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Harpalejeunea molleri subsp. *integra* (R.M. Schuster) Damsholt new to Atlantic Canada

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Abstract

Harpalejeunea molleri subsp. *integra* (R.M. Schuster) Damsholt is reported for the first time in Atlantic Canada. It was found on the base of a large Eastern White Cedar (*Thuja occidentalis*) in a swamp in Nova Scotia. The specimen was examined using light microscopy, diagnosed using standard keys, and compared with reference specimens, including two European collections from the New Brunswick Museum, two North American collections annotated by R.M. Schuster, and the only material that may have been previously collected in Canada, by T. Drummond. We speculate on the original location of Drummond's collection, and the implications of this finding for conservation.

Key words: Liverwort; Nova Scotia; hepatic; Lejeuneaceae

Introduction

Harpalejeunea molleri (Stephani) Grolle (Lejeuneaceae) is a rare leafy liverwort (Note: liverworts typically do not have common names) with a disjunct global distribution, primarily around the North Atlantic, with European and North American populations recognized as subspecies. In Europe, *Harpalejeunea molleri* subsp. *molleri* has been collected on the west coast of Norway and in the United Kingdom, Ireland, and Spain (GBIF 2018), as well as Finland, Italy, Madeira, the Azores, the Canary Islands, and Corsica (Hodgetts 2015). The North American subspecies, *Harpalejeunea molleri* subsp. *integra* (R.M. Schuster) Damsholt, is known primarily from the Appalachian Mountain Range and Atlantic Coastal Plain in the southeastern United States, where it has been collected in Alabama, Georgia, Kentucky, and North and South Carolina (Schuster 1980; Consortium of North American Bryophyte Herbaria 2017), as well as Florida, Mississippi, Tennessee, and Virginia (Breil 1970). A single specimen is thought to have been collected from Canada by Thomas Drummond in the early 19th century, but the collection location is ambiguous, and no other specimens are known to have been collected in Canada since then. Two recent collections are also reported from Brazil, without subspecific designation (GBIF 2018).

The correct name for *H. molleri* and its infraspecific taxa has historically been a source of confusion. Schuster (1980) used the name *Harpalejeunea ovata* (Dickson) Schiffner, and, consequently, much of the material in North American herbaria has been accessioned under that name. However, Grolle (1989) demonstrated that this name is a synonym of *Douinia ovata* (Dickson) H. Buch (Scapaniaceae) and that *H. molleri* is the correct name for the taxon, as recognized recently by European authorities (Paton 1999; Damsholt and Pagh 2002). Nevertheless, the former taxonomic confusion continues to impede accurate delineation of the species' distribution because many herbarium records have not been revised to reflect current taxonomy.

In North America, *H. molleri* subsp. *integra* has been found in old growth swamps or riparian areas with relatively open forest canopies, most commonly as an epiphyte on the base of hardwood trees (Breil 1970; Schuster 1980) and in crevices on sedimentary rock (Consortium of North American Bryophyte Herbaria 2017). It is often in mixed species colonies (Breil 1970), and common liverwort associates in herbarium records include *Frullania asagray-*

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ana Montagneagne, *Lejeunea lamacerina* (Stephani) Schiffner, *Lejeunea ruthii* (A. Evans) R.M. Schuster, *Lejeunea ulicina* (Taylor) Gottsche, Lindenberg & Nees, and *Radula obconica* Sullivant (Consortium of North American Bryophyte Herbaria 2017).

Methods

The collection site was a mixedwood swamp near Hectanooga, Digby County, Nova Scotia (~44.082°N, 66.056°W). Geologically, this part of Digby County is underlain by the Church Point Formation, which is composed primarily of grey to green, fine- to medium-grained metasiltstone and metasandstone, with rare shale deposits (White and Horne 2012). Soils are stony in places and poorly drained, being a mix of peat, sandy loam, and loam-till derived from slate (Hilchey *et al.* 1962). The habitat is a rich swamp forest, dominated by Eastern White Cedar (*Thuja occidentalis* L.), Red Maple (*Acer rubrum* L.), Balsam Fir (*Abies balsamea* (L.) Miller), and Yellow Birch (*Betula alleghaniensis* Britton). Hummock and hollow microtopography characterizes the ground layer, with hummocks dominated by sedges (*Carex* spp.) and Cinnamon Fern (*Osmundastrum cinnamomeum* (L.) C. Presl) and hollows dominated by *Sphagnum* spp. and standing water. The shrub layer is patchy, with Common Winterberry (*Ilex verticillata* (L.) A. Gray) and Grey Alder (*Alnus incana* (L.) Moench).

Collections of *H. molleri* subsp. *integra* were made opportunistically during searches for *Frullania selwyniana* Pearson, also rare in the province. Approximately 40 mature cedar trees were visually inspected during this search; eight were found to host visible mixed-species colonies of leafy liverworts. A mixed-species collection was made from each of the eight host trees and later examined using stereomicroscopy. Liverworts were identified using standard taxonomic keys (Schuster 1980; Paton 1999).

Two of these collections were found to contain *H. molleri* subsp. *integra*. The larger of the two collections was then compared with reference material from three sources: (1) two exsiccatae from the herbarium at the New Brunswick Museum (NBM), (2) two recent collections from the United States that were annotated by liverwort authority R.M. Schuster at the Field Museum (F), and (3) the original (supposedly) Canadian collection by T. Drummond, held by the New York Botanical Garden. Neither S.R.H. nor T.H.N. has since had the opportunity to return to this location to assess the population size or health of the colony.

In this paper, we provide a brief description of the morphology of the specimen that was deposited at the NBM as evidence for our subspecific designation. We also highlight noteworthy aspects of the historical collections for the sake of comparison.

Results

Harpalejeunea molleri subsp. *integra* was collected from two cedar trees in the Hectanooga Cedar Swamp. One of these collections was accessioned at the NBM, while the other is held in the private herbarium of T.H.N. Common species in these colonies included *Frullania asagrayana* Montagne, *Frullania oakesiana* Austin, *Ptilidium pulcherrimum* (Weber) Vainio, and *Radula complanata* (L.) Dumortier, while rarer species included *F. selwyniana*, *Lejeunea cavifolia* (Ehrhart) Lindberg, and *Lejeunea ulicina* (Taylor) Gottsche, Lindenberg & Nees. Both of the (mixed-species) colonies, in which *H. molleri* subsp. *integra* was detected, were ~40 cm^2 on the bases of large Eastern White Cedars (~25 cm diameter at breast height). *Harpalejeunea molleri* subsp. *integra* occupied only a small fraction (<10%) of the colonies and the subsequent collected material, but was distinct from the other species present, being obviously greener than *F. selwyniana*, larger than *L. ulicina*, and with more acutely angled leaves than *L. cavifolia*.

Shoot and colony architecture of *H. molleri* subsp. *integra* in the collected material corresponded to a previously published description (Schuster 1980). The collective, multi-species colony structure for our sample was that of a loose "smooth mat", although each individual species exhibited a thread-like growth form (*sensu* Bates 1998). Shoots of *H. molleri* subsp. *integra* were 0.4–0.6 mm wide (transverse axis, including leaves) and displayed a dichotomous irregular lateral branching pattern. Stem postical cortical cells were 13–15 µm wide on mature shoots. Leaves were two-ranked, spreading, and complicate-bilobed with alternate insertions along the stem (Figure 1). Antical leaf lobes were comma shaped and longer than broad (1.1–1.2 length to width ratio); proximal margins overlapped the stem above the transverse insertion (Figure 2), and distal margins were acute tipped, typically tapering to a single cell, or occasionally two cells and often curved toward the substrate (Figure 3). The smaller, postical lobe (lobule) attached to the stem along the entire length of its proximal margin and folded under the larger, antical lobes, forming a rounded keel along the anterior leaf margin (Figure 3); the angle between the distal edge of the keel and the free antical lobe ranged from 90° to 120°, and the joint was often strongly indented (Figure 2). The distal tips of most lobules bore a slightly elongated, tooth-like cell, located proximal to the distal margin of the keel; this cell projected away from the stem and was ~1.5–2 times the length of a median lobule cell (Figure 3). Immediately proximal

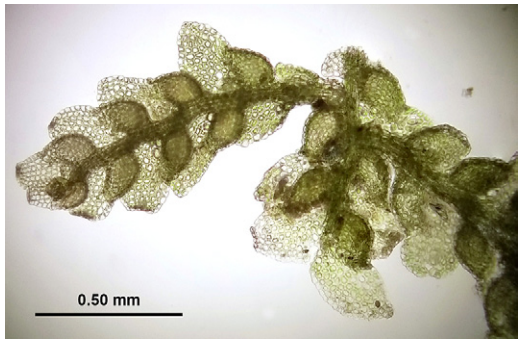

FIGURE 1. Postical view of *Harpalejeunea molleri* subsp. *integra* shoot (*Neily 1629*, New Brunswick Museum). Photo: Sean Haughian.

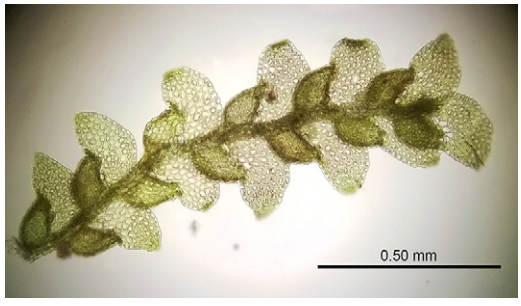

FIGURE 2. Antical view of *Harpalejeunea molleri* subsp. *integra* shoot, from newly collected material (*Neily 1629*, New Brunswick Museum). Photo: Sean Haughian.

to this tooth-like cell, some lobules also had a clavate, hyaline papilla (not shown). Underleaves were 0.12–0.16 mm across, shallowly bilobed, and widely divergent; each lobe was four cells wide at the base and rounded at the apex (Figure 4). The specimen had no obvious reproductive structures.

The two collections from North America (F) were consistent with Schuster's (1980) descriptions of *H. molleri* subsp. *integra*. They exhibited stem postical cortical cells 13–19 µm in width, bilobed underleaves with four cells at the base of each lobe, and strongly indented leaf margins where the distal terminus of the lobule's keel attached to the antical leaf lobe.

The two collections from Spain and Portugal (NBM) had characters consistent with Schuster's (1980) and Paton's (1999) descriptions of *H. molleri* subsp. *molleri*. Compared with the USA material, they had consistently wider postical cortical cells of 19–23 µm, more weakly indented joints (forming angles of ~90–135°) between the lobule and leaf lobe, and slightly more variable underleaf lobe widths (4–7 cells).

Drummond's collection was somewhat transitional between the European and the North American collections examined; the leaf lobe–lobule joints were

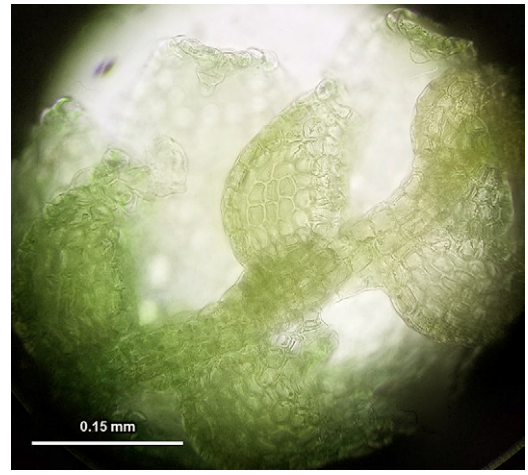

FIGURE 3. Postical view of *Harpalejeunea molleri* subsp. *integra* shoot, showing lobules, underleaves, and antical lobe tips, from newly collected material (*Neily 1629*, New Brunswick Museum). Photo: Sean Haughian.

FIGURE 4. Postical view of *Harpalejeunea molleri* subsp. *integra* shoot, showing underleaves and cortical stem cells, from newly collected material (*Neily 1629*, New Brunswick Museum). Photo: Sean Haughian.

strongly indented on mature stems, and the underleaf lobes were mostly 4 (-6) cells across. However, the postical cortical cells of the stem were wider (19–24 µm) than is typical for *H. molleri* subsp. *integra*. Associated taxa in this packet included *Diplophyllum albicans* (L.) Dumortier and *Frullania tamarisci* (L.) Dumortier. The only writing on the packet was the former Latin name of the species ("*Lejeunea ovata*") and the vague place-name, "British North America".

Discussion

This is the first report of *H. molleri* subsp. *integra* in Atlantic Canada, and the first reliable report of the species in Canada. The apparent disjunction of this occurrence from other known localities in North America suggests that the population is a relic of a previously more contiguous North American distribution, that it is a recent colonist from the southeast, or that the species is present between the new sites and the ones further south but unrecorded. We think the latter is unlikely given the search effort for mosses and liverworts in much of the northeastern United States and the uniqueness of the Nova Scotia habitat.

Alternatively, *H. molleri* subsp. *integra* may be a dispersal-limited disjunct of Nova Scotia's Atlantic Coastal Plain flora. This species is only rarely fertile, even in locations where it is more common and abundant (Breil 1970; Schuster 1980). Consequently, reproductive propagules are unlikely to have colonized any new habitats in recent years. Moreover, other species that are associated with this type of habitat (both vascular plants and epiphytes) are known to be associated with the Atlantic Coastal Plain, for which southwestern Nova Scotia forms a natural northern disjunction (Sweeny and Ogilvie 1993). Regardless, the combination of potential dispersal limitation with habitat and substrate associations, makes *H. molleri* subsp. *integra* an exceptional rarity, even among flora of the Atlantic Coastal Plain.

The first record in Canada?

Although our find was exceptional, it may not be the first detection of this species in Canada; a single collection of *H. molleri* was supposedly made by T. Drummond in the early 19th century and is held by the New York Botanical Garden. The location originally listed in the digital record of the specimen was "British Columbia" (Consortium of North American Bryophyte Herbaria 2018), but the writing on the packet says "British North America", a vague term, which, at the time the collection was made (ca. 1830), could have referred to all of the British territories north of the United States (Nicholson 2006) or primarily those west of Upper Canada, which was both the official name and a more commonly used descriptor for material collected by Drummond from what is now southern Ontario (Consortium of North American Bryophyte Herbaria 2018). If the specimen was indeed from Ontario, Drummond would probably have made this collection at the beginning of his expedition in 1825 (the only time he visited Ontario), which began in the Niagara area, and proceeded toward Lake Superior, and then on to the Rocky Mountains via the Saskatchewan River route (Bird 1967). It is possible that he considered much of northwestern Ontario to be outside of Upper Canada *sensu stricto*.

However, we have reasons to doubt that this collection was from Canada. First, the collection was part of William Mitten's herbarium, which was both extensive and somewhat poorly organized and annotated (Thiers 1983), casting a general doubt on the accuracy of packet labels.

Second, the associated taxa in Drummond's collection (*D. albicans* and *F. tamarisci*) are, in Canada, primarily known from either the British Columbia coast or the Atlantic provinces, where Drummond did not collect; other supposed early records of *D. albicans* (Macoun 1902) probably represent *Diplophyllum taxifolium* (Wahlenberg) Dumortier (Ley and Crowe 1999).

Third, most other Drummond bryophyte collections from the Ontario region list a specific area (e.g., "Lake Superior" or "Niagara Falls"; Consortium of North American Bryophyte Herbaria 2018), many of which would have been considered part of Upper Canada, rather than "British North America".

Fourth, while lands around Lake Superior are known to harbour some rare taxa associated with cedar swamps (e.g., COSEWIC 2019), neither Drummond's own records nor those of others who have studied Drummond's work (Bird 1967) suggest that he sampled extensively in cedar swamps of Ontario.

Fifth, the Drummond *H. molleri* collection could be from another location entirely: the specimen is somewhat morphologically ambiguous, with stem cortical cells suggestive of the European subspecies, perhaps from the United Kingdom (UK), and other morphological aspects suggestive of *H. molleri* subsp. *integra*, perhaps from the southeastern USA.

Drummond is known to have sampled bryophytes extensively in the UK before his work in North America, as exemplified in his two-volume *Musci Scotici* (Geiser 1937), and to have travelled widely throughout the southeastern USA in the 1830s, amassing thousands of specimens, including exsiccatae entitled *Musci Americani* and *Musci Louisiana*, which were posthumously released by Hooker and Wilson (Hooker 1840; Short 1841; Geiser 1937). The associated taxa in his *H. molleri* collection do not provide definitive guidance on alternative localities: in North America, *D. albicans* and *F. tamarisci* are known primarily from the Pacific Northwest or from Atlantic Canada and the Appalachian range of the USA, but have also been recorded in the UK. Nevertheless, we believe the collection was more likely to have been from the southeastern USA. Although hepatics were a minority in all of Drummond's collections and are not fully enumerated in any documents we could locate, Evans (1902) reports that Drummond's "Mosses of the Southern States" contains *Jungermannia serpyllifolia*. Although this name was later consid-

ered a synonym of *L. cavifolia* (Evans 1902), at the time Drummond was collecting, *H. molleri* subsp. *integra* was known as *J. serpyllifolia* subsp. *ovata* (Grolle 1989), and the omission of such a subspecific designation could have been easily overlooked by later handlers of this material. Even if the specimen to which Evans (1902) referred was, indeed, *L. cavifolia*, it suggests that Drummond collected in the right type of habitat to have also recovered *H. molleri*.

Significance and conservation

Although it may be the first Canadian record, our Nova Scotian collection of *H. molleri* subsp. *integra* was not entirely unexpected: the rich swamp forests of southwest Nova Scotia harbour several rare species that are unknown elsewhere (e.g., Neily and Anderson 2010) or are otherwise restricted to the southern Appalachians or Atlantic Coastal Plain of North America (Wisheu and Keddy 1989; Sweeny and Ogilvie 1993). The other liverworts found in the colony with *H. molleri* subsp. *integra* are themselves rare or uncommon in Atlantic Canada, having been reported only a handful of times in Nova Scotia (R. Newell pers. comm. 31 May 2017).

The Hectanooga Cedar Swamp, in which our specimens were collected, has been viewed as rare and exceptional in Nova Scotia for several decades (Ogilvie 1984), but its ecological importance has only been recognized more recently. In addition to an absence of historical disturbance in large parts, with some trees nearly 200 years old (Nova Scotia Department of Environment 2013a), the swamp harbours the largest number of naturally occurring Eastern White Cedar in mainland Nova Scotia (Nova Scotia Nature Trust 2010). The swamp also harbours many rare and at-risk species of lichens (COSEWIC 2009, 2010, 2015, 2016), birds (COSEWIC 2007, 2008), and trees, including Eastern White Cedar (Newell 2005). The Hectanooga Cedar Swamp is, therefore, of considerable value for biodiversity conservation and scientific research.

Historically, much of the Hectanooga Cedar Swamp was privately owned, but large parts are now scheduled to be protected by a provincial Nature Reserve. In 2010, the Nova Scotia Nature Trust purchased 75 ha of this land, and later transferred ownership of it to the provincial government with the protection of a conservation easement. These lands, combined with an adjacent area of Crown land to the north, are proposed as the Hectanooga Cedar Swamp Nature Reserve, including both important swamp forest and some mature mixed hardwood forest to reduce the negative edge influence (Nova Scotia Department of Environment 2013b). On the other hand, logging activities between 2008 and 2012 had already removed a substantial area of adjacent old-growth forest, and several roads run along the edges of the proposed reserve (S.R.H. and T.H.N. pers. obs.). As such, the reserve may yet suffer from negative edge influence, exacerbated by its small size (124 ha), fragmented configuration (divided into three sections), and elongate shape. Such forested wetlands may be declining in Nova Scotia, and these declines may be exacerbated in the future in a warming climate (Newell 2005; Lemieux 2010). We recommend enhancing protections for such unique hotspots of biodiversity by promptly conferring legal protected status upon them wherever possible, by adding additional parcels to make the reserves contiguous, and by increasing reserve sizes to increase protection from adjacent industrial activities.

Vouchers examined

Harpalejeunea molleri subsp. *integra* (R.M. Schust.) Damsh—CANADA, NOVA SCOTIA: Digby Co., Hectanooga Cedar Swamp, 44.082°N, 66.056°W, 17 May 2017, *T. Neily 1629* (NBM BH-2739); *ibidem*: 44.083°N, 66.052°W, 17 May 2017, *T. Neily 1654* (personal collection of T.H.N., Digby Co.); U.S.A., TENNESSEE: Pickett Co., rocky slopes W of Hwy 154 near Scott Co. line, Pickett State Forest, 17 April 1991, *P.G. Davison 1613* (F-C0074242, as *H. ovata* subsp. *integra*); SOUTH CAROLINA: Oconee, gorge of Whitewater River, 0.3–0.4 mi. (0.5–0.6 km) below Lower Falls, *ca.* 3 mi. (4.8 km) above Jocassee, 24 August 1958, *R.M. Schuster 40899a* (F-C0578334, as *H. ovata* subsp. *integra*); BRITISH NORTH AMERICA: *ca.* 1825–1835 (entered as 1906), *T. Drummond s.n.* (NY00265235, as *Lejeunea ovata*).

Harpalejeunea molleri (Steph.) Grolle subsp. *molleri*—SPAIN: 1927, P. Allorge, Exsiccata Bryotheca Iberica No. 11 (NBM BH-00858, as *H. ovata*); PORTUGAL: 1937, P. Allorge, Exsiccata Bryophyta Azorica No. 37 (NBM BH-00519, as *H. ovata*).

Author Contributions

Conceptualization – S.R.H. and T.H.N.; Investigation (specimen discovery & identification) – T.H.N.; Investigation (specimen verifications & comparisons) – S.R.H.; Investigation (nomenclatural & historical research) – S.R.H.; Methods – S.R.H. and T.H.N.; Visualization (photography) – S.R.H.; Writing (original draft preparation) – S.R.H.; Writing (review & editing) – S.R.H. and T.H.N.

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