* sp. are known only in free-living stage and there are no reports on these species as lichen bionts. We consider that the presence of these algal species in the photobiont layer of investigated lichen thalli is caused by their free-living populations in the growing-zone of the lichen. The free-living algae growing in proximity of a lichen can be enveloped with the fungal hyphae and gradually become part of the lichen. Lichens with the facultative (non-trebouxioid) photobiont use the pool of free-living algae as the source of their autotrophic component. For instance, the tropical lichen *Strigula* sp. often colonizes the free-living *Cephaleuros* and uses it as the photobiont (Chapman & Waters, 2001). In most cases the lichens and their free-living algal bionts share the same habitat. Thus, the common terrestrial free-living algae from the genera *Nostoc, Scytonema, Stigonema, Myrmecia, Diplosphaera* and *Stichococcus* are common photobionts of terricolous lichens from the families *Collemataceae*, *Psoraceae*, *Stereocaulaceae* and *Verrucariaceae* (Tschermak-Woess, 1989; Voytsekhovich et al., 2011).

Thus, the finding of recently described lithophilous streptophyte algae *Interfilum massjukiae* and *Interfilum* sp. (Mikhailyuk et al., 2008) inside lichen thalli was unexpected as the localities where lichen specimens with *Interfilum* were collected are new for these algae. This is the first report of *Interfilum* species, and the second of Streptophyte in whole, as the lichen photobionts. This is also the first report on *Neocystis* sp. as a lichen photobiont.

Epiphytes

Most of the investigated epiphytic algae are very common terrestrial algae. The species of *Apatococcus, Bracteacoccus, Parietochloris* and *Trentepohlia* (Fig 2d) are common in aerophytic habitats: tree-bark and rocks (Ettl & Gärtner, 1995; Gärtner & Stoyneva, 2003; Mikhailyuk et al., 2003). *Radiococcus signiensis* is the epibryophyte (Ettl & Gärtner, 1995). The usual habitat of *Chlamydomonas*, *Diplosphaera, Interfilum, Leptosira* and *Pseudococcomyxa* is soil, although they can be found also in aerophytic conditions (Ettl & Gärtner, 1995; Kostikov et al., 2001; Mikhailyuk et al., 2008). In contrast, the species of *Trebouxia* and *Asterochloris* are known only as the obligate photobionts of lichens (Ahmadjian, 1987). The finding of epiphytic algae *Trentepohlia* in lichen apotecium may indicate that the algae that grow in the immediate vicinity of a lichen may be included in its thallus. At the moment we do not know whether this alga can be considered as a photobiont, and such cases require additional investigations.

Lichens

The taxonomical status of *Micarea melanobola* which for a long time was considered to be a variation or synonym of *Micarea prasina* (Hedlund, 1892; Vězda & Wirth, 1976), is still unclarified. The species, *M. melanobola*, was described on the basis of the differences in thallus and epithecium pigmentation, size of apothecia, spores, microconidia and the number of paraphyses in comparison with *M. prasina* (Coppins, 1983). Later, these two species were synonymized because of the absence of distinctions except pigmentation of apothecia and pycnidia (Czarnota, 2007). However, three years later, after molecular phylogenetic analysis of the lichens from *M. prasina*-group, it was noticed that the dark-colored morphotypes of *M. prasina* still required an additional critical investigation

(Czarnota & Guzow-Krzeminska, 2010). Therefore, the question on the species status of *M. melanobola* is still open and any new distinct features might be useful for its taxonomical elaboration. We did not reveal any valuable differences between the photobiont composition of *M. melanobola* and *M. prasina*. The primary photobiont of *M. melanobola* was *Elliptochloris subsphaerica*, while different specimens of *M. prasina* had *E. bilibata, E. subsphaerica* and *Pseudococcomyxa* sp. as primary photobionts. We conclude that the photobiont composition of *M. melanobola* can not be used as a distinct feature in taxonomical clarification of this taxon.

A few specimens of *Placynthiella uliginosa* were collected from sandstones or soil (No. 3, 6, 11), and several (No. 1, 2, 4, 5, 7, 8, 9, 10) from mosses and lignum. *Micarea prasina* is a widespread epiphytic lichen in temperate zone which is not restricted to any certain phorophytes; our specimens were collected from *Betula*, *Fraxinus* and *Quercus*. The specimen of *M. misella* was collected from touchwood (decomposed stub), and *M. subnigrata* from the thallus of another lichen. Based on our data, we suggest that the distribution of studied lichen species does not depend on the habitat of a certain algal species, and that the lichen-forming fungi are labile enough in their photobiont choice. The investigated species of lichen-forming fungi of *Micarea* and *Placynthiella* showed a very low selectivity to their algal component on the generic level. Consequently, the species of these lichen genera are characterized by unstable photobiont composition and unspecific relations between the bionts. Only two species, *Placynthiella uliginosa* and *Micarea prasina*, showed certain selectivity to their primary photobionts on the species level in spite of the presence of some additional photobionts. In our opinion, such a plasticity of studied lichen-forming fungi with respect to their photobionts contributes to their colonization of different substrates in different habitats.

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