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Lectotypification of the threatened endemic Appalachian lichen Alectoria fallacina

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Abstract Alectoria fallacina, described by the prolific 20th century lichenologist Josef Motyka, is a threatened species narrowly endemic to the Appalachian Mountains of eastern North America. The production of a unique unidentified fatty acid as the main secondary metabolite chemically separates A. fallacina from its congeners, especially the morphologically similar A. sarmentosa. Here we show that while A. fallacina and A. sarmentosa are entirely allopatric, the type collection of A. fallacina is a mixture of the two taxa and the holotype is A. sarmentosa. Detailed analyses of the original material support the conclusion that the lichen in the holotype packet was taken from another collection, and is in direct conflict with both the protologue and the current application of the name. We assert that the lichen currently assumed to be the holotype of A. fallacina was erroneously placed in the holotype packet by Motyka after the description, while the actual holotype lichen was likely retained in his personal herbarium now deposited at LBL. This highly unusual scenario is supported by other cases from the literature pertaining to the types of names published by this author. Based on the fact that the currently accepted holotype of A. fallacina directly conflicts with the protologue, that all evidence suggests it could not have been derived from the type locality, and the known working methods of both the collector of the type (Gunnar Degelius) as well as the describing author (Motyka), the holotype of A. fallacina is treated as effectively lost and the name is lectotypified with an isotype that unambiguously represents A. fallacina.

Keywords biodiversity hotspot; conservation; fruticose; fungi; Parmeliaceae

INTRODUCTION

Pendant fruticose lichens are ecologically important and abundant members of many ecosystems (Bohuslavová & al., 2012; Färber & al., 2014; Nystuen & al., 2019; Phinney & al., 2021). Species of Parmeliaceae belonging to the genera *Alectoria* Ach., *Bryoria* Brodo & Hawksw. and *Usnea* Adans. are particularly common and widespread in temperate, boreal and arctic habitats of the Northern Hemisphere (Brodo & Hawksworth, 1977; Arseneau, & al., 1998). These lichens form large, conspicuous colonies (Jaakkola & al., 2006), are used by humans (Brodo & Hawksworth, 1977; Turner & al., 1990; Wang, 2004; Crawford, 2015) and serve as forage or nesting materials for many animals including woodland caribou (*Rangifer tarandus caribou* Gmelin) (Ward & Marcum, 2005; Stevenson & Coxson, 2007). Considering the abundance and conspicuous appearance of fruticose Parmeliaceae, it is not surprising they have a long, complex history of taxonomic study (Mark & al., 2016) that is complicated by divergent treatments of phenotypic plasticity (Boluda & al., 2019; Gerlach & al., 2020) and extensive use of infraspecific taxa (Hawksworth, 1972).

Josef Motyka (b. 1900-d. 1984) was a Polish lichenologist who published prolifically on fruticose Parmeliaceae

(Wójciak & Bystrek, 2016). This included taxa now placed in *Alectoria* Ach., a relatively small genus of species that are abundant and common in Northern Hemisphere boreal and montane systems (Brodo & Hawksworth, 1977). *Alectoria fallacina* Motyka is narrowly endemic to high-elevation spruce-fir forests in the Appalachian Mountains of eastern North America and is of conservation concern (e.g., McMullin & al., 2016; Lendemer & al., 2017; Tripp & Lendemer, 2019). The species has been recognized as distinct from the much more common and widespread *A. sarmentosa* (Ach.) Ach. for nearly a century. There has, however, been long-standing uncertainty as to exactly which phenotypic characters delimit *A. fallacina* (Brodo & Hawksworth, 1977).

Recently, we discovered that this uncertainty stems from the fact that the type gathering is a mixture of *Alectoria fallacina* and *A. sarmentosa*, and the holotype is entirely *A. sarmentosa*. Here we demonstrate that not only is the holotype in direct conflict with the protologue, but it is exceedingly unlikely the holotype could have been part of the type gathering as there is no evidence for the occurrence of *A. sarmentosa* within nearly one thousand miles of the type locality of *A. fallacina*. Instead, it appears that the specimen originally placed in the holotype packet by its collector and used by Motyka to prepare the description, was replaced with a different non-type specimen from an unrelated gathering. This likely was done by Motyka at some point after preparing the description and before being returned to the lending institution. As such, we assert that even though the original packet for the holotype is extant, the holotype that it once contained is now effectively lost and a lectotype must be designated. Typification of the name for this threatened lichen is more complex and unusual than a routine case resolved by synonymy. Resolution of this issue through lectotypification not only preserves the application name of this endemic species, but also provides a case study in addressing issues in typification for the multitude of names published by Josef Motyka in the Parmeliaceae.

MATERIALS AND METHODS

This study is based on specimens of *Alectoria fallacina* and *A. sarmentosa* deposited in CANL and NY, together with extensive fieldwork carried by both others in northeastern North America (McMullin) and the Appalachian Mountains (Lendemer). The first author also visited the type locality of *A. fallacina* repeatedly during the last decade (2012, 2016, 2018, 2019). Type material of *A. fallacina* was borrowed on loan from LBL, UPS and US. Dry herbarium specimens were studied with an Olympus SZ-STB dissecting microscope. Chemistry was studied using standard tests (K, C, KC, P, UV) following Brodo & al. (2001) and with thin-layer chromatography (TLC) using solvents A, B', and C following Orange & al. (2001).

RESULTS AND DISCUSSION

Alectoria fallacina: an evolving delimitation. — Motyka (1960) described Alectoria fallacina and typified the name based on a specimen in US collected in Great Smoky Mountains National Park, Tennessee, U.S.A. by lichenologist Gunnar Degelius on 13 September 1939. No collection number was cited in the protologue because the gathering was unnumbered as was practice for Degelius (e.g., Lendemer & Harris, 2014). The protologue (Motyka, 1960: 447–448) reported the spot test reactions of the lichen to be "K et Pd non coloratur" (i.e., negative with the spot test reagents potassium hydroxide and para-phenylenediamine; Brodo & al., 2001). Motyka (1960) considered A. fallacina to be highly morphologically distinctive and most similar to A. sarmentosa ("Species valde insignis, similis primo aspectu A. sarmentosae deminutae"), differing in its size, habit and minute pseudocyphellae ("Diversa ab ea thallo tenuiore, modo crescendi, pseudocyphellis totaliter diversis, minutis"). He also compared the species to A. lata (Tayl.) Linds. and A. pellucida Mot. ("Proxima est A. laeta (Tayl.) Linds., quae est valde distincte tuberculata, pseudocyphellis elevatis, cicatricosis provisa, et A. pellucida Mot."). While A. lata and A. sarmentosa are currently recognized as distinct taxa, the taxonomic status of A. pellucida remains unclear although it appears to be a species of Bryoria (Brodo & Hawksworth, 1977). In addition to the type collection, Motyka (1960) cited a second unnumbered gathering from New Brunswick, Canada made by Henry Willey in 1879, but did not indicate the herbarium in which it was deposited.

The first author to treat *Alectoria fallacina* after its description was Hawksworth (1972), who included it in the synonymy of *A. sarmentosa* subsp. *sarmentosa* without explanation. Brodo & Hawksworth (1977) then tentatively

recognized A. fallacina as distinct from A. sarmentosa based on similar morphological grounds to those of Motyka (1960). The species was considered endemic to the Appalachian Mountains of eastern North America, a well-known lichen biodiversity hotspot with high-elevation endemic species (Allen & Lendemer, 2016). Brodo & Hawksworth (1977) noted that specimens with this distinctive morphology were deficient in alectoronic acid, a substance typically produced in A. sarmentosa. They also noted some specimens referred to A. fallacina, including the holotype, produced alectoronic acid and differed morphologically in having a yellower coloration and thinner cortex. The latter characters are suggestive of A. sarmentosa, a logical identity given the correlation with the production of alectoronic acid. In subsequent decades, A. fallacina has continued to be accepted as a distinct species endemic to the Appalachian Mountains (e.g., Dey, 1976, 1978; Lendemer & al., 2017; Tripp & Lendemer, 2019). It has even been used in studies of genomic streamlining in lichen symbioses (Pogoda & al., 2019; Tagirdzhanova & al., 2021).

In a molecular phylogenetic study of North American *Alectoria*, McMullin & al. (2016) recovered *A. fallacina* as a strongly supported clade that was distinct from *A. sarmentosa* and its relatives. In that study, material that produced alectoronic acid, but which had been initially assigned to *A. fallacina* based on morphology, was resolved within *A. sarmentosa* rather than *A. fallacina*. This led us to question the taxonomic identity of material assigned to *A. fallacina* that was reported to have alectoronic acid, including the holotype. We revised all the sequenced samples used by McMullin & al. (2016) and found those that were recovered within *A. fallacina* were chemically distinctive in the production of an unidentified fatty acid as an accessory to usnic acid (Fig. 1). The same chemical profile was found in nearly all the Appalachian specimens we examined from New York State southward, including the area around the type locality (Appendix 1). The only specimens from that region that produced alectoronic acid were the holotype and part of an isotype. All the vouchers north of New York State that had been identified as *A. fallacina* produced alectoronic acid and were poorly developed individuals of *A. sarmentosa*, as had been the case with the one alectoronic-acid-producing specimen identified as *A. fallacina* sequenced by McMullin & al. (2016).

Alectoria fallacina and A. sarmentosa are allopatric. — Alectoria sarmentosa is widely distributed in coastal and montane areas of northeastern and western North America (Brodo & Hawksworth, 1977). The species typically produces alectoronic acid and can be recognized by the combination of the pendant thallus, thin cortex and chemistry (Brodo & Hawksworth, 1977). In treating A. sarmentosa, Brodo & Hawksworth (1977) reported an alectoronic-acid-deficient variant that was widespread in northern North America, although all the occurrences of the variant were from outside the range reported for A. fallacina. We examined a selection of specimens cited by those authors as belonging to the deficient variant, and while they had variable chemistries (Appendix 2), none produced the characteristic fatty acid that was detected in A. fallacina. Thus, records of the alectoronic-acid-deficient variant of A. sarmentosa do not appear to be A. fallacina. Based on the specimens we examined, A. fallacina is the only member of the genus that occurs in the Appalachian Mountains of eastern North America from New York State southward (Fig. 2). Prior reports of A. sarmentosa from the region (e.g., Degelius, 1941) instead belong to A. fallacina as has been suggested by McMullin & al. (2016).

Identity of the original material. — The protologue of *Alectoria fallacina* cited two gatherings and only indicated the herbarium in which the holotype had been deposited (US). We located four specimens whose label data suggest they belong to the type gathering. There are two specimens at US, one at LBL where Motyka's herbarium is deposited, and one at UPS where Degelius's herbarium is deposited. The specimen at UPS includes a label in Degelius's standard style, was examined by Motyka in 1964 and was annotated as an isotype of A. fallacina by Irwin Brodo. The specimen at LBL does not include Degelius's label but has a hand-typed label recognizing it as a "syntype", and the lichen itself is mounted on a card recognizing it as a "syntype" and indicating it was determined by Motyka in 1958. Interestingly, the information is handwritten on the card but does not appear to be in Motyka's hand. One of the specimens at US (barcode 00406193) lacks Degelius's label and instead has a typewritten label that indicates it was a duplicate distributed from US that was deposited in MO. Evidently the specimen came to be deposited again at US when MO divested its lichen collection to that institution. The specimen does not bare any indication that it was examined by Motyka and was annotated as an isotype by Brodo in 1973. The holotype (US barcode 00067726) is associated with Degelius's label, and was annotated by Motyka as "Alectoria fallacina Mot. TYPUS SPECIEI" in 1958 and subsequently annotated by David Hawksworth in 1968 as well as by Jonathan Dey in "1973–1974", neither of whom explicitly indicated it was the holotype on their annotations. It is important to note that the holotype (US barcode 00067726) and specimen in LBL were both examined and determined by Motyka in the same year (1958).

Examination of the specimens revealed the material clearly consists of a mixture of two taxa, one with alectoronic acid

corresponding to *Alectoria sarmentosa* and one with an unidentified fatty acid corresponding to *A. fallacina*. The holotype (US barcode 00067726) consists of one thallus with alectoronic acid, which taxonomically belongs to *A. sarmentosa*. Indeed, this was already pointed out by Hawksworth (1972) and Brodo & Hawksworth (1977). The morphology of this specimen is in direct conflict with the protologue of *A. fallacina* in that it has a thin cortex, branches of even thickness, and longer fusiform pseudocyphellae typical of *A. sarmentosa* (Fig. 3A). Meanwhile, the isotype in US consists entirely of material with an unidentified fatty acid that matches all the Appalachian material of *A. fallacina*. It has the thickneed cortex, branches of uneven thickness and shorter punctiform pseudocyphellae typical of *A. fallacina* (Fig. 3B). Like the latter specimen, the specimen in LBL consists of a large thallus with an unidentified fatty acid and matches all the Appalachian material of *A. fallacina*. Interestingly, the specimen at UPS is a mixture and consists of two separate (i.e., not entangled) thalli: one with alectoronic acid and morphology belonging to *A. fallacina*.

Why is the type collection mixed? — The holotype and part of the UPS isotype are the only two specimens of *Alectoria* marked as having been collected within the known range of *A. fallacina* that produce alectoronic acid and are morphologically congruent with *A. sarmentosa*. The anomalous nature of this material, particularly the holotype, has been a source of confusion for decades. Yet it was only the molecular studies of McMullin & al. (2016) that prompted a revision of all *Alectoria* from the Appalachian Mountains and led us to recognize just how strongly aberrant the holotype was.

Previous authors (e.g., Brodo & Hawksworth, 1977) have recognized that the type collection is a mixture of material with and without alectoronic acid but appear to have extrapolated this reflected chemical variation within *Alectoria fallacina*. Our data show that this is not the case, and that instead the type collection is a mixture of *A. fallacina* and *A. sarmentosa*. For some time, we have been perplexed by how to account for the fact that the holotype of *A. fallacina* consists entirely of *A. sarmentosa*, a species otherwise unknown from within nearly one thousand miles of the type locality. There are three plausible explanations.

First, it is possible that *Alectoria fallacina* and *A. sarmentosa* occurred historically at the type locality and both were collected by Degelius, but only the latter was subsequently extirpated during a period of extreme air pollution and habitat changes stemming from the invasive Balsam woolly adelgid (see Allen & Lendemer, 2016; Lendemer & al., 2017). This scenario is extremely unlikely for several reasons, particularly the lack of any historical collections of *A. sarmentosa* from near the type locality or in the Appalachians at all. Also given that both species are fruticose macrolichens with comparable gross morphologies, air pollution and habitat changes would likely have affected the two species similarly rather than only one.

Second, it is possible that Degelius himself inadvertently created an admixture when curating the collections from his 1939 expedition to the United States. During this trip, Degelius collected intensively in two geographically disparate regions: the southern Appalachian Mountains where *Alectoria fallacina* occurs (Degelius, 1941), and coastal Maine in northeastern North America where *A. sarmentosa* occurs (Degelius, 1940). This scenario could explain why the specimen at UPS, in addition to the holotype at US, contains *A. sarmentosa*. However, there are no other documented cases of Degelius creating admixed collections, and the material would have been collected at different times, presumably processed in batches with other specimens from the same geographic region. This scenario also seems unlikely.

The third scenario is that only *Alectoria fallacina* was present at the type locality and collected by Degelius, and that the type gathering came to be admixed later. We believe this is the most likely explanation that accounts for (1) the fact that the holotype of *A. fallacina* at US consists entirely of *A. sarmentosa* and conflicts morphologically with Motyka's protologue, and (2) the isotype in LBL consists entirely of *A. fallacina* and is morphologically congruent with the protologue. Although on the surface this may seem implausible, comparable issues have been documented in typification of other names published by Motyka. For example, there are *Usnea* names where the type is presently missing from the herbarium it was indicated to have been deposited in while a previously uncited duplicate is present in LBL (e.g., *U. moreliana* Motyka fide Truong & Clerc, 2016). Or where the type was stated to have been deposited in one herbarium and then instead retained at LBL (e.g., *U. flaveola* Motyka fide Truong & Clerc, 2013).

The type of *Alectoria fallacina* likely reflects a similar situation, although we cannot explain how or why a thallus of *A. sarmentosa* was then placed in the packet at US. This scenario is also supported by the fact that the duplicate split from the holotype at US, and distributed to MO before Motyka examined the holotype, consists entirely of *A. fallacina*. The admixture of *A. fallacina* and *A. sarmentosa* at UPS is harder to explain, but Motyka did also examine this material. Given the morphological similarity between *A. fallacina* and *A. sarmentosa*, it is possible that either Motyka or a later worker

inadvertently returned a thallus of *A. sarmentosa* to the wrong packet after examination. Issues such as this will be easier to evaluate in the future as collections are imaged as part of digitization efforts.

Resolving typification of Alectoria fallacina. — The name Alectoria fallacina has consistently been applied to an Appalachian endemic species for nearly a century. Recent molecular studies, followed by subsequent morphological and chemical studies, have upheld this delimitation once a small number of questionable occurrences from the northern portion of the range were examined and found to represent depauperate A. sarmentosa. Further, A. fallacina belongs to a cohort of threatened and endangered lichens restricted to high-elevation habitats in the Appalachian Mountains (Allen & Lendemer, 2016; Tripp & Lendemer, 2019). Recognition that the holotype represents A. sarmentosa and is not conspecific with A. fallacina as presently delimited complicates the application of the name to a phenotypically and evolutionarily distinct taxon that is also of conservation concern.

The currently accepted holotype of *Alectoria fallacina* is in direct conflict with the protologue as it does not possess the morphological features considered diagnostic by Motyka (1960). Moreover, the available evidence overwhelmingly suggests that the lichen currently in the holotype packet could not possibly have originated from the type locality. Instead the most likely scenario is that Motyka replaced the holotype of *A. fallacina* that he used to prepare the description, with a non-type specimen of *A. sarmentosa* that originated from an unrelated gathering. While we suspect that the specimen Motyka retained in his herbarium, now at LBL, is the specimen that was originally in the holotype packet, this cannot be determined with certainty. Regardless of how the present situation came to be, it is clear that although the original holotype packet is extant at US, the specimen that was once inside it is no longer present. The currently accepted holotype is not *A. fallacina*, it could not have been part of the type gathering, and it was almost certainly not used to prepare the original description.

In light of the above, we argue that the original specimen Motyka designated as the holotype was at some point replaced with non-type material from an unrelated gathering and it is this latter material that is currently assumed to be the holotype of *Alectoria fallacina*. We assert that the holotype of *A. fallacina* is effectively "lost or destroyed" and that the currently accepted holotype must be excluded from the original material because it was neither used to prepare the description nor is part of the type gathering. Recognizing that the actual holotype is currently lost or destroyed necessitates that the name be lectotypified (Art. 9.3, 9.11 of the *ICN*). Following Art. 9.12 of the *ICN*, we lectotypify the name with the isotype in US that consists entirely of *A. fallacina* and matches both the protologue and the current delimitation of the species.

Alectoria fallacina Motyka in Fragm. Florist. Geobot. 6(3): 447. 1960 – Lectotype (designated here, MBT 10005616): U.S.A., Tennessee, Sevier Co., Great Smoky Mountains National Park, near Alum Cave, 1575 m, 13 Sep 1939, G.B.F. Degelius s.n. (US barcode 00406193!; isolectotypes LBL!, UPS! p.p.).

AUTHOR CONTRIBUTIONS

Both authors contributed equally to the study and designed the overall framework. RTM examined material at CANL and on loan from other institutions. JCL examined material at NY and curated georeferenced data. Both authors interpreted the data, RTM prepared Figs. 1 & 3, JCL led the writing of the manuscript and prepared Fig. 2.—

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- **Fig. 1.** Comparative results of thin-layer chromatography (TLC) between *Alectoria fallacina* (lanes 1 and 2) and *A. sarmentosa* (lanes 3 and 4) using solvent systems A, B' and C. (U = usnic acid; UFA = unknown fatty acid diagnostic of *A. fallacina*; A = alectoronic acid).
- **Fig. 2.** Geographic distribution of *Alectoria fallacina* (black dots) in the Appalachian Mountains based on specimens examined for this study, contrasted against all georeferenced records of *A. sarmentosa* (white dots) from the Consortium of North American Lichen Herbaria. Note that records of *A. sarmentosa* incorrectly tagged based on geography or taxonomy were excluded from mapping, and a record from New York State was excluded after re-examination by S. LaGreca (pers. comm.).

Fig. 3. Comparison of the holotype specimen of *Alectoria fallacina* (**A**, US barcode 00067726) illustrating typical morphology of *A. sarmentosa* and the lectotype specimen of *A. fallacina* (**B**, US barcode 00406193) illustrating typical morphology of *A. fallacina*.

Appendix 1. ...

Alectoria fallacina Motyka, U.S.A., New York, Essex Co., Mount Marcy near Lake Placid, on lignum, 17 Aug 1933, J.L. Lowe 2914 (NY). North Carolina, Burke Co., c. 22.5 km SW of Linville, 14 Jun 1936, W.H. Welch 2524 (NY); Haywood Co., Great Smoky Mountains National Park, Gunter Fork Trail between junction with Balsam Mountain Trail and Walnut Bottoms, on Rhododendron, 13 Oct 2012, E.A. Tripp 3849 (NY); Swain Co., Great Smoky Mountains National Park, Mount Collins, on Betula, 1972, J.P. Dev 2801 (NY); Swain Co., Great Smoky Mountains National Park, Heintooga Overlook & Picnic Area, on Picea, Jul 2003, J.P. Dey 31273 (NY); Swain Co., Great Smoky Mountains National Park, wooded slope adjacent to Newfound Gap parking lot and overlook, on Picea, 11 May 1971, J.G. Guccion 2022A-15 (NY); Swain Co., Great Smoky Mountains National Park, true summit of Luftee Knob, on Abies, 9 Aug 2012, J.C. Lendemer 32951 (NY), J.C. Lendemer 32980 (NY); Yancey Co., Mt. Mitchell in the Black Mountains, on Abies, 1973, J.P. Dey 5993 (NY), J.P. Dey 5997 (NY). Tennessee, Sevier Co., Great Smoky Mountains National Park, High Top of Mount LeConte, on Abies, 1972, J.P. Dey 3255 (NY); Sevier Co., Great Smoky Mountains National Park, N facing slope N of Appalachian Trail, c. 320 m S of summit of Mount Collins, on fallen branch, 6 Jan 2016, J.C. Lendemer 46255 (NY); Sevier Co., Great Smoky Mountains National Park, S facing slope of Mingus Lead, on fallen branch, 6 Jan 2016, J.C. Lendemer 46337 (NY); Sevier Co., Great Smoky Mountains National Park, Sugarland Mountain, Sugarland Mountain Trail c. 320 m E of junction with Rough Creek Trail, on fallen Picea, 28 Mar 2016, J.C. Lendemer 47194 (NY), J.C. Lendemer 47197 (NY); Sevier Co., Great Smoky Mountains National Park, Mount LeConte, E facing slopes along Alum Cave Trail c. 2.4 km S of junction with Rainbow Falls Trail, on fallen Picea, 6 Jun 2018, J.C. Lendemer 56523 (NY); Sevier Co., Great Smoky Mountains National Park, Sugarland Mountain Trail, c. 740 m NW (linear) of trail junction with Appalachian Trail, on bark, 26 Oct 2017, R.T. McMullin 19003 (CANL); Sevier Co., Great Smoky Mountains National Park, Anakeesta Knob to The Jumpoff spur along Boulevard Trail, on lignum, 7 Aug 2012, E.A. Tripp 3447 (NY). West Virginia, Randolph Co., unknown locality, on trees, 30 Aug 1890, C.F. Millspaugh 769 (NY).

Appendix 2. ...

Alectoria sarmentosa (Ach.) Ach. [reported to lack alectoronic acid by Brodo & Hawksworth, 1977], Canada, British Columbia, Vancouver Island, Mount Arrowsmith Massif Regional Park, Mount Arrowsmith, 6 Jul 1969, M. Shchepanek 312A (CANL; usnic acid only); Haida Gwaii, Graham Island, head of Dinan Bay, on Picea, 14 Jul 1971, I.M. Brodo 18387 (CANL; usnic acid and low concentration of alectoronic acid). Newfoundland and Labrador, Notre Dame Bay, Bay of Exploits, on Picea, 26 Jun 1967, Riewe P-50 (CNAL; usnic acid and alectoronic acid). U.S.A., Idaho, Idaho Co., Selway River, Selway Falls, 24 Apr 1954, H.A. Imshaug 16408 (CANL; usnic acid and unidentified fatty acid not equal to A. fallacina).