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Two new species of true morels from Newfoundland and Labrador: cosmopolitan *Morchella eohespera* and parochial *M. laurentiana*

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Abstract: Morphological and molecular phylogenetic studies of true morels (*Morchella*) in the Canadian province of Newfoundland and Labrador resulted in the discovery of two undescribed species in the *M. elata* clade that we initially distinguished by the informal designations *Mel*-19 and *Mel*-36. The latter species, also collected in New Brunswick, Canada, is hitherto known only from the St Lawrence River Basin. *Mel*-36 is described here as a novel, phylogenetically distinct species, *M. laurentiana*. Before the discovery of *Mel*-19 in Newfoundland and Labrador, New Brunswick and Washington state it was only known from central China and central and northern Europe. *Mel*-19 is described here as a novel species, *M. eohespera*.

Key words: Ascomycota, molecular phylogenetics, *Morchella elata* clade, Morchellaceae, Pezizales

Introduction

Phylogenetic analyses of *Morchella* suggest that most species exhibit high continental endemism and provincialism in the northern hemisphere (Du et al. 2012a, b; Taşkın et al. 2010, 2012; O'Donnell et al. 2011; Richard et al. 2015), as illustrated by the 22 North American species with ranges that are largely restricted to areas either east or west of the Great Basin. Only three of these, *M. americana*, *M. prava* and *M. importuna*, are known to be present on both sides of the North American continent (Kuo et al. 2012, Richard et al. 2015). Although seven species in North America are found on other continents (Richard et al. 2015), it has been hypothesized that the majority of transoceanic distributions may be due to anthropogenic activities (O'Donnell et al. 2011). Recent collections of *Morchella* in the Canadian province of Newfoundland and Labrador (NL) resulted in the discovery of two undescribed species within the *M. elata* clade with contrasting distributions (O'Donnell 2014). One, informally designated *Mel*-36, has been reported only from the St Lawrence River Basin, while the other, designated *Mel*-19, hitherto known only from central and northern Europe and the central Chinese provinces Yunnan, Sichuan and Gansu (Du et al. 2012a, b; Taşkın et al. 2012; O'Donnell et al. 2011), also was collected in Washington state (WA), USA, and New Brunswick (NB), Canada. A preliminary report of the discovery of *Mel*-36 and the finding of *Mel*-19 in North America was published previously with illustrations of key morphological features of both species (Beug and O'Donnell 2014, Voitk et al. 2014). Subsequent review of described taxa suggested that *Morchella norvegiensis* (Kristiansen 1990) might be conspecific with *Mel*-19. Efforts to obtain discriminatory multilocus molecular phylogenetic data from the holotype were successful only for ITS and LSU rDNA, placing it in a group containing *Mel*-17, *Mel*-19, *Mel*-20 and *Mel*-34 (Richard et al. 2015); the latter three species have been documented from Europe.

Materials and methods

Specimens and cultures.—Thirty collections of *M. eohespera* and 19 of *M. laurentiana* were analyzed in the present study (Supplementary table I). Specimens were photographed in situ; macroscopic features, including colors (Ridgway 1912, presented between quotes in the descriptions), were recorded from fresh specimens; specimens were air-dried for subsequent deposit in the Canadian National Mycological Herbarium in Ottawa (Index herbariorum code DAOM). Light microscopic observations (Zeiss 043411 with a Ph3 Planapo 100/1.3 objective for *M. eohespera* and Zeiss 392560 with Apo 100/1.25 for *M. laurentiana*) were conducted at 1000× magnification (oil immersion), using water mounts for fresh material and 3% KOH for dried material. Ascospores were measured to 0.5 µm accuracy; measurements deviating from 0.5 µm increments are due to calculation of a lens correction factor. Air-dried ascospores were coated with gold-palladium before examination in a JEOL 6400V scanning electron microscope (SEM, JEOL USA. Peabody, Massachusetts) as described by Elliott et al. (2014). Pure cultures of *M. eohespera* (ex-holotype 02mwb062213 = NRRL 66315 and

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04mwb062114 = NRRL 66314) and *M. laurentiana* (ex-holotype 13.05.18av01 = NRRL 66317 and 13.05.15av01 = NRRL 66316) were obtained, verified by DNA sequence data and deposited in the ARS Culture Collection (NRRL, http://nrrl.ncaur.usda.gov/).

Molecular biology and phylogenetics.—Genomic DNA extraction, PCR amplification and DNA sequencing followed published protocols (O'Donnell et al. 2011). Portions of the following four regions were PCR amplified and sequenced in the present study: translation elongation factor (*TEF1*), RNA polymerase II subunit 1 (*RPB1*), DNA-dependent RNA polymerase I (*RPB2*), and nuclear ribosomal internal transcribed spacer regions and 28S ribosomal RNA gene. Maximum likelihood (ML) and maximum parsimony (MP) phylogenetic analyses were conducted, respectively, with PAUP* 4.0b10 (Swofford 2003) and GARLI 1.0 (Zwickl 2006) as described by Elliott et al. (2014). ML bootstrap analyses were conducted on the CIPRES Science Gateway TeraGrid (Miller et al. 2010) employing the GTR+I+Γ model of molecular evolution. The genealogical exclusivity of putative species-level lineages was assessed by ML and MP bootstrapping (Elliott et al. 2014). Nucleotide sequences of *M. eohespera* and *M. laurentiana* generated in the present study were deposited in GenBank (accession numbers KT819345–KT819389). The 69-taxon, four-locus NEXUS file and one of the most-parsimonious trees were deposited in TreeBASE (accession number S18037, tree number T19798).

RESULTS

Molecular phylogenetics.—Molecular phylogenetic analyses of multilocus DNA sequence data indicated that *Mel*-19 and *Mel*-36 represent phylogenetically distinct species based on genealogical concordance (Taylor et al. 2000). Maximum likelihood (ML) and maximum parsimony (MP) bootstrap (BS) analyses of a four-gene dataset for 69 isolates, representing 22 putative species-level lineages within the *M. elata* clade (FIG. 1), provided only modest support for the genealogical exclusivity of *M. eohespera* (ML-BS/MP-BS = 78%/65%); however, *M. laurentiana* monophyly received strong bootstrap support (ML-BS/MP-BS = 96%/88%). Evolutionary relationships of these species within the *M. elata* clade, however, were unresolved by the present analyses.

TAXONOMY

Morchella eohespera Beug, Voitk & O'Donnell, sp. nov. FIG. 2A–D

MycoBank MB812845

Typification: USA. WASHINGTON. Skamania County, Gifford Pinchot National Forest, Deadhorse Meadows, 46°01′15″N, 121°39′33″W, 1116 m, under *Picea engelmannii*, 22 Jun 2013, *Michael Beug* 02mwb062213 (**holotype** DAOM 574925). Ex-holotype culture: NRRL 66315.

Etymology: Latinized contracted combination of Eos and Hesperos, the Greek gods of dawn (east) and evening/sunset (west), respectively, to highlight the cosmopolitan distribution of this species.

Diagnosis: Ascomata conical to widely conical, 45–100 mm tall; cap with 12–22 longitudinal ridges between rows of slightly irregular pits with horizontal cross ridges, attached to stipe with a distinct sulcus; ridges and pits finely tomentose; ridges pale olive-buff to almost black; pits yellowish tan, darkening with age; cap and stem hollow; inner cavity covered with fine white granules. Ascospores 20–24 × 12–14 μm; ridges with subcapitate to capitate elements. Fruiting singly or in small groups in late spring in grass or calcareous soil or calcareous bedrock near conifers on natural or disturbed sites in North America and Eurasia.

Macroscopic characters: Ascomata 45–100 mm tall. Cap 30–60 mm × 25–50 mm at widest point, hollow, conical to ovate, pitted and ridged, attached to stipe with a sulcus 2–4 mm deep and 3–4 mm wide, often with small white ridges traversing sulcus radially. Ridges 1–4 mm broad; 12–22 primary vertical ridges and some shorter, secondary vertical ridges between irregular pits, with frequent sunken, more or less horizontal transecting ridges; ridges finely tomentose, "pale olive-buff" to "drab" or "pinkish buff" initially, in age "fuscous black", when dried "deep mouse gray", flattened initially, not becoming thin or eroded at maturity; transecting ridges not nearly as dark as vertical ridges. Pits primarily elongated vertically, although in some ascomata pits are wider than tall; finely tomentose; "pale olive buff" to "orange citrine" initially, in age "snuff brown", when dried "pale pinkish buff". Stipe 25–40 mm tall, 15–30 mm wide, cylindrical to tapered downward, sometimes subclavate with a few folds at the base, upper portion ridged in most specimens, with small ridges extending across sulcus to the hymenium; hollow, inner surface finely mealy with whitish granules, "white" to "pale pinkish buff", upper portion 2–3 mm thick, midregion 1–2 mm, layered and chambered near base. Context white to "ivory yellow".

Microscopic characters: Ascospores (164 spores, 10 ascocarps, five collections) (18.5–)20–24(–40) × (10.1–)11–14(–24) μm, Q = 1.4–1.7 (2.0) in water; ellipsoidal, hyaline, content homogeneous, polar oil drops absent, with longitudinal striae that converge at poles when viewed via SEM; ascospore wall ± 1 μm thick. Asci

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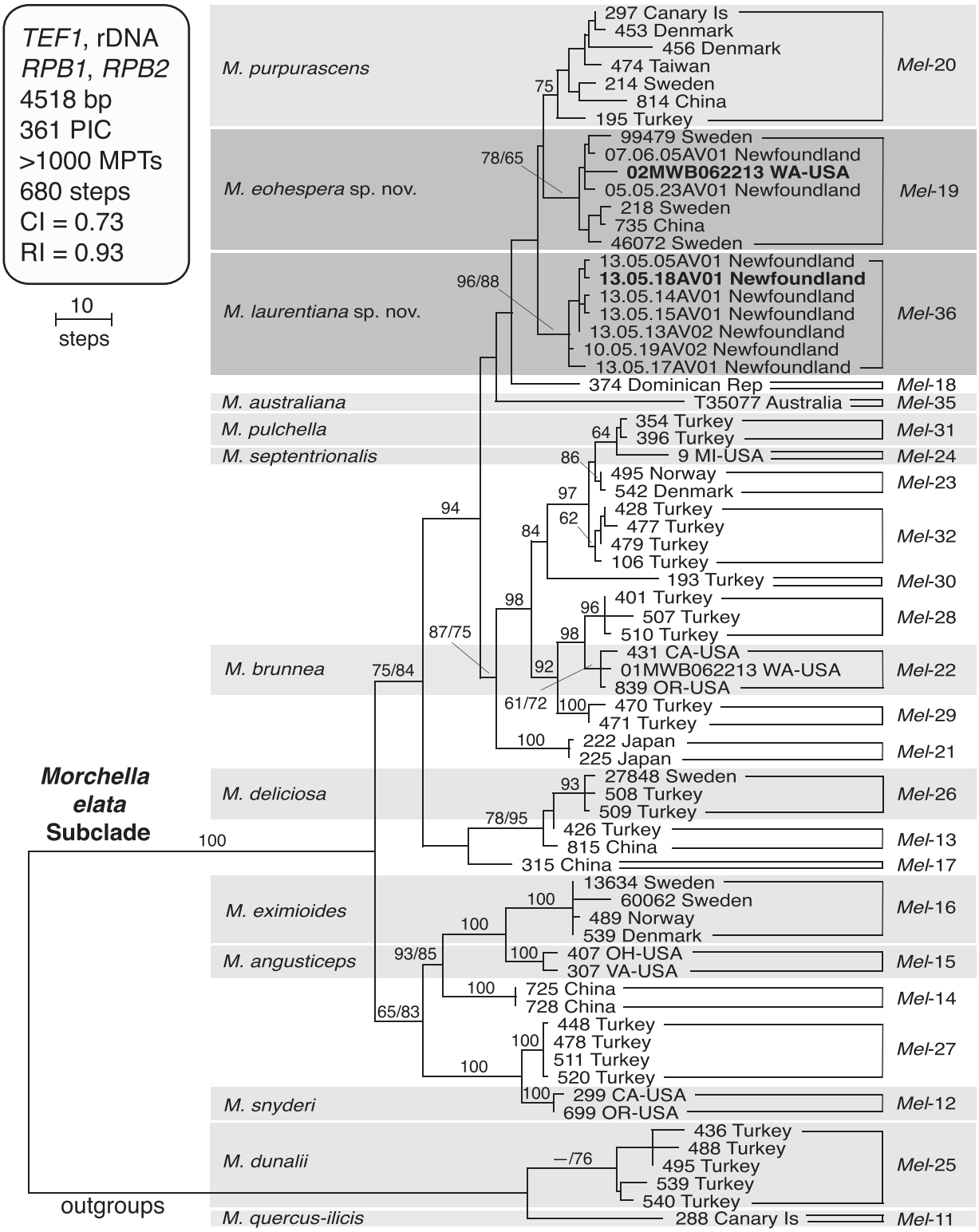
FIG. 1. Maximum-parsimony phylogenetic analysis of a four-gene dataset comprising 69 sequences representing 22 species within the *Morchella elata* clade. The phylogram is one of > 1000 most-parsimonious trees, which is rooted on sequences of



M. dunalii (*Mel*-25) and *M. quercus-ilicis* (*Mel*-11). Only the maximum likelihood bootstrap value (ML-BS) based on 1000 pseudoreplicates of the data is indicated above each node if it differed by ≤ 5% the MP-BS value. Otherwise, the ML-BS/MP-BS values are both indicated. The 22 species within the *M. elata* clade and the two outgroup species are identified by *Mel* followed by a unique Arabic number. Gray highlight is used to identify the 11 ingroup and two outgroup species that have been formally described. Holotype collections of *M. eosphera* and *M. laurentiana* are identified by bold type. CI = consistency index, PIC = parsimony informative character, RI = retention index.

FIG. 2. A–D. *Morchella eohespera*. E–H. *Morchella laurentiana*. A. Mature ascocarp. B. Macro lens view of pit, showing granular to downy surface. C. Clavate to capitate sterile hyphae on ridge. D. SEM of ascospore showing longitudinal striations and some transverse, interconnecting ridges. E. Holotype collection in grassy roadside with characteristic reflexed stipe. F. Macro lens view of pit with glabrous to finely granular surface. G. Sterile clavate to subcapitate hyphae on ridge. H. SEM of ascospore with longitudinal striations and some transverse, interconnecting ridges. Bars: A, E = 10 cm; B, F = 1 cm; C, D, G, H = 10 µm.

200–300 × 18–23 µm, cylindrical, straight to slightly sinuous, hyaline, thin-walled, eight-spored. Paraphyses 120–155 µm long × 4–6 µm wide at base, typically expanding to 9–12 µm at apex, length generally not exceeding asci, scattered, versiform, septate with terminal cell 40–70 µm long, terminal cell typically cylindrical to subclavate but sometimes capitate or lageniform, hyaline. Elements on sterile ridges 120–170 × 14–23 µm, straight to slightly sinuous, lanceolate, clavate, subcapitate or capitate, septate with a 60–90 µm long terminal cell filled with refractory material.

Distribution: Washington state, New Brunswick, Newfoundland and Labrador, Scandinavia, the Netherlands, Germany, Switzerland and China (FIG. 3).

Habitat: Moist, sandy, calcareous soil or calcareous bedrock, in grassy areas, 1–10 m from trees. Elevation ranged from near sea level (NL) to 1100 m (WA). Five sites were remote, unaltered by humans, and two NL sites were significantly affected by anthropogenic activity some decades earlier. At least four of the five wilderness sites were subject to natural disturbance through freeze-thaw heaving (two on limestone barrens) and flooding at spring thaw (two near river edge). Nearby trees were species of *Betula* and *Malus* (NB, NL), *Picea engelmannii* Parry ex. Engelm. (WA), *P. glauca* (Moench) Voss and *P. mariana* (Mill.) Britton Sterns & Poggenburg (NL), *P. rubens* Sarg. (NB), in addition to many shrub species of *Alnus*, *Amelanchier*, *Corylus*, *Salix* etc. (NB, NL), either alone or more commonly lining the edge of coniferous forests.

Season: May–Jun (Newfoundland); Jun (WA); Jul (Labrador). *Morchella eohespera* fruits in Apr in the central provinces of Yunnan, Sichuan and Gansu, China, whereas in northern Europe it fruits Apr–Jun (SUPPLEMENTARY TABLE I).

Additional collections studied: See SUPPLEMENTARY TABLE I.

Comments: Morchella eohespera can be distinguished from other morels in NL (i.e. *M. laurentiana* and *M. importuna*) in that it fruits later, prefers limestone barrens, has finely pruinose pits and sterile capitate elements on the ridges. It is the last morel to fruit in NL, beginning just after *M. laurentiana* has completed fruiting and about 1 wk before *M. importuna* is finished (Voitk et al. 2014). In WA *M. eohespera* differs from *M. brunnea* by the former's association with spruce rather than with hardwoods and later fruiting time than

FIG. 3. Known distribution of *Morchella eohespera* (■) and *M. laurentiana* (○) confirmed by DNA sequence data (TABLE I). *Morchella eohespera* is distributed across the temporal-boreal zone in Eurasia and North America. By contrast *M. laurentiana* is restricted to coastal areas around the St Lawrence River Basin in NL and NB.

other non-burn-site morels. These distinctions are an idealization, and a morphologic identification, both macro- and microscopic, remains problematic in these locations. In other locations with more species from the M. *elata* clade, even these distinctions may not hold. Therefore a partial DNA sequence from *RPB2* is required for a definitive identification.

Morchella laurentiana Voitk, Burzynski, O'Donnell, sp. nov. FIG. 2E–H

MycoBank MB812844

Typification: CANADA. Newfoundland and Labrador, Gros Morne National Park, Berry Hill Campground Road, 49°36′49″N, 57°55′26″W, 100 m, 18 May 2013, *Andrus Voitk* 13.05.18.av01 (**holotype** DAOM 631351). Ex-holotype culture: NRRL 66317.

Etymology: Latin for Laurentian, to indicate its distribution around the St Lawrence River Basin.

Diagnosis: Bluntly conical ascomata 15–140 mm tall; cap with 10–24 longitudinal ridges between rows of slightly irregular pits with a few diagonal cross ridges, attached to stipe with a distinct sulcus; ridges granular, darkening with age; pits glabrous, yellowish tan; cap and stem hollow; inner cavity covered with fine white granules; stipe often reflexed at the base. Ascospores 18.5–25.0 × 12.5–16.5 µm; ridges with cylindrical to clavate, rarely subcapitate elements. Fruiting singly or in small groups in early spring in grass on well-drained sandy soil over calcareous bedrock several meters from the forest edge on disturbed sites in the St Lawrence River Basin.

Macroscopic characters: Ascomata 15–140 mm tall. Cap hollow, oblong, bluntly conical to conical, 20–70 mm × 18–50 mm at widest point, pitted and ridged, attached to stipe with a white sulcus 2–4 mm deep and 3–4 mm wide, radial ridges occasionally span sulcus. Ridges 1–4 mm broad; 10–24 primary vertical ridges and a few shorter, secondary vertical ridges between rows of slightly irregular pits with a few sunken transecting ridges that are more or less vertical, granular rather than hirsute, "yellow ochre" to "orange citrine" initially, "Dresden brown" to "fuscous black" in age, flattened initially, becoming thin in age; transecting ridges not as dark as vertical ones. Pits primarily elongated vertically; glabrous or finely granular; "light buff to "olive buff" or "yellow ochre" initially, "snuff brown" in age; colors lighter when growing during prolonged rain. Stipe 15–70 mm tall, 4–24 mm wide, cylindrical to laterally compressed, usually widening at base with coarse ridges or folds reaching upper portion of stipe and extending across sulcus to hymenium, base often reflexed; hollow, inner surface white and finely granular, "white" to "cinnamon buff", 1–3 mm thick, becoming extensively enfolded and chambered at base with age. Context white.

Microscopic characters: Ascospores (288 spores, 16 ascocarps, 11 collections) 18.3–25.1 × (9.6—)12.1–16.4 µm, Q = 1.4–1.8 in water; ellipsoidal, hyaline, content homogeneous, polar oil drops absent, with longitudinal striae that converge at poles when viewed via SEM; ascospore wall up to 1 µm thick. Asci 200–300 × 17.5–27 µm, cylindrical, straight or slightly curved, hyaline, thin-walled, eight-spored. Paraphyses 120–160 long × 4.8–6.7 µm wide at base, expanding to 7.7–19.3 µm at apex, length generally not exceeding asci, scattered, versiform, terminal cell cylindrical, subclavate, to subcapitate; septate, terminal cell 40–70 µm long. Elements on sterile ridges 110–170 × 11.6–21.2 µm, straight to slightly curved, clavate, lanceolate to subclavate, rarely subcapitate, capitate elements absent; septate with a 60–80 µm long terminal cell, usually filled with refractory material.

Distribution: Known from the west coast of Newfoundland and the north shore of New Brunswick, both facing the Gulf of St Lawrence (FIG. 3).

Habitat: Grows on well-drained, open, grassy slopes on gravel roadsides and sand banks of glacial outwash 1–10 m from the edge of mixed coniferous forests, on limestone bedrock. The single NB site and all seven NL sites had been disturbed by human activity two or more decades before and now appear to be naturally or intentionally kept free of forest. Nearby trees were *Abies balsamea* (L.) Mill., *Betula cordifolia* Regel, *B. papyrifera* Marshall, *Malus* spp., *Picea glauca* (Moench) Voss, *P. mariana* (Mill.) Britton, Sterns & Poggenburg and *Thuja occidentalis* L., in addition to many shrub species of *Alnus*, *Amelanchier* and others. Of all these the shrubs were the closest to fruiting, but the coniferous forest the most consistent, absent only in two sites.

Season: Fruits throughout May in western NL (SUPPLEMENTARY TABLE I). South-facing slopes fruit before north-facing ones and yield slightly larger ascocarps.

Additional collections studied: See SUPPLEMENTARY TABLE I.

Comments: Morchella laurentiana can be distinguished from other morels in NL by its earlier fruiting, tolerance of non-limestone soils, preference for anthropogenically disturbed habitats, longer vertical ridges with fewer cross ridges, longer and glabrous pits and lack of capitate elements on the sterile ridges. In regions where such members of the *M. elata* clade as *M. angusticeps* and *M. septentrionalis* fruit in eastern North America (O'Donnell et al. 2011) DNA sequence data from *RPB2* is needed for a definitive identification.

DISCUSSION

A review of morel species in Newfoundland and Labrador (O'Donnell 2014) led to the discovery of two undescribed species, described in the present report. This limited geographic sampling suggests that future surveys throughout the provinces and territories of Canada might uncover additional novel species, in addition to extending our knowledge of the diversity and distribution of the genus. These two species illustrate two of the most fascinating aspects of morels: their uncanny likeness and distinctive distribution.

Size, shape, color and season make these two species difficult to tell apart, not only from each other but also from most recently identified species of the *M. elata* clade, such as *M. septentrionais* and *M. angusticeps*, and many others. Microscopic examination of these species is not reliable in separating them with certainty. Although we documented some capitate elements in the ridges of one species, they are uncommon and require a long search. Even the longitudinal ascospore striations in *M. eohespera* and *M. laurentiana* match those reported from collections reported as *M. elata* from North America and Europe, *M. esculenta* from North America (Malloch 1973) and *M. anatolica* from Turkey (Işiloğlu et al. 2010).

The most striking difference between our two species is the parochial nature of *M. laurentiana* contrasted to the cosmopolitan nature of *M. eohespera*. In addition, the two species also appear to fruit sequentially and prefer somewhat different habitats. All collections of *M. laurentiana* came from ground disturbed by humans. Some collections of *M. eohespera* also were found on anthropogenically disturbed soils, but the majority grew in natural sites. The wilderness sites for *M. eohespera* in NL were in areas where soil shifted from natural causes: either a sandy island in a river or on limestone barrens, where cryogenic cycles are known to produce significant shifts in the soil, gravel and sand.

The species differ in the degree of bootstrap support that they received in analyses of the combined dataset (FIG. 1). The parochial *M. laurentiana* received high bootstrap support (ML-BS/MP-BS = 98/88), while support for the cosmopolitan *M. eohespera* was only moderate (ML-BS/MP-BS = 78/65). One may speculate that its common regional climate and habitat, coupled with its putative small population limit evolutionary changes in *M. laurentiana*, while *M. eohespera*, dispersed globally, receives a wider range of habitat stimuli that might foster evolutionary change. Natural barriers between disparate genets may make exchange of genetic material difficult, resulting in increased geographic variation.

CONCLUSIONS

Two new species of morels were discovered from Newfoundland and Labrador. Although morphologically very similar, once identified, they showed marked differences in distribution and more subtle differences in other characters. Our study provides the necessary phylogenetic data to differentiate between them and sufficient discriminatory data to describe them formally here.

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