

Gowardia zebrina sp. nov., a new species in a little-known genus of arctic-alpine lichens (*Parmeliaceae*)

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Abstract. The fruticose lichen genus *Gowardia* (*Parmeliaceae*) was recently segregated from *Alectoria* based on phylogeny, morphology, secondary chemistry, ecology and distribution. As currently circumscribed, *Gowardia* comprises two wide-ranging species of arctic-alpine regions. Here we describe a third species, *G. zebrina* sp. nov., apparently endemic to sub-alpine regions in mountainous northwestern North America. *Gowardia zebrina* differs from other species in the genus by its combined subpendent habit, uniformly capillary branches, predominantly isotomic branching, pale-and-dark banding of the terminal branches, and epiphytic ecology. Morphological examination of North American herbarium specimens filed under *A. nigricans* suggests the existence of several additional undescribed species of *Gowardia*. A brief overview of morphological diversity in these species is given, shedding new light on the question of whether *Gowardia* should be subsumed under *Alectoria*, as some have suggested, or is more appropriately recognized as a distinct genus.

Key words: *Alectoria*, Alpine, British Columbia, *Gowardia*, lichen, taxonomy

Introduction

In 2009 the fruticose lichen genus *Gowardia* (*Parmeliaceae*, *Lecanoromycetes*) was segregated from *Alectoria* on the basis of morphology (pseudocyphellae plane versus raised, respectively), cortical chemistry (usnic acid versus alectorialic acid), habitat ecology (mostly epiphytic versus mostly terrestrial), distribution (mostly arctic-alpine versus mostly temperate-boreal) and phylogeny (Halonen et al. 2009; see also Miadlikowska et al. 2014 and Myllys et al. 2014). Only two species of *Gowardia* are currently accepted, both restricted to open, wind-swept habitats in arctic-alpine regions (Halonen et al. 2009). *Gowardia arctica* ranges across northern Canada and Russia (Halonen et al. 2009). *Gowardia nigricans* is more widespread, reported from arctic-alpine regions of both the Northern Hemisphere and Southern Hemisphere (Hawksworth 1972; Galloway 2007).

The recent discovery of a putative third species of *Gowardia* in the Coast Mountains of western Canada prompted a careful morphological review of material filed under *Alectoria nigricans* at the UBC herbarium in Vancouver, British Columbia. In this paper we have four objectives: (1) to formally describe our new species

as *G. zebrina*; (2) to update the genus phylogeny in support of this new species; (3) to provide an overview of morphological diversity in light of recent findings; and (4) to discuss the question, current in the literature, of whether *Gowardia* is more appropriately subsumed within *Alectoria* or treated as a genus in its own right.

Materials and methods

Our study has two parts: morphological, undertaken by the first author at UBC; and molecular, performed by the second author at H. The morphological part involved a search for morphological characters potentially useful for species delimitation and was based on microscopic examination of nearly 150 specimens collected in arctic-alpine North America and filed under *G. nigricans* at UBC, Vancouver. While the main results of this study will be reported elsewhere (in prep.), our findings are nonetheless pertinent to the present paper, making it helpful to summarize our methods here.

Early in our study it became evident that many of the UBC specimens contained mixed collections of *Gowardia*, making it necessary to pre-sort prior to taxonomic evaluation. The contents of each packet were removed and lightly moistened with unchlorinated water. Once moist, the material was teased apart, sorted into distinct morphologies, arranged on sheets of blotting paper, and lightly pressed until dry. The resulting specimens, each now each now presumably taxonomically uniform,

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were then spot-tested for the presence of alectorialic acid – a secondary substance diagnostic for *Gowardia* against *Alectoria* (Halonen et al. 2009) – and finally, as necessary, transferred to new herbarium packets and re-curated. Each specimen was then examined under a dissecting microscope, with careful attention given to repeating morphological discontinuities.

The remainder of this study was undertaken at H, where the second author examined recently collected specimens of *Gowardia* under a dissecting microscope and tested for secondary compounds with thin-layer chromatography (TLC) using solvents A and B (Orange et al. 2001). Subsequent phylogenetic study was based on sequences of nuclear ribosomal ITS regions from 29 specimens (Table 1), including four specimens from the genus *Alectoria* and 24 specimens from *Gowardia*. *Bryocaulon divergens* belongs to the Alectorioid clade *sensu* Divakar et al. (2015) together with *Alectoria* and *Gowardia*, and was used as outgroup. DNA extraction, amplification and sequencing were performed using the methods described in Myllys et al. (2011). The PCR products were cleaned and sequenced by MacroGen Inc. (www.macrogen.com).

The resulting contig sequences of each specimen were assembled using BioEdit v. 7.0.5.3 (Hall 1999). Voucher specimens were deposited in H and UBC.

Seven new ITS sequences were generated for this study. The remaining sequence data were obtained from the NCBI GenBank (www.ncbi.nlm.nih.gov/genbank/), including all available ITS sequences of *Gowardia*. The ITS sequences were aligned with MUSCLE v.3.8.31 (Edgar 2004) using EMBL-EBI's freely available web service (<http://www.ebi.ac.uk/Tools/msa/muscle/>). The ITS alignment is available online from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.51c59zw58>. Phylogenetic relationships were inferred using maximum likelihood (ML) as optimality criteria. The ML analysis was performed in RAxML v.8.1.15 (Stamatakis 2104) located at CSC – IT center for Science (<http://www.csc.fi/english>). We divided the data set into three partitions (ITS1 region, 5,8S gene, ITS2 region) and used a GTR-GAMMA model because GTR is the only substitution model implemented in RAxML. Nodal support was estimated with 1000 bootstrap replicates using the rapid bootstrap algorithm.

Table 1. Specimens used in molecular phylogeny, with GenBank accession numbers. Sequences generated in this study are bolded. The name *G. nigricans* is given in quotes, owing to current nomenclatural uncertainty concerning its application.

Taxon	Locality	Voucher specimen, sequence ID	GenBank accession number
<i>Alectoria imshaugii</i>	Canada, British Columbia	Goward 05-32 (UBC), H131	EU282496
<i>Alectoria ochroleuca</i>	Russia, Murmansk Region	Uotila 49194 (H), L519	KJ947934
<i>Alectoria sarmentosa</i>	Finland, Oulun Pohjanmaa	Halonen s.n. (OULU), H29	EU282494
<i>Alectoria sarmentosa</i>	Canada, British Columbia	Goward 05-38 (UBC), H132	EU282495
<i>Bryocaulon divergens</i>	USA, Alaska	Talbot & Myers UNI062-34 (H), L475	KJ947935
<i>Gowardia arctica</i>	Canada, Nunavut	Mattsson 5115 (UPS), L171	EU282504
<i>Gowardia arctica</i>	Canada, NWT	Mattsson 5255 (UPS, H), L170	EU282502
<i>Gowardia arctica</i>	Russia, Nenetsia	Pajunen s.n. (OULU), S146	EU282503
<i>Gowardia arctica</i>	Canada, Nunavut	Mattsson 5142 (UPS), L169	EU282505
<i>Gowardia 'nigricans'</i>	Finland, Enontekiön Lappi	Virtanen s.n. (OULU), S201	EU282501
<i>Gowardia 'nigricans'</i>	Finland, Inarin Lappi	Hyvärinen s.n. (OULU), H79	EU282499
<i>Gowardia 'nigricans'</i>	Finland, Enontekiön Lappi	Rämä s.n. S203 (OULU)	MT365233
<i>Gowardia 'nigricans'</i>	Norway, Troms	Timdal s.n. (O)	MK812557
<i>Gowardia 'nigricans'</i>	Norway, Buskerud	Rui & Timdal s.n. (O)	MK812358
<i>Gowardia 'nigricans'</i>	Norway, Buskerud	Rui & Timdal s.n. (O)	MK812235
<i>Gowardia 'nigricans'</i>	Norway, Finnmark	Westberg s.n. (O)	KY266967
<i>Gowardia 'nigricans'</i>	Norway, Finnmark	Timdal s.n. (O)	KY266922
<i>Gowardia 'nigricans'</i>	Norway, Finnmark	Holien s.n. (O)	KY266831
<i>Gowardia 'nigricans'</i>	Russia, Nenetsia	Kumpula, Strengell & Moilanen s.n. (OULU), S202	EU282500
<i>Gowardia 'nigricans'</i>	Sweden	Lundqvist 8377 (UPS)	DQ979996
<i>Gowardia 'nigricans'</i>	USA, Alaska	Talbot & Myers #UNI062-34A, L489 (H)	KR857115
<i>Gowardia 'nigricans'</i>	Canada, Quebec	McMullin TL013-B02 (CANL)	KU496936
<i>Gowardia 'nigricans'</i>	Chile	MAF-Lich. 18297 (MAF)	KU647289
<i>Gowardia zebrina</i>	Canada, British Columbia	Goward 96-485, L319 (H, UBC)	MT365234
<i>Gowardia zebrina</i>	Canada, British Columbia	Goward 96-485A, L320 (UBC)	MT365235
<i>Gowardia</i> sp.	Canada, NWT	Björk 24404, L373 (UBC)	MT365237
<i>Gowardia</i> sp.	Canada, NWT	Björk 28956, L617 (UBC)	MT365238
<i>Gowardia</i> sp.	Canada, British Columbia	Goward 06-1624, S187 (UBC)	MT365236
<i>Gowardia</i> sp.	USA, Alaska	Berg 3099, L838 (UBC)	MT365239

Results

Taxonomic diversity

An important finding of our study is that *Gowardia* is likely a much more speciose genus than currently recognized: far from encompassing only two species worldwide,

more than a dozen *Gowardia* species appear to be present in North America alone. Six of these putative new species are illustrated in Figures 1 and 2, while a seventh, the highly distinctive *G. zebrina*, is described below; see also Figure 4. This last species aside, formal description of most putative North American species must proceed

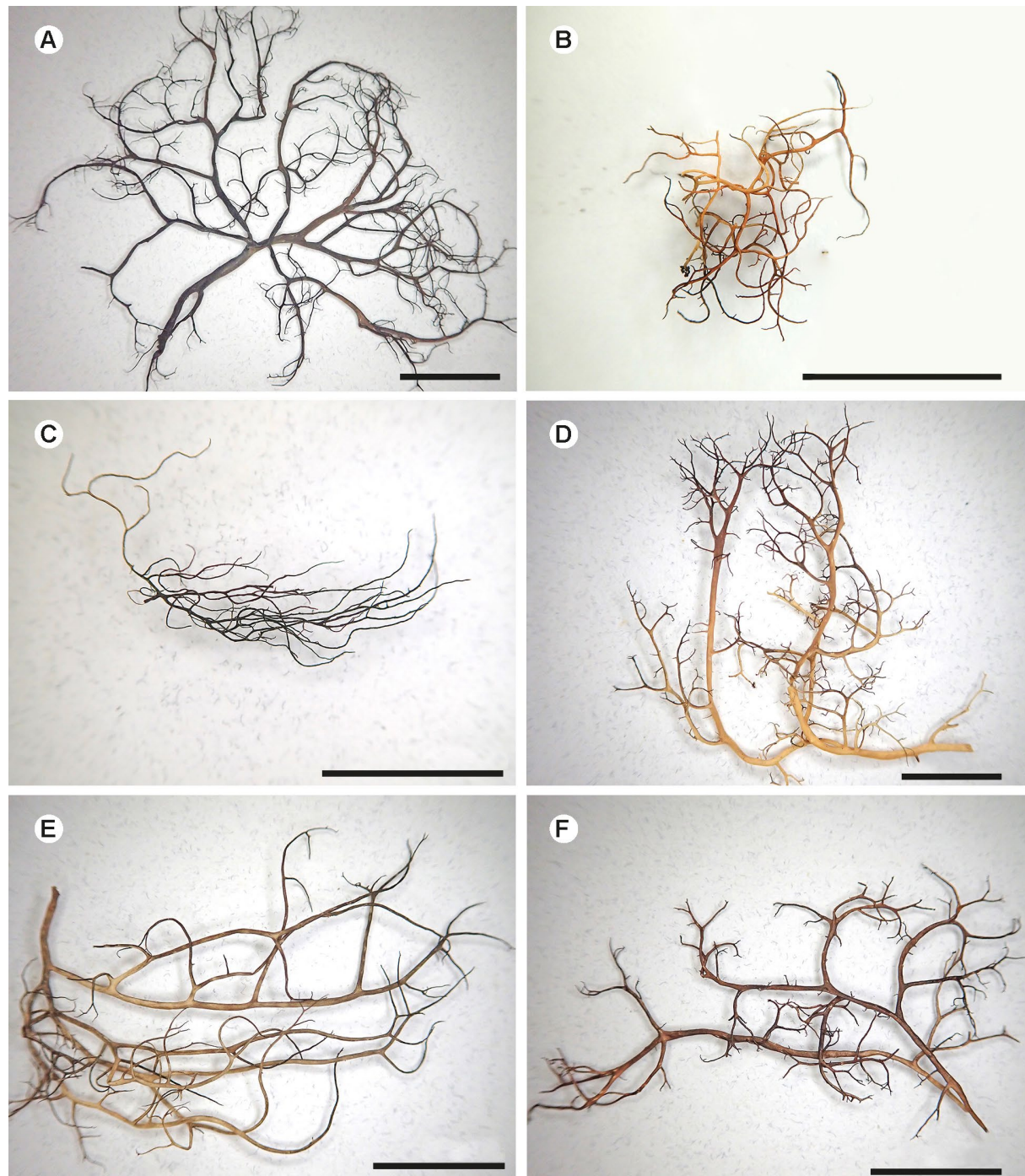


Figure 1. Morphological diversity. Examination of nearly 150 specimens of *Gowardia* at UBC suggests that this genus is much more speciose than hitherto recognized. Illustrated here is a small sampling of putative unnamed species present in North America. A – morph ‘*applanata*’ is decumbent and has flattened and/or foveolate branches that soon become black. Widespread in arctic-alpine habitats. (Otto 5425, UBC); B – morph ‘*salmonescens*’ is small and tufted and turns bright orange with long storage, at least in part. Apparently restricted to alpine elevations in the western cordillera. (Goward 78-773b, UBC); C – morph ‘*crinalis*’ is subpendent and has black capillary branches which tend to be friable when dry. Apparently restricted to subalpine habitats in the western cordillera. (Goward 06-1626, UBC); D – morph ‘*crocea*’ is upright and two-toned, usually orangish below and brownish to blackish above. Widespread both at arctic latitudes and southward at alpine elevations in the western cordillera. (Barrett s.n., L15477, UBC); E – morph ‘*elegans*’ combines decumbent stems with upright branches and has smooth, apically shiny branches that characteristically become whitish toward the base. Known only from the Aleutian Islands. (Talbot CAR001-X-18b, UBC); F – morph ‘*vitrea*’ is blackish and shiny like *G. arctica*, but has glassy, brittle, somewhat angular branches that often bear minute longitudinal striations. Widespread across the North American arctic. (Barrett 36, UBC). Scales: A–F = 10 mm.

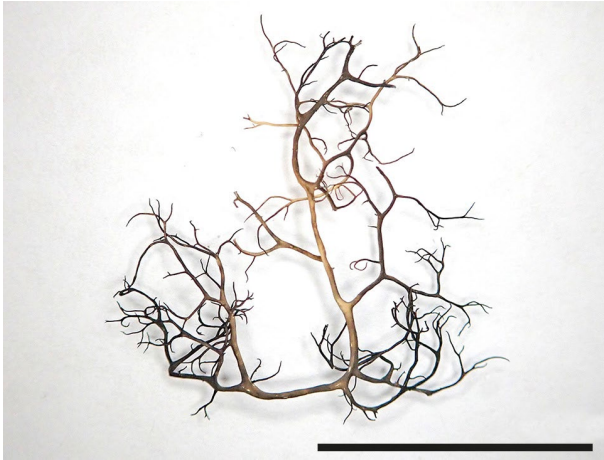


Figure 2. A small thallus of *Gowardia* morph ‘applanata’ (Otto 5360b, UBC). The pale narrow branches in the middle portion of this specimen are termed ‘bone stems’; see text. Scale bar = 10 mm.

with caution: first, owing to difficulties of taxonomic delimitation in a genus having few quantifiable characters, as noted below; and second, owing to the existence, in synonymy, of several published names of uncertain application (Hawksworth 1972; Brodo & Hawksworth 1977; in prep.).

Morphological notes

In most regards, thallus morphology in *Gowardia* is broadly similar to that of other ‘hair lichen’ genera,

permitting direct adoption of the standard descriptive terminology (e.g., Brodo & Hawksworth 1977). On the other hand, it also differs markedly, for example in lacking diagnostic features such as apothecia, soralia, and chemical markers. Quantitative characters are thus few in this genus, and mostly limited to stem length (base to tip), internode length, pseudocyphellae length and cortical thickness. This makes *Gowardia* a taxonomically difficult genus in which species delimitation (in the absence of fresh material suitable for molecular testing) rests primarily on subtle qualitative details.

Still, our search for repeating morphological discontinuities did yield several characters presumed to be taxonomically informative. Of these, the most important are habit (upright, decumbent, mixed), branching (main stems conspicuous, inconspicuous, absent), branch profile (terete, subterete, flattened), surface hue (white, pale yellow, orangish, orangish brown, rust-brown, medium brown, purplish brown, dark brown, black), surface detail (even, weakly foveolate, strongly foveolate), luster (shiny, distinctly matte) and pliancy (pliant, distinctly brittle). Also taxonomically important are various features of the pseudocyphellae, including outline (fissural, hypheniform, narrowly fusiform, broadly fusiform, oval), elevation (immersed, plane, raised) and apical detail (blunt, short-tapered, long-tapered). In a few species the abundance of short pseudocyphellar spinules (absent, sparse, frequent, abundant) appears to be diagnostic, as does the presence/absence of vegetative nodular swellings, interfusing stems and branches, grooved

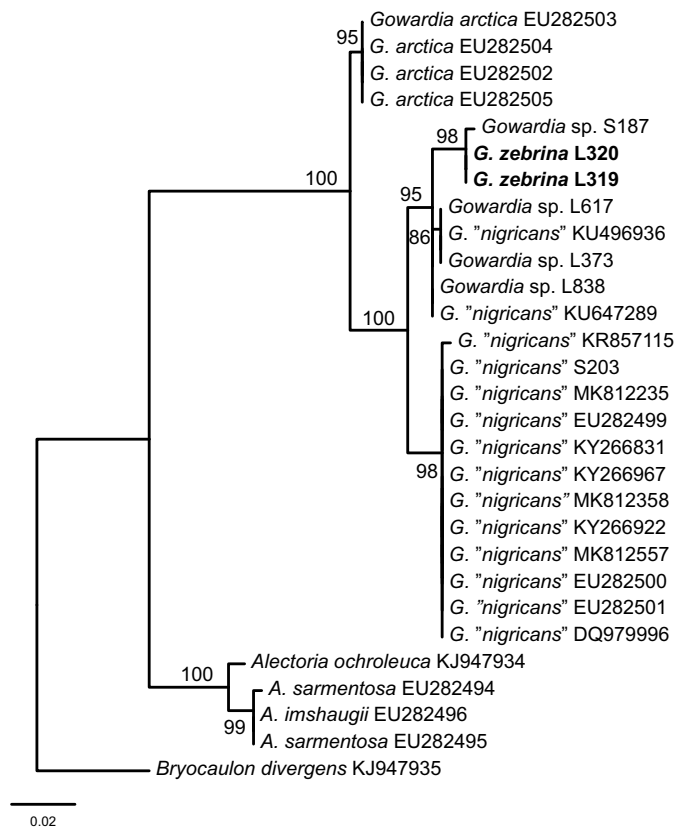


Figure 3. Phylogenetic position of *Gowardia zebrina*. A maximum likelihood phylogram obtained from RAxML analysis based on ITS data. Nomenclatural studies initiated as part of this study reveal the existence of previously published ‘*Alectoria*’ (= *Gowardia*) species of uncertain application, and at the same time call into question the taxonomic identity of *G. nigricans*. In light of these findings, we refrain from accepting earlier applications of that name, pending further study (in prep.).

(sulcate) basal stems and pale-and-dark banding of the terminal branches (as in *G. zebrina*, below).

One additional character apparently informative for species delimitation in *Gowardia* is the presence/absence/position of localized whitish or at any rate anomalously pale cortical patches. Such patches are often associated with distinct narrowings of the stems/branches and are here referred to as ‘bone stems.’ Bone stems appear to be unique to *Gowardia* and may perhaps be compared to the ‘black emorient patches’ recently reported in some species of *Bryoria* (Myllys et al. 2016). With the notable exception of *G. zebrina* (see below), this feature appears to be ubiquitous in *Gowardia*, occurring at any rate in all putative species known to us. In some cases, bone stems are confined to the basal portions of the thallus (where they may become copiously branched), while in others they regularly extend into the middle (Fig. 2) or even terminal portions. In later development they may either darken – in which case they become difficult to distinguish from regular stems – or else broaden into conspicuous, often flattened widenings of the supporting branch. While bone stems usually remain flexible in all stages of development, they become distinctly brittle in at least one of our putative species, hence presumably assisting in fragmentation and dispersal.

Molecular phylogeny

The ITS data set consisted of 487 characters, 45 of which were parsimony-informative. In the ML phylogeny (Fig. 3) both *Gowardia* and *Alectoria* are recovered as strongly monophyletic (100%), a result consistent with earlier multigene phylogenies of Miadlikowska et al. (2014) and Myllys et al. (2014). Within *Gowardia*, two sequences form a strongly supported terminal group (98%) and represent our new species *G. zebrina*. One sequence (S187) obtained from a specimen collected from intermontane BC groups with *G. zebrina*, but the specimen in question differs morphologically, for example, in the presence of bone stems. In addition, several other specimens are shown to be basal to *G. zebrina*, including two from the Canadian NWT, one from Alaska, and two *G. ‘nigricans’* specimens from GenBank. The remaining *G. ‘nigricans’*

specimens form a separate strongly supported group. Note that the specimens identified as *G. ‘nigricans’* are in need of further work before their taxonomic identity can be resolved (see caption to Fig. 3). Comparison of ITS sequences revealed rather high sequence similarity between *G. ‘nigricans’* and *G. zebrina*, (98%), but in the phylogeny these species are clearly separate. *Gowardia ‘nigricans’* and *G. zebrina* also differ in their morphology and distribution (in prep.).

Taxonomy

Gowardia zebrina Goward & Myllys, sp. nov.

(Fig. 4A–B)

MycoBank MB 835591

Diagnosis: Thallus fruticose, subpendent, to 6–8(–10) cm in length, without conspicuous main stems, branches capillary, pale creamy yellow (becoming pale orange in herbarium) except blackening where exposed, superficially resembling *Alectoria sarmentosa* but more delicate and without conspicuously bulging pseudocyphellae, terminal branches repeatedly pale-and-dark banded, usnic acid absent. On trunks and lower branches of conifers at subalpine elevations.

Type: Canada, British Columbia, Vancouver Island, Mt. Cain, 10 km NW of Schoen Lake, 1.5 km NNW of Mt. Cain alpine park society lodge. Open herb meadow with scattered *Tsuga mertensiana*. On lower branches of *Tsuga*. 50°15'N, 126°21'W, alt. 1440 m, 14 Sept. 1996 T. Goward 96-485 (UBC – holotype, BG, CANL, H, HBG, KUN, S, TRH, TUR, UPS – isotypes). GenBank ITS: MT365234.

Description. Thallus up to 7–12(–15) cm in diameter, often with persistent basal points of attachment, also sometimes becoming attached at branch tips; branches capillary, up to 6–8 cm long from base to tip, internodes mostly to 2–4 cm long, terminal branches mostly long and flexuous, often repeatedly banded with pale and dark patches, otherwise pale creamy yellow except brownish or blackish where exposed, becoming pale orange in herbarium, mostly tough and pliant, matte to weakly shiny, of uniform width, 0.2–0.3 mm diam., except to 0.5 mm diam. toward base; medulla well developed, generally filling branch interior. Branching predominantly isotomic

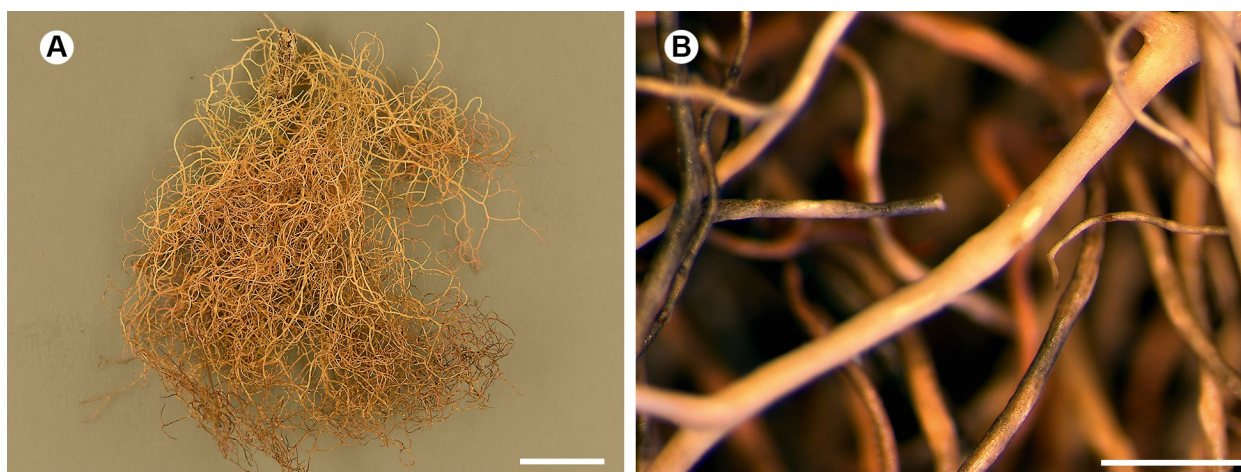


Figure 4. *Gowardia zebrina* (holotype). A – showing habit; B – showing detail of branches with pseudocyphellae and pale-and-dark banding. Scales: A = 10 mm; B = 1 mm.

dichotomous, or at any rate subbasal portions without distinct main stems, angles between branches variable; pseudocyphellar spinules generally absent. Soralia and isidia absent, except (stress-induced) ‘explosion soralia’ rarely present in basal portions. Pseudocyphellae sparse to abundant, \pm inconspicuous, 0.1–0.5 (–1.0) mm long, whitish, fissural to more often narrowly fusiform, occasionally in part hypheniform and/or oval, terminal portions blunt or at most short-tapering, plane or weakly emergent, becoming \pm impressed in age, mostly single, but occasionally in part laterally paired, rarely in threes.

Apothecia rare, lateral, supporting branches often geniculate; apothecial rim concolorous with thallus; disc to 0.8–2 mm wide, reddish brown, initially concave but soon plane or becoming convex in age; asci few-spored; spores ellipsoid, 19–25 \times 8–11 μ m, simple, thick-walled, colourless when young, becoming brownish at maturity.

Conidiomata frequent, generally sparse, brown to blackish, shiny, to 0.05 mm diam., conidiogenous cells not seen.

Chemistry. Cortex and medulla K⁺ pale yellow (filter paper), C⁺ pink (fleeting) or apparently C[–], KC⁺ red (fleeting), PD⁺ yellow. Containing alectorialic acid, unknown substances: A: 2–3, 3/B: 3, 5 brownish yellow.

Etymology. *Zebrina* calls attention to the pale-and-dark banding of the terminal branches, most clearly seen in pale specimens sheltered from high light.

Distribution and habitat. *Gowardia zebrina* appears to be narrowly endemic to coastal northwest North America, where it is currently known from the Insular Mountains of southern Vancouver Island (50°N), northward along the Coastal Mountains to the vicinity of Hazelton (55°N). Here it grows at subalpine elevations on the trunks and lower branches of conifers, especially *Abies* and *Tsuga*, in open old-growth forests subject to wind-scouring of the winter snow. To be sought in adjacent portions of southeast Alaska.

Comments. *Gowardia zebrina* is apparently a rare species currently known from only two localities. On the other hand, the possibility should not be overlooked that it has simply been undercollected owing, for example, to its subalpine distribution and superficial resemblance to *Alectoria sarmentosa*. The pale-and-dark banding characteristic of the terminal branches is diagnostic. Actually, *G. zebrina* is most likely to be confused with alectorialic-containing members of the hair lichen genus *Bryoria*, especially *B. nadvornikiana* (sensu Velmala et al. 2014) and *B. pikei*. Neither of these species occurs at subalpine elevations, however, and both in any case contain barbatic acid and lack the pale-and-dark banding of the terminal branches. Within its habitat, *G. zebrina* grows in proximity to *Alectoria sarmentosa*, readily distinguished by the latter’s coarser branching, yellowish green hue (usnic acid) and distinctly bulging pseudocyphellae.

Additional material seen. CANADA. British Columbia, Vancouver Island, Mt. Cain, 10 km NW of Schoen Lake, 1.5 km

NNW of Mt. Cain alpine park society lodge. On trunk of *Tsuga mertensiana*. 50°15’N, 126°21’W, alt. 1440 m, 14 Sept. 1996 T. Goward 96-485A, 96-493 (UBC) – topotypes; Nass River Drainage, Hazelton area, Nine Mile Mountain. Alpine area with small firs in protected sites. On *Abies*. 55°19’N, 127°30’W, alt 5200’, 8 Aug. 1970. K. E. Ohlsson 2986 (UBC L226).

Discussion

Lichen classification has undergone much scrutiny in recent years, as a constant flow of molecular findings both uphold and challenge traditional taxonomic concepts grounded in morphology, secondary chemistry, spore characters, etc. (Lumbsch & Leavitt 2011; but see also Spribille et al. 2016). At the genus level this has led to debate over the appropriate circumscription of several macrolichen clades, including *Gowardia*.

Lumbsch & Huhndorf (2010) were the first to suggest that *Gowardia* should be subsumed within *Alectoria*, owing to ‘the possibility of errors due to the analysis performed.’ This suggestion was later taken up by Crespo et al. (2016) and Divakar et al. (2017), notwithstanding the prior publication of analyses showing a strongly supported sister group relationship for *Gowardia* and *Alectoria* (Miadlikowska et al. 2014; Myllys et al. 2014). In such a case, the decision on whether to recognize one genus or two is preferably made on the basis of integrated phenotypic discontinuity (Lücking 2019).

In the event, usage over the past decade has clearly supported recognition of *Gowardia* as a distinct genus. Not only was *Gowardia* taken up in the latest Ascomycetes Classification (Lücking et al. 2017 [‘2016’]), it has also been adopted in virtually all recent floristic and vegetational studies within its range: e.g., Piercey-Normore (2010), Hansen (2012), Koroleva (2014), McMullin & Dorin (2016), Wang et al. (2017), Moseev & Sergienko (2018).

Notwithstanding this wide acceptance, the recent introduction of temporal banding into lichenology (Kraichak et al. 2017; Divakar et al. 2017) has once again called the generic status of *Gowardia* into question (Thell et al. 2018). Temporal banding is the practice of linking taxonomic rank to pre-determined cut-off dates on time-calibrated phylotrees, with a view to creating stable, ‘objective’ classification systems ultimately grounded in quantitative data (Hennig 1966). In the temporal banding system promoted by Divakar et al. (2017), the minimum cut-off date for genus recognition is set at 29.5 to 32.5 million years ago – too early to support separate genus status for *Gowardia* and *Alectoria*. In this analysis, the younger genus name *Gowardia* should be subsumed within *Alectoria*.

Yet it is fair to say that the strict application of temporal banding in lichenology has so far received little support (but see McCune et al. 2018). In an extended rebuttal entitled ‘Stop the abuse of time! Strict temporal banding is not the future of rank-based classification in fungi (including lichens) and other organisms’, Robert Lücking (2019) shows that the mechanical application of temporal banding can too often result in significant loss

of morphological, chemical, distributional and evolutionary information, without any compensating benefit.

Certainly this is the case with *Gowardia*, whose optional reduction to synonymy under *Alectoria* obscures several unifying features of substrate ecology, distribution, secondary chemistry and thallus morphology (see, e.g., Table 2 in Halonen et al. 2009), not least being the presence of bone stems, a feature unique to the genus. Crucially, all seven putative *Gowardia* species illustrated in Figures 1 and 2 are morphologically much closer to *Bryoria* (e.g., section *Divaricatae*; Myllys et al. 2011) than to *Alectoria*. ‘Age,’ notes Lücking (2019), ‘is just one trait of clades, but it cannot be the only one to determine rank.’

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