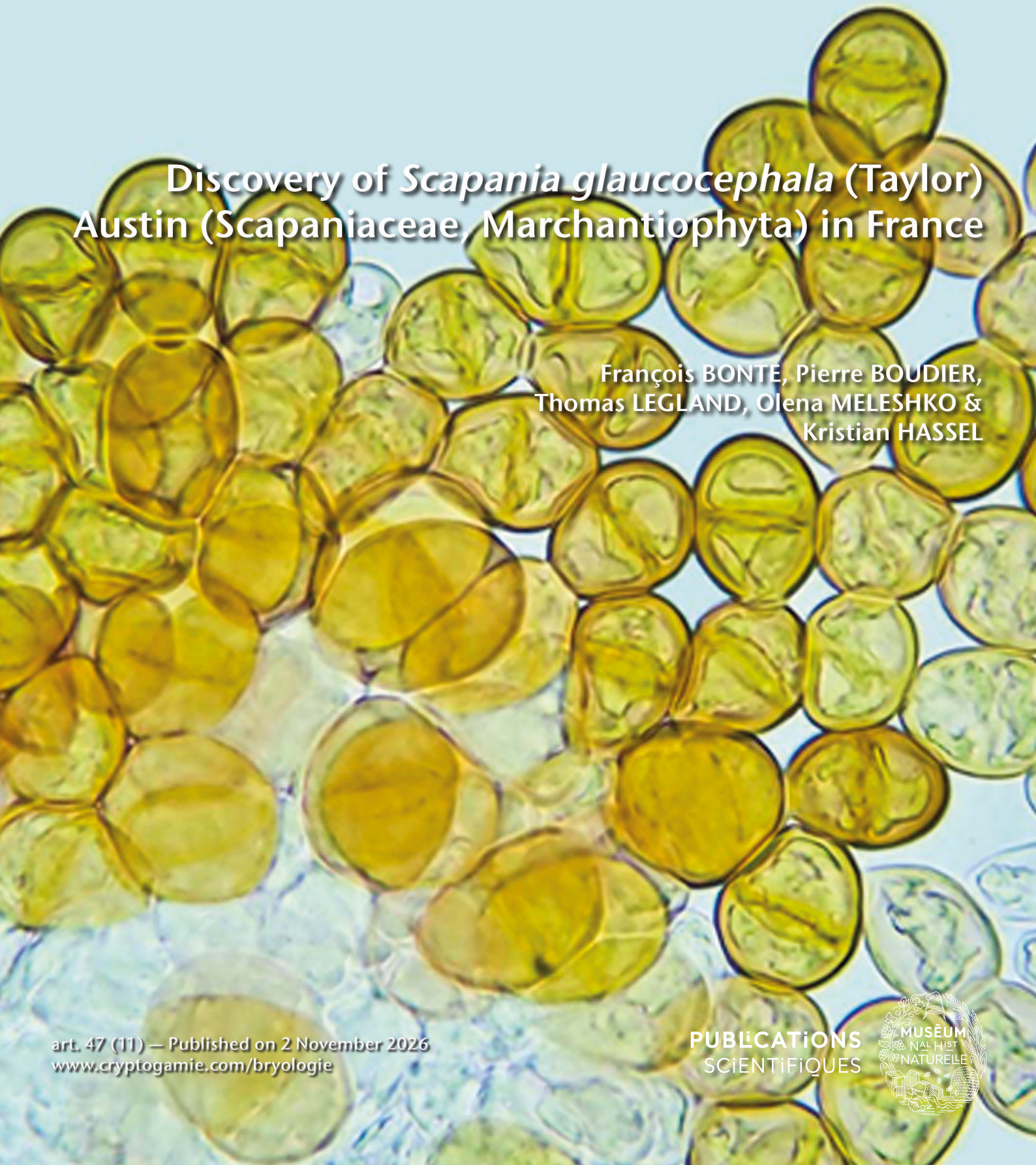
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Discovery of *Scapania glaucocephala* (Taylor) Austin (Scapaniaceae, Marchantiophyta) in France

François BONTE, Pierre BOUDIER, Thomas LEGLAND, Olena MELESHKO & Kristian HASSEL



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Discovery of *Scapania glaucocephala* (Taylor) Austin (Scapaniaceae, Marchantiophyta) in France

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ABSTRACT
Scapania glaucocephala (Taylor) Austin, first described from North America, is a very rare liverwort in Europe, now recorded for the first time in France in the Alps and the Jura. We discuss the nomenclatural history and taxonomic status of this species and similar small *Scapania* (Dumort.) Dumort. taxa with red-brown gemmae growing on decaying wood. We provide genetic data suggesting that most of French samples of *S. glaucocephala* are different from Scandinavian specimens designated by this same name, with the exception of two French samples. The status of the Scandinavian taxon is still to be resolved. A description of the French samples of *S. glaucocephala* with photographic plates is provided, as well as data on distinctive characters, distribution and ecology.

KEY WORDS
Liverworts, rare species, red list, conservation, biogeography, Europe, new record.

RÉSUMÉ

Découverte de Scapania glaucocephala *(Taylor) Austin (Scapaniaceae, Marchantiophyta) en France.*

Scapania glaucocephala (Taylor) Austin, une hépatique très rare en Europe, est signalée pour la première fois en France, dans les Alpes et le Jura. Nous abordons l'histoire nomenclaturale et le statut taxinomique de cette espèce et d'autres petits *Scapania* (Dumort.) Dumort. similaires à propagules rouge-brun poussant sur le bois en décomposition. Nous fournissons des données génétiques suggérant que la plupart des échantillons français de *S. glaucocephala* diffèrent de ceux ayant été désignés sous ce même nom en Scandinavie, à l'exception de deux spécimens français. Le statut du taxon scandinave reste à définir. Une description des échantillons français de *S. glaucocephala*, accompagnée de planches photographiques est fournie ainsi que des données sur leurs caractères distinctifs, leur répartition et leur écologie.

MOTS CLÉS
Hépatiques, espèces rares, liste rouge, conservation, biogéographie, Europe, nouveau signalement.

INTRODUCTION

In the French Alps and the Jura, the forest ravines of the montane level are habitats of great interest for many bryophytes, offering conditions of low light and high humidity that are particularly favorable to their growth and development. Recent targeted surveys of wet decaying wood along streams at the bottom of such ravines have already revealed the presence of two small, rare epixylic liverworts of the genus *Scapania* (Dumort) Dumort.: *S. apiculata* Spruce and *S. carinthiaca* J.B.Jack ex Lindb (Boudier *et al.* 2018; Bonte *et al.* 2020). During the follow up of these surveys, an additional small *Scapania* species resembling *S. glaucocephala* (Taylor) Austin was recorded.

Scapania glaucocephala was described by Taylor (1846) under the name *Jungermannia glaucocephala* based on specimens from western North America (Schuster 1974) and was then placed in the genus *Scapania* by Austin (1876). It was first reported in Europe from Russia close to the Finnish border by Buch & Fagerström (1946). They considered the possibility that their specimen could belong to *Scapania vexata* (C. Massal.) Buch, now considered a synonym to *Scapania scapanioides* (C. Massal.) Grolle. They argue that the non gemmiferous leaves were almost as long as wide, and the cells of the leaf margin were similar in size to other leaf cells, which indicated that their specimen belonged to *S. glaucocephala*. They suggested that *S. vexata* (syn. *S. scapanioides*) has leaves that are longer than wide and leaf marginal cells that are larger than other leaf cells (Buch & Fagerström 1946).

Scapania scapanioides was described by Massalongo on the basis of Italian specimens under the name *Jungermannia scapanioides* (Massalongo 1879). This taxon is considered by some authors to be a species morphologically distinct from *S. glaucocephala* (Buch & Fagerström 1946; Schuster 1974; Grolle 1976; Grolle & Long 2000) or a variety of *S. glaucocephala* (Schumacker & Váňa 2005; Damsholt 2009), while other authors consider the two to be identical (Müller 1951; Potemkin 1998; Köckinger 2017; Kropik & Zechmeister 2023). Müller studied *S. glaucocephala* using specimens from three North American sites and one Finnish site, two Italian specimens of *S. vexata* (syn. *S. scapanioides*) collected by Massalongo, and two specimens from the Swiss Jura. Müller (1951) concluded that there was no difference in leaf shape or cell structure between the two species and proposed that they should be treated as a single species with the older name *S. glaucocephala*. However, Hodgetts *et al.* (2020) include both *S. glaucocephala* and *S. scapanioides* as distinct species in the European checklist.

Schuster (1974) disagreed with the synonymization made by Müller (1951) and agree with Buch & Fagerström (1946) that *S. vexata* (syn. *S. scapanioides*) and *S. glaucocephala* are separate species but partly disagreed on the characters to separate them. Schuster (1974) emphasized that shoots of *S. glaucocephala* are up to 2.3 mm wide, the leaves with a keel less than ½ of the ventral leaf lobe length and with a border of one-two rows of nearly isodiametric equally thick-walled cells (15-18 µm), not larger than the intramarginal and median thin-walled cells. According to Schuster (1974), *S. scapanioides* has shoots up to 1.25 mm wide, the keel more than ½ of the length of the ventral lobe and marginal cells swollen (*c.* 30 µm wide).

The aim of the current study is to: 1) confirm the presence of *S. glaucocephala* in France by genetic data; 2) describe the morphology and ecology for the new records in France; and 3) discuss the nomenclatural history of the species in Europe.

MATERIAL AND METHODS

The sampling was carried out in the Jura mountains and Alpine mountains (Fig. 1) between 2019 and 2022. We targeted the ravine streams that we considered most favorable for small epixylic *Scapania*. Each record of a species was precisely located by GPS in the field and later identified in the laboratory by studying the morphological characteristics described by Schuster (1974). Based on the recognized morphological groups, the specimens were selected for genetic analysis.

Morphology

Specimens were studied morphologically by microscope. All photographs except the one of the gemmae were taken after staining with methyl green and digital processing in black and white in order to accentuate the details. Using the focus stacking technique, each image results from the merger of ten manually micrometrically focused shots with Helicon software. Vouchers of studied specimens are deposited in the bryophyte herbarium in Trondheim (herbarium TRH).

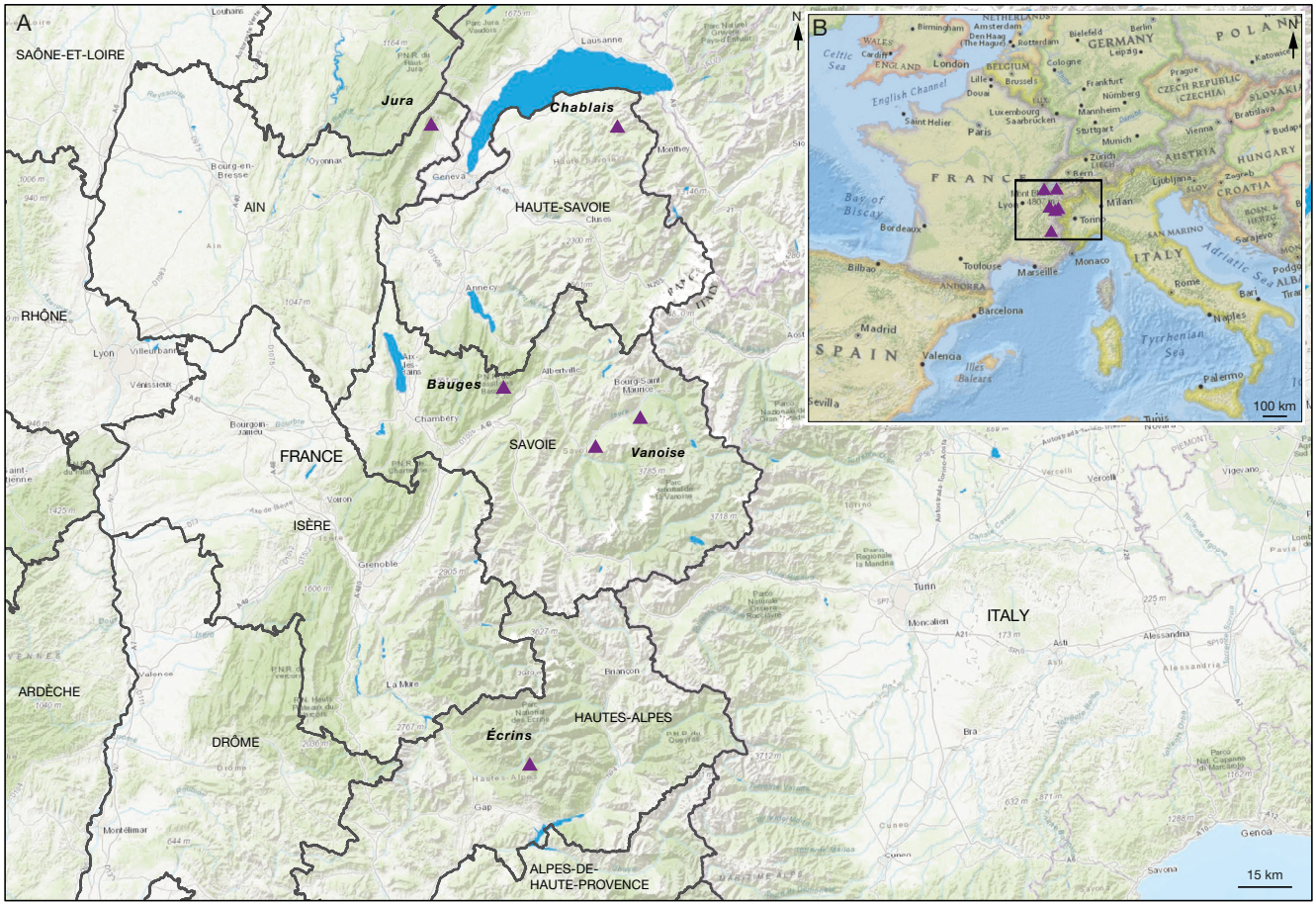


Fig. 1. — Map showing the French localities of *Scapania glaucocephala* (Taylor) Austin: **A**, the French Alps; **B**, map of the French Alps in Europe.

DNA extraction, PCR amplification and sequencing

To evaluate the relationship among the specimens from France determined as *Scapania glaucocephala* based on morphological characters and the species from other regions, we included specimens from Norway, Canada, and Russia. We also included *Scapania nemorea* (L.) Grolle, *S. umbrosa* (Schrad.) Dumort., *S. apiculata, S. cuspiduligera* (Nees) Müll.Frib., and *S. carinthiaca* to rule out morphological misidentification with any of the species with red-brown one-two celled gemmae. Voucher specimens are listed in Table 1. Dried tissue was lysed using a Qiagen Tissues Lyser II (Qiagen) for 120s at 30Hz, and total DNA was extracted using the E.Z.N.A.® HP Plant DNA Mini Kit (Omega Bio-tek) following the manufacturer's protocol (with minor modifications) for dried plant samples. DNA concentration of all extracts was measured using Qubit dsDNA HS kit and Qubit 2.0 Fluorometer (Thermo Fisher Scientific).

Two chloroplast loci were sequenced: *trn*L-*F* and *atp*B-*rbc*L spacer. The amplification was carried out using the Taq PCR Core Kit (Qiagen) and the following protocols:

*trn*L-*F*-5µL of DNA template (containing up to 10 ng of DNA), 1x Taq Polymerase reaction buffer (containing 15 mM $MgCl_2$) , 1x of 5x Q-Solution, 4 µL of $MgCl_2$ (25 mM) to the final concentration of 3.5mM, 0.2 mM of each dNTP, 0.2 mM 5′-primer C (Taberlet *et al.* 1991), 0.2 mM 3′-primer F (Taberlet *et al.* 1991), 1U Taq-DNA-polymerase, Molecular Biology Grade Water to 50 µL. The thermocycling profile was 2 min at 92°C, 30 cycles of 60s at 92°C, 50s at 51°C and 90s at 72°C followed by a final extension step of 10 min at 72°C.

*atp*B-*rbc*L-5µL of DNA template (containing up to 10ng of DNA), 1x Taq Polymerase reaction buffer (containing 15 mM $MgCl_2$), 1x of 5x Q-Solution, 0.5 µL of $MgCl_2$ (25 mM) to the final concentration of 2mM, 0.2 mM of each dNTP, 0.16 mM 5′-primer *atp*B-AD-F (Feldberg *et al.* 2010), 0.16 mM 3′-primer *rbc*L-AD-R (Feldberg *et al.* 2010), 0.5U Taq-DNA-polymerase, Molecular Biology Grade Water to 25 µL. The thermocycling profile was 5 min at 95°C, 35 cycles of 45s at 95°C, 75s at 58°C and 75s at 72°C followed by a final extension step of 8 min at 72°C.

The PCR products were visualized on a 2% agarose gel. For the *trn*L-*F* region, no non-specific bands were present, and the PCR products were purified using illustra™ ExoProStar™ (Cytiva) following the manufacturer's protocol, except for using 10 µl of PCR product. For the *atp*B-*rbc*L spacer, several non-specific bands were detected for most of the samples, and the E.Z.N.A.® Gel Extraction Kit (Omega Bio-tek) was used following the manufacturer's protocol to extract and purify the bands of interest. The purified PCR product was once again visualised on a 2% agarose gel to verify that non-specific bands were no longer present. The purified PCR products

Table 1. — Information on specimens included in the genetic and morphological analysis.

Sample ID	Herbarium ID	Genbank *atp*B-*rbc*L	Genbank *trn*L-F	Species	*leg.*	Date	Country	Locality	Ecology
GSG08	TRH-116881	QB221960	QB221968	*Scapania apiculata* Spruce	S. Vatne	14.VII.2021	Norway	Sør-Trøndelag, Orkland, Vorma	På middels grov gråorlåg i elvekanten
SCA1	TRH-96900	—	QB221974	*Scapania apiculata* Spruce	K. Hassel	10.X.2019	Norway	Sør-Trøndelag, Malvik, Høybydalen E of Brenna	Decaying log of cf. *Alnus incana* by small brook in moist deciduous mixed forest
SCA2	TRH-93682	QB221961	QB221975	*Scapania apiculata* Spruce	T. Høitomt, J.G. Brynjulvsrud	24.V.2017	Norway	Telemark, Notodden, Årlifoss- Kåsa	På dødved av gran langs bekk
SCV1	TRH-112444	QB221962	QB221985	*Scapania apiculata* Spruce	J.G. Brynjulvsrud	11.VIII.2020	Norway	Telemark, Seljord, Djupsåi	På låg i flommark
SCV2	TRH-671555	QB221941	QB221986	*Scapania carinthiaca* J.B.Jack ex Lindb.	G. Gaarder	27.VIII.2007	Norway	Oppland, Sel, Roståe	På trestokk inntil bekken i bekkekløft, eksp. Ø
SCV3	TRH-671047	QB221942	QB221987	*Scapania carinthiaca* J.B.Jack ex Lindb.	J.B. Jordal	18.VIII.2005	Norway	Møre og Romsdal, Sunndal, Grøa-elva mellom Grøa og Dalasetra	På død ved av gråor i flomtransportert dunge av gråorlæger i elvekanten
SCN3	TRH-139519	QB221955	—	*Scapania nemorea* (L.) Grolle	S. Vatne, O. Olsen	05.IX.2023	Norway	Sogn og Fjordane, Stadt, Vedvika	På almelåg i sørvendt, rik edelløvskog
SCN4	TRH-139526	QB221954	QB221983	*Scapania nemorea* (L.) Grolle	S. Vatne	22.IX.2023	Norway	Møre og Romsdal, Surnadal, Gløna	På granlåg i elvekanten Bekkekløft
SCC1	TRH-136669	QB221950	—	*Scapania* sp.	F. Bonte	15.VII.2022	France	Laval-en-Belledonne, Isère, under the Betta edge, 1186 m	On decaying log near a stream
SCC2	TRH-35960	QB221944	QB221976	*Scapania cuspiduligera* (Nees) Müll. Frib.	K. Hassel	31.VIII.2017	Norway	Oppland, Lom, Geitåholet-Geitåtjønne, Hestbrepiggan	Calcareous gravel
SCC3	TRH-690249	QB221946	QB221977	*Scapania cuspiduligera* (Nees) Müll. Frib.	K. Hassel	28.VIII.2006	Norway	Nord-Trøndelag, Verdal, Bekkekløft i Ramsåa, V-siden	Berg v/elv
SCC4	TRH-116886	QB221945	QB221978	*Scapania cuspiduligera* (Nees) Müll. Frib.	O. Olsen, S. Vatne	08.X.2011	Norway	Sør-Trøndelag, Rennebu, Nylendet, Orkla	På stor stein ved elva
SCC5	TRH-675504	QB221957	QB221979	*Scapania* sp.	J.T.R. Klepsland	29.VIII.2008	Norway	Buskerud, Kongsberg, Mørk S (Mørkbekken)	På barkløse furulæger (kantfall) i kalkrik bekkekløft like
GSG01	TRH-136670	—	QB221981	*Scapania* cf. *glaucocephala* (Taylor) Austin	F. Bonte	24.VII.2022	France	Pralognan-la-Vanoise, Savoie, les Fontanettes, 1630 m	On decaying log near a stream
GSG02	TRH-136671	QB221936	QB221964	*Scapania glaucocephala* (Taylor) Austin	F. Bonte	22.VIII.2022	France	Jarsy, Savoie, Coutarse forest, Chéran sream, 1168 m	On decaying log near a stream in forest ravine
GSG03	TRH-136672	QB221938	—	*Scapania glaucocephala* (Taylor) Austin	F. Bonte	12.VIII.2022	France	Vacheresse, Haute-Savoie, Ubine stream, 1078 m	On decaying log near a stream in forest ravine
GSG04	TRH-136673	QB221952	—	*Scapania* cf. *glaucocephala* (Taylor) Austin	F. Bonte	22.VIII.2022	France	Bellevaux, Haute-Savoie, la Chèvrerie, Diomaz sream, 1128 m	On decaying log near a stream in forest ravine

TABLE 1. — Continuation

Sample ID	Herbarium ID	Genbank *atp*B-*rbc*L	Genbank *trn*L-F	Species	*leg.*	Date	Country	Locality	Ecology
GSG05	TRH-136674	QB221937	QB221965	*Scapania glaucocephala* (Taylor) Austin	F. Bonte	13.IV.2019	France	Saint-Marcel, Savoie, Monfort, Hauteville stream, 1024 m	On decaying log near a stream in forest ravine
GSG06	TRH-136675	QB221934	QB221966	*Scapania glaucocephala* (Taylor) Austin	T. Legland	20.VIII.2021	France	Gex, Ain, Creux de l'Envers, along the Journans	On decaying log near a stream in forest ravine
GSG07	TRH-136676	QB221939	QB221967	*Scapania glaucocephala* (Taylor) Austin	F. Bonte	01.VIII.2021	France	Peysey-Nancroix, Savoie, stream Le Ponturin gorges, 941 m	On decaying log near a stream in forest ravine
GSG09	TRH-38544	QB221953	QB221969	*Scapania nemorea* (L.) Grolle	O. Olsen, T.-A. Røsberg	17.X.2016	Norway	Sogn og Fjordane, Sogndal, Mundalsdalen	På råtnende, grov almelåg i gammel alm/gråorskog
GSG10	TRH-116880	QB221949	QB221970	*Scapania* sp.	S. Vatne	01.VIII.2021	Norway	Oppland, Sel, Bjørndalsbekken (øvre del)	På fuktig ved i bekken. Grandominert bekkekløft
GSG11	TRH-693144	—	QB221971	*Scapania glaucocephala* (Taylor) Austin	G.K. Golinski, P. Williston	05.IX.2008	Canada	Alberta, NE of Whitecourt, approx. 110 m N of Athabasca River	Scattered on decorticated log with *Jamesoniella autumnalis* and *Tritomaria exsectiformis* in old growth poplar forest with *Picea glauca* and birch
GSG12	TRH-9448	—	QB221972	*Scapania glaucocephala* (Taylor) Austin	V.A. Bakalin	02.IX.2001	Russia	Far East, central part of Kamchatka Peninsula. Kozyrevskiy District, near Lokhmatka Mtn.	Populus-dwarf-shrubs forest near the stream, on decaying Wood
GSG13	TRH-139525	—	QB221973	*Scapania* sp.	S. Vatne	02.VIII.2023	Norway	Sør-Trøndelag, Melhus, Stjørdalen	På granlåg i sildrebekk. Gammal granskog.
SCN1	TRH-112704	—	—	*Scapania nemorea* (L.) Grolle	T. Prestø	28.VII.2020	Norway	Møre og Romsdal, Rindal, Fossdalen, by river Toråa.	On wet, sandy soil and rocks by river
SCN2	TRH-35996	QB221956	QB221982	*Scapania nemorea* (L.) Grolle	K. Hassel	12.X.2017	Norway	Sør-Trøndelag, Snillfjord, Herdalen, N side of Åstelva.	Boulders in *Alnus incana* forest by stream, flooding zone.
SCU1	TRH-105204	QB221958	QB221984	*Scapania umbrosa* (Schrad.) Dumort.	H. Holien	25.VIII.2018	Norway	Nord-Trøndelag, Flatanger, Sandmohamn vest, Vassleidalen.	På granlåg i fuktig, eldre granskog
SCU2	TRH-96901	QB221959	—	*Scapania umbrosa* (Schrad.) Dumort.	K. Hassel	10.X.2019	Norway	Sør-Trøndelag, Malvik, Høybydalen E of Brenna	Decaying log of cf. *Alnus incana* by small brook in moist deciduous mixed forest
SCX1	TRH-16677	QB221948	QB221988	*Scapania* sp.	F. Bonte	25.VII.2022	France	La Plagne Tarentaise, Savoie, Le Nant Benin Stream, 1750m	On decaying log near a stream
SCX2	TRH-136678	QB221943	QB221989	*Scapania carinthiaca* J.B.Jack ex Lindb.	F. Bonte	06.VIII.2022	France	Livet-et-Gavet, Isère, under les chalets de Poursollet, 1587m	On decaying log near a stream in forest ravine

TABLE 1. — Continuation

Sample ID	Herbarium ID	Genbank *atp*B-*rbc*L	Genbank *trn*L-F	Species	*leg.*	Date	Country	Locality	Ecology
SCX3	TRH-136679	QB221935	QB221990	*Scapania glaucocephala* (Taylor) Austin	F. Bonte	20.VII.2021	France	Orcières, Hautes Alpes, les Côtes du Ranc, 1257m	On decaying log near a stream in forest ravine
SCX4	TRH-92224	QB221940	QB221991	*Scapania* sp.	T. Høitomt, J.G. Brynjulvsrud	12.IX.2014	Norway	Oppland, Øystre Slidre, Ygna	På gråorlåg lang elv
SCX6 #2	TRH-671564	QB221951	QB221992	*Scapania* sp.	G. Gaarder	23.VIII.2007	Norway	Oppland, Nordre Land, Medåa	På morken granlåg i bekk, eksp. Ø

were sequenced by Eurofins Genomics with the same primers used during the PCR.

Phylogenetic analysis

Geneious Prime v 2024.0.5 was used for raw sequence and chromatogram analyses. The raw sequences were trimmed using the default parameters, and the consensus sequences were generated after assembling the forward and reverse sequences together using the default parameters. The consensus sequences were aligned using the PPP MUSCLE v5.1 algorithm with default parameters together with outgroup species, *Douinia ovata* and *Scapania contorta* (Heinrichs *et al.* 2012), and several accessions of the same *Scapania* species used here: *Scapania apiculata*, *S. glaucocephala*, *S. cuspiduligera*, and *S. nemorea* (Table 2) (Heinrichs *et al.* 2012). The alignments were inspected visually. Phylogenetic analyses were performed separately for each of the two genetic markers using IQTREE v1.6.12 (Nguyen *et al.* 2015). The best substitution model was determined first (Kalyaanamoorthy *et al.* 2017), and then the best ML tree was estimated, and 1000 ultrafast bootstraps were performed (Hoang *et al.* 2018). The trees were visualized and manually rooted specifying *Douinia ovata* (Dicks.) H. Buch as an outgroup using FigTree v1.4.4 (Rambaut 2018).

RESULTS

Genetic analysis and conformity of the specimens with those of Canada and Russia

There were three samples which failed to amplify with one of the two markers: SCA1 and GSG01 did not work with the *atp*B-*rbc*L, whereas GSG04 failed with *trn*L-*F*. The results of the phylogenetic analyses are shown in Table 3 and Figure 2. The phylogenetic tree based on *trn*L-*F* (Fig. 2A) shows that the French specimens of *S. glaucocephala* form a clade with the Canadian and the Russian specimens of the same species that is clearly separated from all clades formed by other species with red-brown gemmae. One French specimen with *S. glaucocephala* morphology (GSG01) falls outside all clades on a separate branch. The Scandinavian specimens identified as *S. glaucocephala* form a separate clade together with two French specimens, and we name this clade *Scapania* sp. In the *atp*B-*rbc*L-based phylogeny, *Scapania* sp. is a sister clade to *S. cuspiduligera*, while *S. glaucocephala* is sister to a clade consisting of S. *cuspiduligera, S.* sp., and *S. carinthiaca* (Fig. 2B). Also, here one French specimen with *S. glaucocephala* morphology (GSG04) falls outside all other clades on a separate branch.

Morphology of French plants of *Scapania glaucocephala*

In accordance with the descriptions of North American specimens (Schuster 1974) we observed in our specimens that shoots always grow very erect, and are of two types, which can grow in mixtures or in distinct colonies:

– shoots with few or no gemmae. These are the most developed (Fig. 3A) and have leaves with well differentiated dorsal and ventral lobes (Figs 3B-E); one-three rows of thick-walled cells are present at the edge of the leaves (Fig. 3F);

– shoots which are highly propaguliferous (Fig. 3G). These are smaller and have highly modified leaves with almost equal lobes (Fig. 3H) and without differentiated marginal cells (Fig. 3I).

The sparsely propaguliferous stems have a maximum height of 6 mm. Their leaves have a keel rounded at the base and more pronounced at the top, 0.5-0.8 times the length of the ventral lobe. These leaves are one to three times longer than wide. The tip of the ventral lobe is rounded to acute, often with an apiculus of one-two cells. The dorsal lobe is narrower and is 0.4-0.7 times the size of the ventral lobe. It is also often apiculate at the tip (Fig 3B-E). The median cells of the lobes have weak trigones. The wall thickenings of the marginal cells of leaves are marked (Fig. 3F). Observation of fresh specimens allowed counting of numerous oil bodies in each cell (up to 9), measuring 4-8 µm in diameter. A few gemmae may be present at the tip of the two lobes of some leaves, which in this case have narrow and pointed lobes. Although there is a significant proportion of unicellular gemmae, more than half are bicellular. They are thick-walled and short (8) 10-13 × (12)13-20 (22) µm (Fig. 3K). The highly propaguliferous type has stems of a more or less pronounced "flagelliform" appearance. Stems are very erect and ascending (Fig. 3G). The leaves, strongly modified by the production of gemmae, are very elongated and narrow, the ventral and dorsal lobes are poorly differentiated, and the keel is therefore very short (Fig. 3H). Larger and elongated differentiated cells than the underlying cells are observed in the gemmae production area (Fig. 3I). These

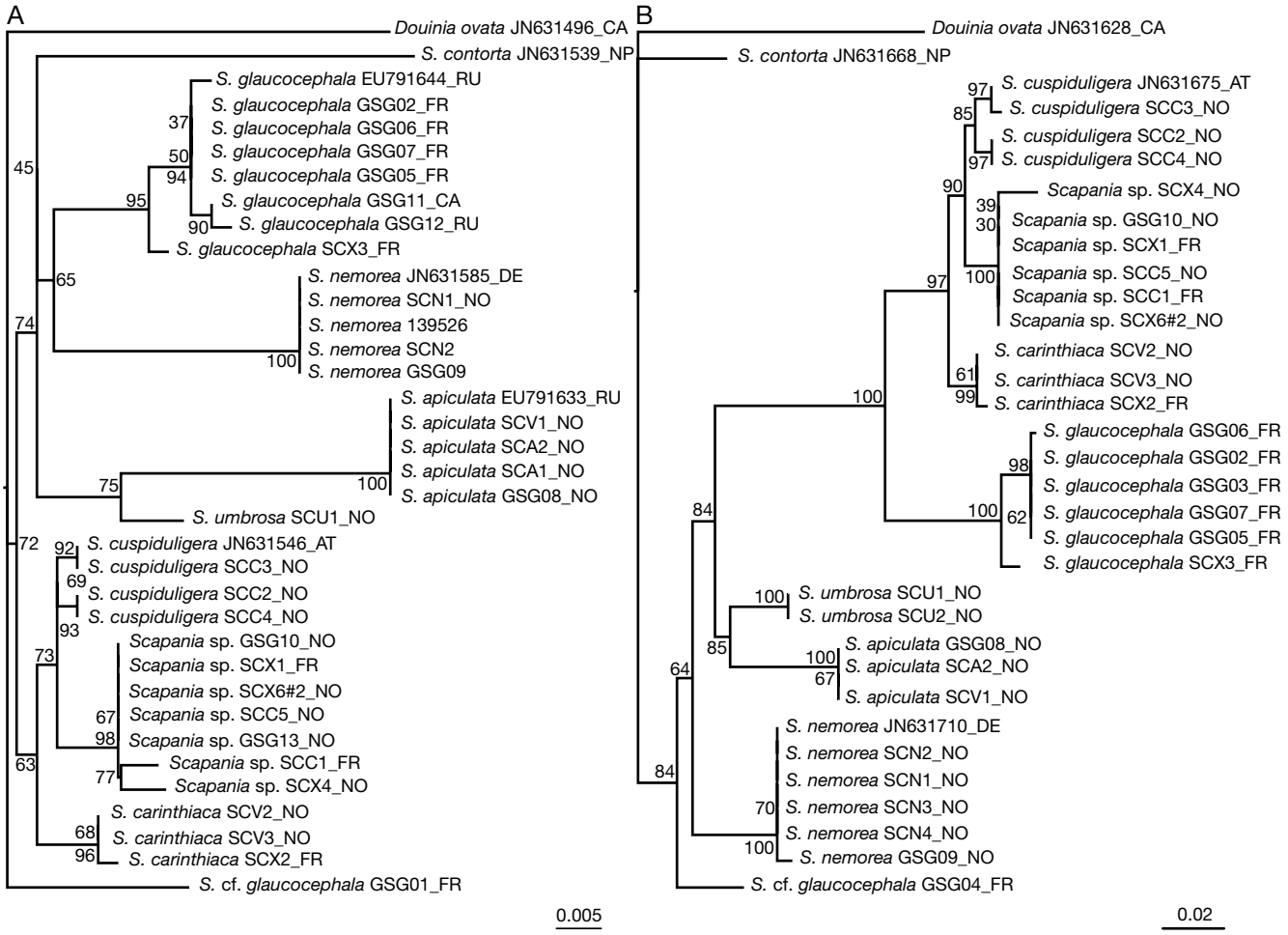


Fig. 2. — Consensus ML phylogenetic trees inferred in the analyses, node labels correspond to bootstrap support: **A**, based on *trn*L-F; and **B**, on *atp*B-*rbc*L. The sample ids refer to specimens in Tables 1 and 2.

Table 2. — Genbank accessions from Heinrichs *et al.* (2012) used in the phylogenetic analyses.

	Genbank accession number	
Species	***trn*L-F**	***atp*B-*rbc*L**
Douinia ovata (Dicks.) H. Buch	JN631496	JN631628
Scapania contorta Mitt.	JN631539	JN631668
Scapania nemorea (L.) Grolle	JN631585	JN631710
Scapania apiculata Spruce	EU791633	—
Scapania cuspiduligera (Nees) Müll. Frib.	JN631546	JN631675
Scapania glaucocephala (Tayl.) Austin	EU791644	—

gemmae are identical to those of the poorly propaguliferous leafy stems type (Fig. 3K).

Scapania glaucocephala is a dioicous species. Two of our specimens allow us to observe male and female sexual organs on sparsely propaguliferous developed stems. The perianths are pleated and have a completely smooth opening at the top (Fig. 3J).

Ecology of the French plants

In the ravines surveyed, *S. glaucocephala* grew in small colonies on the decaying wood of stumps, trunks or large barked branches of *Picea abies* (L.) H. Karst or *Abies alba* Mill., in very dark old forests with a humidity-saturated atmosphere, on the edge or in the major bed of streams. The wood was in a fairly advanced state of decomposition, but not in the final stage. It was always moist, regularly sprayed during low water periods, but sufficiently above the water level to not be regularly stripped during floods.

The most common mixed species was *S. carinthiaca*. We also noted several other strict and non-strict epixylic liverworts: *Nowellia curvifolia* (Dicks.) Mitt., *Blepharostoma trichophyllum* (L.) Dumort., *Lophocolea heterophylla* (Schrad.) Dumort., as well as humicolous species that grew on the thin layers of sediment that were sometimes deposited on the substrate, such as *S. cuspiduligera*.

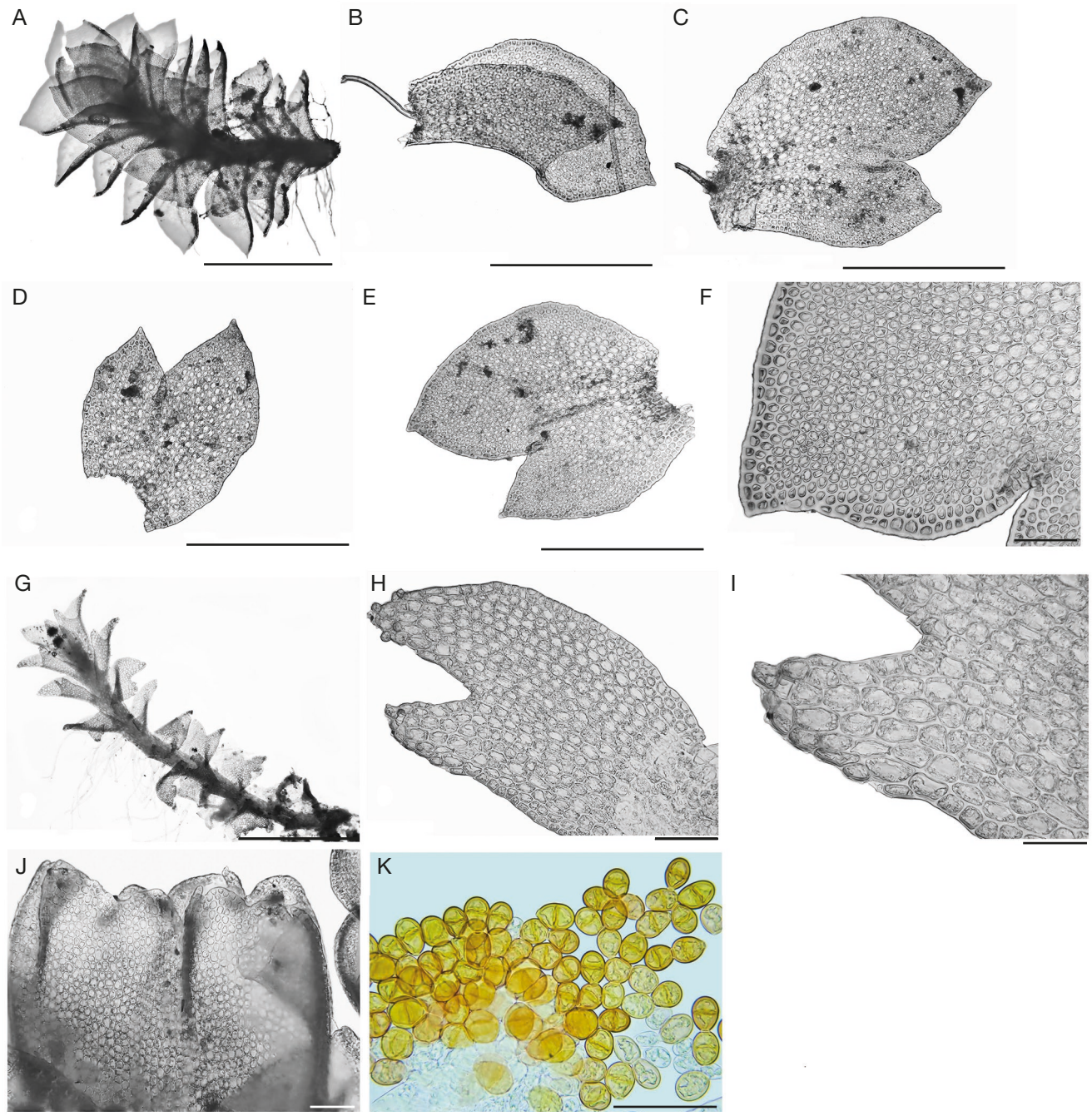


Fig. 3. — *Scapania glaucocephala* (Taylor) Austin: **A**, shoot with gynoecium; **B**, conduplicate leaf of shoot with gynoecium; **C**-**F**, leaves of shoot with gynoecium; **G**, gemmiferous shoot; **H**, **I**, leaf of gemmiferous shoot; **J**, perianth apex; **K**, gemmae. Specimen from: Hauteville, Saint-Marcel, Savoie, France, 1024 m asl. On decaying trunk of *Picea abies* (L.) H. Karst on the stream bank in spruce forest; *leg. F. Bonte 19D327*. Scale bars: A, G, 1 mm; B-E, 500 µm; F, H, J, 100 µm; I, K, 50 µm;

New localities of *Scapania glaucocephala* in France

Family Scapaniaceae Mig.
Genus *Scapania* (Dumort.) Dumort.

Scapania glaucocephala (Taylor) Austin
(Fig. 1)

Examined material. — **France** • Jura Mountains, Gex (Ain dept., Rhône-Alpes), Nature Reserve of the High Jura Mountains at Creux de l'Envers, Journans torrent; 874 m alt.; leg. F. Bonte; *F. Bonte-483*; 20.VIII.2021; TRH-B-136675 • Alpine Mountains, Ecrins, Orcières (Hautes-Alpes dept., Provence-Alpes-Côte d'Azur), the Côtes du Ranc, Pisse stream; 1257 m alt.; leg. F. Bonte; *F. Bonte-122*; 20.VII.2021; TRH-B-136679 • Vanoise, Peysey-Nancroix (Savoie dept., Rhône-Alpes), the Ponturin Gorges; 941 m alt.; leg. F. Bonte; *F. Bonte-7*; 01.VIII.2021; TRH-B-136676 • Saint-Marcel (Savoie dept., Rhône-Alpes), Hauteville stream above the village; 1024 m alt.; leg. F. Bonte; *F. Bonte-327*; 13.IV.2019; TRH-B-136674 • Bauges, Jarsy (Savoie dept., Rhône-Alpes), Chéran stream in the Coutarse forest; 1167 m alt.; leg. F. Bonte; *F. Bonte-238*; 07.VIII.2022; TRH-B-136671 • Chablais Vacheresse (Haute-Savoie dept., Rhône-Alpes),

TABLE 3. — Phylogenetic analyses summary.

Marker	Number of samples	Number of parsimony-informative sites	Number of singleton sites	Number of constant sites	Number of identical sequences ignored in the analysis	Number of identical sequences kept in the analysis	Best-fit substitution model
*trn*F	36	38	35	401	11	4	HKY+F+G4
*rbc*L	33	124	55	461	7	7	HKY+F+I

Ubine stream; 1078 m alt.; leg. F. Bonte; *F. Bonte-238*; 12.VIII.2022; TRH-B-136672.

DISCUSSION

Our genetic data confirm the presence of *S. glaucocephala* in France, and the newly collected French specimens form a clade with Canadian and Russian specimens of the species. However, the Scandinavian specimens identified as *S. glaucocephala* form a separate clade together with two additional French specimens and may represent an undescribed species or *S. scapanioides*. More data is needed to resolve this, and it will be treated elsewhere. The phylogenetic placement of *S. glaucocephala* is not clear from our data as the two markers included show different results which also differ from Heinrichs *et al.* (2012). Two specimens (GSG01 and GSG04) with *S. glaucocephala* morphology fall outside all clades on single branches, the quality of the sequences are good, but more data are needed to evaluate the taxonomic relevance of these specimens.

A preliminary morphological examination of the clade representing specimens named *S. glaucocephala* in Fennoscandia indicates that these plants are smaller, and the cell walls of marginal leaf cells are thinner compared to the true *S. glaucocephala,* thus approaching *S. scapanioides*. We have not seen the specimen of *S. glaucocephala* referred to in Buch & Fagerström (1946), but it could belong to the same taxon as has been named as *S. glaucocephala* in Scandinavia. However, Müller (1951) studied this specimen and concluded that it was similar to specimens of *S. glaucocephala* and *S. vexata* (syn. *S. scapanioides*). We have not been able to locate the type of *S. scapanioides* or to include material from the type locality in this analysis, and we cannot rule out *S. scapanioides*. More recently, Kropik & Zechmeister (2023) consider *S. scapanioides* to be a synonym of *S. glaucocephala* based on their studies in the Austrian alps with reference to Köckinger (2017). Also, Urmi (2020) in his treatment of *Scapania* in central Europe state "The rarity of *S. scapanioides* and *S. glaucocephala*, as well as the lack of detailed descriptions and good illustrations, currently does not allow for a separation of these two taxa."

Scapania glaucocephala can be confused with two other small epixylic *Scapania* with similar morphology and which can grow mixed with it: *S. apiculata* and *S. carinthiaca*. The former also has distinct erect propaguliferous stems with gradually reduced leaves (Damsholt 2009). However, the gemmae of *S. apiculata* are always unicellular, and the leaf margin does not have thick-walled cells. In *S. carinthiaca*, the cells of the leaf margin are tangentially elongated and are at least as large as the cells in the middle of the leaves, and the gemmae are for the most part unicellular and are produced on un-differentiated shoots (Schuster 1974). Reduced forms of *S. cuspiduligera* can sometimes be found on decaying wood and are sometimes difficult to separate from *S. glaucocephala*. *Scapania cuspiduligera* has leaf lobes of almost equal size and the lobes are at least partly reflexed giving the shoots an untidy appearance. Median leaf cells often have strongly convex trigones and usually less than four oil bodies per cell. Usually, the shoots are light to whitish green but rarely shoots can have brownish secondary pigmentation making the colour more similar to *S. glaucocephala*.

Scapania glaucocephala is a boreal-montane species. It occurs in North America, from the west to the east of the United States, in Canada and Greenland (https://explorer.natureserve.org, consulted on 10/11/2024). In Asia, it is reported from Eastern Siberia (Choi *et al.* 2012), Sichuan Province of China (Cao & Sun 2008) and Turkey (Unan *et al.* 2020). The European distribution is uncertain due to the confusion with *S. scapanioides*. However, *S. glaucocephala* is reported from the European part of the Caucasus (Hodgetts & Lockhart 2020; Konstantinova & Savchenko 2021), the Carpathians in Romania and Poland (Vaňa 2002; Unan *et al.* 2020), the Alps in Germany where it seems to have disappeared (Hodgetts & Lockhart 2020). In some other alpine countries, namely Italy, Austria, Switzerland, only *S. scapanioides* is reported (Schröck *et al.* 2019; Hodgetts & Lockhart 2020).

In North America, *Scapania glaucocephala* does not appear to be threatened in the short term (https://explorer.natureserve.org, consulted on 15/11/2024), but Schuster (1974) noted that other epixylic species like *S. apiculata* and *Cephalozia macounii* (Austin) Austin have decreased in frequency due to modern forestry.

In Europe, *S. glaucocephala* and *S. scapanioides*, which are considered distinct on the European red lists (Hodgetts *et al.* 2019) are listed as endangered (EN; Hallingbäck 2019) and critically endangered (CR; Schröck *et al.* 2019), respectively.

Our targeted surveys on dead wood along the streams of the French Alps allow us to consider that *S. glaucocephala* is rare there since it has only been observed in six localities whereas there are more than thirty known localities of *S. carinthiaca*, a species with similar ecology of the Habitat Directive. This relative rarity of *S. glaucocephala* compared to *S. carinthiaca* corroborates the observations of Hassel *et al.* (2006) and Kropik & Zeichmeister (2023). The rarity of *S. glaucocephala* therefore results not only from the small area of habitats favourable to the species, but also from a low occurrence in these environments.

Many human activities are likely to cause, directly or indirectly, a degradation of the habitat of such mountain epixylic liverworts that are highly dependent on atmospheric humidity and the substrate. Climate change leads to an increase in drought episodes causing drastic drying up of streams and, conversely, very rainy episodes causing torrential floods causing landslides that open ravines to light and lead to scouring of stream beds and significant movement of dead wood. Intensive forestry leads to a scarcity of old-growth forests and therefore of rotting wood present on the ground. Finally, watercourse developments are often carried out to compensate for the scarcity of water resources, prevent landslides or floods in valleys and produce electricity in hydroelectric power stations.

CONCLUSIONS

Despite its rarity, the discovery of *S. glaucocephala* in several French locations in the Alps and the Jura in recent years suggests that the species may be under-observed overall. Additional surveys should therefore be planned to better define its distribution. In addition to the surveys, the fresh forest habitats of this liverwort are currently under increasing pressure from human activity, and conservation measures must be taken now, along the lines of those implemented in Sweden (Weibull 2015): population monitoring, protection, as well as site management. Such actions would be highly beneficial not only for *Scapania glaucocephala*, but also for the many other bryophyte species that depend on fresh decaying wood.

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