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Aspicilia goettweigensis (Megasporaceae, lichenized Ascomycetes) – a poorly known and overlooked species in Europe and Russia

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Aspicilia goettweigensis is a poorly known species from xerothermic siliceous rocks in Europe. It is considered to be common in the Czech Republic and it is new to Hungary and Russia. The main diagnostic character is formation of cracked, popcorn-like, areoles in the central parts of the thalli. Analysis of nrITS sequences revealed its close relationship to *Aspicilia subdepressa* and *A. volcanica*. TLC revealed stictic acid in analysed *A. goettweigensis* samples. A key to non-lobate *Aspicilia* with stictic acid known from Europe is provided.

The genus *Aspicilia* s.l. belongs to Megasporaceae (Schmitt et al. 2006) and comprises approximately 200 species worldwide (Owe-Larsson et al. 2007). Despite a rising interest in this genus during the last decade (Nordin et al. 2007, 2010, Sohrabi and Ahti 2010), many uncertainties remain concerning the determination and delimitation of species. As a consequence, there are insufficiently known geographical ranges, and knowledge about ecology and conservation statuses is insufficient. Working with *Aspicilia* collections from the Czech Republic, Hungary and Russia, we realized that a number of them are similar to the type specimen of a poorly known species: *Aspicilia goettweigensis* (Zahlbr.) Hue.

Aspicilia goettweigensis was described by Zahlbruckner (1905, as *Lecanora g.*) on the basis of specimens collected by C. Rechinger and F. Ostermeyer in Austria (Fig. 1A). According to the description in the protologue, the species has a verrucose-areolate greenish-gray thallus, with initially immersed and later appressed apothecia, blackish discs without pruina, submoniliform paraphyses, 8 spores per ascus, 16–22 × 7–12 µm, and 14–18 µm long pycnoconidia. The thallus becomes yellowish after treatment with KOH. Zahlbruckner supposed that this species is related to *Circinaria (Lecanora) gibbosa* (Ach.) A. Nordin et al. Five years later, *Lecanora goettweigensis* was moved to *Aspicilia* by Hue (1910).

Aspicilia goettweigensis is reported from Austria, Czech Republic, Germany, Poland and Switzerland (Magnusson 1939, Lettau 1956, Fałtynowicz 1993, Hafellner and Türk 2001, Clerc and Truong 2012), but it remains a poorly known species and it is not included in keys of European lichens (Clauzade and Roux 1985, Wirth 1995, Wirth et al. 2013). The aim of the study was to clarify the differences between *A. goettweigensis* and other *Aspicilia* species.

Material and methods

Herbarium specimens of *Aspicilia goettweigensis* kept in UPS, S, and specimens collected by the authors in the Ural Mountains, Czech Republic, Austria and Hungary were studied (all details in the attached list of samples). Sections of apothecia were cut by hand and studied in water. The character of paraphyses was studied after treatment with 10% KOH. Spore measurements are given as (min.–) M–SE–[M]–M+ SE(–max.), rounded to the nearest 0.1 µm, where 'min.' and 'max.' are the extreme values recorded, M is the arithmetic mean and SE the corresponding error of the mean. Calculations were made from measurements of 15 specimens (altogether 120 spores and 150 conidia). Secondary lichen substances were determined in all samples using thin layer chromatography (TLC) in solvent systems A and C (Arup et al. 1993, Orange et al. 2001). Other species containing stictic acid were studied in the herbaria H-Nyl, S and UPS. The first and second author appraised types of most such species: i.e. *Aspicilia berntii* A. Nordin, Tibell & Owe-Larss. (S L-4633, lectotype designated by Nordin et al. 2008, isolectotype: UPS), *Aspicilia dudinensis* (H.Magn.) Oxner (holotype: S L-3484, isotype: UPS L-199766), *Aspicilia laevata* (Ach.) Arnold (UPS L-122426, lectotype designated by Nordin 2015), *Aspicilia proluta* (Nyl.) Hue (H-Nyl.

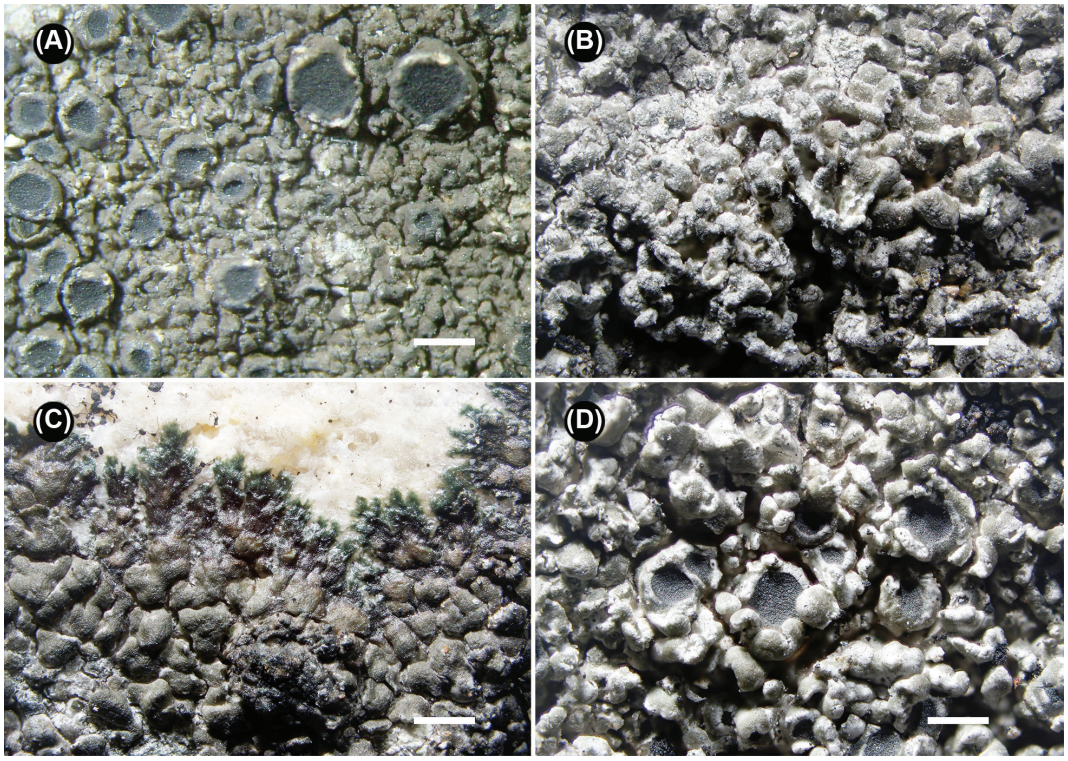

Figure 1. Type specimens of *Aspicilia goettweigensis*. (A) part of the isotype (Zahlbruckner: Krypt. Exs. 1245, UPS L-591845), (B)–(D) topotype (Vondrák 14026, PRA), (B) cracking areoles (white medulla visible), (C) margin of thallus with prothallus, (D) apothecia with granular to lobulate margins. Scale bars = 0.5 mm.

25279, lectotype designated by Motyka 1996), *Aspicilia subdepressa* (Nyl.) Arnold (holotype: H-Nyl. 25538) and *Aspicilia verrucigera* Hue (isotype: H-Nyl., Nyl. et Norrl.: Herb. Lich. Fenn. (Fasc. V). 241).

Sequencing and phylogenetic reconstructions

DNA was extracted with a CTAB-based protocol (Aras and Cansaran 2006). Primers for nrITS DNA sequence amplification were ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). The PCR parameters included an initial hold at 94°C for 5 min, and then 45 cycles with denaturating at 94°C (30 sec), annealing at 62°C with the touch-down to 56°C during the first 7 cycles (30 sec), and extension at 72°C (60 sec).

The alignment was done in the BioEdit 7.2.5 free software (Hall 1999) with the use of the ClustalW application (Thompson et al. 1997), and corrected by hand. Our nine newly generated ITS sequences (Table 1) were aligned together with sixteen sequences of Megasporaceae and outgroup sequences of *Acarospora*, *Myriospora*, *Ochrolechia* and *Polysporina*. A maximum likelihood (ML) phylogenetic analysis was run in the application Phylogeny.fr (Dereeper et al. 2008) without Gblocks, applying the GTR+I+G nucleotide substitution model and the Approximate Likelihood-Ratio Test (aLRT). The ML reconstruction is shown in Fig. 2, modified in CorelDraw, ver. X3.

Results

During revision of *Aspicilia* samples, the first author recognized a high similarity between many of our specimens

Table 1. New nrITS sequences.

Taxon/herbarium number	Altitude (m a.s.l.)	Latitude	Longitude	NCBI acc. no.
Aspicilia cinerea/JV14024/1	400	48.365833	15.609209	KX159287
Aspicilia cinerea/JV14024/2	400	48.365833	15.609209	KX159288
Aspicilia cinerea/AGP20120606-02	326	51.517300	57.575350	KX159290
Aspicilia cinerea/AGP20111016-06	571	55.752367	60.446483	KX159291
Aspicilia goettweigensis/AGP20120513-03	569	55.750383	60.450350	KX159292
Aspicilia goettweigensis/Frolov51	460	50.487250	13.990367	KX159293
Aspicilia goettweigensis/JV14026	400	48.365833	15.609209	KX159289
Aspicilia blastidiata/AGP20120801-01	175	57.356583	61.373400	KX159286
Aspicilia blastidiata/AGP20111009-01	267	56.930400	60.909050	KX129963

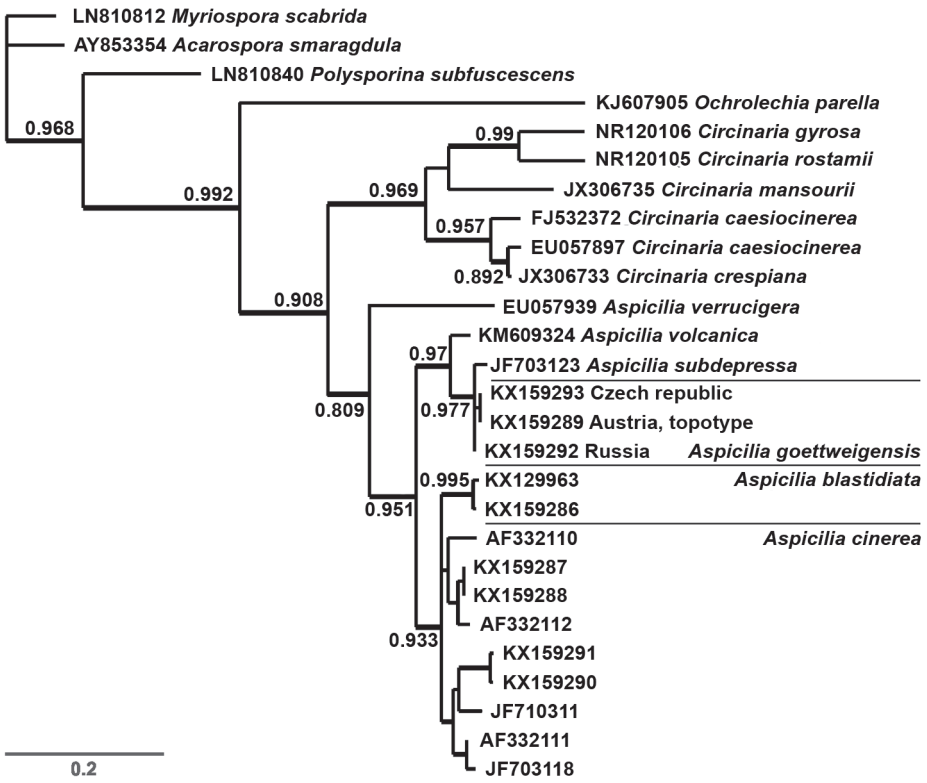

Figure 2. Maximum likelihood reconstruction of the nrITS phylogeny of a part of Megasporaceae including sequences of *Aspicilia goettweigensis* and its related taxa. Supported nodes (aLRT > 0.75) indicated by thicker branch line.

from Czech Republic, Hungary and Russia and the isotypes of *Aspicilia goettweigensis* (Zahlbr.: Krypt. Exs. 1245 seen in UPS and S), as well as with a specimen collected in Baden-Württemberg by J. Flotow that was determined by A. Magnusson as *Lecanora goettweigensis* (UPS L-199810). Our specimens agree well with the description in the protologue (Zahlbruckner 1905, p. 346) and in Magnusson (1939). To increase credibility of this result, the last author collected a rich material of *Aspicilia* from the type locality (see list of specimens). *Aspicilia goettweigensis* was a predominant species in the locality together with *A. cinerea* (L.) Körb.; both species were sequenced from there.

Maximum likelihood reconstruction of nrITS sequences (Fig. 2) revealed that our three sequences of *Aspicilia goettweigensis* (including a sequence of a topotype, Table 1) form a supported clade together with the sequence JF703123 called *A. subdepressa* (aLRT = 0.977). The four sequences are almost identical (in > 99% of nucleotide positions), but JF703123 has a unique deletion of 20 nucleotides in the ITS1 region. This sequence has also four unique substitutions in conservative positions of ITS1 and the 5.8S regions, but they are probably artifactual, caused by incorrect sequence editing. Another closest sister sequence belongs to the type of *A. volcanica* (Ismayil et al. 2015), but it differs from the *A. goettweigensis* clade in 12 nucleotide positions. Other close taxa are *A. cinerea* and the recently described *A. blastidiata* (Paukov et al. 2015), but they are clearly distinct from *A. goettweigensis*.

On the basis of the specimens from different localities, we provide a detailed description of *Aspicilia goettweigensis*:

Aspicilia goettweigensis (Zahlbr.) Hue (1910, p. 112)

MycoBank MB 377609. Basionym: *Lecanora göttweigensis* Zahlbr. (1905, p. 346).

Type: "Austria. Göttweig, ad saxa arenaria aprica, 550 m a.s.l., leg. C. Rechinger and F. Ostermeyer". UPS accession no. L-591845! and S accession no. L-4801!, isotypes distributed as exsiccatae (Zahlbr.: Krypt. Exs. 1245).

Description

Thallus olive-brownish to light-grey, sometimes white-pruinose, up to 1.5 mm thick, areolate, squamulose-areolate, to verrucose-areolate. Lobes absent but elongated marginal areoles may be formed (Fig. 3A). Areoles convex, up to 1.5 mm, soon becoming verruciform (Fig. 3B). Older areoles bullate and often becoming hollow and cracking into popcorn-like tufts (Fig. 1B, 3C) or into upright squamules with exposed white medulla (Fig. 3D). Younger parts of thalli thin, areolate, often producing squamules (Fig. 3E). Cortex paraplectenchymatous, 15–30 µm thick. Medulla white. Prothallus indistinct or distinct, grey, blackish or olive-blackish (Fig. 1C, 3E), sometimes with whitish and fimbriate margin. Apothecia very soon becoming sessile, round to irregular, 0.5–1.5 mm in diameter, 1 per areole. Thalline margin olive-grey to grey, well-developed, at times with lobulate outgrowths (Fig. 1D, 3F). Disc black to brownish-black, smooth or rough, flat to slightly convex, sometimes partly white-pruinose. Proper exciple slightly visible as a thin rim around discs, 22–32 µm wide in upper part, narrowing

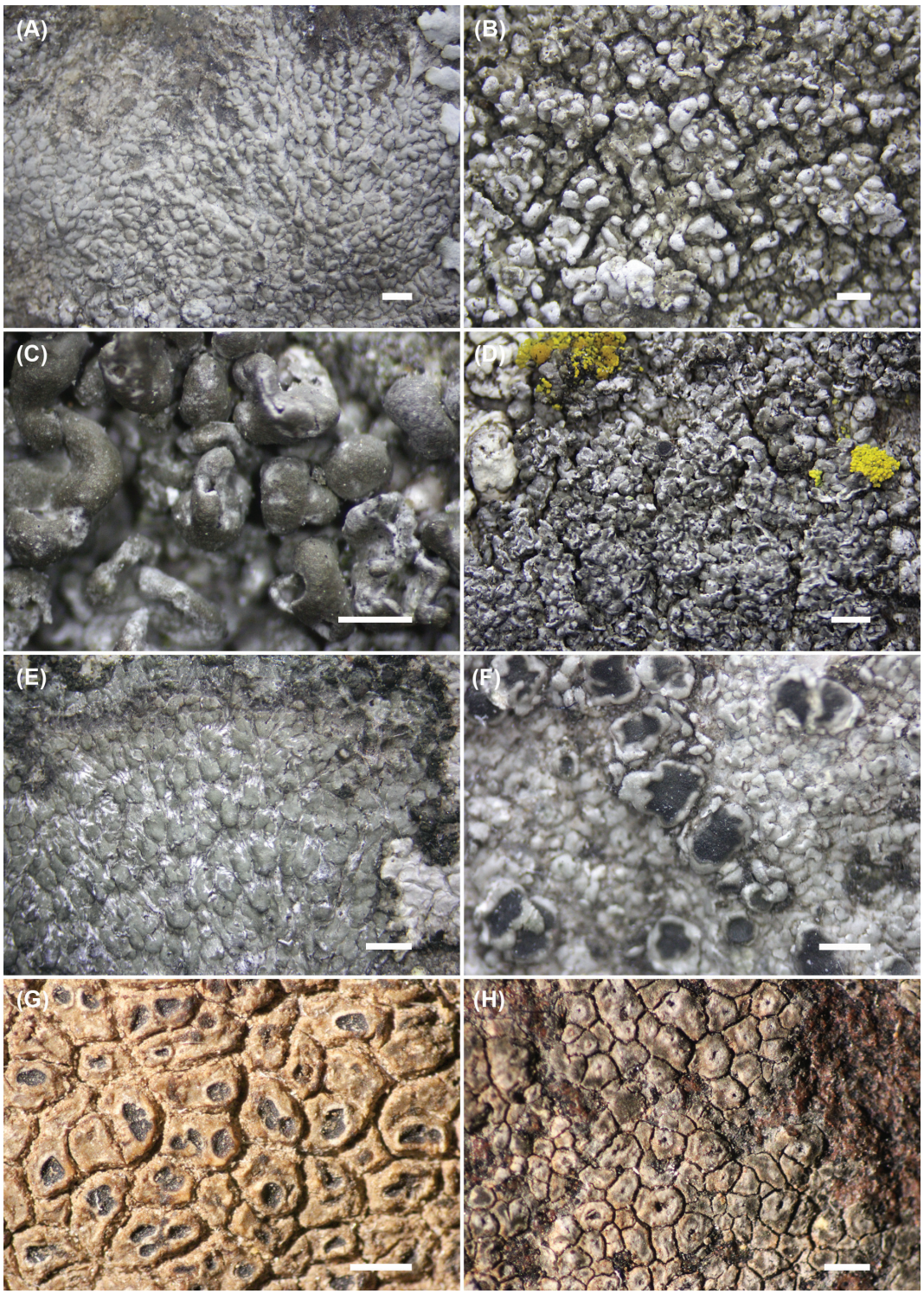

Figure 3. (A)–(F) *Aspicilia goettweigensis*. (A) diffuse thallus margin with some areoles peeled off (Paukov, AGP 20120513-03, UPS, UFU), (B) verrucose thallus (central part) (Vondrák 642, PRA), (C) hollow 'squamules', white medulla seen (Frolov 1279, herb. I. Frolov), (D) squamulose thallus after erosion of verrucae (Frolov 51, herb. I. Frolov, dupl. UPS, UFU), (E) outer part of thallus with prothallus (Paukov 2301, UPS, UFU), (F) apothecia with marginal granules/squamules (Paukov, AGP20130813-01, UFU), (G) *A. subdepressa*, holotype (Nylander, H-Nyl 25538), (H) *A. proluta*, lectotype (Nylander, H-Nyl 25279). Scale bars = 1 mm.

below; cells in upper part elongated, 5–7 µm long, thick-walled, slightly bluish in iodine. Epihymenium greenish-brown, N+ green, K+ brownish. Hymenium hyaline, 75–105 µm tall. Paraphyses submoniliform to moniliform, with 3–5 ± globose apical cells. Asci clavate, ca 60–75 × 12–25 µm; wall and apical dome KJ–. Ascospores hyaline, broadly ellipsoid, (14.5) 17.9–[18.1]–18.3 (21) µm × (9) 10.9–[11.1]–11.3 (14.5) µm (n = 120). Hypothecium

~30–60 µm thick. Conidia filiform, (8.0) 13.9–[14.2]–14.4 (20.0) × 1 µm (n = 150).

Chemistry

Stictic acid (main), norstictic and connorstictic acids (traces or absent) detected.

Distribution and ecology

Aspicilia goettweigensis is widespread in western and middle continental Europe (France, Switzerland, Germany, Austria, Hungary, Czech Republic), and in the southern and middle Urals (Russia). It grows on basic and ultramafic silicate rocks in sun-lit, summer-warm habitats; most findings were made on basalt, serpentinite and sienite. *Aspicilia goettweigensis* is often a predominant species (e.g. in the type locality) in suitable habitats, usual with co-dominants such as *Aspicilia cinerea*, *Bellemerea cupreoatra* (Nyl.) Clauz. et Roux, *Candelariella vitellina* (Ehrh.) Müll. Arg., *Dimelaena oreina* (Ach.) Norman, *Xanthoparmelia pulla* (Ach.) O.Blanco et al., *X. conspersa* (Ach.) Hale, *X. stenophylla* (Ach.) Ahti & D.Hawksw.

Additional specimens examined (paratypes)

Austria. Lower Austria, Krems an der Donau, Stift Göttweig, S-exposed, lit, gneiss outcrops in open oak forest, alt. 400 m, 48.365833N, 15.609209E. 29.11.2015. J. Vondrák 14026 (PRA, topotype). Czech Republic. Central Bohemia, Beroun, Hudlice, sunny rocks in the valley of Libotický potok brook, 300 m ESE of the protected area "Stará ves", alt. 295 m, 49.961550N, 13.987500E, on lime-rich S-exposed rocks, 22.04.2005. J. Vondrak 2897 (PRA); Beroun, Králův Dvůr, Trubín, S-oriented rocks in protected area "Trubínský vrch", alt. 330–350 m, 49.9400N, 13.9900E, on exposed basaltic rock, 25.7.2004, J. Vondrák 2393 (PRA); Beroun, Zdice, S-facing rock on W edge of town, alt. 300 m, 49.906200N, 13.963800E, on sunny basalt rocks, 11.09.2003. J. Vondrak 1354 (PRA); Hořovice, Točník, ruin of castle Točník, 1 km NE of the village, alt. 430 m, 49.889700N, 13.886500E, S-oriented hornfels rock beneath castle, 10.5.2003, J. Vondrák 1121 (PRA); Nový Knín, Chotilsko, 3 km SES of village, protected area Vymyšlenská pěšina, alt. ca 300 m, 49.746329, 14.364733, S-exposed rocky slopes above river Vltava. 01.04.2012. I. Frolov 1279 (herb. I. Frolov); Rakovník, Křivoklát, Městečko, the rock in the valley Rakovnický potok brook, 1 km NW from the town, 50.0533N, on sunny basaltic rock, 26.01.2002. J. Vondrák 1391 (PRA); Rakovnik, Skřiváň, the rock "Valachov", 1 km SE from the village, in the valley of Tyterský potok brook, SW exp., 50.016667N, 13.771667E, on enriched basaltic (spilit) rock. 16.09.2002. J. Vondrák 642 (PRA); Sedlčany, Kamýk nad Vltavou, Velká, rocks on left side of river Vltava, N of the village, alt. 278 m, 49.667033N, 14.250967E, on E-exposed, base-rich granite rock, 14.05.2002, J. Vondrák 2964 (PRA). Northern Bohemia, Libochovice, Klapý, in slope of hill Hazmburg, on sunny basalt outcrop, 22.08.2009, J. Vondrák 7159 (PRA); Lovosice, Třebenice, rocks on S. slope of ruin Košťálov, 50.489522N, 13.984900E, alt. 460 m. 10.05.2012. I. Frolov 51 (UPS, UFU, herb. I. Frolov), 319, 1280-81, 1287 (herb. I. Frolov). South Moravia, Moravský Krumlov, rocky steppe on a slope above Rokytná river, 49.052500N, 16.318533E, on lime-rich conglomerates, 14.5.2004, J. Vondrák 2586 (PRA). Germany. Baden-Württemberg, Festungsberg bei Hirschberg. 26.06.1850. Leg. J. Flotow. Det. A. Magnusson, 05.09.1937. (UPS L-199810). Hungary. Heves county, Bükk mountains, Bükk National park, Szarvaskő: Szarvaskői vár, alt. 300 m, 47.987833N, 20.324350E, on base-rich volcanic outcrop, 04.06.2008. J. Vondrák 6354 (PRA). Russia. Sverdlovsk region, Sysert district, Tokarevo village, rocky outcrops on river Sysert, on basalt, 27.06.1997. A. Paukov, AGP19970627-05 (UFU); Rezhevskoy district, vicinity of Chepchugovo village, rocky outcrops on Rezh river, on basalt, 08.08.1998. A. Paukov, AGP19980808-01 (UFU); Kamensk district, vicinity of Kluchi village, rocky outcrops on river Iset, on basalt, 21.05.1999. A. Paukov, AGP19990521-25 (UFU); Sysert district, 2 km to SW from Dvurechensk, 56.595400N, 61.063017E, serpentine outcrops on river Sysert, on serpentine, 21.07.2000. A. Paukov, AGP20000721-04 (UFU); Nizhniy Tagil town, Golyi Kamen mountain, rocky outcrops, on rock, 19.08.2001. A. Paukov, AGP20010819-04 (UFU); Sysert district, Beklenisheva village, basalt outcrops on river Iset, on basalt, 26.07.2008. A. Paukov, AGP20080726-04 (UFU); Rezh town, Bystrinskiy, rocks on right riverbank of Rezh river, 57.356583N, 61.373400E, alt. 175 m, serpentine outcrops, on serpentine, 01.08.2012. A. Paukov, AGP20120801-13 (UFU); vicinity of Polevskoy town, Azov mountain, 56.473900N, 60.086400E, rocky outcrops under forest canopy, on basalt, 10.09.2011. A. Paukov 2301 (UFU); Beryozovskiy district, Staropyshminsk village, 56.934200N, 60.910300E, alt. 267 m., serpentine outcrops on Pyshma river, on serpentine, 09.10.2011. A. Paukov, AGP20111009-17 (UFU). Chelyabinsk region, Kaslinskiy district, vicinity of Usmanova village, outcrops on Bagaryak river, on basalt, 14.07.2000. A. Paukov, AGP20000714-01 (UFU); Kyshtym district, vicinity of Kyshtym town, Egoza mountain, 55.750383N, 60.450350E, alt. 569 m, serpentine outcrops, on serpentine, 13.05.2012. A. Paukov, AGP20120513-03 (UPS, UFU); Vicinity of Miass town, Ilmenskiy state reserve, 1.6 km to NW from Miasovo biological station, on a bank of Tatkul' lake, 55.189783N, 60.275700E, alt. 312 m, sienite outcrops under pine forest canopy, on rock, 13.08.2013. A. Paukov, AGP20130813-01 (UFU). Bashkortostan, Burzyan district, vicinity of Sargaya village, bazalt outcrops in forest, on basalt, 17.08.2003. I. Frolov, s.n. (UFU); Uchalinskiy district, Mindyak village, 54.021500N, 58.767400E, alt. 726 m, top of a serpentine mountain, steppe communities, on serpentine, 25.05.2010. A. Paukov, AGP20100525-38 (UFU); Beloretskiy district, Shigayevo village, Kraka ridge, 53.807283N, 58.173400E, alt. 765 m, serpentine outcrops, on serpentine, 27.05.2010. A. Paukov, AGP20100527-52 (UFU); Uchalinskiy district, 4 km to SW from Karaguzhino village, Akbura mountain, 53.984433N, 58.739417E, alt. 558 m, serpentine outcrops, on serpentine, 09.06.2012. A. Paukov, AGP20120609-26 (UFU).

Discussion

As here described, *Aspicilia goettweigensis* is a well-delimited species that despite variable thalli is easily distinguished from

other similar species. The areoles that very soon become verruciform in the central part of thalli are characteristic. Older areoles often become hollow and cracking into popcorn-like tufts or into upright squamules with exposed white medulla. These tufts and squamules are better developed in specimens from well lit and dry places. Specimens from shaded sites may lack this character which makes them hardly recognizable from other *Aspicilia* species, but a combination of characters such as the presence of stictic acid, sessile apothecia, length of spores, conidia not exceeding 20 µm, and convex to squamuliform areoles makes it possible to identify such specimens as well.

Aspicilia goettweigensis may be confused with truly sorediate, blastidiate or isidiate species. *Circinaria leprosescens* (Sandst.) A. Nordin et al. contains aspicilin, has bigger spores and a different distribution. *Sagedia simoënsis* (Räsänen) A. Nordin et al. contains norstictic acid, has shorter conidia and usually true soredia or isidia. *Sagedia mastrucata* (Wahlenb.) A. Nordin et al., with convex to papillose areoles and with cylindric outgrowths on thalline margin, contains norstictic acid and lacks the popcorn-like tufts and brittle squamules. *Aspicilia blastidiata* contains norstictic acid, has blastidiate upper surface and shorter conidia. *Circinaria gibbosa*, which was regarded as a relative of *A. goettweigensis* by Zahlbruckner (1905), contains aspicilin and norstictic acid, has taller hymenium, bigger spores and shorter conidia.

European *Aspicilia subdepressa* (Nyl.) Arnold (Fig. 3G, holotype) and central Asian *A. volcanica* are the most close relatives of *A. goettweigensis* according to available nrITS sequence data (Fig. 2). However, neither of these taxa do produce popcorn-like tufts and brittle squamules (Roux et al. 2011, Ismayil et al. 2015). *Aspicilia proluta* (Nyl.) Hue is perhaps another related taxon, but it may also be a synonym to *Aspicilia subdepressa*. Its similarity to *A. subdepressa* was mentioned by G. Clauzade and C. Roux in a notice to the lectotype of *Aspicilia proluta* in H-Nyl 25279 (Clauzade and Roux unpubl.). Roux et al. (2011), however, concluded that they are different species on the basis of differences in thalline colour, form of apothecia and ecology. We consider these taxa conspecific because of their morphological and chemical similarity as well as the same sizes of spores and conidia. Rusty colour of *Aspicilia subdepressa* is likely caused by iron from the substrate, while more crater-form apothecia reported in *Aspicilia proluta* are likely due to their younger age, but additional genetic research is nevertheless needed to resolve this question.

Key to the stictic acid-containing non-lobate species of *Aspicilia* in Europe

The characters in the following key are based on our observations and measurements, and on Nordin et al. (2008):

1. Mature apothecia sessile, clearly constricted at the base to substipitate; thalline margin well-developed …… 2
   – Mature apothecia immersed, slightly projecting to sessile but widely attached with thalline or dark proper margin …… 4
2. Thallus thin, areolate, light to dark-grey; areoles angular, predominantly flat; spores 12.5–20.3 × 7–12.5 µm; conidia 18–25 µm; northern (Sweden, Asian Russia) and alpine (northern Urals, Altai) …… …… *A. dudinensis* (Fig. 2C in Nordin et al. 2008)
   – Thallus thicker, with convex to bullate areoles or squamules; spores or conidia different …… 3
3. Thallus dark-grey, brownish to almost black; areoles convex to substipitate, not cracking to show the medulla; apothecial discs and margin without pruina; apothecial margin without lobules; spores 18–28 × 10–16 µm, conidia 15–22.6 µm long; northern (Greenland and Norway) …… *A. berntii* (Fig. 2A in Nordin et al. 2008)
   – Thallus light-grey to dark gray-olive; younger areoles convex, some squamulose, later strongly convex, becoming hollow, cracking to show white medulla (in well-developed specimens); apothecia occasionally with pruina; apothecial margin often small-lobulate; spores 16–20 × 7–12 µm; conidia (8–) 10–17 (–20) µm long; Europe (not arctic), southern and middle Urals …… *A. goettweigensis*
4. Conidia (7–) 8.7–[9]–9.2 (–12) µm long; spores 18–24 µm long, on average > 20 µm; areoles flat to slightly concave, grayish to gray-olive, rusty of iron from the substrate; younger apothecia crater-like, later with widened disc; externally resembling *Circinaria caesiocinerea*; France, Portugal …… *A. subdepressa* (Fig. 3G)/*A. proluta* (Fig. 3H)
   – Conidia 11–25 µm long; spores 12–22 µm long, on average < 20 µm …… 5
5. Mature apothecia sessile, widely attached; thallus areolate, thin, light to dark-grey; areoles angular, predominantly flat; spores 12.5–20.3 × 7–12.5 µm; conidia 18–25 µm long …… *A. dudinensis* (see couplet 2 above)
   – Apothecia immersed to slightly projecting …… 6
6. In moist or shady habitats; thallus dark, olive-gray to blackish-gray, thin, rimose-areolate, with flat areoles; apothecia with dark margin, immersed, initially crater-like, later with wider disc; spores 13–17 (–22) × 9–13 µm; conidia (14) 17–25 µm long; paraphyses branching, submoniliform; mountains of Europe, Caucasus, Urals, Altai, Far East …… *A. laevata*
   – In drier habitats; thallus light-gray to brownish-gray, usually thick, areolate, areoles convex to verrucose, apothecia not crater-like, with smooth or verrucose thalloid margin, sometimes with dark proper margin, disc often pruinose; spores 15–21.5 × 8–13.5 µm; conidia 11–17 (19) µm; paraphyses simple, moniliform; mountains of Europe, Urals, Altai, Far East …… …… *A. verrucigera* (Fig. 2B in Nordin et al. 2008).

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