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Encalypta driva (sp. nov.) and its relationship to *E. vulgaris* in Scandinavia

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Encalypta vulgaris is well known for its wide morphological variation, here we study morphological and genetic variation of *E. vulgaris* in Scandinavia and compare this with the closely related *E. rhaptocarpa* and the morphologically similar *E. mutica.* Our morphological and genetic results indicate that Scandinavian plants of *E. vulgaris* s.l. includes two taxa, *E. vulgaris* s.s. and a new species here described as *E. driva*. The two species differ genetically by plastid markers while the included nuclear markers do not differentiate between the two. Morphologically they can be separated both by gametophytic and sporophytic characters. We also clarify the distinction between *E. mutica* and the newly described *E. driva* which have been confused in Scandinavia.

Keywords: integrative taxonomy, speciation, mountains, *Encalypta mutica*, threatened bryophytes

The Scandinavian bryophyte flora is still under exploration and new species are continuously discovered new for the region and described new for science (Draper and Hedenäs 2009, Høitomt et al. 2012, Hassel et al. 2014, 2018, Kyrkjeeide et al. 2015, Hedenäs 2018, 2020). The genus *Encalypta* Hedw. is no exception (Høitomt et al. 2016), the genus is easily recognized by the campanulate calyptra completely covering the capsule. Species are mostly easily separated, but the species boundaries in section *Rhabdotheca* have been pointed to as problematic (Horton 1983, Fedosov 2012). *Encalypta vulgaris* Hedw. belongs to section *Rhabdotheca* and is considered a southern species in Scandinavia reaching north to Gästrikland in Sweden and Trøndelag in central Norway (Söderström 1996, Hallingbäck et al. 2006). It is considered to be an easily recognized species in Scandinavia, only to be confused with *Encalypta mutica* I. Hagen from section *Pytomitrium*, with which it shares the obtuse leaves and lack of peristome. There are specimens named *E. vulgaris* from the Scandinavian mountains and northern Scandinavia, but these have by most authors been ignored and/or considered as doubtful and confused with *E. mutica* (Frisvoll and Blom 1997, Nyholm 1998, Hallingbäck et al. 2006).

Both *E. vulgaris* and *E. mutica* are declining in parts of their Scandinavian distribution. *Encalypta mutica* is considered vulnerable (VU) on the Swedish red list, due to declining populations and decreased quality of its habitat (Hallingbäck et al. 2020). It has the same red list category in Norway, the Norwegian population is evaluated to be rather stable, but with few individuals (Høitomt et al. 2021). In Finland it is evaluated as endangered (EN), only occurring close to the Swedish and Norwegian border in Enontekiön Lappi (Juutinen and Ulvinen 2017). *Encalypta mutica* is a rare northern species considered to be at risk of extinction in four out of the six European countries where it is recorded, and is evaluated as VU on the European red list (Hodgetts et al. 2019). *Encalypta vulgaris* on the other hand is evaluated as least concern (LC) in Sweden, but VU in Norway (Hallingbäck et al. 2020, Høitomt et al. 2021). The Norwegian population of *E. vulgaris* is declining due to change in habitat quality and loss of habitats due to various construction works, like building of roads, houses etc.

Most species of the genus *Encalypta* Hedw. prefer base-rich substrates that periodically dry out, and typically the leaves are lingulate with or without a hair point and have densely papillose cells. Globally, about 35 species are recognized (Frey and Stech 2009) and the highest species diversity is found in alpine regions of the northern hemisphere. In Europe, Hodgetts et al. (2020) recognized 15 species in the genus. This treatment follow the work of Fedosov (2012) on the problematic section *Rhabdotheca* where he suggested that

Encalypta obovatifolia Nyholm and *E. intermedia* Jur. should be treated as synonyms of the earlier name *E. pilifera* Funck, and advocated that *E. trachymitra* Ripart should be recognized at the species level. In addition, *Bryobrittonia longipes* (Mitt.) D.G. Horton in Encalyptaceae is known from arctic regions of Europe. All 15 *Encalypta* species and *B. longipes* are known from Scandinavia including Svalbard.

The taxonomic problems of section *Rhabdotheca* Müll. Hal., treated by Fedosov (Fedosov 2012), mainly focused on taxa with morphological similarity to *Encalypta rhaptocarpa* Schwägr. The problematic taxonomy around *E. vulgaris* is still not resolved (cf. Horton 1983). In Scandinavia *E. vulgaris* is recognized by its obtuse epilose leaves, smooth capsules without peristome and an entire to erose base of the calyptra (Nyholm 1998, Hallingbäck et al. 2006). The latter character state separates it from species in section *Pyramitrium* Wallr. ex Hampe (Horton 1982), which includes *E. mutica.* However, when the calyptra is missing as it often is at exposed alpine localities, it is more difficult to separate the two during field work. There are reports of *E. vulgaris* from the Scandinavian mountains, and it has been assumed that this probably is misidentified *E. mutica*. Also the fringes at the base of the calyptra of *E. mutica* are deciduous and can be missing late in the season (Hagen 1899). However, *E. mutica* can be distinguished by the densely papillose costa in upper part of the leaf, which is smooth or with projecting cell ends in *E. vulgaris*. Another character of 'doubtful' specimens is that the capsules often are striate, this is a character state shared with *E. rhaptocarpa* s.l. and one could suspect that the plants represent a form of this taxon with muticous leaves (cf. Gallego et al. 2018) and missing peristome.

The understanding of *E. mutica* is further confused by the descriptions and illustrations provided by Hassel and Høitomt (2016). Afonina and Cernyadjeva (1998) and Hallingbäck et al. (2006), as their illustrations of *E. mutica* show a calyptra with erose base rather than a regularly fringed base (Afonina and Czernyadjeva 1998), striate capsules (Hassel and Høitomt 2016), very strong costa of the leaves (Afonina and Czernyadjeva 1998, Hallingbäck et al. 2006) and the basal cells of the leaves form a strong border (Hallingbäck et al. 2006).

Reliable identification is crucial for correct evaluation of threat status and measures of management and conservation (Bickford et al. 2007). In this paper we clarify the distinction between *E. mutica* and other arctic-alpine taxa with muticous leaves and missing peristome. We investigate the phylogenetic relationship of *E. mutica*, *E. rhaptocarpa* and *E. vulgaris* s.l., based on molecular and morphological analyses we describe *E. driva* sp. nova. We also provide an English translation of the original description of *E. mutica* by Hagen (1898) with illustrations of the type specimen.

Methods

Material

Revision of specimens in herbarium TRH, TROM, BG and O was done to confirm morphological concepts of the included taxa. To reveal genetic relationships of the included taxa, molecular analyses were performed. For molecular analyses we selected 12 specimens of *Encalypta mutica* (n = 2), *E. vulgaris* (n = 2), *E. rhaptocarpa* (n = 2) and *E. driva* (n = 6). A list of included specimens for morphological and molecular analyses are provided in Appendix 1.

Molecular analysis

Encalypta mutica belongs to the section *Pyramitrium* while the other taxa to the section *Rhabdotheca*, thus we assumed that *E. mutica* would act as outgroup in the phylogenetic analysis. Genomic DNA was extracted with DNeasy Plant Mini Kit (Qiagen) according to manufacture protocol. We sequenced all 12 samples with forward and reverse primers for ITS (ITS1, 5.8 and ITS2), and five chloroplast loci (*rbcL*, *rps4*, *trnL–F*, *rpl16* and *trnG*, Appendix 2).

The multiple sequences alignment was performed using the Muscle (Edgar 2004) with visual inspection of the alignments. The phylogenetic analyses were conducted by using the neighbor-joining (NJ) and maximum likelihood (ML) algorithms implemented in MegaX (Kumar et al. 2018). The best fitted substitution model identified with the lowest Bayesian information criterion values for chloroplast and ITS nucleotide sequences were Tamura 3-parameter with a discrete Gamma distribution (+G) and Kimura 2-parameter with a discrete Gamma distribution (+G), respectively. Neighbor-joining analysis was performed based on p distance using the pairwise deletion of gaps. A bootstrap test with 1000 replicates was used to compute the statistical support for internal nods. The graphical representations of the trees (ML) and dendrograms (NJ) were generated with MegaX. A Neighbor-Net network was also conducted to illustrate the genetic relationships among specimens with SplitsTree4 (Huson and Bryant 2006).

Morphological analysis

To explore relative differences in morphology between *E. mutica*, *E. vulgaris*, *E. driva* and *E. rhaptocarpa* morphometric measurements of available specimens, mainly from herbarium TRH, of *E. mutica* (n = 49) and *E. vulgaris* s.l. (n = 104) were included (Appendix 1). For *E. rhaptocarpa* (n = 3) a selection of specimens to represent variation in ecology and distribution were included (Appendix 1). Based on the treatments of *Encalypta* by Horton (1983) and Fedosov (2012) morphological characters of the gametophyte and sporophyte were compared among plants (Table 1, first column lists included characters). Leaves, antheridia and archegonia as well as vaginula, capsule and spores were semi-permanently mounted in glycerol on microscope slides prior to examination. All measurements were taken using a transmission microscope and dissecting microscope, and photomicrographs were made applying a Leica Application Suite ver. 4.5.0 for stacking.

Results

Molecular results

The total aligned sequence length (bp) were 1066 and 2997 positions in the final ITS and combined chloroplast datasets, respectively (Appendix 2). All specimens were success-

Table 1. Morphological characters of the studied taxa.

Character	*E. driva*	*E. vulgaris* s.s.	*E. rhaptocarpa*	*E. mutica*
Plant size (mm)	1–5(–10)	2–10(–20)	2–20(–30)	1–3(–8)
Leaf				
Length (mm)	1.2–2.0(–3.0)	(1.4–)2.0–3.0	2.5–3.5	1.3–1.7(–2.3)
Ratio length/width	(1.5–)1.9–3.0(–3.5)	(2.3–)2.7–3.9(–4.5)	–	–
Shape	ovate-oblong	oblong	ovate-oblong	ovate-oblong
Apex	obtuse	obtuse	apiculate with hairpoint	obtuse
Marginal basal cells	border of 2–5 rows of elongate cells	border of 2–7 rows of elongate cells	border of 4–8 rows of elongate cells	border of 2–3 rows of elongate cells
Costa near apex, dorsal side	denticulate by projecting cell ends	denticulate by projecting cell ends	partly covered by papillae	partly covered by papillae
Vaginula upper part	triangular	triangular	triangular	narrow
Calyptra base	entire-erose	entire-erose	entire-erose	fringed
Capsule				
Surface	broadly and strongly striate to ribbed	smooth-faintly striate, rarely strongly striate	broadly and strongly striate to ribbed	smooth
Peristome	absent	absent	present	absent
Capsule mouth cells (µm)	12.5–17.5	15–25	–	–
Spores size (µm)	25–37	25.0–42.5	31–42	(21–)25–32
Ornamentation	papillose	papillose	papillose	very finely papillose

fully sequenced for all loci except that the ITS sequence for three specimens *Encalypta rhaptocarpa* (B-37814), *E. vulgaris* (B-675760) and *E. driva* (B-693623), were excluded from the analyses because of low quality chromatograms. The locus *rbcL* showed high degree of conserved sites (99%) compared to other chloroplast and ITS regions. The percentage of parsimony informative sites varied from 1% (4 sites) in *rbcL* to 6% in *rpl16* (49 sites) and 6% in *trnG* (33 sites), respectively. The ITS locus consisted of 13% (144 sites) variable sites in which most of them were singletons (10%, 108 sites). The NJ and ML analyses resulted in dendrograms with similar topologies and thus only the ML results are presented. Both nuclear and plastid loci confirm the placement of *E. mutica* section *Pyramitrium* as an outgroup (Fig. 1 and 2). The nuclear ITS locus resolved *E. rhaptocarpa* sister to a clade consisting of *E. vulgaris* and *E. driva* (Fig. 2). However, the combined plastid data (Fig. 1) show that *E. vulgaris* s.s. is sister to a clade consisting of *E. driva* and *E. rhaptocarpa*. Splits Tree analysis of the plastid data confirmed this pattern (Fig. 3).

Morphological results

The morphological characters evaluated for *E. driva*, *E. vulgaris*, *E. mutica* and *E. rhaptocarpa* are summarized in Table 1. The characters are illustrated and compared across the taxa in Fig. 4 and 5. The original description of *E. mutica* by Hagen (1899) is translated (below) and the lectoptype is illustrated (Fig. 9) to avoid further confusion with *E. driva*.

Discussion

Morphological traits combined with molecular data supports the interpretation that Scandinavian plants of *Enca-*

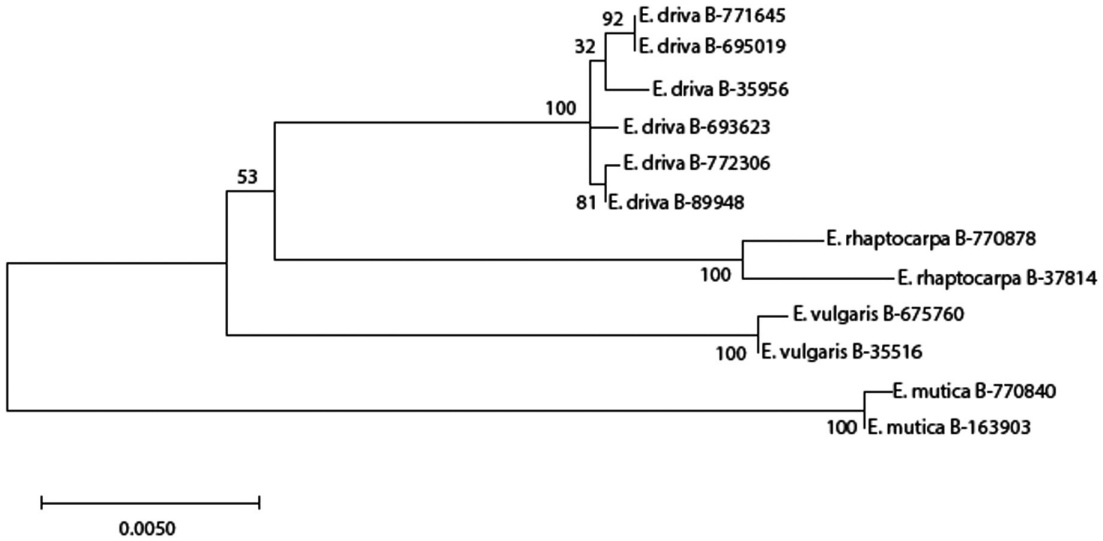

Figure 1. The maximum likelihood phylogenetic tree based on five chloroplast loci. Numbers indicate bootstrap support computed with 1000 replicates. The suffix after species name is the TRH herbarium number.

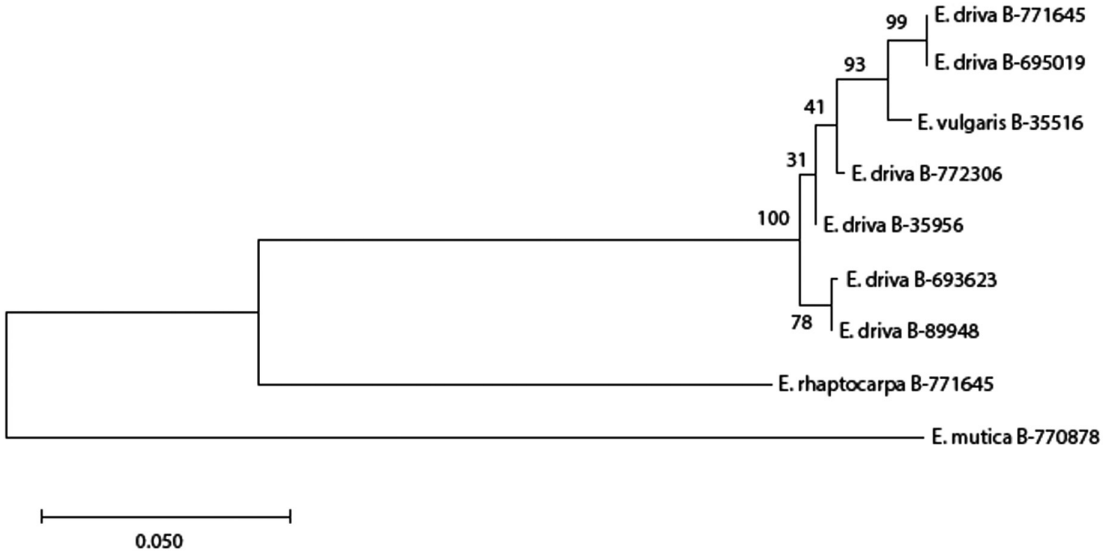

Figure 2. Maximum likelihood phylogenetic tree based on ITS loci. Numbers indicate bootstrap support computed with 1000 replicates. Three specimens are excluded from the three, see text for more detail. The suffix after species name is the TRH herbarium number.

lypta vulgaris s.l. consist of two taxa. *Encalypta vulgaris* s.s. with longly oblong leaves combined with faintly striate to smooth capsules and *E. driva* with ovate to shortly oblong leaves and striate capsules, described below.

The plastid molecular markers included in this study strongly support a clade of *E. driva* that is differentiated from *E. rhaptocarpa* and *E. vulgaris* but the low bootstrap value to the sister clade prevents us to conclude which is the closest clade (Fig. 1). Fedosov (2012) also found poor support for some of the clades in his study of section *Rhabtotheca*, but he only included *trnL–F* as a single marker. Our nuclear markers do not differentiate between *E. driva* and *E. vulgaris* but separates *E. rhaptocarpa* (Fig. 2). The different outcome based on the plastid and nuclear dataset could indicate a polyploid origin of *E. driva* (cf. Kyrkjeeide et al. 2019), where *E. driva* and *E. vulgaris* share the paternal ancestor but have different maternal ancestors for the plastid genome. Chromosome counts of *Encalypta vulgaris* show either n = 13, n = 26 or n = 39 (Fritsch 1982), this could mean events of polyploidisation, and this should be investigated in future studies to understand the speciation processes in *Encalypta* section *Rhabdotheca*. Most species in the genus *Encalypta* are monoecious and produce sporophytes regularly, but mixed stands of *E. vulgaris*/*E. rhaptocarpa* and *E. driva*/*E. rhaptocarpa* are observed and allopolyploidisation could be an important evolutionary process as in other moss genera (Meleshko et al. 2018).

The fact that *E. driva* often is found growing together with *E. rhaptocarpa* has led to suspicion that these plants could be an epilose form of *E. rhaptocarpa* (cf. Gal-

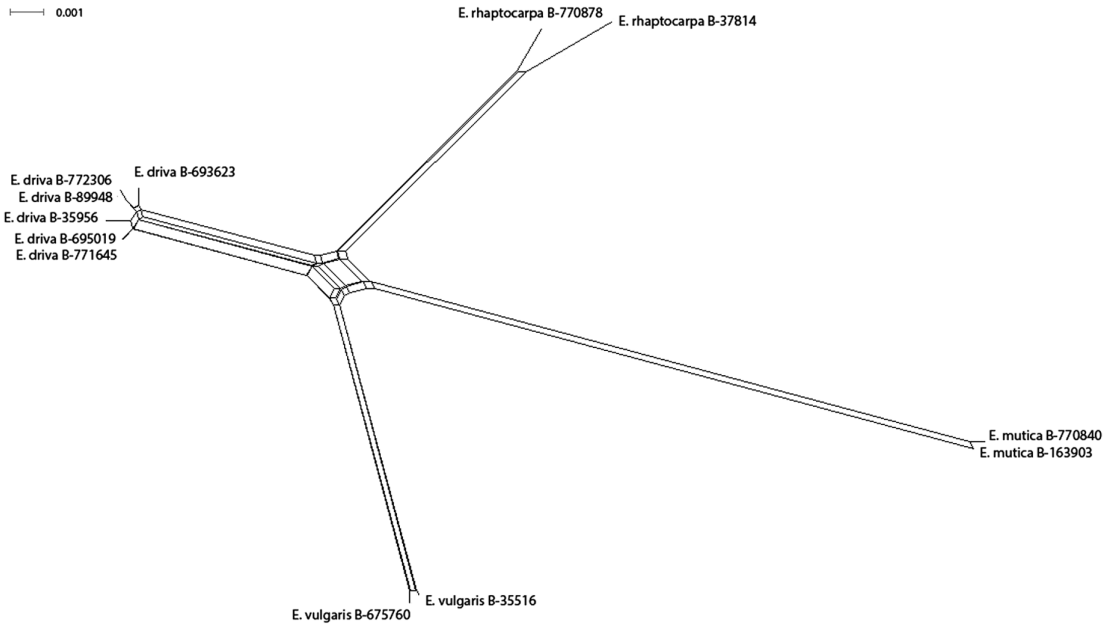

Figure 3. The neighbor-net network obtained from combined chloroplast loci.

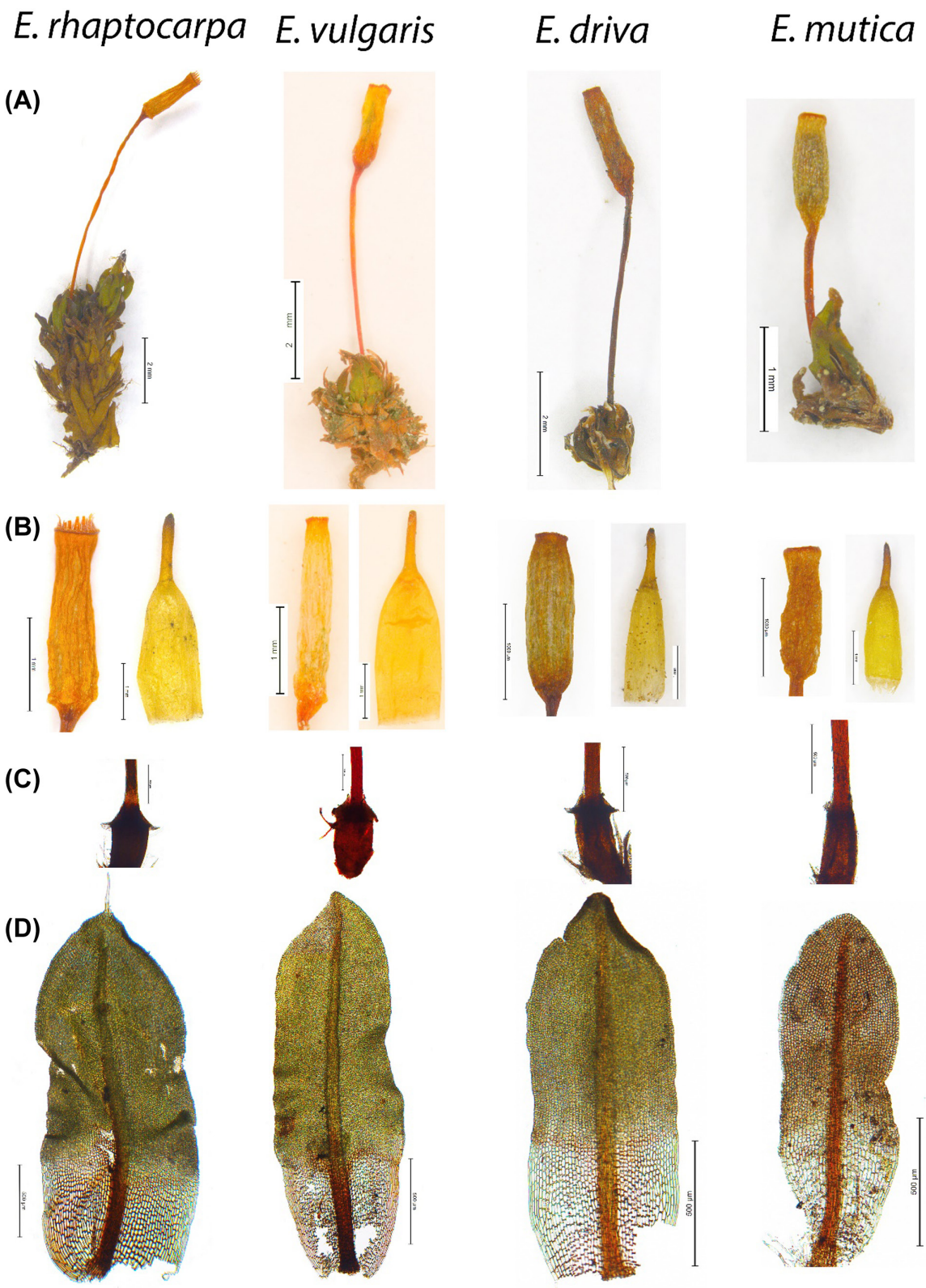

Figure 4. Characters distinguishing the four investigated taxa. (A) Shoots with sporophytes, (B) capsule and calyptra, (C) vaginula, (D) stem leaves. Scale bars: (A) 2 mm except *E. mutica* 1 mm; (B) 1 mm; (C and D) 500 µm. Illustrations of *E. rhaptocarpa* TRH-B-37814 (Dovre, Oppland), *E. vulgaris* TRH-B-35516 (Trondheim), *E. driva* shoot, calyptra TRH-B-35956 (Lom, Oppland), capsule, leaf TRH-B-92190 (Lom, Oppland), vaginula TRH-B-772306 (Storfjord, Troms), *E. mutica* shoot, capsule, vaginula, leaf TRH-B-163903 (Målselv, Troms), calyptra TRH-B-38364 (Trondheim, Trøndelag).

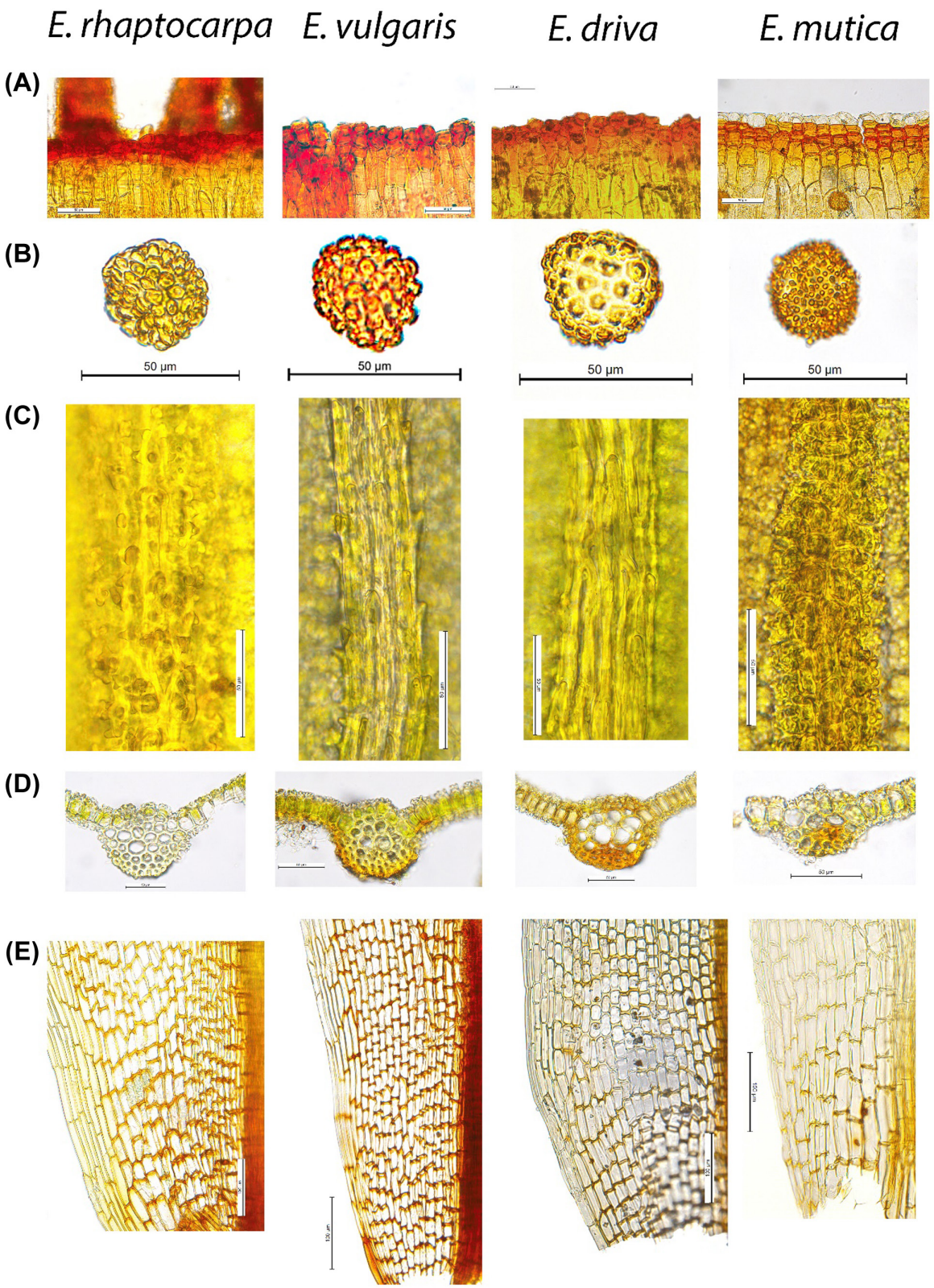

Figure 5. Characters distinguishing the four investigated taxa. (A) Mouth of capsule, (B) spores, distal surface, (C) dorsal side of costa near leaf apex, (D) transverse section of costa, (E) basal cells of leaves. Scale bars: (A, B, C, D) 50 µm; (E) 100 µm. Illustrations of *E. rhaptocarpa* TRH-B-37814 (Dovre, Oppland), *E. vulgaris* TRH-B-35516 (Trondheim), *E. driva* TRH-B-35956 (Lom, Oppland), *E. mutica* TRH-B-163903 (Målselv, Troms).

Figure 6. The type of *Encalypta vulgaris* from Hedwig's herbarium in Geneva. Catalogue des herbiers de Genève (CHG). Conservatoire & Jardin botaniques de la Ville de Genève. 10-03-2022 (<www.ville-ge.ch/musinfo/bd/cjb/chg>).

lego et al. 2018). However, both molecular and morphological results clearly suggest that it is separated from *E. rhaptocarpa*.

Encalypta driva is separated from *E. mutica* by several characters. In the field the entire to erose base of the calyptra and the longitudinal striate capsules are key characters. In *E. mutica* the base of the calyptra has triangular fringes, and the capsule is usually smooth. However, as Hagen (1899) mentioned in his type description, the fringes seem to be deciduous or are worn off by harsh weather conditions (Fig. 9I). In the microscope the species are easily separated by several characters like the leaf border in the leaf base, transverse section of the costa, papillosity of the costa near leaf apex and spore size and ornamentation (Fig. 5, Table 1). The morphological separation from *E. vulgaris* is more problematic in the field, as both have entire to erose base of the calyptra and muticous leaves, but the type of *E. vulgaris* has long capsules thar are rather smooth and it is a larger plant (Fig. 6). Ecologically *E. vulgaris* is a lowland plant with a southern distribution in Scandinavia, while *E. driva* occurs both in lowland and alpine habitats. The capsule mouth cells are 15–25 µm wide in *E. vulgaris* s.s., compared to 12.5–17.5 µm wide in *E. driva*. The leaves of *E. driva* are in general shorter and wider than those of *E. vulgaris*.

Taxonomy

Encalypta driva K. Hassel & Høitomt sp. nov. (Fig. 7, 8, 9)

Holotype: TRH-B-35956, Geitåtjønne, Hestbrepiggan, Lom, Oppland. Soil-covered, calcareous cliff, 1674 m a.s.l., leg. K. Hassel 31 Aug 2017. Isotypes: MHA and S.\

Etymology

Driva is a Gygir in Norse mythology, a female Jotne, and the daughter of Snø (Snow) who is the son of Frost.

Description

Plants small to medium sized 1–5(–10) mm.

Stems irregularly branched, with scattered brown, smooth rhizoids, central strand absent to weakly differentiated, stem cortex formed by 1–3 layers of small thick-walled cells.

Leaves shortly oblong-ovate, rarely longly oblong and undulate (Fig. 8); costa strong, ending before leaf apex, serrulate by protruding cell ends in upper part; costa with ± 3 layers of sterid cells; cells subquadrate, densely papillose in the upper part, rectangular and smooth in the basal part, 2–7 rows of elongate marginal cells in leaf base, forming a border.

Autoicous with a terminal perichaetium with one to several archegonia. Perichaetial leaves ovate obtuse, outer ones larger than stem leaves, inner ones smaller and more ovate. Perigonia each consisting typically of two leaves and one or several antheridia occur in leaf axils just below the perichaetium.

Seta yellow brown to brown. Vaginula in upper part umbrella like.

Capsule cylindrical, slightly to distinctly striate to ribbed, peristome absent, capsule mouth rimmed with 2–3 rows of rounded subquadrate cells.

Spores yellow brown, with few large papillae, on the distal surface 5–6 papillae across the spore, proximal surface only slightly papillose, striate to nearly smooth; spore diameter 25–37 µm.

Calyptra yellowish, base entire to erose.

Distribution

Southeastern Norway, mainly in the lowland Oslofjord area. The southern Scandinavian Mountain range including Jotunheimen and Dovrefjell, from Trøndelag and further north it is known from both lowland and mountain areas in Nordland and eastern part of Troms. In Finnmark it is known from the Alta area and the Varanger Peninsula. A revision of *E. vulagris* s.l. from northern latitudes and high elevations e.g. in the Alps, will probably result in a wider distribution.

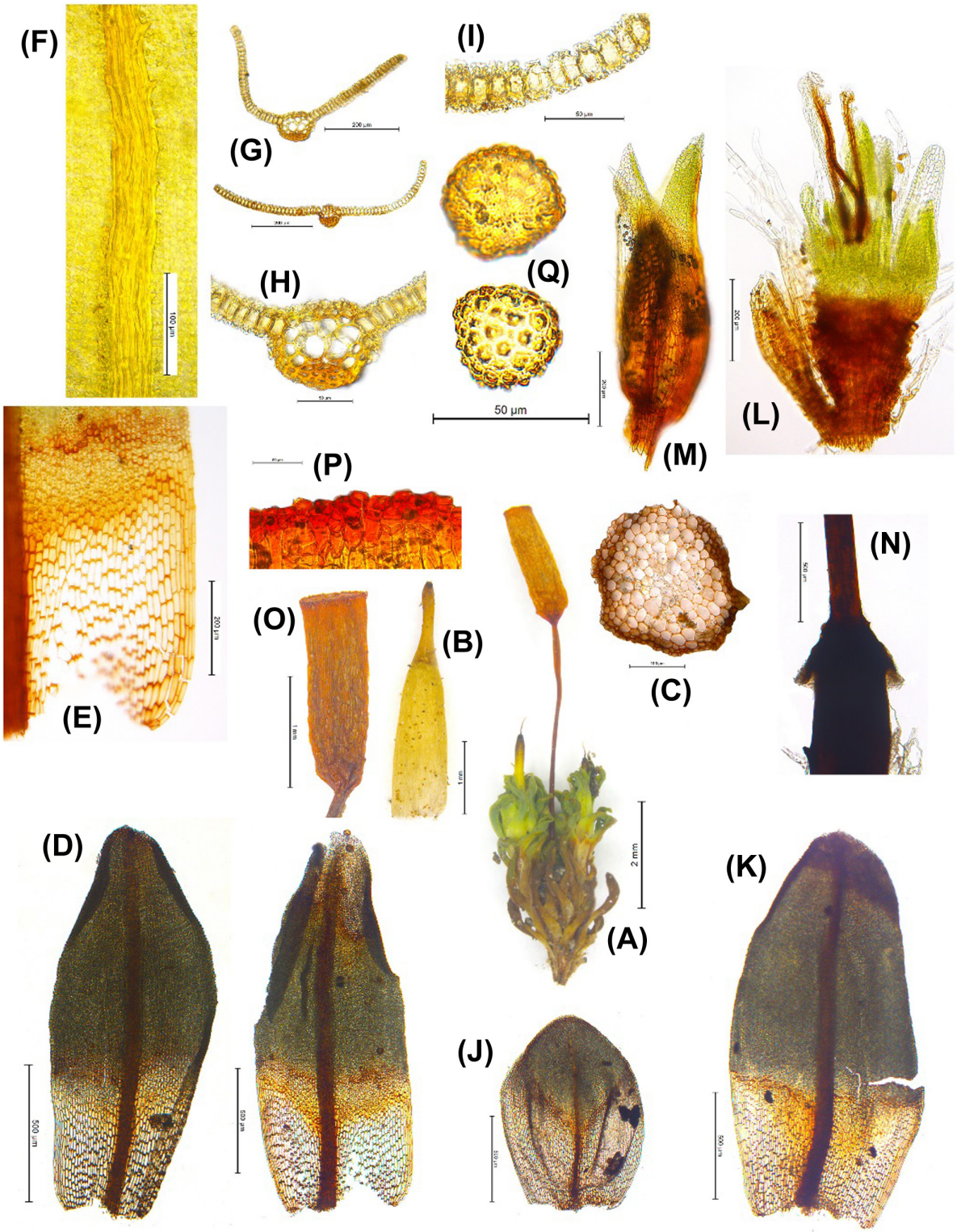

Figure 7. *Encalypta driva*. (A) shoot with sporophyte, (B) calyptra, (C) transverse section of stem, (D) two stem leaves, (E) basal leaf cells, (F) dorsal side of costa near leaf apex with projecting cells, (G) transverse section of leaves, (H) transverse section of costa, (I) leaf lamina cells in transverse section, (J) inner perichaetial leaf, (K) outer perichetal leaf, (L) perichaetium with archegonia, (M) perigonium with antheridia, (N) vaginula with seta attached, (O) capsule, (P) capsule mouth, (Q) spores from proximal and distal side. Scale bars: (A) 2 mm; (B, O) 1 mm; (D, J, K, N) 500 µm; (E, G, L, M) 200 µm; (F, C) 100 µm; (H, I, P, Q) 50 µm. All illustrations are made from the holotype TRH-B-35956.

Figure 8. Two leaves of *Encalypta driva* from a plant growing sheltered from wind, the leaves are longer and more undulate than typical leaves (holotype TRH-B-35956).

Habitat

Calcareous soil over cliffs, with some disturbance and little competition from other species.

Differentiation

Confusion is most likely towards *E. mutica* and *E. vulgaris* s.s. which both have obtuse leaves and capsules without peristome (Fig. 4). *Encalypta mutica* differs by papillose costa on dorsal side in upper part of leaf (Fig. 5C), only weakly differentiated border of elongated cells in basal part of leaf (Fig. 5E), narrow vaginula (Fig. 4C), capsule nearly smooth (Fig. 4B), spores with many small papillae (Fig. 5B) and calyptra with fringes at base (Fig. 4B). *Encalypta vulgaris* s.s. differs by its generally larger size, longer and more narrow leaves, smooth to finely striate capsules (Fig. 4B) and wider cells of the capsule mouth. One source of confusion towards *E. mutica* is that the vaginula of old sporophytes may have a cup-like appearance, but the vaginula is still thicker in upper part compared to *E. mutica* (Fig. 4C, 9).

Encalypta mutica I. Hagen, Tromsø Mus. Aarsh. 21: 91, 1899

Lectotype (selected by Horton 1983): TRH-B163895, Ladehammeren, Trondheim, Sør-Trøndelag, Norway. Northern exposed cliffs by the fjord, 10–20 m a.s.l., leg. I.S. Hagen 16 Aug 1895.

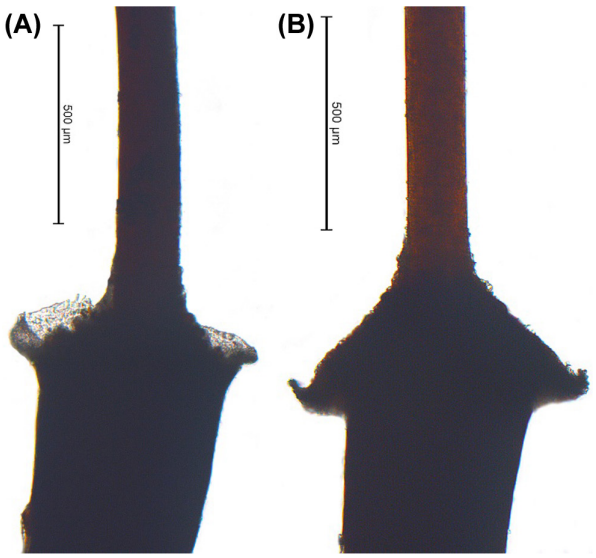

Figure 9. Vaginulas of *Encalypta driva*; old vaginula with a cup shape (A) and (B) a typical umbrella shaped young vaginula, both from the same plant (holotype TRH-B-35956).

In the protologue by Hagen there were no illustrations, but here we illustrate the lectotype in Fig. 10.

Translated original Latin description

Tufts dense, about 8 mm high, rusty red brown inside, green on the outside. Shoot branched, fertile innovations below apex, tomentum yellow-brown scattered. Stem red-brown, 0.17 mm thick, branches in central part 0.04 mm thick, outer cells small thick walled, leptodermis cells turgid. Leaves spreading, recurved, slightly undulate or erect and more lingulate or obovate-lanceolate, up to 2.3 mm long and 0.53–0.62 mm wide, apex rounded or widely triangular or rarely in the upper part quickly tapering, always very obtuse at apex, never with hair point, plane or canaliculated, margin above basal cells roughly papillose; cells in leaf base hyaline with brown walls, rectangular 0.07–0.11 mm long and 0.013–0.016 mm wide, smooth, thin, cells at leaf margin slightly narrower forming a weakly differentiated margin; mid leaf cell regularly hexagonal, 0.011–0.014 mm long and wide, more or less incrassate, papilla bi-trifid; costa with age brownish, 0.045–0.066 mm wide, ends below apex, dorsal papillae multifid low dense, in cross section with 2–4 guide cells and dorsal stereid band, ventral dorsal surface covered with papillose cells, dorsal cells often small, slightly incrassate, always papillose.

Inflorescence autoicous rarely synoicous. Male flower (antheridia) axillar, small, thin, gemmiform; perigonia with two leaves, ovate to ovate-lanceolate, obtuse, and with costa narrow towards apex, with age brownish; antheridia about 4, 0.58 mm long and 0.14 mm wide; paraphyses few, filiform, whitish. Perichaetial leaves, two loosely arranged leaves close to the archegonia, erect-spreading, widely rounded 1.8 mm long and 0.83 mm wide, triangular narrowed in the same way as the stem leaves. Archegonia ca 4–0.56 mm long; paraphyses few to numerous, narrow, almost hyaline.

Vaginula brownish-black, oval-conical, 0.85 mm high and 0.3 mm thick, not pileated, but membrane hyaline erect, forming a pot, glossy, deciduous; Ochrea (sheath) persistent. Seta 5–8 mm long, 0.3 mm wide, brown to dark brown,

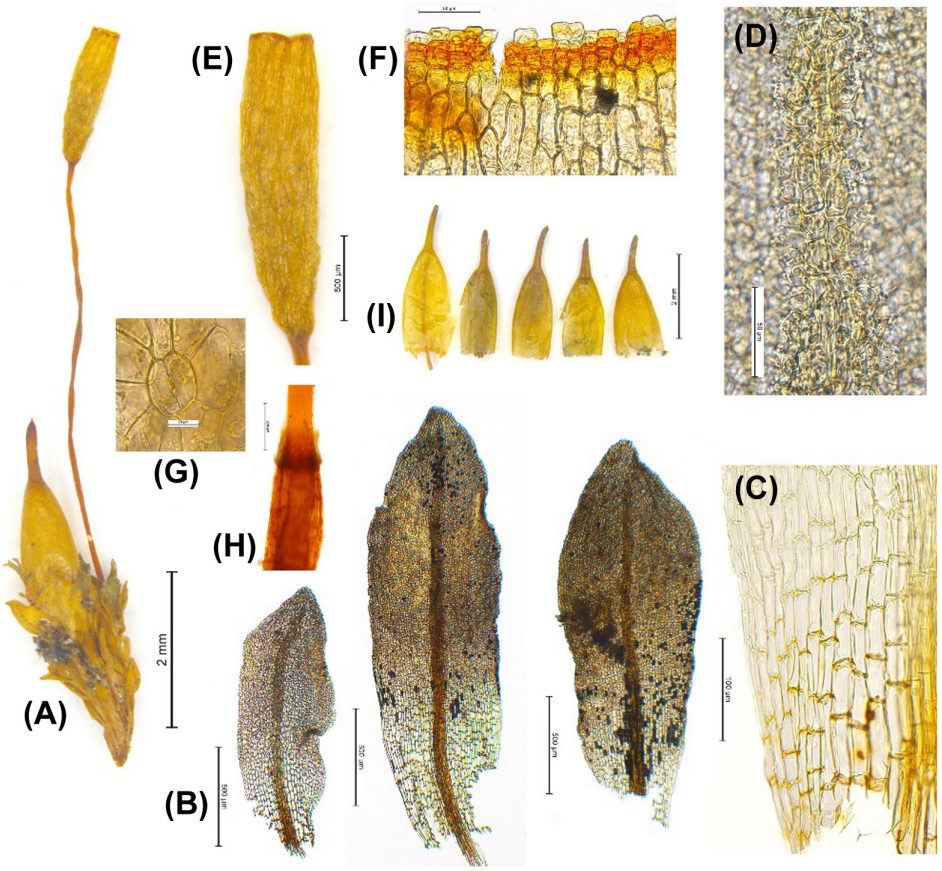

Figure 10. *Encalypta mutica* illustration of the lectotype TRH-B-163895. (A) Shoot with sporophyte, (B) three stem leaves, (C) basal leaf cells, (D) dorsal side of costa near leaf apex, (E) capsule, (F) capsule mouth, (G) stomata in lower half of capsule, (H) vaginula, (I) calyptras where the fringes partly have fallen of. Scale bars: (A) I 2 mm; (B, E) 500 µm; (H) 200 µm; (C) 100 µm; (D, F) 50 µm; (G) 20 µm.

twisted toward the left. Capsule cylindrical with short neck and slightly narrower opening, 2.1 mm long, 0.65 mm wide, brownish-yellow to brown, without longitudinal stria, when dry indistinctly wrinkled. Exothecial cells by the opening in two rows of sub-quadrate, minute, rectangular – rhomboid 0.08–0.11 mm long and 0.022–0.033 mm wide, thin walled. Stomata scattered in the lower part of the capsule, composed of hyaline cells, 0.044 mm long, 0.033 mm wide. Peristome absent. Annulus simple, persistent. Operculum 1.1 mm long, from the convex base forming a beak. Calyptra at the base of the capsule parallel, dirty white – yellowish, slightly shiny, base with narrow regular fringes, reddish brown later deciduous, upper half with scattered obtuse papillae, apex densely dentate rough. Spores 25–32 µm, nearly globose, brown, densely covered by moderate papilla.

Hagen (1899) reported *E. mutica* from four localities all in Norway; 1) Vårstigen, Oppdal, Sør-Trøndelag, leg. Kaurin 1886 (originally identified as *E. vulgaris*, TRH-B-163894); 2) Ladehammeren, Trondheim, Sør-Trøndelag, on chlorite schist, northern exposition, only a few m above the fjord, leg. Hagen 16.08.1895 (TRH-B-163895); 3) Nedre Bergulnesli Saltdal, Nordland, 100 m a.s.l. growing with *E. rhaptocarpa*, leg. Fridtz 02.08.1889; 4) north of Nedrevatnet, Vik, Skjerstad (currently Fauske municipality), Nordland, 100 m a.s.l. on soil over cliffs growing with *E. rhaptocarpa* leg. Hagen 17.08.1893 (TRH-B-163901).

Differentiation according to Hagen in the type description: *E. mutica* is closely related to *E. vulgaris*, but distinguished from it by the more obtuse leaves, the costa is much weaker and on the back very densely papillose, and a much smaller plant. The leaf base is consistently hyaline, while in *E. vulgaris* distinctly yellowish. The base of the seta has a hyaline, cup-shaped upward bent membrane. The seta is turned left, the calyptra has regular fringes at the base. The last feature is very similar to *E. ciliata*.

The first locality mentioned by Hagen (1899) in the protologue of *E. mutica* is Ladehammeren in Trondheim, Norway. This is a lowland locality by the fjord and Hagen describes the habitat as northern exposed cliffs. *Encalypta mutica* has been searched for at this locality, but without success (Frisvoll and Blom 1997). A lot of construction work and harbor development has taken place at Ladehammeren, and *E. mutica* is probably extinct at this locality. During the search for *E. mutica*, we have quite surprisingly, discovered populations of *E. vulgaris* at Ladehammeren (Hassel 2010).

Key to the species included in this study

1. Capsule and calyptra present 2
1. Sporophyte missing 5
2. Calyptra entire-erose, upper part of vaginula triangular ... 3
2. Calyptra fringed at base, upper part of vaginula narrow ..... *E. mutica*
3. Capsule strongly striate to ribbed, with peristome (well developed or not) ..... *E. rhaptocarpa*

3. Capsule smooth, striate or ribbed, peristome absent … 4
4. Capsule smooth-faintly and narrowly striate, capsule mouth cells 15–25 µm …….. *E. vulgaris* s.s.
4. Capsule broadly striate to ribbed, capsule mouth cells 12.5–17.5 µm …… *E. driva*
5. Leaves with hair point …….. *E. rhaptocarpa*
5. Leaves obtuse without hairpoint …….. 6
6. Costa on dorsal side with papillae in upper part … *E. mutica*
6. Costa on dorsal side shiny without papillae, but with denticulations formed by projecting cell ends, in upper part ……... 7
7. Plants normally 2–10 mm, leaves (1.4–)2–3 mm long, oblong, (2.3–)2.7–3.9(–4.5) times longer than wide…… *E. vulgaris* s.s.
7. Plants normally 1–5 mm, leaves 1.2–2(–3) mm long, ovate to shortly oblong, (1.5–)1.9–3.0(–3.5) times longer than wide…… *E. driva*

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Data availability statement

There are no additional data for this paper.

References

Afonina, O. M. and Czernyadjeva, I. V. 1998. New records of *Encalypta mutica* Hag. (Encalyptaceae, Musci) in Russia. – Lindbergia 23: 107–109.

Bickford, D., Lohman, D. J., Sodhi, N. S. et al. 2007. Cryptic species as a window on diversity and conservation. – Trends Ecol. Evol. 22: 148–155.

Draper, I. and Hedenäs, L. 2009. *Sciuro-hypnum dovrense* (Limpr.) Draper et Hedenas comb. nov., a distinct Eurasian alpine species. – Cryptog. Bryol. 30: 289–299.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. – Nucleic Acids Res. 32: 1792–1797.

Fedosov, V. E. 2012. *Encalypta* sect. *Rhabdotheca* in Russia. – Arctoa 21: 101–112.

Frey, W. and Stech, M. 2009. Marchantiophyta, Bryophyta, Anthocerotophyta. – In: Frey, W. (ed.), Syllabus of plant families, 13th edn. Part 3. Bryophytes and seedless vascular plants. Schweizerbart, pp. 9–263.

Frisvoll, A. A. and Blom, H. H. 1997. Trua mosar i Noreg med Svalbard. Førebelse faktaark. – NTNU, Vitenskapsmuseet Botanisk notat, pp. 1–170.

Fritsch, R. 1982. Index to plant chromosome numbers – Bryophyta. – Frans A. Stafleu.

Gallego, M. T., Hugonnot, V. and Cano, M. J. 2018. Taxonomic resurrection of an awnless variety of *Syntrichia ruralis* and comparison with other European muticous taxa in this genus. – J. Bryol. 40: 244–250.

Hagen, I. 1899. Musci Norvegiae Borealis. Bericht über die im nördlichen Norwegen hauptsächlich von den herren Arnell, Fridtz, Kaalaas, Kaurin, Ryan und dem herausgeber in den jahren 1886–1897 gesammelten laubmoose. – Tromsø Mus. Aarsh. 21–22: 1–382.

Hallingbäck, T., Lönnell, N., Weibull, H. et al. 2006. Nationalnyckelen till Sveriges flora och fauna. Bladmossor: Sköldmossor – blåmossor. Bryophyta: Buxbaumia – Leucobryum. – ArtDatabanken, SLU.

Hallingbäck, T., Lönnell, N., Weibull, H. et al. 2020. Rödlista 2020 – expertkommitén för mossor. – In: Eide, W. (ed.), Rödlistade arter i Sverige 2020. SLU Artdatabanken, pp. 59–66.

Hassel, K. 2010. Mosefloraen på Ladehalvøya, Trondheim kommune. – NTNU Vitenskapsmuseet Rapport Botanisk Serie, pp. 1–19.

Hassel, K. and Høitomt, T. 2016. Buttklokkemose *Encalypta mutica* I. Hagen. – <www.artsdatabanken.no/Pages/139404>.

Hassel, K., Appelgren, L., Blom, H. H. et al. 2014. *Colura calyptrifolia* a new oceanic liverwort to Norway and Scandinavia. – Lindbergia 37: 1–5.

Hassel, K., Kyrkjeeide, M. O., Yousefi, N. et al. 2018. *Sphagnum divinum* (sp. nov.) and *S. medium* Limpr. and their relationship to *S. magellanicum* Brid. – J. Bryol. 40: 197–222.

Hedenäs, L. 2018. *Oncophorus demetrii*, a fifth Scandinavian species of *Oncophorus* (Musci) possible to recognize by morphology. – Lindbergia 41: linbg.01098.

Hedenäs, L. 2020. Disentangling Scandinavian species hidden within *Meesia uliginosa* Hedw. s.l. (Bryophyta, Meesiaceae). – Lindbergia 2020: linbg.01125.

Hodgetts, N., Blockeel, T., Konstantinova, N. A. et al. 2019. *Encalypta mutica*. The IUCN Red List of threatened species 2019. – IUCN.

Hodgetts, N. G., Söderström, L., Blockeel, T. L. et al. 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. – J. Bryol. 42: 1–116.

Horton, D. G. 1982. A revision of Encalyptaceae I. – J. Hattori Bot. Lab. 53: 365–418.

Horton, D. G. 1983. A revision of Encalyptacea II. – J. Hattori Bot. Lab. 54: 353–532.

Huson, D. H. and Bryant, D. 2006. Application of phylogenetic networks in evolutionary studies. – Mol. Biol. Evol. 23: 254–267.

Høitomt, T., Appelgren, L., Lönnell, N. et al. 2012. *Pyramidula tetragona* (Brid.) Brid. rediscovered in Fennoscandia and new to Norway. – Lindbergia 35: 33–39.

Høitomt, T., Brynjulvsrud, J. G., Hassel, K. et al. 2016. Frostklokkemose *Encalypta brevipes* ny for Norges fastland på to lokaliteter i Lom i Oppland. – Blyttia 74: 35–38.

Høitomt, T., Hassel, K., Blom, H. H. et al. 2021. Rødlistekomiteen for moser. Norsk rødliste for arter 2021. – Artsdatabanken.

Juutinen, R. and Ulvinen, T. 2017. Suomen sammalien levinneisyys eliömaakunnissa 7. – <www.ymparisto.fi/fi-FI/Luonto/Lajit/Lajiensuojelutyo/Eliotyoryhmat/Sammaltyoryhma/Suomen_sammalet>.

Kumar, S., Stecher, G., Li, M. et al. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. – Mol. Biol. Evol. 35: 1547–1549.

Kyrkjeeide, M. O., Hassel, K., Aguero, B. et al. 2019. *Sphagnum x lydiae*, the first allotriploid peatmoss in the northern hemisphere. – Bryologist 122: 38–61.

Kyrkjeeide, M. O., Hassel, K., Stenøien, H. K. et al. 2015. The dark morph of *Sphagnum fuscum* (Schimp.) H.Klinggr. in Europe is conspecific with the North American *S. beothuk*. – J. Bryol. 37: 251–266.

Meleshko, O., Stenøien, H. K., Speed, J. D. M. et al. 2018. Is interspecific gene flow and speciation in peatmosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits? – Lindbergia 41: linbg.01107.

Nyholm, E. 1998. Illustrated flora of Nordic mosses. Fasc. 4. Aulacomniaceae, Meesiaceae, Catoscopiaceae, Bartramiaceae, Timmiaceae, Encalyptaceae, Grimmiaceae, Ptychomitriaceae, Hedwigiaceae, Orthotrichaceae. – Nordic Bryological Society.

Söderström, L. (ed.) 1996. Preliminary distribution maps of bryophytes in Nortwestern Europe. Vol. 2 Musci (A–I). – Mossornas Vänner.

Appendix 1. List of studied specimens.

Mol. data	Type	Herb.	Regnr	Taxon name	Leg., date	Locality	Municipality, province/ county, country
		TRH	89910	*Encalypta driva*	T. Høitomt & T. Blindheim, 20160806	Øst for Altaelva, sør for Joatkajohka	Alta, Finnmark, Norway
1		TRH	89948	*Encalypta driva*	T. Høitomt et al., 20160813	Sandfjord	Båtsfjord, Finnmark, Norway
		TRH	723485	Encalypta driva	I. Hagen, 18930813	Salten, Fauske, Hankabakken	Fauske, Nordland, Norway
		TRH	723489	*Encalypta driva*	F.E. Conradi, 18930812	Salten, ved Lommi-Javre	Fauske, Nordland, Norway
1		TRH	693623	*Encalypta driva*	K. Hassel, 20100616	Grimsdalen	Dovre, Oppland, Norway
		TRH	93713	*Encalypta driva*	T. Høitomt & A.Thylén, 20170816	Geitåbotn	Lom, Oppland, Norway
		TRH	35906	*Encalypta driva*	K. Hassel, 20170830	Geitåholet-Geitåtjønne, Hestbrepiggan.	Lom, Oppland, Norway
1	Holotype	TRH	35956	*Encalypta driva*	K. Hassel, 20170831	Geitåholet-Geitåtjønne, Hestbrepiggan.	Lom, Oppland, Norway
		TRH	89980	*Encalypta driva*	T. Høitomt & K. Hassel, 20160814	Vesterelva, sør for brua, opp mot Fanthaugen	Vardø, Finnmark, Norway
		TRH	92190	*Encalypta driva*	T. Høitomt et al., 20140904	Høyrokampen – ovenfor Hansbue	Lom, Oppland, Norway
		TRH	693447	*Encalypta driva*	K. Hassel, 20060816	Ved Bøvertun	Lom, Oppland, Norway
		TRH	89518	*Encalypta driva*	A. Breili, 20140601	Leirdalskampen, SV for	Ringebu, Oppland, Norway
		TRH	89543	*Encalypta driva*	A. Breili, 20140707	Siplaus	Vågå, Oppland, Norway
		TRH	93850	*Encalypta driva*	T. Høitomt, 20170921	Øyadalen – sør for Vakkerdalshøin	Vågå, Oppland, Norway
		TRH	5058	*Encalypta driva*	K. Hassel, 20020627	Unndalen, Trongberget	Oppdal, Sør-Trøndelag, Norway
		TRH	691654	*Encalypta driva*	Geir Gaarder, 20090717	Loapmi sør	Kåfjord, Troms, Norway
		TRH	773980	*Encalypta driva*	Geir Gaarder, 20120812	Rihpogaisa	Storfjord, Troms, Norway
1		TRH	772306	*Encalypta driva*	K. Hassel & I.H. Kålås, 20120813	Skibotn. Nuortavággi, S of Buoidenjunni	Storfjord, Troms, Norway
		O	2555605	*Encalypta driva*	E. Jørgensen, 18930722	Venetvara	Nordreisa, Troms, Norway
		O	2554144	*Encalypta driva*	M. Kleiven, 19520624	Ved Sendnes	Vågå, Oppland, Norway
		TRH	695041	*Encalypta driva*	K. Hassel, 20080703	Hjartøya	Steinkjer, Nord-Trøndelag, Norway
1		TRH	695019	*Encalypta driva*	K. Hassel, 20090508	Hovedøya	Oslo, Norway
1		TRH	771645	*Encalypta driva*	T. Høitomt & S. Reiso, 20111117	Ørstvetøya. Skrentene vest på halvøya	Porsgrunn, Telemark, Norway
		TRH	92760	*Encalypta driva*	T. Høitomt et al., 20150902	Jønndalen	Vågå, Oppland, Norway
		TRH	690470	*Encalypta driva*	K. Hassel & K.I. Flatberg, 20070614	Estenstadmarka, Bjønnåsen	Trondheim, Sør-Trøndelag, Norway
		TRH	3618	*Encalypta driva*	K. Hassel, 20130811	Åbakken, Nordherad	Vågå, Oppland, Norway
		TRH	3624	*Encalypta driva*	K. Hassel, 20130811	Valbjør, Nordherad	Vågå, Oppland, Norway
		TRH	36140	*Encalypta driva*	T. Høitomt, 20120804	Bøverdalen, nord-øst for Sulheim.	Lom, Oppland, Norway
		TRH	89489	*Encalypta driva*	A. Breili et al., 20140427	Bergevika S	Ringsaker, Hedmark, Norway
		TRH	93307	*Encalypta driva*	A. Breili, 20140510	Grefsheimberget	Ringsaker, Hedmark, Norway
		TRH	108716	*Encalypta driva*	A. Fjellberg, 20170615	Bøvertunsvatn, S-sida	Lom, Oppland, Norway
		TRH	674944	*Encalypta driva*	H. H. Blom, 20110831	Hellerfjellet.	Rana, Nordland, Norway

	TRH	11025	*Encalypta driva*	K. Hassel, T. Høitomt, 20150409	Nakkholmen	Oslo, Oslo fylke, Norway
	TRH	771618	*Encalypta driva*	T. Høitomt & U. Jansson, 20111103	Malmøya. Sørvestre del av øya	Oslo, Oslo fylke, Norway
	TRH	771655	*Encalypta driva*	T. Høitomt & K. A. Lye, 20111124	Bygdøy, Frognerkilen. N for Oscarshall	Oslo, Oslo fylke, Norway
	TRH	771659	*Encalypta driva*	T. Høitomt & K. A. Lye, 20111124	Bygdøy, Frognerkilen. N for Oscarshall	Oslo, Oslo fylke, Norway
	TRH	772791	*Encalypta driva*	T. Høitomt & K. A. Lye, 20120320	Rambergøya, sørsiden av øya	Oslo, Oslo fylke, Norway
	TRH	116885	*Encalypta driva*	K. Hassel	Varanger	Vardø, Finnmark, Norway
	TRH	38560	*Encalypta driva*	S. Reiso, 20140514	Heistadbukta.	Porsgrunn, Telemark, Norway
	TRH	3337	*Encalypta driva*	S. Reiso et al., 20120813	Spireodden	Asker, Akershus, Norway
	TRH	163914	*Encalypta driva*	E. Ryan, 18870515	Onsö: Fjelle	Fredrikstad, Østfold, Norway
	TRH	37128	*Encalypta driva*	T. Høitomt & T. Blindheim, 20130507	Fornebu, Rolfstangen friområde	Bærum, Akershus, Norway
1	TRH	675760	*Encalypta vulgaris* Hedw.	T. Høitomt et al., 20121018	Jønnevall S	Skien, Telemark, Norway
1	TRH	35516	*Encalypta vulgaris* Hedw.	K. Hassel, 20170911	Ladehammeren	Trondheim, Sør-Trøndelag, Norway
	TRH	730450	*Encalypta vulgaris* Hedw.	P. Hempel, 18700417	Lgl: [=Langeland]	Fyn, Denmark
	TRH	39535	*Encalypta vulgaris* Hedw.	Aug. Hesselbo, 19050514	Zealand: dike at Boserup, west of Roskilde.	Sjælland, Denmark
	TRH	89494	*Encalypta vulgaris* Hedw.	A. Breili, 20140510	Grefsheimberget	Ringsaker, Hedmark, Norway
	TRH	89622	*Encalypta vulgaris* Hedw.	A. Breili, 20140510	Grefsheimberget	Ringsaker, Hedmark, Norway
	TRH	89623	*Encalypta vulgaris* Hedw.	A. Breili, 20140510	Grefsheimberget	Ringsaker, Hedmark, Norway
	TRH	89488	*Encalypta vulgaris* Hedw.	A. Breili, 20150504	Helgeberget NV	Ringsaker, Hedmark, Norway
	TRH	772915	*Encalypta vulgaris* Hedw.	T. Høitomt & S. Reiso, 20120605	Helgeberget, sør på holmen	Ringsaker, Hedmark, Norway
	TRH	108426	*Encalypta vulgaris* Hedw.	T. Høitomt & K. Heistad, 20180621	Tomasodden	Gran, Oppland, Norway
	TRH	3350	*Encalypta vulgaris* Hedw.	S. Reiso, 20130906	Brandbu kirke S	Gran, Oppland, Norway
	TRH	92327	*Encalypta vulgaris* Hedw.	A. Breili, 20150329	Vistehorten NR	Vågå, Oppland, Norway
	TRH	695032	*Encalypta vulgaris* Hedw.	K. Hassel, 20990508	Hovedøya	Oslo, Oslo fylke, Norway
	TRH	163916	*Encalypta vulgaris* Hedw.	F. E. Conradi, 18890428	Frogner	Oslo, Oslo fylke, Norway
	TRH	163918	*Encalypta vulgaris* Hedw.	N. Bryhn, 18750000	Kristiania	Oslo, Oslo fylke, Norway
	TRH	771614	*Encalypta vulgaris* Hedw.	T. Høitomt & U. Jansson, 20111103	Malmøya. Sørvestre del av øya	Oslo, Oslo fylke, Norway
	TRH	692172	*Encalypta vulgaris* Hedw.	K. Hassel, 20090604	Ladehammeren, S-vendt berg v/Norcem	Trondheim, Sør-Trøndelag, Norway

	TRH	695035	*Encalypta vulgaris* Hedw.	K. Hassel, 20080703	Hjartøya, S-sida	Steinkjer, Nord-Trøndelag, Norway
	TRH	692186	*Encalypta vulgaris* Hedw.	K. Hassel, 20090604	Ladehammeren	Trondheim, Sør-Trøndelag, Norway
	TRH	773335	*Encalypta vulgaris* Hedw.	K. Hassel et al., 20121017	Gjermundsholmen	Bamble, Telemark, Norway
	TRH	36088	*Encalypta vulgaris* Hedw.	T. Høitomt et al. 20121017	Sylterøya, vest på øya.	Porsgrunn, Telemark, Norway
	TRH	771631	*Encalypta vulgaris* Hedw.	T. Høitomt & S. Reiso, 20111116	Langesund. Steinvika NR	Bamble, Telemark, Norway
	TRH	3339	*Encalypta vulgaris* Hedw.	S. Reiso, 20120802	Fugleøya V	Larvik, Vestfold, Norway
	TRH	36049	*Encalypta vulgaris* Hedw.	T. Høitomt et al. 20121016	Gunnekleivfjorden Ø, ved inngangen til nedlagt jernbanetunnel.	Porsgrunn, Telemark, Norway
	TRH	91766	*Encalypta vulgaris* Hedw.	T. Høitomt, 20140512	Trosvik, ved Blekebakken, rett øst for eksisterende 2-felts E18	Porsgrunn, Telemark, Norway
	TRH	112467	*Encalypta vulgaris* Hedw.	J. G. Brynjulvsrud, 20190618	Bø, nordre	Skien, Telemark, Norway
	TRH	773264	*Encalypta vulgaris* Hedw.	K. Hassel et al., 20121016	Ø for Herøya, Gunnekleivfjorden	Porsgrunn, Telemark, Norway
	TRH	773274	*Encalypta vulgaris* Hedw.	K. Hassel et al., 20121016	Jernbanebrua til Herøya, Gunnekleivfjorden	Porsgrunn, Telemark, Norway
	TRH	773277	*Encalypta vulgaris* Hedw.	K. Hassel et al., 20121016	Ørstvedthalvøya	Porsgrunn, Telemark, Norway
	TRH	12558	*Encalypta vulgaris* Hedw.	T. Høitomt et al., 20160506	Nedre Ljøsne N	Lærdal, Sogn og Fjordane, Norway
	TRH	12563	*Encalypta vulgaris* Hedw.	T. Høitomt et al., 20160507	Nedre Ljøsne N	Lærdal, Sogn og Fjordane, Norway
	TRH	35612	*Encalypta vulgaris* Hedw.	H. H. Blom, 20170510	Lustrafjorden. Between Helvetesberget and Sauadrogi, Gaupne	Luster, Sogn og Fjordane, Norway
	TRH	163915	*Encalypta vulgaris* Hedw.	I. Hagen, 18850405	Kongssten, østre Fredrikstad	Fredrikstad, Østfold, Norway
	TRH	93310	*Encalypta vulgaris* Hedw.	A. Breili, 20140516	Lillelien	Asker, Akershus, Norway
	TRH	674775	*Encalypta vulgaris* Hedw.	T. Høitomt & S. L. Olsen, 20110415	Bili. Skråning ned mot hovedveien.	Hole, Buskerud, Norway
	TRH	37024	*Encalypta vulgaris* Hedw.	T. Høitomt & S. Reiso, 20130604	Lille Svartøya Ø	Hole, Buskerud, Norway
	TRH	772799	*Encalypta vulgaris* Hedw.	T. Høitomt, 20120323	Solbergfjellet, i den bratte, sørvendte lia	Drammen, Buskerud, Norway
	TRH	37032	*Encalypta vulgaris* Hedw.	T. Høitomt & S. Reiso, 20130603	Pålerud SV	Hole, Buskerud, Norway
	TRH	771620	*Encalypta vulgaris* Hedw.	T. Høitomt, 20111109	Konglungen. Spirebukta	Asker, Akershus, Norway
	TRH	3343	*Encalypta vulgaris* Hedw.	S. Reiso, 20130524	Brattstad Ø	Ringerike, Buskerud, Norway
	TRH	37250	*Encalypta vulgaris* Hedw.	T. H. Hofton, 20120813	Spirodden NR	Asker, Akershus, Norway
	TRH	163919	*Encalypta vulgaris* Hedw.	I. Hagen, 18980530	Eker, Lilleby	Øvre Eiker, Buskerud, Norway

	TRH	3342	*Encalypta vulgaris* Hedw.	S. Reiso, 20120828	Borgenvika S	Hole, Buskerud, Norway
	TRH	4021	*Encalypta vulgaris* Hedw.	T. Høitomt, 20111202	Storøya, skrenten helt vest på øya	Hole, Buskerud, Norway
	TRH	36441	*Encalypta vulgaris* Hedw.	L. Appelgren et al., 20111015	Bili, 100 m sør for	Hole, Buskerud, Norway
	TRH	37017	*Encalypta vulgaris* Hedw.	T. Høitomt & S. Reiso, 20130604	Bønsnestangen	Hole, Buskerud, Norway
	TRH	37242	*Encalypta vulgaris* Hedw.	T. H. Hofton & S. Reiso, 20120827	Herøya S	Hole, Buskerud, Norway
	TRH	92442	*Encalypta vulgaris* Hedw.	T. Høitomt & K. Hassel, 20150409	Husbergøya	Nesodden, Akershus, Norway
	TRH	163917	*Encalypta vulgaris* Hedw.	F. E. Conradi, 18880527	Asker	Asker, Akershus, Norway
	TRH	694307	*Encalypta vulgaris* Hedw.	K. Hassel, 20110505	Burudåsen	Hole, Buskerud, Norway
	TRH	694310	*Encalypta vulgaris* Hedw.	K. Hassel, 20110505	Burudåsen	Hole, Buskerud, Norway
	TRH	771579	*Encalypta vulgaris* Hedw.	T. Høitomt et al. 20111024	Bili. Rett sør for gården	Hole, Buskerud, Norway
	TRH	104980	*Encalypta vulgaris* Hedw.	C. Sandberg, 1924	Bohuslän. Tanum. På .... vid Kuserö.	Bohuslän, Sweden
	TRH	82495	*Encalypta vulgaris* Hedw.	K. Johansson, 1888	Visby, Fröborg	Gotland, Sweden
	TRH	97613	*Encalypta vulgaris* Hedw.	B. Pettersson, 19340331	Gotland, Västerhejde sn., Hallbrosslott	Gotland, Sweden
	TRH	730454	*Encalypta vulgaris* Hedw.	E. Hjertman, 1913	Hönö, vid Fotösund	Göteborg, Sweden
	TRH	730455	*Encalypta vulgaris* Hedw.	O. J. Hasslow, 19140430	Scania: Hanaskog	Skåne, Sweden
	TRH	730456	*Encalypta vulgaris* Hedw.	A. Arvén, 1887	Jönköping, Östra Kyrkogården	Småland, Sweden
	TRH	39932	*Encalypta vulgaris* Hedw.	Erik Evers, 19240525	Sörmland: Andervik i Vagnhärads sn.	Södermanland, Sweden
	TRH	730453	*Encalypta vulgaris* Hedw.	K. Fr. Thedenius, 1840	Stockh. [=Stockholm], Skanstull	Södermanland, Sweden
	TRH	730457	*Encalypta vulgaris* Hedw.	O. Gjærevoll, 19440527	Ved Ekeby, Uppsala	Uppland, Sweden
	TRH	112297	*Encalypta vulgaris* Hedw.	C. Osc. Hamnström, ca 1875	Ostrogothiæ.	Östergötland, Sweden
	TRH	37814	*Encalypta rhaptocarpa* Schwägr.	K. Hassel, 20160804	Geitberget by Hjerkinn	Dovre, Oppland, Norway
1	TRH	772910	*Encalypta rhaptocarpa* Schwägr.	T. Høitomt & S.L. Olsen, 20120602	Vikerkilen NV	Hvaler, Østfold, Norway
1	TRH	770878	*Encalypta rhaptocarpa* Schwägr.	K. Hassel, 20110606	Station Linné	Öland, Sweden
	TRH	82478	*Encalypta mutica* I. Hagen	D.G. Horton, 19770723	Whirlpool Canyon: At confluence of Coal & Liard Riv. 41.4 mi. NW of Liard Riv. crossing at Liard Hot Springs	British Columbia, Canada

	TRH	692699	*Encalypta mutica* I. Hagen	K. Hassel & T. Prestø, 20090818	Zackenberg, by the research station, Wollastone Forland	Greenland
	TRH	163905	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19830810	N for Joatkajåkka	Alta, Finnmark, Norway
	TRH	163907	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19830818	Mazejåkka	Kautokeino, Finnmark, Norway
	TRH	163906	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19830814	Mazeniilasajåkka	Kautokeino, Finnmark, Norway
	TRH	163908	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19830815	Mazeniilasjåkka	Kautokeino, Finnmark, Norway
	TRH	163904	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19830817	Virdneguoika	Kautokeino, Finnmark, Norway
	TRH	163910	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19830815	Virdneguoika	Kautokeino, Finnmark, Norway
	TRH	723487	*Encalypta mutica* I. Hagen	E. Ryan, 18940724	Porsangerfjord, Kolvik	Porsanger, Finnmark, Norway
Paralectotype	TRH	163901	*Encalypta mutica* I. Hagen	I. Hagen, 18930817	juxta Nedrevand	Fauske, Nordland, Norway
	TRH	92076	*Encalypta mutica* I. Hagen	T. Høitomt et al., 20140806	Junkerdalen	Saltdal, Nordland, Norway
	TRH	163899	*Encalypta mutica* I. Hagen	I. Hagen, 18920829	Vik	Saltdal, Nordland, Norway
	TRH	163900	*Encalypta mutica* I. Hagen	I. Hagen, 18920829	Vik	Saltdal, Nordland, Norway
	TRH	163902	*Encalypta mutica* I. Hagen	I. Hagen, 18920821	Strömsnæsset	Sørfold, Nordland, Norway
	TRH	163898	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19820624	Otersjøen, nordsida	Lierne, Nord-Trøndelag, Norway
	TRH	3990	*Encalypta mutica* I. Hagen	T. Høitomt, 20130917	Brennberget NV, ovenfor Aunet	Verdal, Nord-Trøndelag, Norway
	TRH	3094	*Encalypta mutica* I. Hagen	T. Høitomt, 20130709	Lieslia skytefelt	Dovre, Oppland, Norway
	TRH	690684	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19730721	Nordfjorden NE, Kapp Wijk. Crevice in Kongressfjellet E of Oxaashytta	Dickson Land, Svalbard, Norway
	TRH	66591	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19730721	Nordfjorden NØ. Kapp Wijk. Bekkekløft i Kongressfjellet Ø for Oxaashytta (Gryta).	Dickson Land, Svalbard, Norway
	TRH	66592	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19730721	Nordfjorden NØ. Kapp Wijk. Bekkekløft i Kongressfjellet Ø for Oxaashytta (Gryta).	Dickson Land, Svalbard, Norway
	TRH	66593	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19730707	Nordfjorden. Kapp Wijk, Varm bekkekløft Ø for Oxaashytta (Gryta).	Dickson Land, Svalbard, Norway
	TRH	690683	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19740719	Kongsfjorden, Lovénøyane, Juttaholmen	Oscar II Land, Svalbard, Norway
	TRH	47811	*Encalypta mutica* I. Hagen	H.H. Blom, 19850527	Hommelvik, Høgbydalen sydøstre del, kalkberg ved veien.	Malvik, Sør-Trøndelag, Norway
	TRH	163892	*Encalypta mutica* I. Hagen	I. Hagen, 19030825	Losløkken	Oppdal, Sør-Trøndelag, Norway
	TRH	163897	*Encalypta mutica* I. Hagen	I. Hagen, 19030825	Loslökken	Oppdal, Sør-Trøndelag, Norway
	TRH	163896	*Encalypta mutica* I. Hagen	I. Hagen, 19030712	Nestavollan	Oppdal, Sør-Trøndelag, Norway

	Paralectotype	TRH	163894	*Encalypta mutica* I. Hagen	C. Kaurin, 18860000	Vaarstien	Oppdal, Sør-Trøndelag, Norway
		TRH	164295	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19930904	Vinstradalen	Oppdal, Sør-Trøndelag, Norway
	Paralectotype	TRH	47771	*Encalypta mutica* I. Hagen	Chr. Kaurin, 18860000	Vst. [= Vårstigen]	Oppdal, Sør-Trøndelag, Norway
	Lectotype	TRH	163895	*Encalypta mutica* I. Hagen	I. Hagen, 18950816	Ladehammeren	Trondheim, Sør-Trøndelag, Norway
		TRH	38364	*Encalypta mutica* I. Hagen	E. Værnes, 20171021	Storbranden	Trondheim, Sør-Trøndelag, Norway
		TRH	163893	*Encalypta mutica* I. Hagen	I. Hagen, 18880713	Trondhjem, bag K. sten	Trondheim, Sør-Trøndelag, Norway
		TRH	773673	*Encalypta mutica* I. Hagen	T. Høitomt et al., 20120814	Sinaidvárri	Kåfjord, Troms, Norway
1		TRH	163903	*Encalypta mutica* I. Hagen	A.A. Frisvoll, 19850607	Finnbrua	Målselv, Troms, Norway
		TRH	773910	*Encalypta mutica* I. Hagen	T. Høitomt & K. Hassel, 20120813	Luhcavarri N	Storfjord, Troms, Norway
		TRH	93752	*Encalypta mutica* I. Hagen	T. Høitomt et al., 20170826	Stoalpojeakkit	Storfjord, Troms, Norway
1		TRH	770840	*Encalypta mutica* I. Hagen	K. Hassel, 20110605	Resmo	Öland, Sweden
		TRH	119985	*Encalypta mutica* I. Hagen	K. A. Lye & T. Høitomt, 20130807	Oppland: Vågå k.: Vistdal, ovanfor hovudvegen	Vågå, Innlandet, Norway
		TRH	671076	*Encalypta mutica* I. Hagen	G. Gaarder, 20060914	Breidvaelva ved Valosen nær Bertnes	Bodø, Nordland, Norway
		TRH	89980	*Encalypta mutica* I. Hagen	T. Høitomt & K. Hassel, 20160814	Vesterelva, sør for brua, opp mot Fanthaugen	Vardø, Finnmark, Norway
		TRH	93752	*Encalypta mutica* I. Hagen	T. Høitomt & A. Breili, et al., 20170826	Stoalpojeakkit	Storfjord, Troms, Norway
		TRH	121474	*Encalypta mutica* I. Hagen	K. Hassel & T. Høitomt, 20130923	Ven, S for gården.	Melhus, Sør-Trøndelag, Norway
		TRH	38820	*Encalypta mutica* I. Hagen	G. Gaarder & O. Olsen, 20160705	Svartvika ved Muruvika.	Malvik, Sør-Trøndelag, Norway
		TRH	37604	*Encalypta mutica* I. Hagen	K. Hassel, 20150604	Bergsåsen by Navlus	Snåsa, Nord-Trøndelag, Norway
		TRH	112627	*Encalypta mutica* I. Hagen	K. Hassel, 20180520	Storbranden, N side of Ratåsdalen.	Trondheim, Sør-Trøndelag, Norway
		O	40739	*Encalypta mutica* I. Hagen	A. Pedersen, 19790921	S-enden av Tisjøen	Eidsvoll, Akershus, Norway
		BG		*Encalypta mutica* I. Hagen	E. Jørgensen, 18880701	Talvik	Alta, Finnmark, Norway
		TROM	10041	*Encalypta mutica* I. Hagen	A.A. Frisvoll & A. Elvebakk, 19850706	Kirkesdalen, Finnbru, nedest i Iselvdalen	Målselv, Troms, Norway
		TROM	10040	*Encalypta mutica* I. Hagen	A. Elvebakk, 19830818	Vir'dnejaroaivos S, A-sida	Kautokeino, Finnmark, Norway

Appendix 2. The primer sequences and number of specimens, the number of variable and parsimony informative sites for chloroplast and ITS loci.

Locus	Primer name	Sequence (5′–3′)	GeneBank accession no.	Reference	No. of sequences	Aligned sequence length (bp)	Singleton variable sites	Parsimony informative sites
ITS	ITS5-bryo	GGAAGGAGAAGTCGTAACAAGG	ON603580-ON603588	Stech 1999	9	1068	108	36
	ITS4R	TCCTCCGCTTATTGATATGC		Stech 1999				
rbcL	rbcl-aF	ATGTCACCACAAACAGAG	ON528145-ON528156	Miwa et al. 2009	12	551	2	4
	rbcl-aR	CTTCTGCTACAAATAAGAATGGATCTG		Miwa et al. 2009				
rps4	rps4_rps5'	ATGTCCCGTTATCGAGGACCT	ON528157-ON528168	Souza-Chies et al. 1997	12	617	1	15
	rps4_trnS	TACCGAGGGTTCGAATC		Souza-Chies et al. 1997				
trnL-F	trnF	ATTTGAACTGGTGACACGAG	ON548434-ON548445	Taberlet et al. 1991	12	509	2	23
	trnC	CGAAATCGGTAGACGCTACG		Taberlet et al. 1991				
rpl16	rpl16_F71	GCTATGCTTAGTGTGTGACTCGTT	ON548446-ON548457	Jordan et al. 1996	12	787	6	49
	rpl16R	GTAATCCAAGCTGGTTCAAGTGC		Olsson et al. 2009				
trnG	trnGF	ACCCGCATCGTTAGCTTG	ON548458-ON548469	Pacak and Szweykowska-Kulinska 2000	12	533	4	33
	trnGR	GCGGGTATAGTTTAGTGG		Pacak and Szweykowska-Kulinska 2000				