



RESEARCH ARTICLE

a open access



Arthonia dokdoensis and Rufoplaca toktoana – Two New Taxa from Dokdo Islands (South Korea)

Sergij Kondratyuk^a, László Lőkös^b, Josef Halda^c, Beeyoung Gun Lee^d, Seol-Hwa Jang^e, Jeong-Jae Woo^f, Jung Shin Park^f, Soon-Ok Oh^f, Sang-Kuk Han^f and Jae-Seoun Hur^e

^aM. H. Kholodny Institute of Botany, Kiev, Ukraine; ^bDepartment of Botany, Hungarian Natural History Museum, Budapest, Hungary; ^cDepartment of Biology, University of Hradec Králové, Hradec Králové, Czech Republic; ^dBaekdudaegan National Arboretum, Bonghwa, Korea; ^eKorean Lichen Research Institute, Sunchon National University, Suncheon, Korea; ^fKorea National Arboretum, Pocheon, Korea

ABSTRACT

Arthonia dokdoensis sp. nov., a lichenicolous fungus from the subcosmopolitan Arthonia molendoi complex growing on crustose thalli of species of the genus Orientophila (subfamily Xanthorioideae, Teloschistaceae), as well as the lichen species Rufoplaca toktoana sp. nov. (subfamily Caloplacoideae, Teloschistaceae) similar to Rufoplaca kaernefeltiana, both from Dokdo Islands, Republic of Korea, are described, illustrated, and compared with closely related taxa. In the phylogenetic tree of the Arthoniaceae based on 12S mtSSU and RPB2 gene sequences, the phylogenetic position of the A. dokdoensis and the relationship with the A. molendoi group are illustrated, while the position of the newly described R. toktoana is confirmed by phylogenetic tree based on ITS nrDNA data.

ARTICLE HISTORY

Received 6 December 2018 Revised 28 October 2019 Accepted 28 October 2019

KEYWORDS

New species; *Orientophila*; phylogenetic analysis; taxonomy

1. Introduction

During a recent investigation of lichen-forming and lichenicolous* fungi (*lichenicolous, i.e., growing or inhabiting on lichen thalli [or thalli of lichen-forming fungi]) of Dokdo Islands, two members of the genera *Arthonia* (Ach.) (*Arthoniaceae*) and *Rufoplaca* Arup, Søchting & Frödén (subfamily Caloplacoideae of the Teloschistaceae) were newly found.

Within our study from combined phylogenetic analysis of the Arthoniaceae based on mtSSU and RPB2 sequences, the Arthonia molendoi group was positioned in the monophyletic branch. Several arthonioid species were already known to grow on foliose or fruticose members of the Teloschistaceae, namely Arthonia sytnikii S. Y. Kondr., Arthonia anyutae S. Y. Kondr. et Alstrup and Arthonia descruens var. nana Grube et Hafellner, as well as A. molendoi (Heufl. ex Frauenf.) R. Sant. All of them infect the thallus, and some of them also develop fruiting bodies on the apothecia (hymenia) of their hosts. Selected characters of taxa mentioned above have been recently summarized by Fleischhacker et al. [1], who described a new taxon, Arthonia parietinaria Hafellner et A. Fleischhacker, a member of the A. molendoi group, and compared with Arthonia anjutae, A. sytnikii, as well as Arthonia epiphyscia,

and A. molendoi. It was concluded that the status of taxa mentioned at the species level had been confirmed by the taxonomic position of hosts in separate genera of the Teloschistaceae, which recently have been proved by three-gene phylogeny (see [2]). Thus A. parietinaria has hosts of the genus Xanthoria Th. Fr. (as it is correctly stressed by Fleischhacker et al. [1]), while lichenicolous fungi previously recorded on Massjukiella polycarpa (Hoffm.) S.Y. Kondr., Fedorenko, S. Stenroos, Kärnefelt, Elix, Hur & A. Thell and/or Oxneria huculica S.Y. Kondr. are highly likely to belong to different taxa. A. anjutae was confirmed as a species of the genus *Teloschistes* Norm. (the subfamily Teloschistoideae of the Teloschistaceae), A. as a species of the genus Jackelixia S. Y. Kondr., Fedorenko, S. Stenroos, Kärnefelt & A. Thell, and A. molendoi as a species of the genus Rusavskia S. Y. Kondr. & Kärnefelt (both latter genera, i.e., Jackelixia and Rusavskia of the subfamily Xanthorioideae of the Teloschistaceae). The further taxon from the A. molendoi complex, which was confirmed as a species of the genus Orientophila Arup, Søchting & Frödén (subfamily Xanthorioideae, Teloschistaceae), is segregated in this article.

The genus *Rufoplaca* Arup, Søchting & Frödén (subfamily Caloplacoideae, Teloschistaceae) was introduced in 2013 for six species and two



additional species have subsequently been described [3-5]. Additionally, to eight species of the genus Rufoplaca, hitherto known from various regions of the Northern Hemisphere, was added one new species found among Dokdo lichens.

The aim of this article was to present legal descriptions of these two taxa of the genera Arthonia and Rufoplaca.

2. Materials and methods

2.1. Taxon sampling

More than 230 lichen specimens were collected in 17 localities of Dokdo Islands, the Republic of Korea in September 2017. The Dokdo specimens, as well as previous collections included in comparative studies and kept in the KoLRI and other herbaria (BP, KW-L, LE, LWG, and VBI), were examined using standard microscopic techniques and handsectioned under a dissecting microscope (Nikon SMZ 645; Nikon, Tokyo, Japan). Anatomical descriptions were based on observations of these preparations under a microscope (Nikon Eclipse E200; Nikon, Tokyo, Japan, and Zeiss Scope, A1; Carl Zeiss, Oberkochen, Germany) with digital camera AxioCam ERc 5s. A section of apothecia was tested with water and with potassium (K) and iodine-potassium iodide (IKI) (10% aqueous potassium iodide) for identification [4,5]. Well-preserved and freshly collected lichen specimens lacking any visible symptoms of fungal infection were selected for DNA isolation. Although not possible for all taxa, an attempt was made to achieve a sample series with at least two specimens of each newly sequenced species, preferably from different localities, to ensure species determination by avoiding contamination through unintentional sampling of a wrong individual or sequencing errors.

A total of 11 new sequences (6 nrITS, 2 mtSSU, and 3 RPB2 sequences) from 8 specimens belonging to 3 species in Dokdo and Ulleung-do islands (Table 1), as well as approximately 150 sequences from GenBank (27 ITS nr DNA, 71 mtSSU, and 78 RPB2), were used for phylogenetic analysis.

2.2. Molecular data

Genomic DNA was isolated from lichen specimens using the CTAB extraction protocol [21]. For some tiny crustose species (e.g., Arthonia or Rufoplaca), contaminations with co-occurring fungi are frequent when using standard DNA isolation protocols on large parts of the lichen thalli. To avoid such contamination, hand-made sections of the hymenium or the thallus were used for direct polymerase chain reaction (PCR) [22]. Any pigmented or crystalencrusted portions were removed with a razor blade. In addition, the lichen material was sometimes washed with acetone or a 1% KOH solution, and then rinsed with water to remove remnants of pigments.

The material was then added to a tube containing the PCR reaction mixture and amplified directly. Amplification reactions were prepared for a 50 µL final volume containing 5 µL 10× DreamTaq Buffer (Fermentas, Waltham, MA), 1.25 µL of each of the $20 \,\mu\text{M}$ primers, $5 \,\mu\text{L}$ of $2.5 \,\text{mg mL}^{-1}$ bovine serum albumin (Fermentas #B14), 4 mL of each of the 2.5 mM dNTPs (Fermentas), 1.25 U DreamTag DNA polymerase (Fermentas) and 1 µL of template genomic DNA or tiny fragments of lichen material.

The nuclear ribosomal RNA gene region including the internal transcribed spacers 1 and 2 and the 5.8S subunit (ITS) was amplified using the primers ITS1F [23] and ITS4 [24], the 28S LSU using the primer LR5 [25], and the 12S mtSSU using the primers mtSSU1-mtSSU3R and mtSSU2R [14,20]. Methods of DNA extractions, data on primers, and phylogenetic analysis are provided in our previous article [26].

A fragment of about 1kb of the RPB2 proteincoding gene was amplified using primers fRPB2-7cF and fRPB2-11aR [27]. The yield of the PCRs was verified by running the products on a 1% agarose gel using ethidium bromide. The amplicons were sequenced by Macrogen® using the amplification primers. Two additional primers, RPB2-2488F and RPB2-2492R [28], were used for sequencing RPB2. See also Park et al. [29] and Kondratyuk et al. [26] amplifications, for extractions, and ing procedures.

Sequence fragments were assembled Sequencher version 4.6 (Gene Codes Corporation, Ann Arbor, MI). Sequences were subjected to MEGABLAST searches to verify their closest relatives and to detect potential contaminations.

2.3. Phylogenetic analyses

The NucITS, mtSSU, and RPB2 sequences for taxa listed in Table 1 were aligned manually using MacClade version 4.05 (Sunderland, MA) [30].

A conflict was assumed to be significant if two different relationships (one being monophyletic and the other being non-monophyletic) for the same set of taxa were both supported with bootstrap values \geq 70% [31].

The mtSSU and RPB2 datasets were concatenated. The combined two-locus dataset consisted of 180 terminals and 1777 unambiguously aligned sites: 856 for the mtSSU and 921 for RPB2. Bayesian inference, maximum likelihood, and parsimony were

Table 1. Species of the *Arthoniaceae* and the *Caloplacoideae* of the *Teloschistaceae* included in the phylogenetic analyses and the GenBank accession numbers of the sequences. New sequences generated are indicated in bold.

Species name	Voucher specimen/reference	ITS	12S mt SSU	RPB2
1. Alyxoria ochrocheila	Ertz et al. [6]		EU704073	EU704035
2. Alyxoria ochrocheila	Ertz et al. [6]		EU704072	EU704037
3. Alyxoria ochrocheila	Ertz et al. [6]		EU704071	
4. Alyxoria varia	Frisch et al. [7]		KJ851006	KJ851147
5. Alyxoria varia	Frisch et al. [7]		KF707642	KF707664
5. Alyxoria varia	Miadlikowska (unpubl.)		KT232221	
7. Alyxoria varia	Ertz et al. [6]		EU704075	EU704039
8. Alyxoria varia	Schoch et al. [8]		FJ772243	
9. Arthonia apatetica	Frisch et al. [7]		KJ850994	KJ851126
10. Arthonia apotheciorum	Frisch et al. [7]		KJ850970	KJ851148
11. Arthonia biatoricola	Frisch et al. [7]		KJ850990	KJ851149
12. Arthonia calcarea	Ertz et al. [6]		EU704065	EU704028
13. Arthonia calcarea	Ertz et al. [6]			EU704029
14. Arthonia calcarea	Frisch et al. [7]		KJ850974	
15. Arthonia didyma	Ertz et al. [6]		EU704047	
16. Arthonia didyma	Frisch et al. [7]		KJ851106	
17. Arthonia dokdoensis	SK L06, South Korea,	171029	171029	171029
	Dokdo Islands,			
	07.09.2017 J. J.Woo			
	171029 (KoLRI 045310)			
18. Arthonia dokdoensis	SK L05, South Korea,			171032
	Dokdo Islands,			
	07.09.2017 J. J.Woo			
	171032 (KoLRI 045313)			
19. Arthonia dokdoensis	SK L04, South Korea,		171034	171034
	Dokdo Islands,			
	07.09.2017 J. J.Woo			
	171034 (KoLRI 045315)			
20. Arthonia granitophila	Frisch et al. [7]		KJ850981	KJ851107
21. Arthonia incarnata	Frisch et al. [9]		KY983975	KY983983
22. Arthonia incarnata	Frisch et al. [9]		KY983976	KY983984
23. Arthonia lapidicola	Frisch et al. [7]		KJ850997	KJ851119
24. Arthonia lobariellae	Frisch et al. [7] as Arthonia		KJ851001	KJ851127
	sp. <i>"lobariicola"</i>			
25. Arthonia lobariellae	Frisch et al. [7] as <i>Arthonia</i> sp. "lobariicola"		KJ851002	KJ851128
26. Arthonia molendoi	Frisch et al. [7]		KJ851000	KJ851117
27. Arthonia neglectula	Frisch et al. [7]		KJ850989	KJ851118
28. Arthonia peltigerina	Frisch et al. [7]		KJ850998	KJ851122
29. Arthonia phaeophysciae	Frisch et al. [7]			KJ851112
30. Arthonia physcidiicola	Frisch et al. [7]		KF707646	KF707657
31. Arthonia radiata	Ertz and Tehler [10]			HQ454651
32. Arthonia radiata	Tehler and Irestedt [11]			EF081373
33. Arthonia radiata	Ertz et al. [6]		EU704048	EU704011
34. Arthonia radiata	Frisch et al. [7]			KJ851109
35. Arthonia stereocaulina	Frisch et al. [7]		KJ850999	
36. Arthonia subfuscicola	Frisch et al. [7]		KJ850971	KJ851111
37. Arthonia subfuscicola	Frisch et al. [7]		KJ850972	
38. Brigantiaea ferruginea	SK 780; Kondratyuk	KF264623	KF264685	
	et al. [12]			
39. Brigantiaea ferruginea	SK 779; Kondratyuk	KF264622	KF264684	
	et al. [12]			
40. Bryostigma muscigenum	Frisch et al. [7]		KJ850991	KJ851124
41. Caloplaca areolata	SK 714; Kondratyuk			
	et al. [13]			
42. Caloplaca cerina	FNM 185; Fedorenko	EU681284	EU680863	
	et al. [14]			
43. Caloplaca stillicidiorum	Gaya et al. [15]	KT291510		KT291649
44. Oxneria huculica	FNM 199; Fedorenko		EU680931	
	et al. [14]			
45. Oxneria huculica	Gaya et al. [16]	JQ301687		JQ301776
46. Oxneria ulophyllodes	FNM 198; Fedorenko	EU691342	EU680930	
• •	et al. [14]			
47. Oxneria ulophyllodes	Gaya et al. [16]			JQ301779
48. Rufoplaca arenaria	Arup et al. [3]	KC179455		
49. Rufoplaca arenaria	Halici et al. [17]	KF007908		
50. Rufoplaca arenaria	Vondrák and Malicek [18]	KT934385		
51. Rufoplaca kaernefeltiana	South Korea, Ulleung-do	162024		
,	Island, Dodong Port,			
	11.07.2016 Kondratyuk			
	S. Y. & L. Lőkös 162024			
	(KoLRI 040262)			
52. Rufoplaca kaernefeltiana	South Korea, Ulleung-do	162044		
==:p.aca racincicidina	Island, Dodong Port,	.02011		
	11.07.2016 Kondratyuk			

(continued)

Table 1. Continued.

	Voucher			
Species name	specimen/reference	ITS	12S mt SSU	RPB2
	S. Y. & L. Lőkös 162044			
	(KoLRI 040282)			
53. Rufoplaca oxfordensis	Arup et al. [3]	KC179456		
54. Rufoplaca scotoplaca	Gaya et al. [16]	JQ301618	JQ301497	JQ301756
55. Rufoplaca scotoplaca	Arup et al. [3]	KC179457	KC179573	
56. Rufoplaca sp. 43	Arup et al. [3]	KC170458	KC179574	
57. Rufoplaca sp. JV 14429	JV 14429, Vondrák et al. [19]	KU926986		
58. Rufoplaca sp. JV 18681	Vondrák et al. (unpubl.)	MG954203		
59. Rufoplaca sp. D 17245	Vondrák et al. (unpubl.)	MG954209		
60. Rufoplaca subpallida	Arup et al. [3]	KC179459		
61. Rufoplaca toktoana	SK L03, South Korea, Dokdo Islands, 07.09.2017 JJ.Woo 171044 (KoLRI 045325)	SK L03		
62. Rufoplaca toktoana	SK L07, South Korea, Dokdo Islands, 07.09.2017 JJ.Woo 171045 (KoLRI 045326)	SK L07		
63. Rufoplaca toktoana	SK L08, South Korea, Dokdo Islands, 07.09.2017 JJ.Woo 171045 (KoLRI 045326)	SK L08		
64. Rufoplaca toktoana	162040, South Korea, Ulleung-do Island, Dodong Port, 11.07.2016 Kondratyuk S. Y. & L. Lőkös 162040 (KoLRI 040278)	162040		
65. Rufoplaca tristiuscula	Arup et al. [3]	KC179460	KC179575	
66. Xanthoria coomae	Arup et al. [3]	NR_120253		
67. Xanthoria mediterranea	Fedorenko et al. [14]	EU681297		
68. Xanthoria monofoliosa	SK 3191, Fedorenko et al. [20]	JN984136		
69. Xanthoria parietina	FNM 177; Fedorenko et al. [14]	EU681297		

used to estimate the phylogeny of Arthoniaceae based on a concatenated sequence matrix of the two loci. For the Bayesian and the maximum likelihood analyses, the best fit model for the two loci, as well as for the codon positions in the RPB2 gene, were calculated by applying the Akaike Information Criterion [32] and the program MrModeltest version 2.2 (Uppsala, Sweden) [33] in conjunction with PAUP* [34]. The prior selection of substitution models supported the $GTR + I + \Gamma$ model for both the two individual loci, as well as for each codon position in RPB2. In the Bayesian analysis, the dataset was analyzed in four partitions, mtSSU and by codon positions for RPB2. Posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MrBayes version 3.2.1 (Uppsala, Sweden) [35]. In parsimony analysis, the concatenated dataset was analyzed using the same settings as those used for testing the topological incongruence. The phylogenetic tree of the Arthoniaceae obtained from parsimony analysis based on the concatenated mtSSU and RPB2 sequences as the most illustrative one was included in the article (Figure 1).

Three outgroup species Oxneria ulophyllodes, Oxneria Alfredii, and O. huculica were chosen for the *Arthoniaceae* tree, but *Brigantiaea ferruginea* for the *Rufoplaca* phylogenetic tree. These taxa were used as the rooting taxa in all the analyses. In total, the dataset for the multilocus phylogenetic tree included 141 sequences and ca. Hundred specimens representing approximately 70 species, while the final tree presented in this article included 38 specimens representing 23 species.

3. Results and discussion

3.1. New taxa

Arthonia dokdoensis S. Y. Kondr., L. Lőkös, B. G. Lee, J.-J. Woo et J.-S. Hur, sp. nov. (Figure 2)

MycoBank No.: MB 831133.

This species is similar to *A. parietinaria* but differs in causing much smaller infection spots, and in having smaller ascomata, a lower mean number of ascomata per infection spot, more common conidiomata, and bacilliform conidia.

Type: Republic of Korea, Gyeongsangbuk-do, Ulleung-gun, Dokdo-ri, Seodo (= Western) Island, on rocks, growing on thalli of *Orientophila yokjidoensis*, growing together with *Polyozosia* aff. *dispersa* and *Orientophila dodongensis*. Lat.: 37° 14′ 27″ N, Long.: 131° 51′ 54″ E, Alt.: 100 m a.s.l.

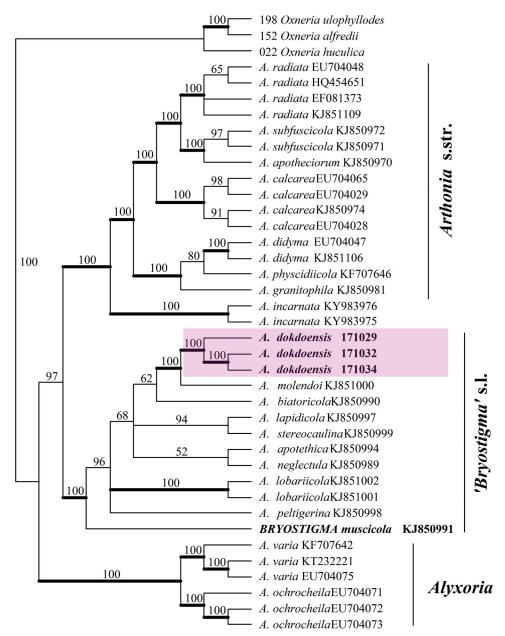


Figure 1. Position of the newly described Arthonia dokdoensis in the phylogenetic tree of the Arthoniaceae obtained from parsimony analysis based on concatenated mtSSU and RPB2 sequences.

Coll:. Woo, J. J. (171028), 07.09.2017 (KoLRI 045309 sub Polyozosia - holotype); the same locality, growing on thalli of O. yokjidoensis, growing together with Physciella aff. melanchra Lecanora sp. Coll.: Woo, J. J. (171029), 07.09.2017 (KoLRI 045310 sub O. yokjidoensis - holotype); the same locality, growing on thalli of O. yokjidoensis, growing together with Polyozosia aff. dispersa. Coll.: Woo, J. J. (171030), 08.09.2017 (KoLRI 045311 sub *Polyozosia* – isotype); the same locality, growing on thalli of O. yokjidoensis, growing together with Polyozosia aff. dispersa, Physciella aff. melanchra and Diplotomma alboatra. Coll.: Woo, J. J. (171032), 08.09.2017 (KoLRI 045313 Polyozosia - isotype); the same locality, growing on thalli of O. yokjidoensis, growing together with Polyozosia aff. dispersa, Physciella aff. melanchra,

Buellia ulleungdoensis and Lecanora sp. Coll.: Woo, J. J. (171034), 08.09.2017 (KoLRI 045315 sub Polyozosia - isotype); the same locality, growing on thalli of O. yokjidoensis, growing together with Polyozosia aff. dispersa, Physciella aff. melanchra, Diploicia canescens, and B. ulleungdoensis. Coll.: Woo, J. J. (171036), 08.09.2017 (KoLRI 045317 sub D. canescens - isotype).

Morphology: Lichenicolous fungus forming very indistinct infection spots (from very indistinct to more or less recognizable to 0.5-1 mm across) in the central areolate portion of lobate lichen O. yokjidoensis, where the peripheral zone of host thalli to 1.5-2.5 mm wide with radially orientated lobes usually not damaged; infection spots often include very small, punctiform, scattered, and distant ascomata or conidiomata.

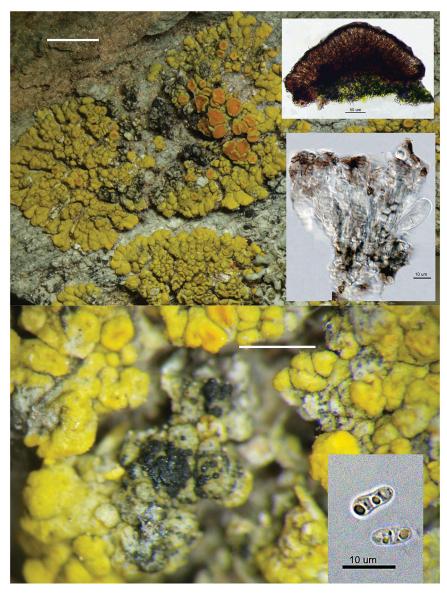


Figure 2. Arthonia dokdoensis (holotype), general habit. Scale 2 mm (top, with enlarged section of apothecium, scale 50 µm and enlarged portion of hymenium, scale 10 μm) and 500 μm (bottom, with enlarged ascospores, scale 10 μm).

Ascomata (0.08-)0.1-0.13(-0.14) mm wide, single, round and more or less regular, scattered and distant, and rather inconspicuous, or aggregated in very irregular shape aggregations with 5-10 apothecia together in spots to 0.4-0.6 mm diam./across, often covering one side/portion of the host thalline areole, and better seen. In section, epihymenium olivaceous brown to blackish brown, 4.6-8 μm thick; hymenium 32-40 µm high, in the middle and lower portions more or less hyaline; interascal hyphae branched and anastomosing ca. 2 µm wide; subhymenium (48-)56-64(-80) µm thick, hyaline or light brown; asci clavate, 8-spored; ascospores hyaline (0-)1-septate; lower cell slightly attenuated, $9.6-12.8 \times 4-4.8 \ \mu m$ (42 measurements).

Conidiomata very often observed below ascomata and probably especially numerous at first stages of infection development; conidia bacilliform, $3-4 \times 0.8 \mu m$.

Ascomatal gel I + red; KI + blue; asci with KI + blue ring-structure.

Ecology: The species grows in the crustose central portion of thalli of lobate lichens O. yokjidoensis and O. dodongensis growing on siliceous rock.

Etymology: It is named after the type locality, namely Dokdo Islands, Republic of Korea, Eastern Asia.

Distribution: It is so far known only from the type collection in Dokdo Islands, Republic of Korea, Eastern Asia, where it is rather abundant.

Taxonomic notes: The lichenicolous fungus A. dokdoensis usually damages the central portion to 0.5-1 mm across, while it hosts thalli to 7-8 mm across with peripheral zone to 1.5-2.5 mm wide with radially orientated lobes, which are usually not damaged by lichenicolous fungi.

Very small ascomata (ca. 80-120 μm in diam. at first) are rather scattered and distant, and are very

barely noticeable. Lichenicolous fungus is usually better distinguished when aggregated ascomata form irregular, often confluent aggregations to 0.4-0.5 mm wide. At this stage, ascomata of lichenicolous fungus often entirely cover the areoles of the central portion of host thalli. The A. dokdoensis infection on thalli of O. yokjidoensis can be most easy to be recognized at the latest stage.

Sometimes numerous brown hyphae rounded cells to 4-4.8 µm wide are also observed in host thalli damaged by A. dokdoensis. On the other hand, they probably belong to another lichenicolous fungus.

Additional specimens examined: Republic of Korea, Gyeongsangbuk-do, Ulleung-gun, Dokdo-ri, Seodo (= Western) Island, on rock, growing on thalli of O. yokjidoensis growing together with Buellia halonia, and Lecanora sp. Lat.: 37° 14' 29.04" N, Long.: 131° 51′ 51.4" E, Alt.: 20–25m a.s.l. Coll.: Park, J. S. (170860), 07.09.2017 (KoLRI 045141 sub B. halonia); Dongdo Island, on rock, growing on thalli of O. yokjidoensis, growing together with O. dodongensis, Polyozosia aff. Dispersa, and Physciella aff. melanchra. Lat.: 37° 14' 21.61" N, Long.131° 52′ 5.71" E, Alt.: 12 m a.s.l. Coll.: Oh, S. O. (171086), 08.09.2017 (KoLRI 045367 sub Polyozosia aff. dispersa); Seodo Island, near the top level of the trail, on rock, growing on thalli of O. yokjidoensis growing together with Myriolecis aff. dispersa, B. ulleungdoensis and Physciella aff. melanchra. Lat.: 37° 14′ 30.02″ N, Long.: 131° 51′ 50.44" E, Alt.: 25 m a.s.l. Coll.: Lee, B. G. (170928), 07.09.2017 (KoLRI 045209 sub O. yokjidoensis); Seodo Island, on rocks, growing on thalli of O. yokjidoensis, growing together with Rufoplaca toktoana. Lat.: 37° 14′ 27″ N, Long.: 131° 51′ 54″ E, Alt.: 100 m a.s.l. Coll.: Woo, J. J. (171044), 07.09.2017 (KoLRI 045325 sub R. toktoana).

R. toktoana S. Y. Kondr., L. Lőkös et J.-S. Hur, **sp. nov.** (Figure 3)

MycoBank No.: MB 825110.

Similar to Rufoplaca kaernefeltiana but different in having well distinct and much larger thallus, thinner and K - cortical layer of thallus, larger and biatorine-like apothecia, lower hymenium and narrower paraphysis tips and shorter and narrower ascospores, and mainly hardly visible and narrower ascospore septum.

Type: Republic of Korea, Gyeongsangbuk-do, Ulleung-gun, Dokdo-ri, Seodo Island, on rocks, growing together with O. yokjidoensis damaged by A. dokdoensis, Lecanora sp. and Physciella sp. Lat.: 37° 14′ 27" N, Long.: 131° 51′ 54" E, Alt.: 100 m a.s.l. Coll: Woo, J. J. (171044), 07.09.2017 (KoLRI 045325 - holotype of R. toktoana); the same locality, growing together with O. yokjidoensis, Coll: Woo, J.

J. (171045), 07.09.2017 (KoLRI 045326 - isotype of R. toktoana).

Morphology: Thallus rather thick, areolate to continuous, whitish gray, or grayish-white; apothecia seem to be biatorine, orange, or somewhat reddishorange. Thalline areoles (0.5–)1.5–2.5 mm across. Thallus in section to (64-)80-160(-280) µm thick, cortical layer 8-11.2(-12.8)[-24] µm thick, very thin, paraplectenchymatous, cell lumina rounded to 4.8 µm in diam.; algal zone filling in the whole thallus below cortical layer to 80(-96) µm thick; algal cells trebouxioid, 16-19.2(-22.4) µm in diam.

Apothecia to 0.9-1 mm in diam. and 0.2-0.27 mm thick in section, seem to be biatorine, while lecanorine or zeorine in section; 1-3(-5) per areole; in section thalline exciple to 80–96(–112) μm thick, cortical layer not distinct or very thin, to 8-16 µm thick, better seen on underside, paraplectenchymatous; true exciple (56-)80-96(-112)[-144] µm wide in the uppermost lateral portion, more or less scleroplectenchymatous, hyphal lumina to 1.6 μm, and to 16-32(-48) μm thick in lower lateral and to 16 µm thick in the basal portion, more or less Blastenia-type in the latter two portions or scleroplectenchymatous; hymenium 64-72 µm high, epihymenium 8–11.2 μm thick, dark brown; paraphysis tips more or less brownish, richly branched to 2.4-4 µm in diam. in K brownish color disappearing; subhymenium (48–)80–96 μm thick, hyaline, without oil; asci 8-spored, but usually only simple ascospore seen (in K too); ascospores narrowly ellipsoid, mainly simple observed, sometimes becoming slightly darker or slightly brownish (9.6-)11.2-12.8(-14.4)×3-4.8 μm in water (45 measurements) and $11.8-13.4(-14.4)\times$ 3.6-3.9(-4.5) µm in K (37 measurements); septum very rarely observed, usually seen only at sides of equatorial portions in water to (0.5-)1-2.4 μm wide in water and better seen in K (0.5-)1.5-2(-2.5) µm thick. Conidiomata and conidia not observed.

Chemistry: Epihymenium K + crimson-purple, while brownish color disappearing. Cortical layer of thalline exciple K+purple only in the uppermost lateral portion. Cortical layer of thallus K-.

Ecology: It grows on siliceous rock in the supralitoral zone.

Etymology: It is named after the type locality, namely Dokdo Islands (in Korean Tokto Islands), Republic of Korea, Eastern Asia.

Distribution: The species is so far known from the type collection Dokdo Islands, as well as Ulleung-do Island, both the Republic of Korea, Eastern Asia, where it was rather abundant in some places.

Taxonomic notes: R. toktoana is similar to R. kaernefeltiana S. Y. Kondr., L. Lőkös et J. S. Hur, recently described from Ulleung-do Island, South Korea (Eastern Asia), but differs in having well distinct



Figure 3. Rufoplaca toktoana (holotype), general habit with enlarged section of apothecium (top, scale 25 µm) and with enlarged ascospores (bottom, scale 25 μm). Scale 500 μm.

and much larger thallus and larger thalline areoles or often forming almost continuous thallus (thalline areoles (0.5-)1.5-2.5 mm vs. (0.2-)0.4-0.8 mm across, usually very indistinct, distant, and scattered), in having thinner and K – cortical layer of thallus (8–11(–13) μ m vs. 30–40(–50) μ m thick, K + purple), in having larger and biatorine-like apothecia (vs. seem to be lecanorine), in having lower hymenium (65-70 µm vs. 70–90 µm high) and narrower paraphysis tips $(2.4-4 \mu m \ vs. \ to \ 5(-6) \mu m \ in \ diam.)$, and in having shorter and narrower ascospores ((9.5-) $11-13(-14.5)\times$ 3–4.8 μ m vs. (10–)12–15(–16) \times 7–8 μ m) and mainly hardly visible and narrower ascospore septum $((0.5-)1-2.4 \mu \text{m vs.} (4-) 5-6(-7) \mu \text{m wide}) [4].$

Additional specimens examined: Republic of Korea, Gyeongsangbuk-do, Ulleung-gun, Dokdo-ri, Seodo Island, on rocks, growing together with Lecanora cf. campestris. Lat.: 37° 14′ 27" N, Long.: 131° 51′ 54″ E, Alt.: 100 m a.s.l. Coll.: Woo, J. J. (171042), 07.09.2017 (KoLRI 045323 sub Lecanora

cf. campestris); Republic of Korea, Gyeongsangbukdo, Ulleung-gun, Dokdo-ri, Seodo Island, on rocks, growing together with Caloplaca dodongensis. Lat.: 37° 14′ 26.66″ N, Long.: 131° 51′ 51.50″ E, Alt.: 20 m a.s.l. Coll.: Lee, B. G. (170909), 07.09.2017 (KoLRI 045190 sub R. toktoana); the same locality, growing together with B. ulleungdoensis, Coll.: Lee, B. G. (170910, 170911), 07.09.2017 (KoLRI 045191, KoLRI 045192 sub R. toktoana); Republic of Korea, Gyeongsangbuk-do, Ulleung-gun, Ulleung-eup, Dodong-ri, Dodong Port, on siliceous rocks. Lat.: 37° 28′ 59.9″ N, Long.: 130° 54′ 40.7″ E, Alt.: 20 m a.s.l. Coll.: Kondratyuk, S. Y., Lőkös, L. (162040), 11.07.2016 (KoLRI 040278).

3.2. Discussion

A. dokdoensis is similar to the recently described A. parietinaria in having ascomata distributed over the surface of the host thallus, including apothecial

Table 2. Comparison of morphological/anatomical characters of Arthonia dokdoensis, A. parietinaria and A. molendoi.

Characters	Arthonia dokdoensis	Arthonia parietinaria	Arthonia molendoi
Infection spots	to 0.5 mm across, often rather indistinct	to 3–5 mm in diam.	to 3–5 mm in across
Mean number of ascomata per infection spot	to 5–10	(10–)20–30(–50)	1–5(–10)
Ascomata (in diam.)	(80–120(–140) μm	up to 0.25 mm	0.1-0.24 mm
Hymenium (µm high)	32–40	30-45	45-50
Subhymenium (μm thick)	64–80	[data not provided in the original description][1]	50–60 μm
Ascospores (μm)	9.6–12.8 × 4–4.8, hyaline	(9-)10-12(-13.5)×(3-)4-5(-6), hyaline with thin hyaline perispore (getting condensed and brownish with age)[1]	11–14 \times 5–6.5, slightly pigmented with age
A gelatinous epispore	absent		present
Conidiomata	being often aggregated, more common while ascomata rarely observed	usually indistinct while ascomata well developed	pycnidia of <i>Arthonia molendoi</i> still not observed after Grube [30]
Conidia	bacilliform	ellipsoid; unfortunately measurements on conidia not provided in the original description)[1]	pycnidia of <i>Arthonia molendoi</i> still not observed after Grube [30]
Hosts	Orientophila spp.	Xanthoria parietina	Rusavskia spp.

margins and hymenia, but differs in causing much smaller infection spots (to 0.5 mm across, often rather indistinct, vs. to 3-5 mm in diam.), in having smaller ascomata (80-120(-140) µm vs. up to 0.25 mm in diam.), in having lower mean number of ascomata per infection spot (to 5-10 vs. (10-)20-30(-50)), in having more common conidiomata being often aggregated, while ascomata rarely observed (vs. ascomata well developed while conidiomata usually indistinct), and in having bacilliconidia (vs. ellipsoid; unfortunately measurements on the conidia of A. parietinaria were not provided in the original description)[1] (Table 2).

A. dokdoensis is similar to A. molendoi but differs in causing much smaller infection spots (to 0.5 mm in diam. often rather indistinct vs. to 3-5 mm diam. across), in having higher mean number of ascomata per infection spot (5-10 vs. 1-5(-10) in A. molendoi), in having smaller ascomata (80-120(-140) μm vs. 0.1-0.24 mm in diam.), in having lower hymenium (32-40 vs. 45-50 µm high) and thicker subhymenium (64-80 µm vs. 50-60 µm thick), in having shorter and narrower ascospores $(9.6-12.8 \times 4-4.8 \ \mu m \ vs. \ 11-14 \times 5-6.5 \ \mu m)$, as well as being hyaline ascospores (not being slightly pigmented with age), and in having bacilliform conidia (pycnidia of A. molendoi still not observed after Grube [36]), as well as in the lack of a gelatinous epispore [36].

Unfortunately, a relatively recent full description of A. molendoi published only in Grube [36] is still incomplete. Fleischhacker et al. [1] also provided some data on the diagnostic characters of A. molendoi. Unfortunately, data on some measurements of ascomata, subhymenium, and shape or morphology of conidia are still missing.

Thus far, all species of the A. molendoi aggregation have been recorded from the members of the subfamily Xanthorioideae of the Teloschistaceae (see [2]), i.e., genera Rusavskia (type host of A. molendoi s. str.), Xanthoria (type host of A. parietinaria), Orientophila (type host of A. dokdoensis) and Calogaya. On the other hand, material of A. molendoi previously recorded from members of the genus Calogaya is in urgent need of revision and may belong to another taxon.

The data confirm the conclusion of Grube [36] in that careful studies of the A. molendoi complex are still needed in the future to determine if specimens on different lineages in Caloplaca and Xanthoria belong to the same species.

Arthonia destruens differs from taxa of the A. molendoi aggr. in having permanently brownish ascospores at overmaturity.

Fleischhacker et al. [1] segregated Ar. parietinaria growing on the members of the Xanthoria s. str. from the A. molendoi complex, which was believed to be foliose lichens of the genera Xanthoria and Rusavskia, as well as crustose lichens of the genus Calogaya (the former Caloplaca saxicola group). After segregation of A. parietinaria from the complex mentioned, A. molendoi is confirmed to Rusavskia elegans (type host) and to other species of Rusavskia, genus as well as of genus Calogaya.

The suggestion about the worldwide distribution of A. parietinaria and Holarctic is somewhat doubtful given that the host lichen species Xanthoria parietina itself is confirmed only from a few collections outside Europe and the Mediterranean region. Most records of Xanthoria parietina from outside Europe belong to other taxa (Kondratyuk, in prep.) and even to various genera of the Teloschistaceae in current stage (see [2]). Fleischhacker et al. [1] hesitated to use modern generic groups of the Teloschistaceae, but the generic groups Jackelixia, Rusavskia, Massjukiella, and Oxneria, recently received further confirmation [2,37].

Unfortunately, the diagnostic character of the A. molendoi complex, such as fast vine red reaction of hymenium (in contrast to I + blue then red in case of Arthonia destruens or Arthonia incarnata), was not discussed in the description of A. parietinaria [1].

Initially, close relations of the Korean material of A. dokdoensis to Arthonia patellaria (ITS sequences FR799123, FR799124) were found after ITS phylogeny of the members of the Arthoniaceae. On the other hand, only very limited data exists on the ITS nrDNA sequences of the family Arthoniaceae, while phylogeny of this family and the entire Arthoniales is built mainly on nrLSU, mtSSU, and RPB2 sequences. An attempt was made to obtain the three sequences mentioned above. On the other hand, only the mtSSU and RPB2 sequences for the new taxon could be obtained.

A separate mtSSU and RPB2 analysis (not shown) revealed that A. molendoi is positioned in a separate branch from the Arthonia s. str. branch. The same results were obtained in the combined phylogenetic analysis based on concatenated mtSSU and RPB2 sequences (Figure 1).

It was firstly found in this study that the A. molendoi group is positioned within the Bryostigma clade of the combined phylogenetic tree of the Arthoniaceae based on concatenated mtSSU and RPB2 sequences. The Bryostigma clade includes the genus Bryostigma Poelt et Döbbeler with type species Bryostigma muscigenum (Th. Fr.) Frisch et G. Thor, as well as members of the A. molendoi group [38]. We agree with previous authors [9] that there is probably more than one generic group within the Bryostigma clade. Positions of seven of ten taxa of the Bryostigma clade are confirmed by combined mtSSU and RPB2 sequences (Figure 1), as well as by nrLSU phylogeny [1].

A. dokdoensis, together with the following two species, i.e., Arthonia phaeophysciae and A. parietinaria, for which molecular data were provided, are the members of the A. molendoi complex. Unfortunately, only data on nrLSU sequences of A. parietinaria were recorded and illustrated in phylogenetic tree by Fleischhacker et al. [1] from this species of the A. molendoi complex. These data could not be obtained from GenBank within this study. A. epiphyscia, the position of which should be confirmed by molecular data in the future, is highly likely to be a member of the Bryostigma molendoi complex. These taxa, which are characterized by

lichenicolous habit, as well as numerous ascomata forming very characteristic aggregations in host thallus, may be segregated in the future in a separate genus. On the other hand, only insufficient data exist on differences of lichenicolous taxa and lichenforming fungi of the Bryostigma s. l. clade, as well as epibryophilous Bryostigma muscigenum (Th. Fr.) Frisch et G. Thor itself (i.e., the genus Bryostigma s. str.).

These results provide further evidence for the still incomplete understanding of the character evolution in Arthonia s. l. and the relevance of morphological characters used for the delimitation of genera and species groups in Arthoniaceae, as was previously shown, e.g., by the studies of Frisch and Thor [39], Frisch et al. [40,41], and Aptroot et al. [42]. Given the combination of morphological characters presented above, in addition to the isolated position on the phylogenetic tree in Figure 1, A. incarnata appears to be a rather common species in oldgrowth forests in Japan (collected only once in Korea) [9], and cannot be connected easily with any of the generic names currently accepted in the synonymy of Arthonia [43]. At the current state of knowledge and with a proper revision of Arthonia s. 1. still pending, this species should be in Arthonia for the time being instead of describing it for another poorly monotypic genus.

R. toktoana is also similar to the recently described Rufoplaca ulleungensis S. Y. Kondr., L. Lőkös et J. S. Hur, from Ulleung-do Island, South Korea (Eastern Asia), but differs in having much better developed and often almost continuous thallus (vs. rather indistinct and consisting of distant and scattered areoles), in having larger apothecia (to 0.9-1 mm vs. (0.2-)0.3-0.8 mm diam.), and in having shorter and narrower ascospores ((9.5-) $11-13(-14.5)\times 3-4.5 \ \mu m \ vs. \ 14-16(-18) \times 4-5.5(-6)$ μ m), while ascospore septum ((0.5–)1–2.4 μ m vs. $1.5-2(-2.5) \mu m$ wide) is similar [5] (Table 3).

R. toktoana is similar to "Caloplaca" fraudans (Th. Fr.) H. Olivier growing on sea coastal rock, rarely on wood or bones, in Arctic regions of the Holarctic, but differs in having well distinct, thick thallus, in having concave or plane light reddish orange apothecia (vs. convex, dark orange, or rusty red), in having rather thin own margin and concolorous with apothecium disc (vs. to 0.1-0.2 mm wide slightly shiny and lighter of disc, bright orange, or yellow), in having thinner subhymenium (vs. 60-100(-130) μm thick), in having lower hymenium (65-70 μm vs. 85-100 μm high), in having shorter narrower ascospores ((9.6-) $(-14.5)\times 3-4.8$ µm vs. $(10-)12-14(-15)\times 4-6$ µm), and in having slightly narrower (or mainly

Table 3. Comparison of morphological/anatomical characters of Rufoplaca toktoana, Rufoplaca kaernefeltiana, and Rufoplaca ulleungdoensis.

Characters	Rufoplaca toktoana	Rufoplaca kaernefeltiana	Rufoplaca ulleungdoensis
Thallus	well distinct and large	usually very indistinct	rather indistinct and consisting of distant and scattered areoles
Thalline areoles mm across	(0.5–)1.5–2.5, well distinct or often forming almost continuous thallus	(0.2–)0.4–0.8, usually very indistinct, distant and scattered	0.3–0.7(–1.3), distant and separate to aggregated in small groups
Cortical layer of thallus (µm thick)	8-11(-13) and K-	30–40(–50), K $+$ purple	7–8 and K–
Apothecia	to 0.9–1 mm, biatorine-like	0.3–0.7 mm, seem to be lecanorine	(0.2–)0.3–0.8 mm, often in groups, biatorine
Hymenium (µm high)	65–70	70–90	70–80
Paraphysis tips (µm in diam.)	2.4-4	to 5(-6)	to 4
Ascospores (µm)	(9.5-) 11-13(-14.5)×3-4.5	(10-)12-15(-16)×7-8	14-16(-18)×4-5.5(-6)
Ascospore septum(µm wide)	(0.5–)1–2.4, mainly hardly visible	(4–) 5–6(–7)	1.5-2(-2.5)

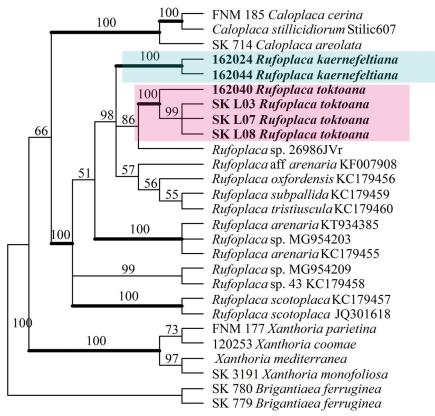


Figure 4. Phylogenetic tree of the genus Rufoplaca based on ITS nrDNA showing position of the new species R. toktoana and the recently described Rufoplaca kaernefeltiana.

undeveloped) ascospore septum ((0.5–)1–2.4 μ m vs. 2.5-4.5 μm wide) [44].

R. toktoana is similar and can be keyed to Caloplaca erythrocarpa (Pers.) Zwackh growing on limestones, sandstones enriched by calcium in Europe, the Caucasus, Asia (Syria, Israel, Jordania, and Egypt), and North Africa, but differs in having larger apothecia (0.9-1 mm vs. 0.2-0.5(-0.8) mm in diam.), in having biatorine, but lecanorine or zeorine in section apothecia (vs. zeorine), in having superficial (vs. seem to be immersed) apothecia; in having irregular and larger thalline areoles $(0.5-1(-1.5) \text{ mm } vs. \ 0.2-0.5(-1) \text{ mm across}), \text{ in hav-}$ ing 1 apothecium per areole (vs. (1-)2-3 apothecia per areoles in peripheral and 1(-2) per areoles in the center of thallus); in having dull orange or dull reddish orange disc (vs. dark red, dark rusty red, to

dark rusty brown), in having weakly developed, seen at sides or on underside thalline margin (vs. own margin lighter of disc, red-orange, thin, and permanent), in having narrower and shorter ascospores ((9.6–) $11-13(-14.5)\times 3-4.8~\mu m$ vs. $12-16(-18)\times$ (5-)7-9(-10) µm, and in having narrower ascospore septum $((0.5-)1-2.4 \,\mu\text{m} \text{ vs. } 3-5 \,\mu\text{m} \text{ wide } [40].$

Twenty-five sequences are available for members of the genus Rufoplaca in GenBank. The main portion of data was provided by Arup et al. [3], while a few specimens were added by J. Vondrák et al. [17-19]. On the other hand, after ITS phylogeny, the Eastern Asian material, i.e., R. toktoana and R. kaernefeltii, for which molecular data are for the first time provided in this article, form a separate branch within the genus Rufoplaca (Figure 4). Both Eastern Asian taxa have the highest level of



bootstrap support. Therefore, the material of both taxa mentioned is rather homogenous from the molecular point of view.

4. Conclusion

The species diversity of the Bryostigma s. lat. clade includes 13 species based on a combined phylogenetic analysis of the Arthoniaceae based on mtSSU and RPB2 gene sequences. Data on ITS nrDNA sequences are provided herein for the first time for A. dokdoensis, R. kaernefeltiana, and R. toktoana.

Acknowledgments

We are thankful to Dr Edit Farkas (Vácrátót, Hungary) for kind help with getting photos of new taxa described above, and Dr Konstanze Bensch (the MycoBank team, UK) for nomenclature comments.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by a grant from the Korean Forest Service Program through the Korea National Arboretum (KNA1-1-22, 17-2), the Korean National Research Resource Center Program (NRF-2017M3A9B8069471), the Korean Brain Pool Program (161S-4-3-1659), and the Ministry of Education and Science of Ukraine (M/172-2017).

References

- Fleischhacker A, Grube M, Frisch A. Arthonia parietinaria - a common but frequently misunderstood lichenicolous fungus on species of the Xanthoria parietina-group. Fungal Biol. 2016; 120(11):1341-1353.
- Kondratyuk SY, Lőkös L, Upreti DK, et al. New monophyletic branches of the Teloschistaceae (lichen-forming Ascomycota) proved by three gene phylogeny. Acta Bot Hung. 2017;59(1-2):71-136.
- Arup U, Søchting U, Frödén P. A new taxonomy of the family Teloschistaceae. Nord J Bot. 2013;31: 16 - 83.
- Kondratyuk SY, Lőkös L, Halda J, et al. New and noteworthy lichen-forming and lichenicolous fungi 6. Acta Bot Hung. 2017;59(1-2):137-260.
- Kondratyuk SY, Lőkös L, Halda JP, et al. New and noteworthy lichen-forming and lichenicolous fungi 7. Acta Bot Hung. 2018;60(1-2):115-184.
- Ertz D, Miadlikowska J, Lutzoni F, et al. Towards the new classification of Arthoniales (Ascomycota) based on a three-gene phylogeny focussing on the genus Opegrapha. Mycol Res. 2009;113(1):141-152.

- Frisch A, Thor G, Ertz D, et al. The Arthonialean challenge: restructuring Arthoniaceae. Taxon. 2014; 63(4):727-744.
- Schoch CL, Sung GH, López-Giráldez F, et al. The Ascomycota tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Syst Biol. 2009; 58(2):224-239.
- [9] Frisch A, Thor G, Moon KH, et al. Arthonia incarnata (Arthoniaceae), a rare and poorly known oldgrowth forest lichen new to Asia. Nord J Bot. 2017;35(5):587-594.
- [10] Ertz D, Tehler A. The phylogeny of Arthoniales (Pezizomycotina) inferred from nucLSU and RPB2 sequences. Fung Divers. 2011;49(1):47-71.
- [11] Tehler A, Irestedt M. Parallel evolution of lichen growth forms in the family Roccellaceae (Arthoniales, Euascomycetes). Cladistics. 2007; 23(5):432-454.
- [12] Kondratyuk S, Jeong MH, Yu NH, et al. Four new genera of teloschistoid lichens (Teloschistaceae, Ascomycota) based on molecular phylogeny. Acta Bot Hung. 2013;55(3-4):251-274.
- Kondratyuk SY, Jeong MH, Yu NH, et al. A [13] revised taxonomy of the subfamily Caloplacoideae (Teloschistaceae, Ascomycota) based on molecular phylogeny. Acta Bot Hung. 2014;56(1-2):93-123.
- Fedorenko NM, Stenroos S, Thell A, et al. A [14] phylogenetic analysis of xanthorioid lichens (Teloschistaceae, Ascomycota) based on ITS and mtSSU sequences. Bibl Lichenol. 2009;100:49-84.
- [15] Gaya E, Fernández-Brime S, Vargas R, et al. The radiation of adaptive lichen-forming Teloschistaceae is associated with sunscreening pigments and a bark-to-rock substrate shift. Proc Natl Acad Sci USA. 2015;112(37):11600-11605.
- [16] Gaya E, Högnabba F, Holguin Á, et al. Implementing a cumulative supermatrix approach for a comprehensive phylogenetic study of the Teloschistales (Pezizomycotina, Ascomycota). Mol Phylogen Evol. 2012;63(2):374-387.
- Halıcı MG, Vondrák J, Demirel R, et al. [17] Teloschistaceae (lichenized Ascomycetes) in Turkey II. Some poorly known taxa. Supported by molecular data. Nova Hedw. 2014;98(3):449-458.
- Vondrák J, Malíček J. Teloschistaceae of the local-[18] ities Velká kotlina and Petrovy kameny in the Hrubý Jeseník Mts. Bryonora. 2015;56:45-55.
- [19] Vondrák J, Ismailov A, Urbanavichus G. Lichens of the family Teloschistaceae in Dagestan, an eastern part of the Caucasian biodiversity hot-spot. Nova hedw. 2017;104(4):483-498.
- Fedorenko NM, Stenroos S, Thell A, et al. [20] Molecular phylogeny of xanthorioid lichens (Teloschistaceae, Ascomycota), with notes on their morphology. Bibl Lichenol. 2012;108:45-64.
- [21] Doyle JJ, Doyle JL. Isolation of plant DNA from fresh tissue. Focus. 1990;12:13-15.
- Lawrey JD, Binder M, Diederich P, et al. Phylogenetic diversity of lichen-associated homobasidiomycetes. Mol Phylogen Evol. 2007;44(2): 778-789.
- Gardes M, Bruns TD. ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Mol Ecol. 1993;2(2):113-118.

- [24] White TJ, Bruns T, Lee S, et al. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR Protocols. 1990;38:315-322.
- [25] Vilgalys R, Hester M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. J Bacteriol. 1990;172(8):4238-4246.
- [26] Kondratyuk SY, Persson P-E, Hansson M, et al. Upretia, a new caloplacoid lichen genus (Teloschistaceae, Lichen-Forming Ascomycota) Biodiversity from India. Cryptogam Assessment. 2018;2018(01):22-31.
- [27] Liu YJ, Whelen S, Hall BD. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. Mol Biol Evol. 1999;16(12): 1799-1808.
- [28] Reeb V, Lutzoni F, Roux C. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. Mol Phylogen Evol. 2004;32(3):1036-1060.
- [29] Park JS, Park SY, Park CH, et al. Taxonomic revision of the lichen genera Pertusaria, Varicellaria, and Variolaria (Pertusariales, Ascomycota) in South Korea. Mycobiology. 2017;45(4):270-285.
- [30] Maddison DR, Maddison WP. MacClade 4: analysis of phylogeny and character evolution, version 4.05. Sunderland (MA): Sinauer; 2002.
- [31] Mason-Gamer RJ, Kellogg EA. Testing for phylogenetic conflict among molecular data sets in the Tribe Triticeae (Gramineae). Syst Biol. 1996;45(4): 524-545.
- [32] Akaike H. Information theory and an extension of the maximum likelihood principle In: Petrov BN, Casaki F, editors. Second international symposium on information theory. Budapest, Hungary: Akadémiai Kiadó; 1973. p. 267-281.
- [33] Nylander JAA. MrModeltest v.2.2. Uppsala, Sweden: Computer Program Distributed by the Author; 2005.

- Swofford DL. PAUP*. Phylogenetic Analysis Using [34] Parsimony (* and other methods). Version 4. Sunderland (MA): Sinauer Associates; 1998.
- [35] Ronquist F, Huelsenbeck JP. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics. 2003;19(12):1572–1574.
- [36] Grube M. Arthonia In: Nash III TH, Gries C, Bungartz F, editors. Lichen flora of the greater Sonoran desert region. Vol. 3. Tempe (AZ): Lichens Unlimited, Arizona State University; 2007. p. 51-52.
- [37] Kondratyuk SY, Kärnefelt I, Thell A, et al. A revised taxonomy of the subfamily Xanthorioideae (Teloschistaceae, Ascomycota) based on molecular phylogeny. Acta Bot Hung. 2014;56(1-2):141-178.
- Poelt J, Dobeler P. Bryostigma leucodontis nov., gen. et spec., eine neue Flechte mit fast unsichtbaren Fruchtkörpern. Plant Syst Evol. 1979;131(3-4): 211-216.
- [39] Frisch A, Thor G. Crypthonia, a new genus of byssoid Arthoniaceae (lichenised Ascomycota). Mycol Progress. 2010;9(2):281-303.
- [40]Frisch A, Thor G, Sheil D, et al. Four new Arthoniomycetes from Bwindi Impenetrable National Park, Uganda - supported by molecular data. Nova Hedw. 2014;98(3):295-312.
- [41]Frisch A, Ohmura Y, Ertz D, et al. Inoderma and related genera in Arthoniaceae with elevated white pruinose pycnidia or sporodochia. Lichenologist. 2015;47(4):233-256.
- [42] Aptroot A, Ertz D, Silva JDR, et al. The phylogenetic position of Coniarthonia and the transfer of Cryptothecia miniata to Myriostigma (Arthoniaceae, lichenized ascomycetes). Phytotaxa. 2015;218(2):128-136.
- [43] Sundin R, Frisch A, Thor G. A literature review of Arthonia s. lat. Bibl Lichenol. 2012;108:257-290.
- [44] Kondratyuk SY, Oxner AN, Khodosovtsev AY. Caloplaca In: Andreev MP, Roms EG, editors. Handbook of the lichens of Russia. Teloschistaceae. Sankt-Peterburg, Fuscideaceae, Russia: Nauka; 2004. p. 38-235.