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

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Haughian, S.R., and T.H. Neily. 2019. Harpalejeunea molleri subsp. integra (R.M. Schuster) Damsholt new to Atlantic Canada. Canadian Field-Naturalist 133(3): 199–205. https://doi.org/10.22621/cfn.v133i3.2052

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) 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-
Osmundastrum cinnamomeum (Taylor) Gottsche, Lindenberg & Nees, larger than Ilex verticillata 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 cm² 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 (lobe) 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).

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 cm² 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.

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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 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”.

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**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.

**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.
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 from the Pacific Northwest or from Atlantic 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 have been 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 exsiccatea 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. cavi-
folia*, 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 spe-
cies 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; Sweeney
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 har-
bours 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 con-
servation 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 pur-
 chased 75 ha of this land, and later transferred owner-
ship of it to the provincial government with the pro-
tection 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 nega-
tive edge influence, exacerbated by its small size (124
ha), fragmented configuration (divided into three sec-
tions), and elongate shape. Such forested wetlands
may be declining in Nova Scotia, and these declines
may be exacerbated in the future in a warming cli-
mate (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 addi-
tional 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 (en-
tered as 1906), T. Drummond s.n. (NY00265235, as
*Lejeunea ovata*).

*Harpalejeunea molleri* (Steph.) Grolle subsp.
molleri—SPAIN: 1927, P. Allorge, Exsiccata Bryo-
theca 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.; Investiga-
tion (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 (ori-
ginal draft preparation) – S.R.H.; Writing (review &
editing) – S.R.H. and T.H.N.

**Acknowledgements**

This work was self-funded by the authors. We
wish to thank Stephen Clayden and Kendra Driscoll
for assistance in accessing specimens at the New
Brunswick Museum, Ruth Newell for assistance with
searching for Nova Scotian liverwort records at the

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lection of *Bryo phyta* 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
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Acadia University Herbarium, Barbara Thiers for assistance in locating the Drummond record at the New York Botanical Garden, the Field Museum and New York Botanical Garden Herbaria for loans of material, and three anonymous reviewers, Jennifer Doubt, Jeff Saarela, and Dwayne Leptizki for their insightful feedback on our draft manuscript.

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Received 26 February 2018
Accepted 17 December 2019