

CONTRIBUTIONS TO MOLECULAR PHYLOGENY OF LICHEN-FORMING FUNGI 2. REVIEW OF CURRENT MONOPHYLETIC BRANCHES OF THE FAMILY PHYSICIACEAE

S. Y. KONDRATYUK^{1*}, L. LÓKÖS², I. KÄRNEFELT³, A. THELL³, M.-H. JEONG⁴
S.-O. OH⁵, A. S. KONDRATIUK¹, E. FARKAS⁶ and J.-S. HUR⁴

¹M. H. Kholodny Institute of Botany, Tereshchenkivska str. 2, 01004 Kiev, Ukraine

*E-mail: ksy_a_net@ukr.net; corresponding author

²Department of Botany, Hungarian Natural History Museum
H-1431 Budapest, Pf. 137, Hungary

³Botanical Collections, Biological Museum, Lund University
Box 117, SE-221 00 Lund, Sweden; E-mail: arne.thell@biol.lu.se

⁴Korean Lichen Research Institute, Suncheon National University
Suncheon 540-742, Republic of Korea; E-mail: jshur1@suncheon.ac.kr

⁵Korea National Arboretum, Gwangneungsumogwon-ro 415, Pocheon-si, Gyeonggi-do 11186,
Republic of Korea

⁶Institute of Ecology and Botany, Centre for Ecological Research
H-2163 Vácrátót, Alkotmány u. 2–4, Hungary

(Received: 26 May 2021; Accepted: 30 August 2021)

Seven genera new to science, i.e.: *Helmutiopsis*, *Huriopsis*, *Johnsheardia*, *Klauskalbia*, *Kudratovia*, *Kurokawia* and *Poeltonia* of the Physciaceae are proposed for the ‘*Rinodina*’ *atrocineria*, the ‘*Rinodina*’ *xanthophaea*, the ‘*Rinodina*’ *cinnamomea*, the ‘*Heterodermia*’ *obscurata*, the ‘*Rinodina*’ *straussii*, the ‘*Anaptychia*’ *isidiata* and the ‘*Physconia*’ *grisea* groups consequently that all form strongly supported monophyletic branches in a phylogeny analysis based on a combined matrix of nrITS and mtSSU sequences.

Phylogenetic positions of species belonging to the genera *Kashiwadia* s. l., *Leucodermia*, *Mischoblastia*, *Oxnerella*, *Phaeorrhiza* s. l., *Polyblastidium* and *Rinodinella* s. l. are discussed. *Oxnerella afghanica* which for the first time recorded as parasitic lichen species from both epiphytic and saxicolous crustose lichens is designated as type species for the genus *Oxnerella*.

Sequences of the recently described *Physcia orientostellaris* as well as *Huriopsis xanthophaea* and additional sequences of *Kashiwadia* aff. *orientalis* and *Mischoblastia* aff. *oxydata* are submitted to the GenBank.

The positions of *Polyblastidium casaterrinum* from Costa Rica, ‘*Rinodina*’ *efflorescens* from Białowieża, Poland, and ‘*Mischoblastia*’ *confragosula* from Cambodia in the Physciaceae are confirmed in a phylogeny analysis based on the nrITS sequences.

The presence of ‘extraneous mycobiont DNA’ in lichen associations is exemplified with earlier incorrect identifications of *Heterodermia*, *Kashiwadia*, *Kurokawia*, *Oxnerella* and *Poeltonia* specimens.

Fifty-six new combinations are presented: *Helmutiopsis alba* (for *Rinodina alba* Metzler ex Arn.), *Helmutiopsis aspersa* (for *Lecanora aspersa* Borrer), *Helmutiopsis atrocineria* (for *Parmelia atrocineria* Fr.), *Huriopsis chrysiidiata* (for *Rinodina chrysiidiata* Sheard), *Huriopsis chrysome-laena* (for *Rinodina chrysome-laena* Tuck.), *Huriopsis lepida* (for *Lecanora lepida* Nyl.), *Huriopsis luteonigra* (for *Rinodina luteonigra* Zahlbr.), *Huriopsis plana* (for *Rinodina plana* H. Magn.), Hu-

riopsis thiomela (for *Lecanora thiomela* Nyl.), *Huriopsis xanthomelana* (for *Rinodina xanthomelana* Müll. Arg.), *Huriopsis xanthophaea* (for *Lecanora xanthophaea* Nyl.), *Johnsheardia cinnamomea* (for *Rinodina mniaroea* var. *cinnamomea* Th. Fr.), *Johnsheardia herteliana* (for *Rinodina herteliana* Kaschik), *Johnsheardia jamesii* (for *Rinodina jamesii* H. Mayrhofer), *Johnsheardia reagens* (for *Rinodina reagens* Matzer et H. Mayrhofer), *Johnsheardia zwackhiana* (for *Lecanora zwackhiana* Kremp.), *Kashiwadia austrostellaris* (for *Physcia austrostellaris* Elix), *Kashiwadia jackii* (for *Physcia jackii* Moberg), *Kashiwadia littoralis* for *Physcia littoralis* Elix, *Kashiwadia nubila* (for *Physcia nubila* Moberg), and *Kashiwadia tropica* (for *Physcia tropica* Elix), *Klauskalbia crocea* (for *Heterodermia crocea* R. C. Harris), *Klauskalbia flabellata* (for *Parmelia flabellata* Fée), *Klauskalbia obscurata* (for *Physcia speciosa* (Wulfen) Nyl. **obscurata* Nyl.), *Klauskalbia paradoxa* (for *Heterodermia paradoxa* Schumm et Schäfer-Verwimp), *Kudratovia bohlinii* (for *Rinodina bohlinii* H. Magn.), *Kudratovia candidogrisea* (for *Rinodina candidogrisea* Hafellner, Muggia et Obermayer), *Kudratovia luridata* (for *Buellia luridata* Körb.), *Kudratovia metaboliza* (for *Rinodina metaboliza* Vain.), *Kudratovia pycnocarpa* (for *Rinodina pycnocarpa* H. Magn.), *Kudratovia roscida* (for *Lecanora roscida* Sommerf.), *Kudratovia straussii* (for *Rinodina straussii* J. Steiner), *Kudratovia terrestris* (for *Rinodina terrestris* Tomin), *Kurokawia bryorum* (for *Anaptychia bryorum* Poelt), *Kurokawia isidiata* (for *Anaptychia isidiata* Tomin), *Kurokawia mereschkowskii* (for *Physcia mereschkowskii* Tomin), *Kurokawia palmulata* (for *Psoroma palmulatum* Michx.), *Kurokawia runcinata* (for *Lichen runcinatus* With.), *Kurokawia stippea* (for *Parmelia aquila* var. *stippea* Ach.), *Lecania safavidiorum* (for *Oxnerella safavidiorum* S. Y. Kondr., Zarei-Darki, Lökös et Hur), *Leucodermia erinacea* (for *Lichen erinaceus* Ach.), *Mischoblastia confragosula* (for *Lecanora confragosula* Nyl.), *Mischoblastia destituta* (for *Lecidea destituta* Nyl.), *Mischoblastia moziana* (for *Lecanora moziana* Nyl.), *Mischoblastia moziana* subsp. *parasitica* (comb. et stat. nova for *Rinodina moziana* var. *parasitica* Kaschik et H. Mayrhofer), *Mischoblastia ramboldii* (for *Rinodina ramboldii* Kaschik), *Mischoblastia vezdae* (for *Rinodina vezdae* H. Mayrhofer), *Oxnerella afghanica* (for *Rinodina afghanica* M. Steiner et Poelt), *Oxnerella castanomelodes* (for *Rinodina castanomelodes* H. Mayrhofer et Poelt), *Physciella nigricans* (for *Lecanora nigricans* Flörke), *Poeltonia elegantula* (for *Physconia elegantula* Essl.), *Poeltonia grisea* (for *Lichen griseus* Lam.), *Poeltonia isidiomuscigena* (for *Physconia isidiomuscigena* Essl.), *Poeltonia perisidiosa* (for *Physcia perisidiosa* Erichsen), *Poeltonia venusta* (for *Parmelia venusta* Ach.), and *Polyblastidium albicans* (for *Parmelia albicans* Pers.) are proposed.

Key words: East Asia, *Helmutiopsis*, *Huriopsis*, *Johnsheardia*, *Kashiwadia*, *Klauskalbia*, *Kudratovia*, *Kurokawia*, *Lecania*, *Leucodermia*, *Mischoblastia*, *Oxnerella*, *Physcia*, *Poeltonia*

INTRODUCTION

The nrITS is hitherto the most frequently used molecular marker used for phylogeny of species and genera in the Physciaceae, followed by the 12S mtSSU. Other markers have been used to a much lesser extent. All taxa of the Physciaceae for which nrITS sequences were available, in total more than 500 sequences, were studied. The combined analysis contains only taxa for which both nrITS and mtSSU sequences were available.

During the last decade, the large and well-known genera *Anaptychia*, *Heterodermia*, *Phaeophyscia*, and *Physcia* have been revised in phylogeny analyses. In some cases new and strong monophyletic branches were distinguished

(Cubero *et al.* 2004, Grube *et al.* 2001, Helms *et al.* 2003, Lohtander *et al.* 2000, 2008, etc.).

Several sequences of the genus *Rinodina* (Ach.) Grey have been accumulated in the GenBank. It is obvious that the genus is polyphyletic and the species of the crustose genus are dispersed also among foliose and fruticose groups, occasionally forming more or less supported subclades (Hafellner *et al.* 2012, Nadyeina *et al.* 2010).

Two genera, *Polyblastidium* Kalb and *Leucoderma* Kalb, were segregated from *Heterodermia* without confirmation from molecular data (Mongkolsuk *et al.* 2015).

Elix *et al.* (2009) described new Australian species of the *Physcia aipolia* group, *P. austrostellaris* Elix, *P. tropica* Elix, *P. littoralis* Elix, and *P. jackii* Moberg, illustrated by a phylogenetic tree based on nrITS and mtSSU sequences of the *Physcia aipolia* group. However, after including these species in a phylogenetic tree of the Physciaceae it seemed that they are closer related with the recently proposed East Asian genus *Kashiwadia* S. Y. Kondr., Lökös et Hur. Consequently, five new combinations for the genus *Kashiwadia* are proposed here.

In phylogenetic studies (Grube *et al.* 2001, Helms *et al.* 2003, Lohtander *et al.* 2000) *Anaptychia* was found to be rather distantly related with *Heterodermia*. Instead, it forms a sister group to the genus *Physconia*, while *Heterodermia* appeared closely related with *Physcia* (Schreb.) Michx. *Anaptychia* is characterised by brown, thin-walled, 1-septate spores of *Physconia*-type and a prosoplectenchymatous upper cortex. The spores of *Heterodermia* have thick walls of *Pachysporaria*-type (Poelt 1965). The species of *Heterodermia* contain atranorin (K+ yellow cortex), a substance lacking in *Anaptychia* or is present in very low concentrations (K-). *Physconia* is characterised by the sclero- or paraplectenchymatous, pruinose upper cortex and squarrose rhizinae (Moberg 2002).

In the papers by Lohtander *et al.* (2000) and Grube *et al.* (2001), *Anaptychia* appeared paraphyletic, however, few specimens were included in their analyses and the studies were based on nrITS sequences only. In a study by Cubero *et al.* (2004) *Anaptychia* and *Physconia* formed two separate monophyletic groups, however, with only two species of *Anaptychia* included. Lohtander *et al.* (2008) illustrated that *Anaptychia* and *Physconia* formed distinct monophyletic groups in an analysis based on two independent gene regions (nrITS and mtSSU rDNA).

The earlier molecular studies in the Physciaceae seemed to be performed for single or few genera or for checking positions of new species.

The original aim of this paper was to clarify positions of species described from eastern and central Asia and southeastern Europe (Hur *et al.* 2016, 2018), however, the study developed into a re-evaluation of the current monophyletic branches of the entire family.

MATERIAL AND METHODS

Morphological and chemical analyses. Hand-cut sections were prepared with a razor blade under a stereomicroscope (Olympus SZ51; Olympus, Tokyo, Japan), examined under a compound microscope (Nikon Eclipse E400; Nikon, Tokyo, Japan) and imaged using a software program (NIS-Elements D; Nikon, Tokyo, Japan) and a DS-Fi3 camera (Nikon, Tokyo, Japan) mounted on a Nikon Eclipse Ni-U microscope (Nikon, Tokyo, Japan). The ascospores were investigated at 1,000× magnification in water. The length and width of the ascospores were measured and the range of spore sizes was shown with average, standard deviation, and number of measured spores. Thin-layer chromatography (TLC) was performed using solvent systems A and C according to standard methods (Orange *et al.* 2010).

Isolation, DNA extraction, amplification, and sequencing. Hand-cut sections of ascomata or thallus from all collected specimens were prepared for DNA isolation and DNA was extracted with a NucleoSpin Plant II Kit in line with the manufacturer's instructions (Macherey-Nagel, Düren, Germany). PCR amplification for the internal transcribed spacer region (ITS1-5.8S-ITS2 rDNA), the mitochondrial small subunit, and the nuclear large subunit ribosomal RNA genes were achieved using Bioneer's AccuPower PCR Premix (Bioneer, Daejeon, Korea) in 20 µL tubes and primers ITS5 and ITS4 (White *et al.* 1990), mrSSU1 and mrSSU3R (Zoller *et al.* 1999), and LR0R and LR5 (Rehner and Samuels 1994), respectively. The PCR thermal cycling parameters used were 95 °C (15 s), followed by 35 cycles of 95 °C (45 s), 54 °C (45 s), and 72 °C (1 min), and a final extension at 72 °C (7 min) based on Ekman (2001). DNA sequences were generated by the genomic research company GenoTech (Daejeon, Korea).

Phylogenetic analyses. All ITS and mtSSU sequences were aligned and edited manually using ClustalW in Bioedit V7.2.6.1 (Hall 1999). All missing and ambiguously aligned data and parsimony-uninformative positions were removed and only parsimony-informative regions were finally analysed in MEGA X (Kumar *et al.* 2018, Stecher *et al.* 2020). There were a total of 1,423 positions in the final dataset. The final alignment comprised 878 (ITS), and 900 (mtSSU) columns. Phylogenetic trees with bootstrap values were obtained in RAxML GUI 2.0 beta (Edler *et al.* 2021) using the maximum likelihood method with a rapid bootstrap with 1,000 bootstrap replications and GTR GAMMA for the substitution matrix. The posterior probabilities were obtained in BEAST 2.6.4 (Bouckaert *et al.* 2019) using the HKY (Hasegawa, Kishino and Yano) model, as the appropriate model of nucleotide substitution based on the Bayesian Information Criterion (BIC) (Schwarz 1978) as evaluated by bModelTest (Bouckaert and Drummond 2017), empirical base frequen-

cies, gamma for the site heterogeneity model, four categories for gamma, and a 10,000,000 Markov chain Monte Carlo chain length with a 10,000-echo state screening and 1,000 log parameters. Then, a consensus tree was constructed in TreeAnnotator 2.6.4 (Bouckaert *et al.* 2019) with a burn-in of 5,000, no posterior probability limit, a maximum clade credibility tree for the target tree type, and median node heights. All trees were displayed in FigTree 1.4.2 (Rambaut 2014) and edited in Microsoft Paint. The bootstrapping and Bayesian analyses were repeated three times for the result consistency and no significant differences were shown for the tree shapes and branch values.

RESULTS

Altogether 553 nrITS sequences were included in the analysis, whereas 175 vouchers were used in the combined phylogeny analysis based on nrITS and 12S mtSSU sequences. The species of the genus *Oxneria*, *O. alfredii* (S. Y. Kondr. et Poelt) S. Y. Kondr. et Kärnefelt, *O. huculica* (S. Y. Kondr.) S. Y. Kondr. *et al.*, and *O. ulophyllodes* (Räsänen) S. Y. Kondr. et Kärnefelt, were used as out group (Table 1).

List of specimens with GenBank accession numbers of sequences included in the phylogeny of the Physciaceae. Names proposed in this paper are provided in bold.

Results of combined phylogeny

About half of the more than 500 nrITS sequences available in the GenBank were included in the paper with a focus on species groups in need of urgent revision. The discussion is concentrated on such groups and the five subclades identified in the combined tree: 1. the *Physcia* s. l. subclade, 2. the *Rinodina* / *Tornabea* s. l. subclade, 3. the *Phaeophyscia* s. l. subclade, 4. the *Anaptychia* / *Physconia* s. l. subclade and 5. the *Heterodermia* s. l. subclade. (Fig. 1).

1. The *Physcia* s. l. subclade includes *Physcia* s. l., *Kashiwadia*, and the *Helmutiopsis* (i.e. genus proposed here for the '*Rinodina*' *atrocinerea* branch) branches. Thus, the *Helmutiopsis* is positioned in the *Physcia* s. l. subclade, far separated from *Rinodina* s. str. *Rinodina* remains polyphyletic and needs to be revised in a future analysis.

2. The *Rinodina* / *Tornabea* s. l. subclade includes *Rinodina* s. str., *Tornabea*, *Coscinocladium*, the '*Rinodina*' *orculata* group according to the combined analysis (Fig. 1).

3. The *Phaeophyscia* s. l. subclade includes the *Oxnerella* branch, the '*Rinodina*' *bischoffii* branch including two species, i.e., '*Rinodina*' *calcareae* (Hepp ex Arn.) Arn. and '*R.*' *bischoffii* (Hepp) A. Massal. in sister position to *Oxnerella*.

Table 1

List of specimens with GenBank accession numbers of sequences included in the phylogeny of the Physciaceae

Species name	voucher	nrITS	mtSSU
<i>Anaptychia ciliaris</i>	BCN-Lich 15484	GU247148	GU247182
<i>Anaptychia crinalis</i>	isolate 66A	EF582785	EF582833
<i>Anaptychia elbursiana</i>	isolate 63A	EF582782	EF582830
<i>Anaptychia setifera</i>	SK C77	KP747674	KP747680
<i>Anaptychia setifera</i>	SK D05, this paper	OK138527	
<i>Coscinocladium gaditanum</i>	MAF 9856	AY449721	AY464074
<i>Coscinocladium gaditanum</i>	MAF 9855	AY449720	AY464073
<i>Helmutiopsis alba</i>	GZU 000272655	GU553290	GU553310
<i>Helmutiopsis atrocineria</i>	H. Mayrhofer 13.740 & U. Arup (GZU)	AF540544	
<i>Helmutiopsis atrocineria</i>	M280	AF250806	
<i>Heterodermia speciosa</i>	MP34	KX512927	KX512975
<i>Heterodermia speciosa</i>	Wetmore 88030 (UPS)	JX000105	JX000125
<i>Heterodermia speciosa</i>	O-L-176824	MK811755	
<i>Huriopsis lepida</i>	[Sweden]?	AY143413	AY143424
<i>Huriopsis</i> sp.	J. Malíček 10238 (hb. Malíček)	MK778639	MK778575
<i>Huriopsis</i> sp.	J. Vondrák 15298 (PRA)	MK778640	
<i>Huriopsis xanthophaea</i>	KoLRI 34212, this paper	OK138528	
<i>Huriopsis xanthophaea</i>	161619 KoLRI, this paper	OK138529	
<i>Huriopsis xanthophaea</i>	KoLRI 34208, this paper	OK138530	
<i>Hyperphyscia adglutinata</i>	BCN-Lich 17031	GU247155	GU247189
<i>Hyperphyscia adglutinata</i>	BCN-Lich 17046	GU247154	GU247188
<i>Hyperphyscia crocata</i>	voucher South Korea S. Y. Kondratyuk 120413	MN150490	
<i>Johnsheardia</i> aff. <i>reagens</i>	161264 KoLRI, this paper	OK138531	
<i>Johnsheardia cinnamomea</i>	T807	KX015689	KX015709
<i>Johnsheardia cinnamomea</i>	T806	KX015688	KX015708
<i>Johnsheardia cinnamomea</i>	P268	KX015685	KX015704
<i>Johnsheardia hertelii</i>	M. Lambauer 0177 (GZU)	DQ849300	
<i>Johnsheardia jamesii</i>	H. Mayrhofer 10810 (GZU)	DQ849303	
<i>Johnsheardia mniaraea</i>	T803	KX015687	KX015706
<i>Johnsheardia mniaraea</i>	M249	AF250811	
<i>Johnsheardia mniaroeiza</i>	P280	KX015686	KX015713
<i>Johnsheardia mniaroeiza</i>	T831	KX015690	KX015711
<i>Johnsheardia reagens</i>	M. Lambauer 0218 (GZU)	DQ849316	
<i>Johnsheardia zwackhiana</i>	H. Mayrhofer 13.848 (GZU)	AF540552	

Table 1 (continued)

Species name	voucher	nrITS	mtSSU
<i>Kashiwadia</i> aff. <i>orientalis</i>	Hur 40164		KM397365
<i>Kashiwadia</i> aff. <i>orientalis</i>	Hur 40044		KM397366
<i>Kashiwadia</i> aff. <i>orientalis</i>	KoLRI 40620, this paper	OK138532	KM397364
<i>Kashiwadia austrostellaris</i>	Australia, Elix 38832 (F)	FJ822881	FJ816690; GU074408
<i>Kashiwadia austrostellaris</i>	Australia, New South Wales, Elix 36682 (CANB)	FJ822880	FJ816689
<i>Kashiwadia jackii</i>	Australia, Elix 28862 (CANB)	FJ822885	FJ816694
<i>Kashiwadia jackii</i>	Australia, Elix 36023 (CANB)	FJ822884	FJ816693
<i>Kashiwadia jackii</i>	Australia, Elix 32564 (CANB)	FJ822883	FJ816692
<i>Kashiwadia nubila</i>	Australia, Elix 39083 (CANB)	FJ822888	FJ816696
<i>Kashiwadia orientalis</i>	Hur 040164	EU670210	KM397365
<i>Kashiwadia orientalis</i>	Hur 040044	EU670209	KM397366
<i>Kashiwadia orientalis</i>	Hur 040849		KM397367
<i>Kashiwadia</i> sp.	AFTOL-ID 84	DQ782836	DQ912290
<i>Kashiwadia tropica</i>	Australia, Northern Territory, Elix 36320 (CANB)	FJ822890	FJ816698
<i>Kashiwadia tropica</i>	Australia, Northern Territory, Elix 37727 (CANB)	FJ822889	FJ816697
<i>Klauskalbia flabellata</i>	Hur 040623	EU045436	KM397361
<i>Klauskalbia obscurata</i>	BCN-Lich 16794	GU247152	GU247186
<i>Klauskalbia obscurata</i>	BCN-Lich 15527	GU247151	GU247185
<i>Kudratovia bohlinii</i>		MT435940	
<i>Kudratovia bohlinii</i>	G112	MT435939	
<i>Kudratovia candidogrisea</i>	Hafellner 73533	JN211109	
<i>Kudratovia candidogrisea</i>	Hafellner 75179	JN211107	
<i>Kudratovia luridata</i>	H. Mayrhofer 12122 (GZU)	DQ849304	
<i>Kudratovia luridata</i>	GZU 000272660	GU553298	GU553316
<i>Kudratovia metaboliza</i>	G170	MT260863	
<i>Kudratovia metaboliza</i>	G169	MT260864	
<i>Kudratovia pycnocarpa</i>	G79	MT435947	
<i>Kudratovia roscida</i>	S. Kholod plot515 (GZU)	DQ849317	
<i>Kudratovia straussii</i>	G53	MT435945	
<i>Kudratovia straussii</i>	G54	MT435942	
<i>Kudratovia terrestris</i>	G98	MT435946	
<i>Kurokawia bryorum</i>	U383 nrITS / 57B mtSSU	AF250781	EF582825
<i>Kurokawia isidiata</i>	as <i>Heterodermia isidiophora</i> voucher Hur 060480-2	EU045430	

Table 1 (continued)

Species name	voucher	nrITS	mtSSU
<i>Kurokawia isidiata</i>	162011 KoLRI, this paper	OK138533	
<i>Kurokawia isidiata</i>	162012 KoLRI, this paper	OK138534	
<i>Kurokawia isidiata</i>	060480 KoLRI, this paper	OK138535	
<i>Kurokawia isidiata</i>	121046 KoLRI, this paper	OK138536	
<i>Kurokawia palmulata</i>	isolate 59A	EF582779	KJ766523; EF582827
<i>Kurokawia runcinata</i>	isolate 54A	EF582775	KX512977; EF582824
<i>Leucodermia boryi</i>	S2_11_HL3	KU862952	
<i>Leucodermia boryi</i>	D3_42_HL2	KU862951	
<i>Leucodermia boryi</i>	Hur 040340	EU045422	
<i>Leucodermia boryi</i>	Hur 040754	EU045423	KM397356
<i>Leucodermia erinacea</i>	isolate 2A / 2B	EF582746	EF582789
<i>Leucodermia leucomelos</i>	MAF 7638	AY449725	AY464072
<i>Leucodermia subascendens</i>	Hur 040847	EU045442	KM397363
<i>Leucodermia subascendens</i>	Hur 040658	EU045427	
<i>Leucodermia subascendens</i>	KoLRI 30895, this paper	OK138537	
<i>Leucodermia subascendens</i>	Hur 040619	EU045441	KM397362
<i>Leucodermia vulgaris</i>	isolate AFTOL-ID 320	HQ650704	DQ912288
<i>Leucodermia vulgaris</i>	isolate HV	KX512928	KX512989
<i>Oxnerella afghanica</i>	SK 513 as <i>O. safaavidiorum</i> , (Kondratyuk <i>et al.</i> 2014a)	KM410153	KN410156
<i>Oxnerella afghanica</i>	SK 512 as <i>O. safaavidiorum</i> , (Kondratyuk <i>et al.</i> 2014a)	KM410152	KN410155
<i>Oxnerella afghanica</i>	SK 511 as <i>O. safaavidiorum</i> , (Kondratyuk <i>et al.</i> 2014a)	KM410151	KN410154
<i>Oxnerella afghanica</i>	G152	MT260858	
<i>Oxnerella afghanica</i>	G151	MT260860	
<i>Oxnerella afghanica</i>	G153	MT260859	
<i>Oxnerella castanomelodes</i>	G74	MT435948	
<i>Oxneria alfredii</i>	FNM 152	EU681345	EU680933
<i>Oxneria huculica</i>	Aftol-ID 406 / FNM 199	HQ650706	EU680931
<i>Oxneria ulophyllodes</i>	FNM 198	KC179144; EU681342	EU680930
<i>Phaeophyscia ciliata</i>	Tehler 7914 / MP8	AF224457	KX512958
<i>Phaeophyscia endococcina</i>	17A / B	EF582753	EF582804
<i>Phaeophyscia hirsuta</i>	BCN-Lich 15109	GU247167	GU247201
<i>Phaeophyscia insignis</i>	BCN-Lich 17035	GU247169	GU247204

Table 1 (continued)

Species name	voucher	nrITS	mtSSU
<i>Phaeophyscia nigricans</i>	Moberg 12046 / 14B	AF224375	EF582801
<i>Phaeophyscia orbicularis</i>	Tehler 7913 / MP49	AF224452	KX512967
<i>Phaeophyscia pusilloides</i>	BCN-Lich 17036	GU247170	GU247203
<i>Phaeophyscia rubropulchra</i>	141271	MN150493	
<i>Phaeophyscia rubropulchra</i>	160391 KoLRI, this paper	OK138538	
<i>Phaeorrhiza nimbose</i>	U386	AF250800	KX015707
<i>Phaeorrhiza nimbose</i>	KUN-L ZZY-10	MW133638	MW133653
<i>Phaeorrhiza nimbose</i>	voucher KUN-L 19-65695	MW133637	MW133652
<i>Phaeorrhiza nimbose</i>	voucher KUN-L 19-65328	MW133635	MW133650
<i>Phaeorrhiza sareptana</i>	E35	AF250801	AY143421
<i>Phaeorrhiza sareptana</i>	KUN-L 19-65347	MW133636	MW133651
<i>Phaeorrhiza sareptana</i>	KUN-L 19-65326	MW133634	MW133649
<i>Phaeorrhiza sareptana</i>	KUN-L 18-62379	MW133630	MW133645
<i>Physcia aipolia</i>	Nordin 3847	AF244391	EU682128
<i>Physcia almophila</i>	Ahti 64008	EU682210	EU682153
<i>Physcia biziana</i>	BCN-Lich 17044	GU247178	GU247212
<i>Physcia caesia</i>	Urbanavichus C-01566	EU682197	EU682139
<i>Physcia leptalea</i>	Moberg 12031 / BCN-Lich 16792	AF224428	GU247210
<i>Physcia orientostellaris</i>	Hur 050213 as <i>Physcia stellaris</i>	EU670220	
<i>Physcia orientostellaris</i>	KoLRI 41671, this paper	OK138539	
<i>Physcia orientostellaris</i>	101264 KoLRI, this paper	OK138540	
<i>Physcia orientostellaris</i>	120788 KoLRI, this paper	OK138541	
<i>Physcia orientostellaris</i>	KoLRI 41642, this paper	OK138542	
<i>Physcia orientostellaris</i>	KoLRI 41649, this paper	OK138543	
<i>Physcia stellaris</i>	4Sb / FNM 160	AY860537	EU680859
<i>Physcia stellaris</i>	BIOUG24047-D07	KT695388	
<i>Physcia stellaris</i>	20Sa / Moberg 12012	AY860547	EU682115
<i>Physcia subalbinea</i>	Vitikainen 14417	EU682188	EU682121
<i>Physcia ucrainica</i>	SK C01, Ukraine (Kondratyuk <i>et al.</i> 2015)	KP747679	KP747685
<i>Physciella chloantha</i>	BCN-Lich 15519	GU247162	GU247196
<i>Physciella melanchnra</i>	170857 KoLRI, this paper	OK138544	
<i>Physciella melanchnra</i>	171055 KoLRI, this paper	OK138545	
<i>Physciella melanchnra</i>	171779 KoLRI	MN150501	
<i>Physconia detersa</i>	Esslinger 14682 (hb. Esslinger)	AY368115	EF582815; EF582811
<i>Physconia distorta</i>	SK C88, this paper / 31B SK C88	OK138546	EF582814

Table 1 (continued)

Species name	voucher	nrITS	mtSSU
<i>Physconia enteroxantha</i>	SK C89, this paper	OK138547	EF582816
<i>Physconia enteroxantha</i>	MAF 6257	AY368123	EF582817
<i>Physconia grumosa</i>	isolate 39A	EF582769	EF582818
<i>Physconia jacutica</i>	<i>Physconia</i> sp. KL-2007b	EF594742	EF594746
<i>Physconia muscigena</i>	Malíček: 10468	LS483212	EF594747
<i>Physconia rossica</i>	17-0612	MN103157	EF594745; EF594744
<i>Poeltonia elegantula</i>	22A	EF582757	EF582808
<i>Poeltonia grisea</i>	SK C78, this paper	OK138548	
<i>Poeltonia grisea</i>	MAF 9788	AY368126	AY464077
<i>Poeltonia grisea</i>	SK D04, this paper	OK138549	
<i>Poeltonia grisea</i>	MAF 9783	AY368125	AY464067
<i>Poeltonia perisidiosa</i>	23A & 23B	EF582758	EF582809
<i>Poeltonia venusta</i>	MAF-Lich 14123	DQ862497; EF582759	JQ301538; EF582810
<i>Polyblastidium casarettianum</i>	<i>Heterodermia casarettiana</i> voucher 15441a	DQ337305	
<i>Polyblastidium japonicum</i>	Hur 61140	KM397355	
<i>Polyblastidium japonicum</i>	China: Hu, G. R. and Chen, J. B.	AY498687	
<i>Polyblastidium japonicum</i>	Hur 60291	EU045432	KM397359
<i>Polyblastidium propaguliferum</i>	Hur 041134	EU045437	
<i>Polyblastidium</i> sp.	<i>Heterodermia</i> sp. 16606a	DQ337327	
' <i>Polyblastidium</i> ' <i>hypoleucum</i>	Hur 060232	EU045428	KM397358
' <i>Polyblastidium</i> ' <i>hypoleucum</i>	personal: Hara Kojiro: 0034	LC533098	
' <i>Polyblastidium</i> ' <i>microphyllum</i>	Hur 060494	EU045434	
' <i>Polyblastidium</i> ' <i>microphyllum</i>	Hur 060173	EU045433	KM397360
<i>Rinodina glauca</i>	GZU 000272662	GU553295	GU553295
<i>Rinodina milvina</i>	H. Mayrhofer 13.702 (GZU)	AF540546	GU553317
<i>Rinodina septentrionalis</i>	GZU 000272561	GU553303	GU553320
<i>Rinodina sophodes</i>	GZU 000272661	GU553304	
' <i>Rinodina</i> ' <i>albana</i>	GZU 000272651 / P266	GU553297	KX015703
' <i>Rinodina</i> ' <i>balanina</i>	O-L-195705 Norway	KY266842	
' <i>Rinodina</i> ' <i>bischoffii</i>	KW 63380 Ukraine	GU553291	GU553311
' <i>Rinodina</i> ' <i>calcareo</i>	GZU 000272654	GU553292	GU553312
' <i>Rinodina</i> ' <i>capensis</i>	GZU 000272663	GU553293	GU553313
' <i>Rinodina</i> ' <i>capensis</i>	W. Obermayer 09230 (GZU)	DQ849296	
' <i>Rinodina</i> ' <i>confragosa</i>	M287	AF250808	

Table 1 (continued)

Species name	voucher	nrITS	mtSSU
' <i>Rinodina</i> ' <i>confragosa</i>	W. Obermayer 09091 (GZU)	DQ849297	
' <i>Rinodina</i> ' <i>degeliana</i>	P232	KX015679	KX015698
' <i>Rinodina</i> ' <i>degeliana</i>	P231	KX015678	KX015697
' <i>Rinodina</i> ' <i>exigua</i>	GZU 000272652	GU553294	GU553314
' <i>Rinodina</i> ' <i>interpolata</i>	M263	AF250809	
' <i>Rinodina</i> ' <i>oleae</i>	B42740a Greece	AJ544186	GU553318
' <i>Rinodina</i> ' <i>orculata</i>	H. Mayrhofer 15754 (GZU)	DQ849309	
' <i>Rinodina</i> ' <i>plana</i>	E34	AF250812	AY143425
' <i>Rinodina</i> ' <i>pyrina</i>	P. Bilovitz, H. Mayrhofer 483 (GZU)	AF540549	GU553319
' <i>Rinodina</i> ' <i>subpariata</i>	P235	KX015682	KX015700
' <i>Rinodina</i> ' <i>subpariata</i>	P101	KX015673	KX015693
' <i>Rinodina</i> ' <i>teichophila</i>	GZU 000272659	GU553305	GU553322
' <i>Rinodina</i> ' <i>trevisanii</i>	P264	KX015684	KX015702
<i>Tornabea</i> <i>scutellifera</i>	BCN-Lich 16791	GU247172	GU247206
<i>Tornabea</i> <i>scutellifera</i>	BCN-Lich 16804	GU247173	GU247207
<i>Tornabea</i> <i>scutellifera</i>	AFTOL-ID 1061	JQ301698	DQ972985

Names proposed in this paper are provided in **Bold**

This subclade furthermore includes the *Physciella* branch, the *Phaeophyscia* s. str. branch, the *Kudratovia* (i.e. the former '*Rinodina*' *straussii* group) branch, as well as the '*Rinodina*' *teichophila* branch.

4. The *Anaptychia* / *Physconia* s. l. subclade includes the *Johnsheardia* branch (i.e. the former '*Rinodina*' *cinnamomea* group), the *Poeltonia* branch (the former '*Physconia*' *grisea* group), the *Phaeorrhiza* branch, the *Anaptychia* s. str. branch and the *Kurokawia* branch (the former '*Anaptychia*' *isidiata* group). Our results confirm the conclusion of Lohtander *et al.* (2008) that the support for the *Physconia* / *Anaptychia* clade is rather weak, while almost all monophyletic branches within this clade, except the *Poeltonia* branch, are strongly supported (Fig. 1). *Kurokawia* is positioned as sister position to the *Anaptychia* s. str. branch. The support for *Poeltonia* varies between different trees, however, species strongly supported as members of this genus are *P. grisea* (Lam.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *P. elegantula* (Essl.) S. Y. Kondr., L. Lőkös et J.-S. Hur and *P. perisidiosa* (Erichsen) S. Y. Kondr., L. Lőkös et J.-S. Hur, *P. venusta* (Ach.) S. Y. Kondr., L. Lőkös et J.-S. Hur, whereas the support is weaker for *P. isidiomuscigena* (Essl.) S. Y. Kondr., L. Lőkös et J.-S. Hur, as well as *Physconia muscigena* (Ach.) Poelt, and *P. rossica* Urbanav.

5. The single *Hyperphyscia* branch is positioned in out position to the *Physcia* s. l. and *Anaptychia* – *Physconia* s. l. subclades.

6. The *Huriopsis* s. l. subclade includes the *Huriopsis* (i.e. the former '*Rinodina*' *xanthophaea* group), the '*Rinodina*' *capensis* branch with the '*Rinodina*' *exigua* single species branch as single sister to the '*Rinodina*' *capensis* branch, as well as the '*Rinodina*' *oleae* branch.

7. The *Heterodermia* s. l. subclade includes the genera *Leucodermia*, *Polyblastidium*, *Heterodermia* s. str., *Klauskalbia* (the former '*Heterodermia*' *obscurata* group), and the '*Polyblastidium*' *hypoleucum* group, forming a separate branch. The genera *Leucodermia* is confirmed as monophyletic, whereas *Polysporidium* appears to be polyphyletic.

Comments on phylogeny based on nrITS sequences

The genera *Mischoblastia*, *Mobergia* and *Rinodinella* are supported only by nrITS phylogeny, thus are not included in the combined phylogenetic analysis (not included in the tree, Fig. 1) (Table 2).

Some additional branches of species groups exist outside the subclades.

Comments to the *Kashiwadia* s. l. subclade being a member of the *Physcia* s. l. subclade are placed under revised genera (see below). New sequences for *Kashiwadia* aff. *orientalis* have been submitted to the GenBank within this study (Table 1, Fig. 1).

Sequences for Korean *Physcia orientostellaris* S. Y. Kondr., Lökös (Kondratyuk *et al.* 2017) are provided for the first time, too. This recently described species forms a separate branch within the *Physcia* s. str. clade (Fig. 1).

Rinodina s. str., situating in the *Rinodina* / *Tornabea* s. l. subclade includes *Rinodina sophodes* (Ach.) A. Massal., *R. septentrionalis* Malme, *R. glauca* Ropin, *R. milvina* (Wahlenb.) Th. Fr., *R. anomala* (Zahlbr.) H. Mayrhofer et Giral, *R. obnascens* (Nyl.) H. Olivier and *R. roboris* (Dufour ex Nyl.) Arn. Only nrITS sequences are available for the latter three species. Position of the first five taxa of the *Rinodina* s. str. confirms the data of previous authors (Nadyeina *et al.* 2010).

Rinodina anomala and *R. roboris* are sometimes found together with the *Rinodina efflorescens* group in sister position to the *Kashiwadia* / *Physcia* subclade after nrITS phylogeny.

According to the phylogeny based on mtSSU phylogeny, the *Rinodina* s. str. branch includes also *Rinodina freyi* H. Magn., and *R. malangica* (Norman) Arn., however, nrITS sequences are missing for these species. Therefore, *R. freyi* and *R. malangica* are not included into the combined analysis.

The '*Rinodina*' *orculata* branch (as '*Rinodina*' 2 in Fig. 1), including '*Rinodina*' *orculata* H. Mayrhofer et Poelt, '*R.*' *trevisanii* (Hepp) Körb., '*R.*' *interpolata* (Stirt.) Sheard, '*R.*' *balanina* (Wahlenb.) Vain., *Rinodina archaea* (Ach.) Arn., '*R.*' *plana* H. Magn., and '*R.*' *olivaceobrunnea* C. W. Dodge et G. E. Baker, is positioned in the *Physcia* s. l. subclade. The '*Rinodina*' *orculata* branch sometimes forms a common clade with the '*R.*' *efflorescens* branch, including also '*Rino-*

Table 2
Monophyletic branches of the Physciaceae proved by combined or nrITS phylogeny

Subclades after combined phylogeny	Genera proved by combined phylogeny		Branches proved by nrITS phylogeny	
	accepted	newly proposed	accepted genera	branches
the <i>Anaptychia</i> / <i>Physconia</i> s. l.	<i>Anaptychia</i> s. str., <i>Coscinodiscus</i> , <i>Phaeorrhiza</i> , <i>Physconia</i> s. str., <i>Tornabea</i>	<i>Johansheardia</i>, <i>Kurokavia</i>, <i>Poelttonia</i>	<i>Mischoblastia</i> s. l.	' <i>Rinodina</i> ' <i>anomala</i> gr., ' <i>R.</i> ' <i>disjuncta</i> gr., ' <i>R.</i> ' <i>efflorescens</i> gr., ' <i>R.</i> ' <i>gallowayi</i> gr., ' <i>R.</i>' <i>orculata</i> gr. [as ' <i>Rinodina</i> ' 2 in Fig. 1], ' <i>R.</i> ' <i>turfacea</i> gr.
the <i>Heterodermia</i> s. l.	<i>Heterodermia</i> s. str., <i>Leucodermia</i> , <i>Polyblastidium</i>	<i>Klauskalbia</i>		' <i>Polyblastidium</i> ' <i>hypoleucum</i> gr.
the <i>Huriopsis</i> s. l.		<i>Huriopsis</i>		' <i>Rinodina</i> ' <i>capensis</i> gr., ' <i>R.</i> ' <i>exigua</i> , ' <i>R.</i> ' <i>oleae</i> gr., ' <i>R.</i> ' <i>subpariata</i> gr.
the <i>Phaeophyscia</i> s. l.	<i>Oxnerella</i> , <i>Phaeophyscia</i> s. str., <i>Physciella</i>	<i>Kudratovia</i>	<i>Rinodinella</i>	' <i>Rinodina</i> ' <i>bischoffii</i> gr., ' <i>R.</i> ' <i>teichophyla</i> gr.
the <i>Physcia</i> s. l.	<i>Physcia</i> s. str., <i>Kashiwadia</i> (s. l.)	<i>Helmutiopsis</i>	<i>Mobergia</i>	
the <i>Hyperphyscia</i> branch	<i>Hyperphyscia</i>			
the <i>Rinodina</i> s. str.	<i>Rinodina</i> s. str.			
Total	15	7	3	12

Genera proposed or revised in this paper are in bold

dina' *anomala* and '*R.*' *roboris*, in sister position to the *Tornabea* branch.

The single species '*Rinodina*' *anomala*, represented by two specimens, is situated in the sister position to the *Tornabea* and the *Coscinodiscus* branches.

'*Rinodina*' *efflorescens* is another single species. A specimen identified as *Rinodina* sp. 17776 from Białowieża, Poland most likely represents '*R.*' *efflorescens*.

The *Rinodinella* s. str. branch and *Mischoblastia* s. l. branch, which are supported only by nrITS phylogeny are in the sister position to the '*R.*' *bischoffii* group, whereas all three branches are in sister position to the *Hyperphyscia* branch of the *Phaeophyscia* s. l. subclade.

The *Rinodinella* s. str. branch includes *Rinodinella controversa* (A. Massal.) H. Mayrhofer et Poelt and *R. dubyanoides* (Hepp) H. Mayrhofer et Poelt. Both *Rinodinella* and the '*Rinodina*' *bischoffii* group belong to the *Oxnerella* / *Rinodinella* s. l. subclade. Our results confirm the previous data (Nadyeina et al. 2010) that '*Rinodina*' *bischoffii* (Hepp) A. Mas-

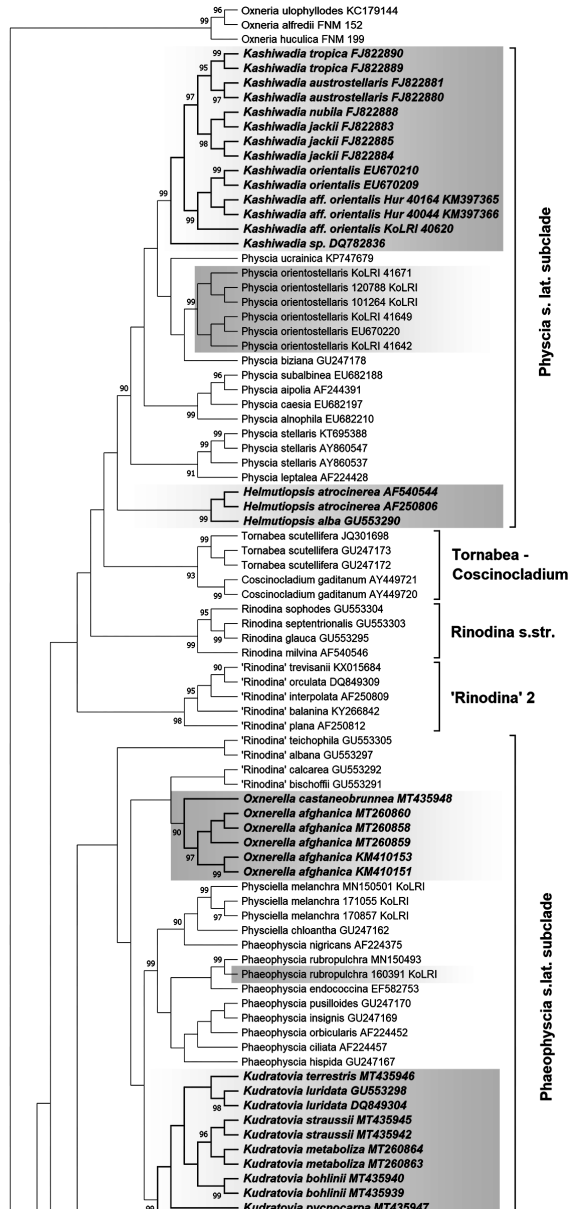


Fig. 1. Phylogenetic relationships among available species in the Physciaceae based on a maximum likelihood analysis of the combined dataset based on nrITS and of the 12S mitochondrial small subunit (mtSSU) sequences. The tree was rooted with three sequences of the genus *Oxneria*. Maximum likelihood bootstrap values $\geq 90\%$ and posterior probabilities $\geq 95\%$ are shown above internal branches. Branches with new genera and with bootstrap values $\geq 90\%$ are shown in bold. All species names are followed by the GenBank accession numbers or voucher information

sal, '*R.* calcarea (Hepp ex Arn.) Arn., '*R.* immersa (Körb.) J. Steiner, '*R.* tunicata H. Mayrhofer et Poelt and one more additional, undescribed species from Iran all belong to the '*Rinodina* bischoffii' group, whereas the presumed position for '*Rinodina* guzzinii Jatta in this group remains unclear because of lack of mtSSU

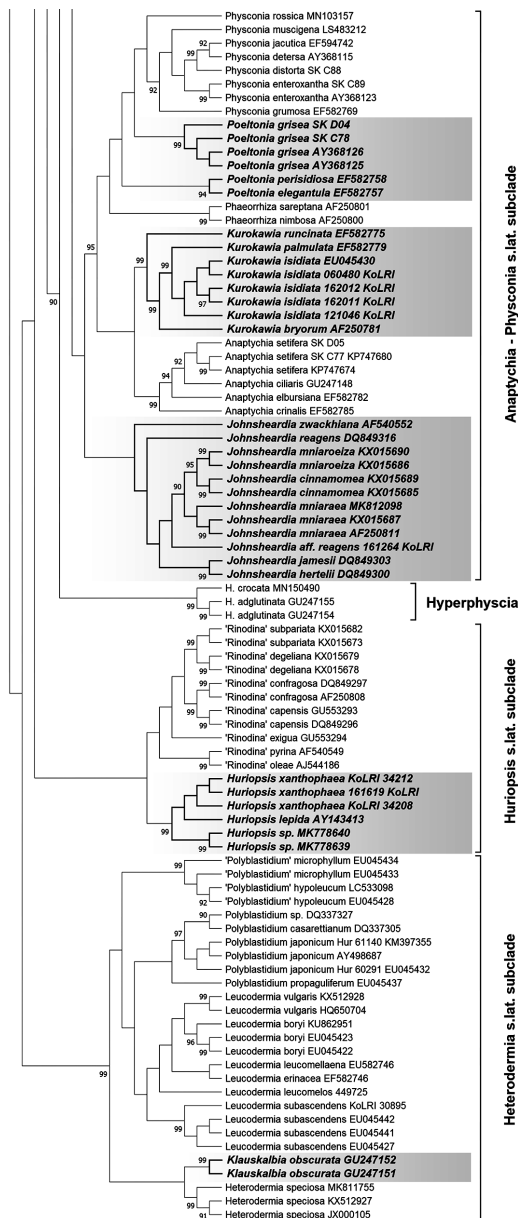


Fig. 1 (continued)

sequences. Only two species of the group, '*R.* *bischoffii*' and '*R.* *calcarea*', are represented by mtSSU sequences. Therefore, *Rinodinella* s. str. branch is therefore not included into the combined phylogenetic tree.

The position and delimitation of the genus *Mischoblastia* A. Massal. according to the phylogeny based on nrITS sequences data are discussed below.

The '*Rinodina*' *luridescens* branch of the *Hyperphyscia* s. l. subclade, includes '*Rinodina*' *luridescens* (Anzi) Arn., '*R.*' *parvula* H. Mayrhofer et Poelt, and '*R.*' *lindigerii* (Erichsen) Giralt et van den Boom. '*Rinodina*' *luridescens* has a thick grey-violet-black thallus with large immersed apothecia without a perceptible exciple. The ascospores appear intermediate between the *Physcia*- and *Milvina*-types. It contains gyrophoric acid and zeorin and is widely distributed in the Northern Hemisphere on maritime rock in xeric-supralittoral habitat. It is mainly an Atlantic and Mediterranean species reaching the Black Sea. Nadyeina *et al.* (2010) and Hafellner *et al.* (2012) revealed '*Rinodina*' *luridescens* group to include also '*Rinodina*' *parvula* and '*R.*' *lindigerii* with maximum support.

From our nrITS phylogeny the '*Rinodina*' *luridescens* branch is usually positioned in sister position to both the '*Rinodina*' *gallowayi* branch including '*R.*' *gallowayi* H. Mayrhofer, '*R.*' *cacaotina* Zahlbr., and the *Hyperphyscia* s. str. branch. However, the status of the '*Rinodina*' *luridescens* discerned in the phylogeny based on nrITS sequences within the *Hyperphyscia* s. l. subclade can not be confirmed in the combined phylogeny analysis since data on mtSSU are lacking.

Within the *Phaeophyscia* s. l. subclade the *Physciella melanchra* (Hue) Essl. branch with several additional specimens from Dokdo Islands is positioned in a separate branch together with *P. chloantha* (Ach.) Essl., while *Physciella denigrata* (Hue) Essl. is positioned within the *Phaeophyscia* s. str. branch. Thus, *Phaeophyscia denigrata* (Hue) Moberg is probably the correct name for this taxon.

Position of the single species '*Rinodina*' *disjuncta* Sheard et Tønsberg is hitherto somewhat contradictory. It forms a branch between the *Mischoblastia* and *Physcia* s. l. subclades. In the phylogeny based on nrITS sequences only, the '*Rinodina*' *disjuncta* (MK812529 and MK812438) and the '*Rinodina*' *turfacea* (Wahlenb.) Körb. branches are positioned in sister position to the *Phaeorrhiza* branch within the *Physconia* / *Anaptychia* s. l. subclade. The '*Rinodina*' *turfacea* group takes a sister position of the *Phaeorrhiza* branch and is also a member of the *Anaptychia* / *Physconia* s. l. subclade according to the combined phylogeny analysis, too.

The position and delimitation of the genus *Oxnerella* positioning within the *Oxnerella* / *Rinodinella* s. l. subclade at the base of the *Phaeophyscia* s. l. subclade are discussed below.

After the nrITS phylogeny within the *Physcia* s. l. subclade (while after combined phylogeny within the *Huriopsis* s. l. subclade, see Fig. 1) the '*Rinodina*' *capensis* group and *Mobergia*, for which 12S mtSSU sequences are lacking, have a preliminary position. The *Rinodina capensis* group / branch includes *R. capensis* Hampe, *R. cana* (Arn.) Arn. and *R. confragosa* (Ach.) Körb.

The '*Rinodina*' *oleae* branch, containing '*Rinodina*' *oleae* Bagl., '*R.*' *nimisii* Giralt et H. Mayrhofer, '*R.*' *gennarii* and '*R.*' *pyrina* (Ach.) Arn., is positioned in sister position to the *Phyiscia* subclade (while after combined phylogeny it is positioned within the *Huriopsis* s. l. subclade, see Fig. 1).

The *Heterodermia* branch was the subject in two pioneering phylogeny papers by Lohtander *et al.* (2000) using nrITS sequences and both nrITS and mtSSU sequences (Lohtander *et al.* 2008). The *Heterodermia* subclade as monophyletic has rather weak support but contains several strongly supported monophyletic branches, the genus *Leucodermia* Kalb being one of those. A new combination, *L. erinacea* is proposed here supported both by phylogeny using nrITS sequences only and a combined matrix (Fig. 1). On the contrary, the recently accepted genus *Polyblastidium* Kalb does not form one but two strongly supported monophyletic branches, *Polyblastidium* s. str. and the '*Polyblastidium*' *hypoleucum* group, however, represented by two species only, *P. hypoleucum* (Ach.) Kalb and *P. microphyllum* (Kurok.) Kalb, therefore a future revision is necessary.

The '*Heterodermia*' *subascendens* branch including '*H.*' *subascendens* (Asahina) Trass, '*H.*' *comosa* (Eschw.) Follmann et Redón, and '*H.*' *hypochraea* (Vain.) Swinscow et Krog appears to be as sister group of the *Leucodermia* branch in some trees, however, mostly with weak support.

A new genus, *Klauskalbia* is proposed for the '*Heterodermia*' *obscurata* branch including '*H.*' *obscurata* (Nyl.) Trevis., '*H.*' *flabellata* (Fée) D. D. Awasthi and two specimens preliminary identified as '*H.*' *obscurata* (Hur 40623 and Hur 50136 in herb. KoLRI), however, perhaps belonging to *H. flabellata*, since specimens identified as '*H.*' *obscurata* are found also in the *Kashiwadia orientalis* and *K. aff. orientalis* branches.

Heterodermia s. str. includes *H. speciosa* (Wulfen) Trevis., *H. pseudospeciosa* (Kurok.) W. L. Culb., *H. isidiophora* (Nyl.) D. D. Awasthi, and *H. diademata* (Taylor) D. D. Awasthi.

The genus *Chaudhuria* Zahlbr. has been considered as synonymous with *Heterodermia* (<http://www.speciesfungorum.org/Names/SynSpecies.asp?RecordID=2316>). However, we discovered that *Chaudhuria indica* Zahlbr. has never been combined in *Heterodermia*. Furthermore, *Anaptychia indica* H. Magn. (Awasthi 1960) and *Heterodermia indica* (H. Magn.) D. D. Awasthi (Awasthi 1973) has to be listed as illegitimate names. No molecular data and no recent records exist for the species.

The '*Rinodina*' *degeliana* branch forms a sister group to the *Heterodermia* s. l. subclade after nrITS phylogeny, while after combined data set it is positioned in the *Huriopsis* s. l. subclade (Fig. 1). According to both nrITS and mtSSU phylogeny analyses separately, the '*Rinodina*' *degeliana* branch include '*R.*' *degeliana* Coppins and '*R.*' *subpariata* (Nyl.) Zahlbr., the latter often listed as synonym to *R. degeliana*.

Sometimes the '*Rinodina*' *degeliana* branch is joined by the '*Rinodina*' *capensis* branch (see above) forming a basally placed subclade in the Physciaceae.

Specimens with GB accession numbers EU045436 (Hur 040623) and EU045453 (Hur 50136), both from the Republic of Korea submitted under name '*Heterodermia obscurata*' were revealed to belong to '*Heterodermia*' *flabellata* (Fée) D. D. Awasthi, at least in a wide sense.

The specimen '*Heterodermia*' *diademata* (Taylor) D. D. Awasthi with GB accession number AF540518 is positioned in the '*Heterodermia*' *subscendens* branch, while '*H.*' *diademata* is positioned in the *Polyblastidium hypoleucum* branch.

Incorrectly identified specimens labelled as *Heterodermia* often belong to *Anaptychia* and *Kurokawia* (see below).

Single species molecular data on which are waiting for confirmation

The separate nrITS phylogeny analysis of *Physcia halei* J. W. Thomson (MN989317) and *Rinodina violascens* H. Magn, (several specimens) are found in an isolated position in the Physciaceae (these taxa are not shown in Fig. 1).

MtSSU phylogeny

Both *Rinodina freyi* H. Magn. and *R. malangica* (Norman) Arn. belong to the *Rinodina* s. str. branch according to the phylogeny based on mtSSU sequences.

Physcia halei is represented by a single specimen (MN989316). It has a basal position in the Physciaceae according to the mtSSU sequences, which is in line with the phylogeny based on nrITS phylogeny.

Rinodina griseosoralifera Coppins, an additional species represented by a single specimen (MK778573), also has a basal position in the Physciaceae according to mtSSU phylogeny, however, a nrITS sequence is lacking for this specimen.

Additional samples are needed for both *Physcia halei* and *Rinodina griseosoralifera*.

New and revised genera

Helmutiopsis S. Y. Kondr., L. Lőkös et J.-S. Hur, *gen. nova*

MycoBank No.: MB 841013

Similar to the genus Rinodina but differs in having Pachysporaria-type of ascospores, in having atranorin and gyrophoric acid as well as in the position in the Physcia s. l. subclade of the Physciaceae.

Type species: *Helmutiopsis atrocineria* (Fr.) S. Y. Kondr., L. Lőkös et J.-S. Hur

Thallus thin, areolated or rimoso-areolated, grey or whitish grey. Apothecia usually numerous, lecanorine; ascus of *Lecanora*-type. Ascospores of *Pachysporaria*-type with thickenings of ascospore walls.

Chemistry: Atranorin, gyrophoric (and 2''-O-methylgyrophoric acid in *Helmutiopsis alba*) and lecanoric acid present.

Ecology: Three taxa of this genus are saxicolous.

Etymology: The new genus is named after the Austrian lichenologist Helmut Mayrhofer (Graz, GZU) in recognition of his extensive contribution to the knowledge of rinodinoid lichens and to lichenology in general.

Distribution and species diversity: The genus hitherto includes three species which rather rare in the Northern Hemisphere, among which *H. alba* seem to be more widely distributed.

Taxonomic notes: Our combined analysis confirms the data of previous authors that the *Helmutiopsis atrocinerea* branch including two species (i.e. *H. atrocinerea* and *H. alba*) is positioned in sister position to the *Physcia* s. l. subclade (Nadyeina *et al.* 2010, clade B). However, from our data the '*Rinodina*' *capensis* and '*R.*' *oleae* are positioned in the *Huriopsis* s. l. subclade in contrast to previous data, where these two branches were positioned in distant from the *Physcia aipolia* branch position (clade A and clade E in Nadyeina *et al.* 2010, consequently).

After nrITS phylogeny where larger number of monophyletic branches found (see above) the *Helmutiopsis* branch positioning between the *R. efflorescens* and the *Physcia* s. str. branches includes *H. atrocinerea* (Fr.) S. Y. Kondr., L. Lőkös et J.-S. Hur and *H. alba* (Metzler ex Arn.) S. Y. Kondr., L. Lőkös et J.-S. Hur. This genus probably also includes the Atlantic species *Helmutiopsis aspersa* (Borrer) S. Y. Kondr., L. Lőkös et J.-S. Hur, however, molecular data for the latter are still lacking. Sometimes the type species, i.e. *H. atrocinerea* was considered as infraspecific taxon of the latter taxon (*Rinodina aspersa* var. *atrocinerea* (Fr.) Cl. Roux or *R. aspersa* subsp. *atrocinerea* (Fr.) Cl. Roux) (Roux *et al.* 2006).

Huriopsis S. Y. Kondr. et L. Lőkös, *gen. nova*

Mycobank No.: MB 841014

Similar to Rinodina but differs in having a citrine coloured thallus or yellow-green soralia, ascospores of Pachysporaria-type and presence of xanthone thiomelin in cortex and medulla.

Type species: *Huriopsis xanthophaea* (Nyl.) S. Y. Kondr. et L. Lőkös

Thallus thin to moderately thick, golden yellow or grey; areolate to continuous; surface otherwise plane and matt; vegetative propagules (soredia and true isidia) present or absent, developing as marginal, labriform soralia,

often becoming circular, sometimes with a central perforation, then pustulate; soredia as larger consoredia sometimes present, which may develop into blastidia; thallus indeterminate; soralia or true isidia yellow-green; prothallus typically present, black, entire, then sometimes thick, rimose-areolate, or fimbriate at the margins, particularly when overgrowing foliose lichens. Apothecia frequent but often absent in sorediate thalli, rarely contiguous, narrowly attached; disc dark reddish brown, plane; margin concolorous with the thallus, 0.15–0.25 mm wide, flexuose and persistent. Reddish orange crystals present in the cortex of the thalline exciple and the medulla obscuring the structure of both, less dense in the medulla. Ascospores with Type A development, *Physcia*- or *Pachysporaria*-type, walls not ornamented.

Chemistry: Secalonic acid A or W (major), thiomelin in some species, atranorin [minor or trace], and three unknown eumitrin derivatives (eumitrin Y (submajor), eumitrin X (minor), eumitrin U (minor)) (Lendemer *et al.* 2012); xanthone pigments present in the cortex or in the medulla. Spot tests: K⁻, C⁺ yellow-orange, KC⁺ yellow-orange, P⁻, UV⁺ dull orange.

Ecology: On bark of deciduous trees (*Abies nephrolepis*, *A. sachalinensis*, *Betula costata*, *B. mandshurica*, *Fraxinus mandshurica*, *Larix gmelinii*, *Maackia amurensis*, *Magnolia obovata*, *Phellodendron amurense*, *Picea ajanensis*, *Pinus koraiensis*, *Quercus mongolica*, *Q. dentata*, *Salix caprea*, *Tilia amurensis*, *T. mandschurica*, etc.), on wood and on detritus over rocks, at elevations of 70–1,535 m. It is sometimes found growing over decaying thalli of *Parmelia* species. Three species are also saxicolous.

Etymology: The new genus is named after the Korean lichenologist Jae-Seoun Hur (Sunchon, Republic of Korea) in recognition of his significant studies of the East Asian lichens.

Distribution and species diversity: The genus includes eight species of which *H. lepida* is known from Central and South America (Florida, Gulf of Mexico and the Galapagos Islands), *H. xanthophaea* from East Asia region (Japan, Russia, and Republic of Korea), whereas *H. chrysideiata* is a North American–East Asian species. Finally, both *H. thiomela* and *H. xanthomelana* are tropical.

Taxonomic notes: The genus *Huriopsis* forms a strong monophyletic branch. The *Huriopsis* species are similar to *Rinodina*, but differ in morphological and chemical characters, i.e., a citrine coloured thallus or yellow-green soralia, ascospores of *Pachysporaria*-type (sensu Sheard 2010) and presence of xanthone thiomelin in the cortex and medulla.

The new combinations *Huriopsis chrysideiata*, *H. chrysomelaena*, *H. luteonigra*, *H. xanthomelana* and *H. thiomela* are proposed based on morphological and chemical data.

According to the nrITS phylogeny where larger number of monophyletic branches found (see above), the genus *Huriopsis* includes *H. lepida* (Nyl.) S. Y.

Kondr. et L. Lőkös (AY143413), *H. xanthophaea* (Nyl.) S. Y. Kondr. et L. Lőkös (34212, 39837 and 34208) and one still unidentified species ('*Rinodina*' sp. Malíček MK778639 and '*Rinodina*' sp. Vondrák MK778640), both from Russian Caucasus. Since both nrITS and mtSSU sequences were obtained for both two unidentified specimens it was possible to confirm their position in *Huriopsis*. Thus, three species, of which one is still undescribed, are confirmed as members of *Huriopsis*, however, we dare to include also *Huriopsis chrysidata*, *H. chrysomelaena*, *H. thiomela* and *H. xanthomelana* in *Huriopsis* based on chemical characters but without molecular data. However, the status for some additional *Rinodina* species, usually mentioned in connection with the *Huriopsis* species, remains unsolved, i.e., *Rinodina citrinisidiata* Aptroot et Wolseley, *R. isidioides* (Borrer) H. Olivier, *R. fuscoisidiata* Giralt, Kalb et Elix, *R. brasiliensis* Giralt, Kalb et H. Mayrhofer, *R. guianensis* Aptroot, *R. colobinoides* (Nyl.) Müll. Arg. and *R. flavosoralifera* Tønsberg.

The strongly supported *Huriopsis* branch, according to nrITS phylogeny, includes *H. xanthophaea* (Nyl.) Zahlbr. and *H. lepida* (Nyl.) Müll. Arg., as well as '*Rinodina*' *plana* H. Magn. However, the position '*Rinodina*' *plana* within the *Huriopsis* branch was not confirmed in the combined analysis, and therefore excluded.

Johnsheardia S. Y. Kondr., I. Kärnefelt et A. Thell, *gen. nova*

Mycobank No.: MB 841015

Similar to the genus Rinodina but differs in having Physcia- and Bicinctatypes of ascospores, and in the position in the Physconia / Anaptychia s. l. subclade of the Physciaceae.

Type species: *Johnsheardia cinnamomea* (Th. Fr.) S. Y. Kondr., I. Kärnefelt et A. Thell

Thallus from thin to rather thick, areolated or rimoso-areolated, brownish grey, brownish to brownish green to dark brown or reddish brown. Medulla yellow or orange and K+ reddish violet in type species or white in other species. Hypothallus dark, blackish. Apothecia usually numerous. Ascospores of *Physcia*-type.

Chemistry: Skirin, atranorin, variolaric acid and anthraquinones are detected by TLC in the type species. No lichen substances confirmed for other species. In some species epihymenium K+ and N+ reddish violet.

Ecology: On bryophytes, plant remnants and calcareous rocks. Only one species grows on bark.

Etymology: The new genus is named after the Canadian lichenologist John Wilson Sheard (Saskatoon, Canada) in recognition of his extensive contribution to the knowledge of rinodinoid lichens and to lichenology in general.

Distribution and species diversity: The genus hitherto includes seven species of which the type species and *J. mniaraea* are widely distributed in the Northern Hemisphere. *Johnsheardia zwackhiana* is rare but has a similar wide distribution, whereas other species have more restricted distributions, i.e., the New Zealand species *J. herteliana*. Finally, *J. jamesii* and *J. reagens* are known from South Africa and New Zealand.

Taxonomic notes: The *Johnsheardia* branch has a basal position in the *Physconia* / *Anaptychia* s. l. subclade, thus being sister group to the *Physconia*, *Anaptychia*, *Phaeorrhiza* and *Kurokawia* branches. The position is confirmed both by nrITS sequences separately and the combined matrix (Fig. 1).

Johnsheardia is similar to the genera *Rinodina* and *Mischoblastia*, but differs in having *Physcia*- and *Bicincta*-types of ascospores, and in the position in the *Physconia* / *Anaptychia* s. l. subclade of the Physciaceae.

In previous papers (Nadyeina *et al.* 2010) after nrITS data *Johnsheardia zwackhiana* (Kremp.) S. Y. Kondr., I. Kärnefelt et A. Thell was only illustrated in sister position to *Kudratovia roscida* (Sommerf.) S. Y. Kondr., L. Lőkös et J.-S. Hur (see also below). However new set of data has allowed to clarify position of taxa mentioned.

Klauskalbia S. Y. Kondr., L. Lőkös, E. Farkas et J.-S. Hur, *gen. nova*

Mycobank No.: MB 841016

Similar to Heterodermia s. str., but differs in the lack of lower cortex, in having lower surface mostly dull and never with rhizines, as well as in having a lower surface with a superimposed layer of cotton-woolly hyphae, impregnated by yellow to orange-brown pigments.

Type species: *Klauskalbia obscurata* (Nyl.) S. Y. Kondr., L. Lőkös, E. Farkas et J.-S. Hur

Thallus foliose, orbicular to irregularly spreading, moderately to loosely adnate. Lobes plane to convex, sublinear-elongate, irregularly branched, radiating; apices not ascending, contiguous to discrete, with short lateral lobes, eciliate. Upper surface grey-white to greenish white, ±partly blackened or darkened in the centre, lacking soredia, isidia and pruina or sorediate; soredia farinose to granular, in labriform to capitate soralia at the apices of lateral and terminal lobes, rarely spreading along lobe margins. Medulla white; lower medulla dark yellow to orange-brown. Lower surface ecorticate, with a su-

perimposed layer of cotton-woolly hyphae, impregnated by yellow to orange-brown pigments, in some species arachnoid. Marginal rhizines, black, simple or squarrosely branched. Apothecia rare or common, laminal, sessile to substipitate, margin initially crenulate, then soreciate or lobulate at maturity; disc concave, dark brown to brown-black, epruinose or weakly white-pruinose. Ascospores *Polyblastidia*-type, ellipsoidal, with 2 or 3 small sporoblastidia present particularly at maturity or *Pachysporaria*-type, ellipsoidal, without sporoblastidia. Conidia bacilliform or short bacilliform.

Chemistry: Cortex K⁺ yellow, C⁻, KC⁻, P⁺ yellow; medulla or its upper portion K⁺ yellow, C⁻, P⁻; lower surface K⁺ violet; containing atranorin (major), zeorin (major), 16 β -acetoxyhopane-6 α ,22-diol (major), leucotylin (minor), 7-chloroemodin (minor), flavo-obscurins A, B1, B2 (minor), 5,7-dichloroemodin (trace), AO-1 anthrone (trace), AO-2 anthrone (trace), emodin (minor).

Ecology: On bark of trees (*Acacia auriculiformis*, *Acer pseudoplatanus*, *Betula alnoides*, *Cassia bakeriana*, *Cinnamomum porrectum*, *Garuga* sp., *Holigarna kurzii*, *Phyllanthus emblica*, *Rhododendron microphyton* and *Pinus clausa*), on dead wood and on rocks in savanna, hill evergreen forest, dry evergreen forest, dry dipterocarp forest, tropical rainforest, lower montane scrub, secondary forest, coniferous forest, dry evergreen forest, lower montane scrub, lower montane rainforest, mixed deciduous forest and secondary forest from 630 to 2,565 m a.s.l.

Etymology: This genus name honours the German lichenologist Klaus Kalb in recognition of his outstanding contribution to lichenology, not least the genus *Heterodermia* in a large sense.

Distribution and species diversity. This genus so far includes four species, of which *Klauskalbia flabellata* is known in Australia, North, Central and South America, Africa, Asia (China, India, Japan?) and Fiji, where can be the most common of the four species. *Klauskalbia obscurata* is rather common in North, Central and South America, Africa, Asia, Australia, New Zealand, and Europe?, while *K. paradoxa* and *K. crocea* are known exclusively from Indonesia and North America, respectively.

Taxonomic notes: The genus *Klauskalbia* is similar to *Heterodermia* s. str., but differs in the lack of lower cortex. The lower surface is mostly dull and never supplied with rhizines. In *Heterodermia*, the lower cortex or a pseudo-cortex is present, shiny and often with rhizines. Furthermore, *Klauskalbia* is characterised by a lower surface with a superimposed layer of cotton-woolly hyphae, impregnated by yellow to orange-brown pigments.

The genus *Klauskalbia* is similar to *Polyblastidium* in having a thallus with marginal rhizines, which soon become jet-black. However, *Polyblastidium* differs in having a lower surface formed by \pm arachnoid hyphae, without pigments or the pigments only patchy.

The position of two of the four species, i.e. *Klauskalbia obscurata* and *K. flabellata*, are confirmed in the phylogeny analyses.

Kudratovia S. Y. Kondr., L. Lőkös et J.-S. Hur, *gen. nova*

MycoBank No.: MB 841017

Similar to the genus Rinodina of the Tornabea s. l. or the Physcia s. l. subclades, but differs in having Bicincta- or Physcia-types of ascospores, in having thallus containing zeorin, variolaric acid, and unknown fatty acid, as well as in positioning in the Phaeophyscia s. l. subclade.

Type species: *Kudratovia straussii* (J. Steiner) S. Y. Kondr., L. Lőkös et J.-S. Hur

Thallus crustose, thin and endolithic to well developed, epilithic, areolate to squamulose, umbilicate or indistinctly lobate in peripheral parts, with pruina or without, whitish, greyish to lightly yellowish or brownish. Cortical layer paraplectenchymatous, medulla unclear or sometimes containing oxalate crystals. Apothecia lecanorine, sometimes the thalline margin is disappearing, disc with or without pruina. Ascospores of *Bicincta-* or *Physcia-*types, sometimes with elongated hyaline ends (*K. terrestris*). Conidia bacilliform.

Chemistry: Thallus containing zeorin in various quantities, sometimes small amounts of variolaric acid, unknown fatty acid or lichen substances not detected by TLC / absent.

Ecology: Mostly on calcareous rocks (including calcareous sandstone), on mosses or plant remnants / remains, rarely on soil particularly Ca-containing, in arid and alpine conditions.

Etymology: *Kudratovia* is named after the Tajik lichenologist Imomnazar Kudratov (Dushanbe) for his distinguished contribution to the knowledge of the high mountain lichen flora in Central Asia, and on occasion of his 75th anniversary.

Distribution and species diversity: The genus includes eight species of which some are widely distributed in arctic and alpine ecosystems of the Northern Hemisphere (*K. roscida*), while some are known only from mountains of Eurasia (*K. straussii*, *K. luridata*) or from the Asian continent (*K. bohlii*, *K. pycnocarpa*, *K. terrestris*) and the Alps (*K. candidogrisea*).

Taxonomic notes: *Kudratovia* is similar to the genus *Rinodina*, but differs in having *Bicincta-* or *Physcia-*types of ascospores (vs. *Milvina-*type), in having thallus containing zeorin, variolaric acid, and unknown fatty acid, as well as in positioning in the *Phaeophyscia* s. l. subclade.

Kudratovia is similar to the genus *Mischoblastia* of the *Phaeophyscia* s. l. subclade but differs in having often pruinose discs of the apothecium or pruina on the thallus surface, in having *Bicincta-* or *Physcia-*types of ascospores (vs. *Milvina-*type).

In the phylogeny based on the nrITS sequences the *Kudratovia* branch is positioned in sister position to the *Oxnerella* and the *Rinodinella* s. l. subclades. However, in the phylogenetic tree based on the combined matrix, *Kudratovia* is positioned within the *Phaeophyscia* s. l. subclade (Fig. 1). In previous papers based only on nrITS data *Kudratovia roscida* (Sommerf.) S. Y. Kondr., L. Lőkös et J.-S. Hur and *K. luridata* (Körb.) S. Y. Kondr., L. Lőkös et J.-S. Hur shown to be positioned as separate branches in sister position to *Phaeophyscia ciliaris* (Clade C after Nadyeina *et al.* 2010).

Within the *Kudratovia* branch two main subgroups can be discerned, i.e., the *Kudratovia straussii* and *K. roscida* groups according to the nrITS phylogeny. The *Kudratovia straussii* group includes *K. straussii* (J. Steiner) S. Y. Kondr., L. Lőkös et J.-S. Hur, *K. bohlinii* (H. Magn.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *K. metaboliza* (Vain.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *K. pycnocarpa* (H. Magn.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *K. luridata* (Körb.) S. Y. Kondr., L. Lőkös et J.-S. Hur and *K. terrestris* (Tomin) S. Y. Kondr., L. Lőkös et J.-S. Hur.

The strongly supported *Kudratovia roscida* group contains two species, i.e., *K. roscida* (Sommerf.) S. Y. Kondr., L. Lőkös et J.-S. Hur and *K. candidogrisea* (Hafellner, Muggia et Obermayer) S. Y. Kondr., L. Lőkös et J.-S. Hur. The two species form a species pair, where *K. candidogrisea* is a sorediate counterpart of the fertile *K. roscida* (Hafellner *et al.* 2012).

The '*Rinodina*' *lecanorina* sequence GU553298 from the GenBank, voucher from Crete, Greece is identical with the *Kudratovia luridata* sequence DG849304. Thus, we consider the former to be a *K. luridata*.

The '*Rinodina*' *teicholyta*–'*Rinodina*' *alba* (GU553297) branch is in sister position to the *Kudratovia* branch according to nrITS phylogeny. However, we hesitate to include '*Rinodina*' *teicholyta* in *Kudratovia*, having *Mischoblastia*- or *Pachysporaria*-types of ascospores, and rather wider conidia (to 1.5 µm wide), no lichen substances, and a distribution in Eurasia, North Africa and New Zealand. Also '*Rinodina*' *alba* Metzler ex Arn., distributed in the Northern Hemisphere, is hitherto excluded from *Kudratovia* because the latter taxon is the member of the *Helmutiopsis* branch (see Fig. 1).

Kurokawia S. Y. Kondr., L. Lőkös et J.-S. Hur, *gen. nova*

Mycobank No.: MB 841018

Similar to Anaptychia, but differs in having foliose and closely attached to the substrate thallus, with dull olive green upper surface, when moist, in having well-developed lower cortex, in having simple rarely branched rhizines, and in having somewhat shorter ascospores, and wider conidia, as well as in the lack of pale grey-white lateral cilia and tomentum on the upper surface.

Type species: *Kurokawia isidiata* (Tomin) S. Y. Kondr., Lőkös et J.-S. Hur

Thallus distinctly foliose, often plate-like, closely attached to the substrate, upper surface light to dark brown when dry and to dull olive green when moist, with smooth surface of cortical layer, isidia or soredia present in some taxa, underside light to light brownish; both upper and lower cortical layer well developed, prosoplectenchymatous; lower surface pale or dark brown with simple, rarely branched, scattered white or pale brown to black, scattered rhizines; lateral cilia and tomentum on upper surface absent. Apothecia lecanorine, asci 8-spored, *Lecanora*-type, ascospores dark brown, 1-septate, ellipsoid, medially constricted, thin walled, sculptured with minute spines or ridges. Conidia from bacilliform to widely bacilliform, straight, colourless, $3\text{--}5 \times 1\text{--}1.5 \mu\text{m}$.

Chemistry: Atranorin and zeorin (trace) recorded.

Ecology: On hard coastal rock, also on turf and soil, some species on bark of trees, especially on wayside trees.

Etymology: The genus *Kurokawia* is named after the distinguished Japanese lichenologist Syo Kurokawa (1926–2010) who published a world monograph of the genus *Anaptychia* (Kurokawa 1962, 1973).

Distribution: Four species, i.e. *K. bryorum*, *K. isidiata*, *K. palmulata*, and *K. runcinata*, are confirmed as members of the genus in the combined analysis. *K. runcinata* is a Mediterranean European and North African species, while *K. bryorum* and *K. palmulata* are rare in the Northern Hemisphere. *Kurokawia isidiata* is present in East Asia and North America (Alaska).

Taxonomic notes: The branch including *Kurokawia bryorum*, *K. isidiata*, *K. palmulata*, and *K. runcinata* was identified by Lohtander *et al.* (2008). *Kurokawia* is similar to *Anaptychia* Körb. in having a prosoplectenchymatous upper cortical layer, but differs in having a foliose and closely attached thallus. *Kurokawia* has a dull olive green, when moist, upper surface, in having a well developed lower cortex. In *Anaptychia* the lower cortex is mostly absent or poorly developed. *Kurokawia* is furthermore characterised by simple, rarely branched (brush-like) rhizines, and in having shorter ascospores ($30\text{--}36 \times 15\text{--}18 \mu\text{m}$, compared with $40\text{--}45\text{--}54 \times 18\text{--}24 \mu\text{m}$ in *Anaptychia*). Finally, *Kurokawia* lacks pale grey-white lateral cilia / fibrils and tomentum on the upper surface.

After segregating *Kurokawia*, the *Anaptychia* branch is rather homogeneous although including two groups, i.e., the *Anaptychia ciliaris* group having a fruticose thalli, with hyaline spinules or tomentum on the upper surface and lacking a lower cortical layer. The *Anaptychia* s. str. is strongly supported (97PP). It includes the following species: *A. elbursiana*, *A. desertorum*, *A. crinalis*, and *A. ciliaris*.

The second group corresponds the section *Protoanaptychia* Poelt, characterised by a foliose, closely attached thallus, a well-developed prosoplectenchymatous lower cortex and simple rhizines. The delimitation of this group is

not settled. It usually includes *Anaptychia desertorum* (Rupr.) Poelt, *A. elbursiana* (Szatala) Poelt, *A. mereschkowskii* (Tomin) Kulakov, with hyaline spinules and sorediate crevices on the upper surface, and *A. roemeri* Poelt. Morphological characters indicate a relationship with the *Kurokawia* branch. However, according to nrITS phylogeny *Anaptychia elbursiana* rather belongs to *Anaptychia* s. str. Molecular data for other species are hitherto lacking.

The *Kurokawia* branch has a basal position in the *Physconia* / *Anaptychia* s. l. subbranch (Fig. 1).

It could be mentioned that *Kurokawia isidiata* has been submitted to GenBank under different names, for example *Heterodermia isidiophora*.

Poeltonia S. Y. Kondr., Lőkös et J.-S. Hur, *gen. nova*

Mycobank No.: MB 841019

Similar to Physconia, but differs in having a paraplectenchymatous or scleroplectenchymatous upper cortex, in having a whitish or pale brown underside in the central part, in having whitish to brownish or grey, simple or rarely brush-like rhizines, as well as in having somewhat wider conidia and several unidentified substances.

Type species: *Poeltonia grisea* (Lam.) S. Y. Kondr., L. Lőkös et J.-S. Hur

Thallus distinctly foliose, irregular or sometimes orbicular, more or less closely attached to the substrate, upper surface grey to grey-brown when dry and to dull olive green when moist, isidia or soredia present in some taxa, underside light to light brownish in central parts; the upper cortical layer well developed, pseudoparenchymatous or scleroplectenchymatous, lower cortex paraplectenchymatous or prosoplectenchymatous; lower surface pale or dark brown with simple, rarely branched, scattered whitish to brownish or grey simple rhizines (but black bottle-brush-like in *P. perisidiosa*); lateral cilia and tomentum on upper surface absent. Apothecia lecanorine, asci 8-spored, *Lecanora*-type, ascospores dark brown, 1-septate, ellipsoid, medially constricted, thin walled, sculptured with minute spines or ridges. Ascospores of *Physconia*-type, 22–34 × 12–17 μm. Conidia narrowly bacilliform to widely bacilliform, 3–5 × 1–1.5 μm.

Chemistry: Up to four still unidentified substances by TLC recorded for the type species of the genus is recorded.

Ecology: On hard coastal rock, also on turf and soil, some species on bark of trees.

Etymology: The genus *Poeltonia* is named after the famous German lichenologist Josef Poelt. The name reflects the similarity with the genus *Physconia* of the Physciaceae described by Poelt (1965).

Distribution: The positions of five species, i.e. *Poeltonia elegantula*, *P. grisea*, *P. isidiomuscigena*, *P. perisidiosa*, and *P. venusta*, are confirmed by the phylogeny based on the combined matrix. The European-Caucasian species *P. grisea*, characterised by an upper paraplectenchymatous and a lower prosoplectenchymatous cortex, both well developed, is probably replaced by *Physconia rossica*, having an upper scleroplectenchymatous and a lower paraplectenchymatous layer, poorly developed, on the Asian continent. *P. grisea* is recorded from Europe, North America, Nepal, Australia, New Zealand.

Taxonomic notes: The genus *Poeltonia* is similar to *Physconia* Poelt in having foliose thallus more or less loosely attached to the substrate, but differs in having pseudoparenchymatous (= paraplectenchymatous) or scleroplectenchymatous upper cortical layer (vs. scleroplectenchymatous), in having whitish or pale brown underside in the central parts (vs. blackish in the centre), in having whitish to brownish or grey, simple rarely branched or brush-like rhizines (vs. black bottle-brush-like rhizines), in having shorter and narrower ascospores of *Physconia*-type, as well as in having wider conidia and larger number of unidentified substances.

The genus *Poeltonia* is similar to *Kurokawia* in having a foliose, dull olive green (best seen as moist) upper surface, a well-developed lower cortex, with simple, rarely branched, brush-like rhizines, however, differs from *Anaptychia* by a paraplectenchymatous or scleroplectenchymatous upper cortex and a prosoplectenchymatous or paraplectenchymatous lower cortex. In *Anaptychia* both the upper and lower cortices are well developed and prosoplectenchymatous. It also differs from *Poeltonia* by the lack of atranorin and zeorin.

The phylogeny analyses, both the combined and separate strongly support the *Poeltonia grisea* branch to include *P. grisea*, *P. perisidiosa* and *P. venusta*, while *P. rossica*, *P. muscigena* and *P. isidiomuscigena* Essl. have weaker support and it is possible that the '*Poeltonia*' *muscigena* branch, including *P. muscigena* as *P. isidiomuscigena*, will be segregated as a separate genus in future.

Position of *Physconia californica* Essl. has to be confirmed in the future since it lacks molecular data. It is similar to *P. venusta*, having an upper paraplectenchymatous and a lower prosoplectenchymatous cortex, both well developed. '*Physconia*' *elegantula* Essl. belongs to *Poeltonia* according to the nrITS phylogeny. The three species *Poeltonia elegantula*, *Physconia californica*, and *P. isidiigera* are restricted to North America. In Lohtander *et al.* (2008) the three species *Poeltonia elegantula*, *P. perisidiosa* and *P. venusta* formed a branch together with *Poeltonia grisea*, based on the nrITS and mtSSU sequences, however, without support.

Finally, *Physconia* s. str., i.e., the *Physconia distorta* group, including *P. servitii* (Nád. v.) Poelt, *P. subpulverulenta* (Szatala) Poelt, *P. leucoleiptes* (Tuck.) Essl., *P. kurokawae* Kashiw., *P. americana* Essl. and *P. isidiigera* (Zahlbr.) Essl. were delimited only by nrITS sequences.

Comments to some genera of the Physciaceae

Kashiwadia S. Y. Kondr., Lőkös et Hur, in Kondratyuk, Lőkös, Kim, Jeong, Kondratiuk, Oh et Hur, *Acta Bot. Hung.* 56(3–4): 375 (2014). – Type species: *Kashiwadia orientalis* (Kashiw.) S. Y. Kondr., Lőkös et Hur, in Kondratyuk, Lőkös, Kim, Jeong, Kondratiuk, Oh et Hur, *Acta Bot. Hung.* 56(3–4): 375 (2014). – Originally *Kashiwadia* was described as a monotypic genus including only the East Asian species *K. orientalis*, a species earlier studied by Kondratyuk *et al.* (2014b). However, several additional specimens are investigated here. We suggest that at least two additional, East Asian species, closely related to *K. orientalis*, exist, revealed in the phylogenetic tree (Fig. 1). The former '*Physcia*' species '*P.*' *austrostellaris* Elix, '*P.*' *jackii* Moberg, '*P.*' *nubila* Moberg, and '*P.*' *tropica* Elix are found in a sister position to the genus *Kashiwadia*, whereas other species of the genus forms a separate monophyletic branch rather distant from *Kashiwadia* s. l. Australian species which also show a close relationship with *Kashiwadia* s. str. are placed in the *Kashiwadia* s. l. clade. A future analysis complemented with mtSSU sequences is needed, including particularly the '*Kashiwadia*' *austrostellaris* group, i.e., '*K.*' *austrostellaris*, '*K.*' *jackii*, '*K.*' *nubila*, and '*K.*' *pumila*. One additional '*Kashiwadia*' s. l. species (DQ782836 as *Physcia aipolia* in GB) is included in the analysis as *Kashiwadia* sp. (Fig. 1). However, molecular data (nrITS, 18S nrSSU, 12S mtSSU and RPB2) of this taxon were provided within project voucher AFTOL-ID 84 identified as '*Physcia aipolia*'. This specimen was not available for a revision within our study. Furthermore, we have suggestion that one more species is included in the *K. orientalis* complex, sometimes misidentified as *Heterodermia obscurata* (=> *Klauskalbia obscurata*). At any case, there are still several species of *Kashiwadia* s. l. waiting for a revision.

Mischoblastia A. Massal., *Ric. auton. lich. crost.* (Verona): 40 (1852) – Type species: *Mischoblastia oxydata* A. Massal. – Massalongo (1852) proposed the genus for two species, i.e. *M. oxydata* A. Massal. and *M. lecanorina* A. Massal. characterised by *Mischoblastia*-type of ascospores. Later one more species, i.e., *Mischoblastia physciospora* (M. Choisy et Werner) M. Choisy et Werner was proposed. Molecular data for this species is lacking why the position of this species is not discussed here. – The strongly supported *Mischoblastia* branch is situated in sister position to the *Hyperphyscia* branch in the tree based on nrITS phylogeny, supporting genus status for *Mischoblastia*. The branch includes three species, i.e., *M. destituta*, *M. vezdae* and *M. oxydata*, while the position of the South Korean '*M.*' aff. *oxydata*, and '*M.*' *ramboldii* in the same branch is uncertain because of weak support. The position of '*Mischoblastia*' *lecanorina* A. Massal. in the genus *Mischoblastia* is not confirmed in this study as far one voucher specimen from Greece (GU553298) as shown above found to be *Kudratovia luridata*, while another voucher specimen (AF540545) belongs

to *Rinodina parvula* (see Nadyeina *et al.* 2010). Additional molecular markers would be desirable for this group. *Mischoblastia* in a large sense includes also *M. moziana* subsp. *parasitica* (Kaschik et H. Mayrhofer) S. Y. Kondr., L. Lökös et J.-S. Hur, distributed in New Zealand, South Korean *M. aff. oxydata* ad int., *M. confragosula* (Nyl.) S. Y. Kondr., L. Lökös et J.-S. Hur, described from South Africa but now known from several continents, here reported from Cambodia for the first time, found in the GenBank under the name 'Physciaceae sp. KWS 3' (Kawasaki *et al.* 2013), *M. moziana* subsp. *moziana* (Nyl.) S. Y. Kondr., L. Lökös et J.-S. Hur, and *M. ramboldii* (Kaschik) S. Y. Kondr., L. Lökös et J.-S. Hur. Sometimes '*M. ramboldii*' is positioned together with '*Rinodina albana*'. According to Sheard *et al.* (2017) the Asian *Mischoblastia moziana* has eastern North American–Eastern Asian European distribution, well aware that the authors included *Rinodina destituta* and *R. vezdae* in *Mischoblastia moziana*. A close relationship between the three species is confirmed in our analysis, however, without finally proving the taxonomy. *Mischoblastia moziana* subsp. *parasitica* is positioned close to *M. destituta* (Nyl.) S. Y. Kondr., L. Lökös et J.-S. Hur, *M. vezdae* (H. Mayrhofer) S. Y. Kondr., L. Lökös et J.-S. Hur and *M. oxydata*, while *M. moziana* subsp. *moziana* appears more distantly related. The topology of the tree indicates species status for *M. moziana* subsp. *parasitica*, however, we will wait until more data is available not to forget that the name already exists for a different taxon, *Rinodina parasitica* H. Mayrhofer et Poelt. A final conclusion is that our knowledge of the East Asian *Mischoblastia* and *Helmutiopsis* biodiversity is still fragmentary.

Oxnerella S. Y. Kondr., Lökös et Hur, in Kondratyuk, Lökös, Kim, Kondratiuk, Jeong, Zarei-Darki et Hur, *Acta bot. hung.* 56(3–4): 388 (2014). – Type species: *Oxnerella afghanica* (M. Steiner et Poelt) S. Y. Kondr., L. Lökös et J.-S. Hur, designated here (see below). – '*Rinodina afghanica*' M. Steiner et Poelt was originally described as parasitic lichen from epiphytic lichen *Lazarenkoella polycarpoides* (J. Steiner) S. Y. Kondr. et L. Lökös (syn. *Caloplaca polycarpoides* (J. Steiner) M. Steiner et Poelt) (Steiner and Poelt 1987), later recorded from another epiphytic lichen *Buellia* (Steiner and Mayrhofer 1987), and now known from saxicolous lichen, for example, *Lecania safavidiorum*, here reported as host for the first time. Molecular data earlier published for *Oxnerella safavidiorum* was probably based on the mycobiont of a parasiting '*Rinodina afghanica*' (Resl *et al.* 2016), since three recently submitted nrITS sequences of '*Rinodina afghanica*' are identical with the *Oxnerella safavidiorum* sequence. This is another example of 'extraneous mycobiont DNA' in a lichen association, reported by Kondratyuk *et al.* (2019) from the Ramalinaceae. With this knowledge, we designate *Oxnerella afghanica* as type species of the genus of the Physciaceae, and propose a new combination for the host, *Lecania safavidiorum* for *O. safavidiorum* below. The position of the rare Eurasian lichen *Oxnerella castanomelodes* (H. Mayrhofer et Poelt) S. Y. Kondr., L. Lökös et J.-S. Hur as sister to *O. af-*

ghanica is uncertain. The support in the combined analysis is weak. Currently, *O. castanomelodes* is considered as a synonym of '*Rinodina*' *bischoffii*, however, in our analysis the two species are positioned on different branches (Fig. 1).

New combinations

Totally 56 new combinations proposed for taxa discussed above based on combined or on the nrITS phylogeny of the Physciaceae are listed below.

Helmutiopsis alba (Metzler ex Arn.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841020 – Basionym: *Rinodina alba* Metzler ex Arn., *Flora, Regensburg* 55(3): 35 (1872).

Helmutiopsis aspersa (Borrer) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841021 – Basionym: *Lecanora aspersa* Borrer, in Hooker et Sowerby, *Suppl. Engl. Bot.* 2: tab. 2728 (1834). – Syn.: *Rinodina aspersa* (Borrer) J. R. Laundon, *Lichenologist* 18(2): 175 (1986).

Helmutiopsis atrocineria (Fr.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841022 – Basionym: *Parmelia atrocineria* Fr., *Lich. eur. reform.* (Lund): 151 (1831). – Syn.: *Rinodina atrocineria* (Fr.) Körb., *Syst. lich. germ.* (Breslau): 125 (1855).

Huriopsis chrysiidiata (Sheard) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841023 – Basionym: *Rinodina chrysiidiata* Sheard, in Lendemer et al., *Lichenologist* 44(2): 180 (2011). – Type: USA, North Carolina, Clay Co., Nantahala National Forest, 1–1.5 mi N of US 64 on Buck Creek Rd., c. 5 mi NE of Shooting Creek, mesic upland forest, on *Liriodendron*, 10 November 2007, J. C. Lendemer 10425 (NY – holotypus; BG – isotypus).

Huriopsis chrysomelaena (Tuck.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841024 – Basionym: *Rinodina chrysomelaena* Tuck., *Gen. lich.* (Amherst): 123 (1872).

Huriopsis lepida (Nyl.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841025 – Basionym: *Lecanora lepida* Nyl., *Mém. Soc. Imp. Sci. Nat. Cherbourg* 5: 115 (1857). – Syn.: *Rinodina lepida* (Nyl.) Müll. Arg., *Flora, Regensburg* 64(32): 515 (1881).

Huriopsis luteonigra (Zahlbr.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841026 – Basionym: *Rinodina luteonigra* Zahlbr., *Bot. Mag. Tokyo* 41: 360 (1927).

Huriopsis plana (H. Magn.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841027 – Basionym: *Rinodina plana* H. Magn., *Meddn Göteb. Bot. Trädg.* 17: 298 (1947).

Huriopsis thiomela (Nyl.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841028 – Basionym: *Lecanora thiomela* Nyl., *Flora, Regensburg* 48: 338 (1865). – Syn.: *Rinodina thiomela* (Nyl.) Müll. Arg., *Flora, Regensburg* 64(32): 515 (1881).

Huriopsis xanthomelana (Müll. Arg.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841029 – Basionym: *Rinodina xanthomelana* Müll. Arg., *Nuovo G. bot. ital.* 23(3): 390 (1891).

Huriopsis xanthophaea (Nyl.) S. Y. Kondr. et L. Lőkös, *comb. nova* – MycoBank No.: MB 841030 – Basionym: *Lecanora xanthophaea* Nyl., *Lich. Jap.* 41 (1890). – Type: Japan, Magayesi, 1879, E. Almquist (H-NYL 29084 – lectotype, designated by Lendemer *et al.* (2012); H-NYL 29085 – isolectotype pro parte). – Syn.: *Rinodina xanthophaea* (Nyl.) Zahlbr., *Cat. Lich. Univers.* 7: 559 (1931); *Rinodina xanthophaea* f. *sorediosa* Pczelkin, *Nov. sist. nizsh. rast.* 24: 167 (1987). – Type: [Russia:] USSR Far East, Sikhote-Alin' Nature Reserve, along the sea, 2 km from the River Belimbe [approximately 45.320937° N, 137.012290° E], on oak bark, 1982, A.V. Pczelkin (LE – holotype!).

Johnsheardia cinnamomea (Th. Fr.) S. Y. Kondr., I. Kärnefelt et A. Thell, *comb. nova* – MycoBank No.: MB 841079 – Basionym: *Rinodina mniaroea* var. *cinnamomea* Th. Fr., *Nova Acta R. Soc. Scient. upsal.*, Ser. 3, 3: 228 (1861) [1860]. – Syn.: *Rinodina cinnamomea* (Th. Fr.) Räsänen, *Die Flecht. Estl.* 1: 137 (1931).

Johnsheardia herteliana (Kaschik) S. Y. Kondr., I. Kärnefelt et A. Thell, *comb. nova* – MycoBank No.: MB 841032 – Basionym: *Rinodina herteliana* Kaschik, *Bibl. Lichenol.* 93: 57 (2006).

Johnsheardia jamesii (H. Mayrhofer) S. Y. Kondr., I. Kärnefelt et A. Thell, *comb. nova* – MycoBank No.: MB 841033 – Basionym: *Rinodina jamesii* H. Mayrhofer, *Lichenologist* 15(3): 272 (1983).

Johnsheardia reagens (Matzer et H. Mayrhofer) S. Y. Kondr., I. Kärnefelt et A. Thell, *comb. nova* – MycoBank No.: MB 841034 – Basionym: *Rinodina reagens* Matzer et H. Mayrhofer, *Acta Bot. Fenn.* 150: 116 (1994).

Johnsheardia zwackhiana (Kremp.) S. Y. Kondr., I. Kärnefelt et A. Thell, *comb. nova* – MycoBank No.: MB 841035 – Basionym: *Lecanora zwackhiana* Kremp., *Flora, Regensburg* 37: 145 (1854). – Syn.: *Rinodina zwackhiana* (Kremp.) Körb., *Syst. lich. germ.* (Breslau): 126 (1855).

Kashiwadia austrostellaris (Elix) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841039 – Basionym: *Physcia austrostellaris* Elix, in Elix et al., *Syst. Biodiv.* 7(4): 482 (2009).

Kashiwadia jackii (Moberg) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841040 – Basionym: *Physcia jackii* Moberg, *Bibl. Lichenol.* 78: 298 (2001).

Kashiwadia littoralis (Elix) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841041 – Basionym: *Physcia littoralis* Elix, in Elix et al., *Syst. Biodiv.* 7(4): 484 (2009).

Kashiwadia nubila (Moberg) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841042 – Basionym: *Physcia nubila* Moberg, *Nordic J. Bot.* 10(3): 335 (1990). – Syn.: *Heterodermia desertorum* Kalb, *Lich. Neotrop.*, Fasc. VIII (Neumarkt): no. 324 (1984).

Kashiwadia tropica (Elix) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841043 – Basionym: *Physcia tropica* Elix, in Elix et al., Syst. Biodiv. 7(4): 485 (2009).

Klauskalbia crocea (R. C. Harris) S. Y. Kondr., L. Lőkös, E. Farkas et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841036 – Basionym: *Heterodermia crocea* R. C. Harris, Some Florida Lichens (New York): 78 (1990).

Klauskalbia flabellata (Fée) S. Y. Kondr., L. Lőkös, E. Farkas et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841037 – Basionym: *Parmelia flabellata* Fée, Essai Cryptog. Écorc. Exot. Officin., Deuxième partie: 122 (1837). – Syn.: *Anaptychia flabellata* (Fée) A. Massal., Mem. Lichenogr. 41 (1853); *Heterodermia flabellata* (Fée) D. D. Awasthi, Geophytology 3: 113 (1973).

Klauskalbia obscurata (Nyl.) S. Y. Kondr., L. Lőkös, E. Farkas et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841080 – Basionym: *Physcia speciosa* (Wulfen) Nyl. **obscurata* Nyl., Acta Soc. Sci. Fenn. 7: 440 (1863). – Type: Colombia, s. loc., alt. 2,900 m, Lindig 704; (H-NYL, holotype n.v.). – Syn.: *Heterodermia speciosa* var. *obscurata* (Nyl.) Trevis., Atti Soc. Ital. Sci. Nat. Milano 11: 614 (1869 [1868]); *Anaptychia obscurata* (Nyl.) Vain., Acta Soc. Fauna Fl. Fenn. 7(1): 137 (1890); *Heterodermia obscurata* (Nyl.) Trevis., Nuovo Giorn. Bot. Ital. 1: 114 (1869).

Klauskalbia paradoxa (Schumm et Schäfer-Verwimp) S. Y. Kondr., L. Lőkös, E. Farkas et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841038 – Basionym: *Heterodermia paradoxa* Schumm et Schäfer-Verwimp, Herzogia 19: 36 (2006). – Type: Indonesia. North-Sumatra: Highland of Brastagi, ascent from lake Lau Kawar to Gunung Sinabung, in the canopy of a fallen tree, 1,520 m, 18 May 2005, A. Schäfer-Verwimp et I. Schäfer-Verwimp 24902 (B, holotype n.v.).

Kudratovia bohlinii (H. Magn.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841044 – Basionym: *Rinodina bohlinii* H. Magn., Lichens Central Asia: 149 (1940).

Kudratovia candidogrisea (Hafellner, Muggia et Obermayer) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841045 – Basionym: *Rinodina candidogrisea* Hafellner, Muggia et Obermayer, Bibl. Lichenol. 108: 80 (2012).

Kudratovia luridata (Körb.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841046 – Basionym: *Buellia luridata* Körb., Parerga lichenol. (Breslau) 2: 188 (1860) [1865]. – Syn.: *Rinodina luridata* (Körb.) H. Mayrhofer, Scheid. et Sheard, in Jahns, Bibl. Lichenol. 38: 346 (1990).

Kudratovia metaboliza (Vain.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841047 – Basionym: *Rinodina metaboliza* Vain., in Almqvist, Kolemman. tutkim. Länsi-Siperiassa 4: 87 (1928).

Kudratovia pycnocarpa (H. Magn.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841048 – Basionym: *Rinodina pycnocarpa* H. Magn., Lichens Central Asia 1: 152 (1940).

Kudratovia roscida (Sommerf.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841049 – Basionym: *Lecanora roscida* Sommerf.,

Suppl. Fl. lapp. (Oslo): 97 (1826). – Syn.: *Rinodina roscida* (Sommerf.) Arn., Verh. zool.-bot. Ges. Wien 37: 133 (1887).

Kudratovia straussii (J. Steiner) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841050 – Basionym: *Rinodina straussii* J. Steiner, Ann. Mycol. 8(2): 242 (1910). – Syn.: *Rinodina kansuensis* H. Magn., Lichens Central Asia: 151 (1940).

Kudratovia terrestris (Tomin) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841051 – Basionym: *Rinodina terrestris* Tomin, Prirod. sel'skoe chozjajst. zasuch.-pustyn S.S.S.R. (The Nature and Agricult. in the arid Regions of the U.S.S.R.) (no. 3): 59 (1928). – Syn.: *Rinodina mucronatula* H. Magn., Meddn Göteb. Bot. Trädg. 17: 293 (1947).

Kurokawia bryorum (Poelt) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841052 – Basionym: *Anaptychia bryorum* Poelt, Bryologist 74(2): 154 (1971).

Kurokawia isidiata (Tomin) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841053 – Basionym: *Anaptychia isidiata* Tomin, Bull. South. Ussuri Branch State Russ. Geograph. Soc.: 220 (1926). – Syn.: *Anaptychia isidiza* Kurok., Beih. Nova Hedwigia 6: 19 (1962).

Kurokawia mereschkowskii (Tomin) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841054 – Basionym: *Physcia mereschkowskii* Tomin, Neue Flecht. Süd-Russl.: 7 (1926). [в: Природа и Сельское Хозяйство засушливых областей СССР. 1927, 1-2: 5. Lectotypus (designated by Kulakov 2003): Астраханская губ. окр. Баскунчакского оз. по склонам холмов на выходах гипса. VIII. 1927 №55 М. Томин. (LE).] – Syn.: *Physcia desertorum* (Ruprecht) Savicz, (1938) в: Бот. мат. Отд. Споров. Раст. БИН АН СССР, 4, 10-12: 1-4 р.р. excl. typo; *Physcia caesia* var. *melops* auct. non (Duf.) Wain.: Мережковский (1911a): 21, 41; *Anaptychia mereschkowskii* (Tomin) Kulakov, Bot. Zhurnal 88(9): 100 (2003).

Kurokawia palmulata (Michx.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841055 – Basionym: *Psoroma palmulatum* Michx., Fl. Boreali-Americ. 2: 321 (1803). – Syn.: *Anaptychia palmulata* (Michx.) Vain., Term. Füz. 22: 299 (1899).

Kurokawia runcinata (With.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841056 – Basionym: *Lichen runcinatus* With., Bot. arr. veg. Gr. Brit. (London) 2: 714 (1776). – Syn.: *Anaptychia aquila* (Ach.) A. Massal., Memor. Lich.: 36 (1853); *A. fusca* (Huds.) Vain., Term. Füz. 22: 299 (1899); *A. fusca* var. *caesiopruinosa* (Lamy) Zahlbr., Cat. Lich. Univers. 7: 722 (1931); *A. runcinata* (With.) J. R. Laundon, Lichenologist 16(3): 225 (1984); *Lichen aquilus* Ach., Lich. suec. prodr. (Linköping): 109 (1799) [1798]; *Lichen fuscus* Huds., Fl. Angl., Edn 2 2: 533 (1778); *Lichen pullus* Lightf., Fl. Scot. 2: 825 (1777); *Lichen rugosus* Pers., in Nylander, Lich. Scand. (Helsinki): 161 (1861).

Kurokawia stippea (With.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841057 – Basionym: *Parmelia aquila* var. *stippea* Ach., Methodus, Sectio post. (Stockholmiae): 202 (1803). – Syn.: *Anaptychia stippea* (Ach.) Nádv., Stud. Bot. Čechoslov. 8(2–4): 75 (1947).

Lecania safavidiorum (S. Y. Kondr., Zarei-Darki, Lőkös et Hur) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841058 – Basionym: *Oxnerella safavidiorum* S. Y. Kondr., Zarei-Darki, Lőkös et Hur, in Kondratyuk et al., Acta bot. hung. 56(3–4): 388 (2014).

Leucodermia erinacea (Ach.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841059 – Basionym: *Lichen erinaceus* Ach., Lich. univ.: 499 (1810). – Syn.: *Anaptychia erinacea* (Ach.) Trevis., Flora, Regensburg 44: 52 (1861); *Heterodermia erinacea* (Ach.) W. A. Weber, in Egan, Bryologist 90(2): 163 (1987).

Mischoblastia confragosula (Nyl.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841060 – Basionym: *Lecanora confragosula* Nyl., in Crombie, J. Linn. Soc., Bot. 15: 172 (1876) [1877]. – Syn.: *Rinodina confragosula* (Nyl.) Müll. Arg., Revue mycol., Toulouse 9(34): 79 (1887).

Mischoblastia destituta (Nyl.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841061 – Basionym: *Lecidea destituta* Nyl., Sert. Lich. Trop. Labuan Singapore: 41 (1891). – Syn.: *Rinodina destituta* (Nyl.) Zahlbr., Cat. Lich. Univers. 7: 510 (1931).

Mischoblastia moziana (Nyl.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841062 – Basionym: *Lecanora moziana* Nyl., Lich. Japon.: 40 (1890). – Syn.: *Rinodina moziana* (Nyl.) Zahlbr., Cat. Lich. Univers. 7: 544 (1931).

Mischoblastia moziana subsp. *parasitica* (Kaschik et H. Mayrhofer) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. et stat. nova* – MycoBank No.: MB 841063 – Basionym: *Rinodina moziana* var. *parasitica* Kaschik et H. Mayrhofer, in Kaschik, Bibl. Lichenol. 93: 76 (2006).

Mischoblastia ramboldii (Kaschik) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841064 – Basionym: *Rinodina ramboldii* Kaschik, Bibl. Lichenol. 93: 105 (2006).

Mischoblastia vezdae (H. Mayrhofer) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841065 – Basionym: *Rinodina vezdae* H. Mayrhofer, J. Hattori Bot. Lab. 55: 473 (1984).

Oxnerella afghanica (M. Steiner et Poelt) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841066 – Basionym: *Rinodina afghanica* M. Steiner et Poelt, Pl. Syst. Evol. 155(1–4): 139 (1987).

Oxnerella castanomelodes (H. Mayrhofer et Poelt) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841067 – Basionym: *Rinodina castanomelodes* H. Mayrhofer et Poelt, Bibl. Lichenol. 12: 81 (1979).

Physciella nigricans (Flörke) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841068 – Basionym: *Lecanora nigricans* Flörke, Deutsche Lich. 5: 10 (no. 91) (1819). – Syn.: *Phaeophyscia nigricans* (Flörke) Moberg, Symb. bot. upsal. 22(no. 1): 42 (1977).

Poeltonia elegantula (Essl.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841069 – Basionym: *Physconia elegantula* Essl., Mycotaxon 51: 92 (1994).

Poeltonia grisea (Lam.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841070 – Basionym: *Lichen griseus* Lam., Encycl. Méth. Bot. (Paris) 3(2): 480 (1792). – Syn.: *Physconia grisea* (Lam.) Poelt, Nova Hedwigia 9: 30 (1965).

Poeltonia isidiomuscigena (Essl.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841071 – Basionym: *Physconia isidiomuscigena* Essl., Bull. Calif. Lichen Soc. 7(1): 5 (2000).

Poeltonia perisidiosa (Erichsen) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841072 – Basionym: *Physcia perisidiosa* Erichsen, Verh. bot. Ver. Prov. Brandenb. 72: 57 (1930). – Syn.: *Physconia perisidiosa* (Erichsen) Moberg, Symb. bot. upsal. 22(no. 1): 90 (1977).

Poeltonia venusta (Ach.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841073 – Basionym: *Parmelia venusta* Ach., Methodus, Sectio post. (Stockholmiaë): 211 (1803). – Syn.: *Physconia venusta* (Ach.) Poelt, Nova Hedwigia 12(1–2): 130 (1966).

Polyblastidium albicans (Pers.) S. Y. Kondr., L. Lőkös et J.-S. Hur, *comb. nova* – MycoBank No.: MB 841074 – Basionym: *Parmelia albicans* Pers., Ann. Wetter. Gesellsch. Ges. Naturk. 2(1): 17 (1810). – Syn.: *Heterodermia albicans* (Pers.) Swinscow et Krog, Lichenologist 8(2): 113 (1976).

Presence of 'extraneous mycobiont DNA' in lichen associations

Presence of 'extraneous mycobiont DNA' in lichen association was recently described for species in the Ramalinaceae (Kondratyuk *et al.* 2019). Further examples are presented here. One is the case with the lectotypification of the genus *Oxnerella*. Additional examples are connected with incorrect identification of specimens of the genera *Heterodermia*, *Kashiwadia*, *Poeltonia* and *Kurokawia*.

Revisions of different groups in the Physciaceae were perhaps never published, because of contradictory results and wrong identifications explained by 'extraneous mycobiont DNA'.

CONCLUSIONS

Sixteen genera of the Physciaceae are confirmed by molecular data, 14 of these in the analysis based on the combined matrix of nrITS and mtSSU sequences and two in the nrITS phylogeny only. Seven new genera are proposed, i.e., *Helmutiopsis*, *Huriopsis*, *Johnsheardia*, *Klauskalbia*, *Kudratovia*, *Kurokawia* and *Poeltonia* and the circumscription of the genera *Oxnerella* and *Mischoblastia* is discussed. Fifty-six new combinations were proposed for *Helmutiopsis*, *Huriopsis*, *Johnsheardia*, *Klauskalbia*, *Kashiwadia*, *Kudratovia*, *Kurokawia*, *Lecania*, *Leucodermia*, *Mischoblastia*, and *Poeltonia*.

The results obtained from the combined and separate analysis are compared and discussed. Further revisions of the Physciaceae using a multilocus phylogeny are needed to clarify monophyletic groups of the polyphyletic genus *Rinodina*, found in the *Phaeophyscia*, *Physcia*, and *Physconia*–*Anaptychia* s. l. subclades in this study.

‘Extraneous mycobiont DNA’ are still present in the GenBank representing incorrectly identified specimens of the genera *Heterodermia* s. l., *Kashiwadia*, *Kurokawia*, *Poeltonia*, *Physconia* and other genera in the Physciaceae. The increased knowledge that more and more sequences in the GenBank entail, will make it possible to seek out and eliminate these inaccuracies.

*

Acknowledgements – We are grateful to Dr Konstanze Bensch (MycoBank, UK) for valuable comments on nomenclature and to two anonymous reviewers for comments on manuscript. This work was supported by the Korean National Research Resource Centre Program (NRF-2017M3A9B8069471) and the Korean Forest Service Program through the Korea National Arboretum (KNA1-1-22, 17-2), and (for SK) in parts by The Ministry of Education and Science of Ukraine (M/172-2017, M/53-2019 and M/30-2020) and by Korean Brain Pool Program (161S-4-3-1659). The work was supported by the research project of the Hungarian National Research Development and Innovation Fund (NKFI K124341).

REFERENCES

- Awasthi, D. D. (1960): Contributions to the lichen flora of India and Nepal. II. The genus *Anaptychia* Körb. – *J. Indian Bot. Soc.* **39**(3): 415–442.
- Awasthi, D. D. (1973): On the species of *Anaptychia* and *Heterodermia* from India and Nepal. – *Geophytology* (Lucknow) **3**: 113–116.
- Bouckaert, R. R., Drummond, A. J. (2017): bModelTest: Bayesian phylogenetic site model averaging and model comparison. – *BMC Evol. Biol.* **17**(1): 42.
<https://doi.org/10.1186/s12862-017-0890-6>
- Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., du Plessis, L., Poppinga, A., Rambaut, A., Rasmussen, D., Sive-

- roni, I., Suchard, M. A., Wu, C.-H., Xie, D., Zhang, C., Stadler, T. and Drummond, A. J. (2019): BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. – *PLoS Comp. Biol.* **15**(4): e1006650. <https://doi.org/10.1371/journal.pcbi.1006650>
- Cubero, O. F., Crespo, A., Esslinger, T. L. and Lumbsch, H. T. (2004): Molecular phylogeny of the genus *Physconia* (Ascomycota, Lecanorales) inferred from a Bayesian analysis of nuclear ITS rDNA sequences. – *Mycol. Res.* **108**: 498–505. <https://doi.org/10.1017/s095375620400975x>
- Edler, D., Klein, J., Antonelli, A., and Silvestro, D. (2021): raxmlGUI 2.0: a graphical interface and toolkit for phylogenetic analyses using RAxML. – *Methods Ecol. Evol.* **12**(2): 373–377. <https://doi.org/10.1111/2041-210X.13512>
- Ekman, S. (2001): Molecular phylogeny of the Bacidiaceae (Lecanorales, lichenized Ascomycota). – *Mycol. Res.* **105**: 783–797. <https://doi.org/10.1017/S0953756201004269>
- Elix, J. A., Corush, J. and Lumbsch, T. H. (2009): Triterpene chemosyndromes and subtle morphological characters characterize lineages in the *Physcia aipolia* group in Australia (Ascomycota). – *Syst. Biodiv.* **7**(4): 479–487. <https://doi.org/10.1017/S1477200009990223>
- Grube, M. and Arup, U. (2001): Molecular and morphological evolution in the Physciaceae (Lecanorales, lichenized Ascomycotina), with special emphasis on the genus *Rinodina*. – *Lichenologist* **33**(1): 63–72. <https://doi.org/10.1006/lich.2000.0297>
- Hafellner, J., Muggia, L. and Obermayer, W. (2012): *Rinodina candidogrisea*, a new sorediate species from high altitudes in the Alps. – *Bibl. Lichenol.* **108**: 75–102.
- Hall, T. A. (1999): BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucl. Acids Symp. Ser.* **41**: 95–98.
- Helms, G., Friedl, T. and Rambold, G. (2003): Phylogenetic relationships of the Physciaceae inferred from rDNA sequence data and selected phenotypic characters. – *Mycologia* **95**(6): 1078–1099. <https://doi.org/10.2307/3761914>
- Hur, J.-S., Oh, S.-O. *et al.* (eds) (2016): *Flora of macrolichens in Korea*. – Korea National Arboretum, Seoul, 520 pp. (In Korean and English)
- Hur, J.-S., Oh, S.-O., Kondratyuk, S., Lökös, L. and Park, J.-S. (2018): *Flora of microlichens in Korea*. – Korea National Arboretum, Seoul, 486 pp.
- Kawasaki, F., Matsui, T., Yamamoto, Y. and Hara, K. (2013): The documentation method using lichens growing on stoneworks in order to protect cultural heritage stone monument – the case of Angkor monuments of Cambodia. – *Lichenology* **11**: 39–52.
- Kondratyuk, S. Y., Lökös, L., Kim, J. A., Kondratiuk, A. S., Jeong, M.-H., Zarei-Darki, B. and Hur, J.-S. (2014a): *Oxnerella safavidiorum* gen. et spec. nov. (Lecanoromycetidae, Ascomycota) from Iran (Asia) proved by phylogenetic analysis. – *Acta Bot. Hung.* **56** (3–4): 379–398. <https://doi.org/10.1556/abot.56.2014.3-4.13>
- Kondratyuk, S., Lökös, L., Kim, J., Jeong, M.-H., Kondratiuk, A., Oh, S.-O. and Hur, J.-S. (2014b): *Kashiwadia* gen. nov. (Physciaceae, lichen-forming Ascomycota), proved by phylogenetic analysis of the Eastern Asian Physciaceae. – *Acta Bot. Hung.* **56**(3–4): 369–378. <https://doi.org/10.1556/abot.56.2014.3-4.12>
- Kondratyuk, S. Y., Lökös, L., Kapetz, N. V., Pleskach, L. Ya., Kim, J., Kondratiuk, A. S. and Hur, J.-S. (2015): *Physcia ucrainica* sp. nova (Physciaceae, Ascomycota) from the Crimean peninsula, proved by molecular phylogeny. – *Acta Bot. Hung.* **57**(1–2): 143–163. <https://doi.org/10.1556/abot.57.2015.1-2.11>
- Kondratyuk, S. Y., Lökös, L., Halda, J. P., Roux, C., Upreti, D. K., Schumm, F., Mishra, G. K., Nayaka, S., Farkas, E., Park, J. S., Lee, B. G., Liu, D., Woo, J.-J. and Hur, J.-S. (2017): New and noteworthy lichen-forming and lichenicolous fungi 6. – *Acta Bot. Hung.* **59**(1–2): 137–260. <https://doi.org/10.1556/034.59.2017.1-2.7>

- Kondratyuk, S. Y., Lőkös, L., Jang, S.-H., Hur, J.-S. and Farkas, E. (2019): Phylogeny and taxonomy of Polyozosia, Sedelnikovaea and Versegghya of the Lecanoraceae (Lecanorales, lichen-forming Ascomycota). – *Acta Bot. Hung.* **61**(1–2): 137–184. <https://doi.org/10.1556/034.61.2019.1-2.9>
- Kulakov, V. G. (2003): Foliose and fruticulose lichens of Baskunchak Lake vicinity. – *Bot. Zhurnal* **88**(9): 96–104.
- Kumar, S., Stecher, G., Li, M., Knyaz, C. and Tamura, K. (2018): MEGA X: Molecular Evolutionary Genetic Analysis across computing platforms. – *Mol. Biol. Evol.* **35**: 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Kurokawa, S. (1962): A monograph of the genus Anaptychia. – *Beih. Nova Hedwigia* **6**: 1–115.
- Kurokawa, S. (1973): Supplementary notes on the genus Anaptychia. – *J. Hattori Bot. Lab.* **37**: 563–607.
- Lendemer, J. C., Sheard, J. W., Thor, G. and Tønsberg, T. (2012): Rinodina chrysiadiata, a new species from far eastern Asia and the Appalachian Mountains of North America. – *Lichenologist* **44**(2): 179–187. <https://doi.org/10.1017/s0024282911000764>
- Lohtander, K., Källersjö, M., Moberg, R. and Tehler, A. (2000): The family Physciaceae in Fennoscandia: phylogeny inferred from ITS sequences. – *Mycologia* **92**(4): 728–735. <https://doi.org/10.2307/3761429>
- Lohtander, K., Ahti, T., Stenroos, S. and Urbanavichus, G. (2008): Is Anaptychia monophyletic? A phylogenetic study based on nuclear and mitochondrial genes. – *Ann. Bot. Fennici* **45**: 55–60. <https://doi.org/10.5735/085.045.0106>
- Moberg, R. (2002): Anaptychia. – *Nordic Lichen Flora* **2**: 9–10.
- Mongkolsuk, P., Meesim, S., Poengsungnoen, V., Buaruang, K., Schumm, F. and Kalb, K. (2015): The lichen family Physciaceae in Thailand II. Contributions to the genus Heterodermia sensu lato. – *Phytotaxa* **235**(1): 1–66. <https://doi.org/10.11646/phytotaxa.235.1.1>
- Nadyeina, O., Grube, M. and Mayrhofer, H. (2010): A contribution to the taxonomy of the genus Rinodina (Physciaceae, lichenized Ascomycotina) using combined ITS and mtSSU rDNA data. – *Lichenologist* **42**(5): 521–531. <https://doi.org/10.1017/s0024282910000186>
- Orange, A., James, P. W. and White, F. J. (2010): *Microchemical methods for the identification of lichens*. – British Lichen Society, London, 101 pp.
- Poelt, J. (1965): Zur Systematik der Flechtenfamilie Physciaceae. – *Nova Hedwigia* **9**: 21–32.
- Rambaut, A. (2014): *FigTree v1.4.2*. – University of Edinburgh, Edinburgh, <http://tree.bio.ed.ac.uk/software/figtree>
- Rehner, S. A. and Samuels, G. J. (1994): Taxonomy and phylogeny of Gliocladium analysed from nuclear large subunit ribosomal DNA sequences. – *Mycol. Res.* **98**: 625–634. [https://doi.org/10.1016/S0953-7562\(09\)80409-7](https://doi.org/10.1016/S0953-7562(09)80409-7)
- Resl, P., Mayrhofer, H., Clayden, S. R., Spribille, T., Thor, G., Tønsberg, T. and Sheard, J. W. (2016): Morphological, chemical and species delimitation analyses provide new taxonomic insights into two groups of Rinodina. – *Lichenologist* **48**(5): 469–488. <https://doi.org/10.1017/s0024282916000359>
- Roux, C., Coste, C., Masson, D. and Bauvet, C. (2006): Lichens et champignons lichénicoles du parc national des Cévennes. 3. Les basses Cévennes. – *Bull. Soc. Linn. Provence* **57**: 59–84.
- Schwarz, G. (1978): Estimating the dimension of a model. – *Ann. Statist.* **6**: 461–464. <https://doi.org/10.1214/aos/1176344136>
- Sheard, J. W. (2010): *The lichen genus Rinodina (Ach.) Gray (Lecanoromycetidae, Physciaceae) in North America, North of Mexico*. – NRC Research Press, Ottawa.

- Sheard, J. W., Ezhkin, A. K., Galanina, I. R., Himelbrant, D., Kuznetsova, E., Shimizu, A., Stepanchikova, I., Thor, G., Tønsberg, T., Yakovchenko, L. S. and Spribille, T. (2017): The lichen genus *Rinodina* (Physciaceae, Caliciales) in north-eastern Asia. – *Lichenologist* **49**(6): 617–672. <https://doi.org/10.1017/s0024282917000536>
- Stecher, G., Tamura, K. and Kumar, S. (2020): Molecular Evolutionary Genetics Analysis (MEGA) for macOS. – *Mol. Biol. Evol.* **37**(4): 1237–1239. <https://doi.org/10.1093/molbev/msz312>
- Steiner, M. and Mayrhofer, H. (1987): Flechten aus Afghanistan IV. Die Gattungen *Buellia*, *Dimelaena* und *Rinodina*. – *Nova Hedwigia* **45**(3–4): 315–326.
- Steiner, M. and Poelt, J. (1987): Drei parasitische Flechten auf *Caloplaca polycarpoides*. – *Plant Syst. Evol.* **155**: 133–141. <https://doi.org/10.1007/bf00936295>
- White, T. J., Bruns, T., Lee, S. and Taylor, J. W. (1990): Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – *PCR protocols* **18**(1): 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Zoller, S., Scheidegger, C. and Sperisen, C. (1999): PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. – *Lichenologist* **31**(5): 511–516. <https://doi.org/10.1006/lich.1999.0220>