COMPREHENSIVE PLANT BIOLOGY

https://doi.org/10.2298/CPB2502351B

(2025) 49 (2): 351–373
ISSN 3042-3201
formerly Botanica Serbica

Review Paper

Axenic cultivation of bryophytes: cultivated species checklist

Djordje P. Božović[1*], Marija V. Vesović[1], Bojana Z. Jadranin[1], Nikolina A. Matić[1], Aneta D. Sabovljević[1,2] and Marko S. Sabovljević[1,2,3]

1 Institute of Botany and Botanical Garden Jevremovac, Faculty of Biology, University of Belgrade, Takovska 43, 11000 Belgrade, Serbia
2 Center of Plant Biotechnology and Conservation (CPBC), Takovska 43, 11000 Belgrade, Serbia
3 Department of Plant Biology, Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Mánesova 23, 04001 Košice, Slovakia

Corresponding author: djordje.bozovic@bio.bg.ac.rs

ABSTRACT:
Bryophytes represent the second largest group of land plants and play key ecological roles in colonisation, water regulation, and habitat formation. In addition to their ecological significance, they are also a rich source of biologically active compounds with potential applications in medicine, agriculture, and biotechnology. However, bryophytes remain challenging to cultivate under controlled, particularly axenic conditions, due to their slow growth, strict ecological requirements, and the limited knowledge of their nutritional and reproductive biology, particularly in less common species. As a result, only a small fraction of species have been successfully maintained in axenic culture, and information on cultivation methods is scattered and often overlooked. To bridge this gap, we conducted an in-depth survey of the published literature on axenically cultivated bryophytes, compiled a comprehensive checklist with references to the original sources, and highlighted emerging model species. This checklist and literature database provide a valuable resource by consolidating dispersed knowledge, serving both as a foundation for future studies in bryophyte biology and conservation and as a platform to expand their biotechnological potential.

Keywords: moss, liverwort, hornwort, *in vitro*, diversity, bryophyta

Received:
25 April 2025

Revision accepted:
01 September 2025

UDC: 57.086.83:82.32

INTRODUCTION

Bryophytes, the second largest group of land plants, are known as a significant component in numerous ecosystems (Vanderpoorten & Goffinet 2009). They are often the first colonisers of bare or degraded substrates, facilitating soil formation and creating conditions suitable for other organisms. By forming dense mats and cushions, bryophytes prevent soil erosion, retain moisture, and buffer microclimatic conditions, thereby enabling other organisms to survive in otherwise harsh environments (Saxena & Harinder 2004). Their sponge-like properties regulate water retention and release, contributing significantly to habitat water balance and ecosystem water regimes. In this way, bryophytes also mitigate flood risk and provide microhabitats for a diverse array of cohabitants, including invertebrates, fungi, algae, and microorganisms (Longton 1992). Beyond their ecological importance, bryophytes also possess considerable practical and economic potential, which has often been underestimated due to challenges in species identification, biomass production, and obtaining axenic cultures. Nevertheless, mosses are widely used in bonsai cultivation, Japanese-style gardening, green roofs, and surface

Published by Institute of Botany and Botanical Garden Jevremovac, Belgrade
Faculty of Biology, University of Belgrade, Belgrade, Serbia
www. cpb.bio.bg.ac.rs

coverings, where they serve both aesthetic and functional purposes such as moisture retention and energy savings. In addition, bryophytes also hold great promise in biotechnology, as they produce a wide range of unique bioactive compounds with medicinal, industrial, and ecological applications, although this potential remains largely underexploited (Asakawa *et al.* 2003).

Bryophytes represent a rich source of diverse chemical compounds with significant biological potential and broad applications in medicine, pharmacy, and agriculture (Commisso *et al.* 2021; Dziwak *et al.* 2022). Several volatile compounds produced by bryophytes exhibit repellent, nematicidal, and herbicidal properties, highlighting their potential for improving crop protection and yield (Abay *et al.* 2012). In addition, secondary metabolites and extracts from numerous bryophyte species have demonstrated pronounced antifungal, antimicrobial, and antioxidant properties (Drobnik & Stebel 2021). However, harvesting bryophytes directly from natural habitats for the preparation of extracts or other products poses a risk to wild populations and may contribute to environmental degradation (Horn *et al.* 2021; Dziwak *et al.* 2022). To address this challenge, *in vitro* culture techniques provide an efficient means of propagating large numbers of individuals and generating sufficient biomass within a relatively short period, thereby reducing the negative impacts on natural ecosystems (Horn *et al.* 2021).

Nevertheless, cultivating bryophytes remains a complex task. Many species are restricted to moist, shaded habitats, and excessive insolation can rapidly lead to photooxidative damage and mortality. Due to the absence of roots, bryophytes are functionally dependent on high and continuous humidity. Their inherently slow growth rates (and yields) also make large-scale cultivation costly and time-consuming. In addition, significant challenges stem from their reproductive biology and physiology, including insufficient knowledge of their nutrient requirements, the induction of sex organs, spore storage and germination (including dormancy control), rare phenomena such as apogamy and apospory, endoreduplication (endopolyploidy) patterns, species-specific biological traits, and the requirement of water for fertilisation among others. These limitations not only hinder the establishment of efficient propagation systems, but also restrict experimental studies under axenic conditions. A more detailed overview of the challenges associated with axenic bryophyte cultures is provided by Duckett *et al.* (2004), Rowntree *et al.* (2011), and Sabovljević *et al.* (2014, 2022).

Overall, these challenges indicate that axenic, small-scale cultures represent a practical alternative for bryophyte cultivation despite the existence of considerable difficulties in both the establishment and long-term maintenance of axenic cultures (Duckett *et al.* 2004).

In vitro cultures of bryophytes are essential for both fundamental and applied research, enabling the study of diverse phenomena in morphogenesis, reproductive biology, evolution, development, and functional traits. They are also crucial for the maintenance and investigation of biological characteristics in rare or threatened species, supporting conservation efforts, reintroduction programmes, species sustainability, and the acquisition of new knowledge. According to Duckett *et al.* (2004), approximately 95% of bryophyte taxa have never been successfully cultured. Drawing on experience with around 300 moss species and 50 liverworts, these authors emphasised that axenic cultivation is far from a straightforward process, contrary to assumptions derived from the so-called *physcomitrellocentric* perspective. In fact, the majority of bryophyte *in vitro* studies have focused almost exclusively on three moss species: *Physcomitrium* (*Physcomitrella*) *patens* (Hedw.) Mitt., *Ceratodon purpureus* (Hedw.) Brid., and *Funaria hygrometrica* Hedw.

Data on the axenic cultivation of different bryophyte species are scattered throughout the literature and are often overlooked. Nevertheless, valuable

protocols and methodological approaches have been reported for certain species, which can be replicated directly or adapted to target specific species, ecologically or physiologically similar taxa, morpho-anatomical counterparts, or simply to phylogentically related species. To address this gap, we conducted an extensive survey and now present a comprehensive list of bryophyte species successfully cultivated under axenic conditions worldwide, accompanied by a thorough analysis of the available data. This study builds upon our previous work, which analysed the types of cultivation media used globally for bryophyte cultivation (Ćosić *et al.* 2025).

MATERIALS AND METHODS

Literature search. A comprehensive literature review was conducted to identify relevant scientific publications (for details, see Ćosić *et al.* 2025). The bibliographic units included in this study consisted of original scientific articles, conference proceedings and reviews presenting new data published between 1925 and 2024, retrieved from the Scopus (https://www.scopus.com/standard/marketing.uri#basic) and Google Scholar (http://www.scholar.google.com) databases. The complete list of publications used in this study is given in Supplement 1. The keyword search in Scopus employed the terms "*in vitro*" and "bryophyte," while the Google Scholar search was expanded with the additional terms "culture" and "axenic" to enhance the retrieval of pertinent records.

Following a thorough review of all the publications and the references therein, a database comprising 633 individual observations was created. Each entry includes the original taxon name as reported in the source publication, the currently accepted taxon name, classification details including phylum, order, and family, the number of references in which the taxon was reported, and the corresponding source(s) from which the data were extracted (see Supplement 2).

Nomenclature revision. Prior to further analysis, a comprehensive nomenclatural revision was undertaken to account for any taxonomic changes which have occurred over time. Certain taxa were recorded under different names depending on the publication year. To standardise the nomenclature and ensure consistency, taxonomic information, including accepted names and classifications, was obtained from Checklist and country status of European bryophytes – update 2020 (Hodgetts & Lockhart 2020) for mosses, and was combined with the World Checklist of Liverworts and Hornworts (Söderström *et al.* 2016) for liverworts and hornworts. In instances where information was unavailable, the Tropicos database (https://www.tropicos.org) was used for the supplementation of the missing data.

In accordance with the currently accepted nomenclature, all taxa included in our database were standardized to their current accepted scientific names, i.e. original names were replaced with their corresponding accepted ones. However, in certain instances, multiple taxa (original entry) belonged to a single revised taxon name. In such cases, an asterisk (*) was used in the tables (in the Results section) to indicate that these entries were consolidated under a single taxon record. The supplementary material (Supplement 2) provides a detailed list of all taxa, including both original and currently accepted names. For the purposes of analysis in this study, only data corresponding to the currently accepted taxonomic names and classifications were used.

Selection of emerging model bryophytes. In addition to the well-known model bryophyte species, this study aimed to identify additional taxa which are frequently cultivated, as inferred from the currently available data. For each of the three bryophyte phyla—mosses, liverworts, and hornworts, we selected candidate model species based on the frequency of their occurrence in scientific

publications. The selection criteria were adjusted for each phylum due to discrepancies in the number of species and the volume of literature available in the database. To account for these differences, we calculated the percentage of publications in which each taxon appeared (taxa publication occurrence) and proposed the most frequently cited taxa as emerging model species.

RESULTS AND DISCUSSION

Mosses. Out of 633 originally identified bryophyte taxa, 601 remained after taxonomic revision. Mosses accounted for 440 of the revised taxa (nomenclature), representing 73.2% of the total. Overall, 28 orders and 64 families of mosses have been the subject of *in vitro* cultivation to date. The most abundant orders were Hypnales (24%), Bryales (19.1%), Pottiales (13.9%), Dicranales (11.1%), and Sphagnales (8%) (Fig. 1A). Among the families, Pottiaceae (11.8%), Bryaceae (11.1%), and Sphagnaceae (8%) were the most dominant (Fig. 1B). The list of moss taxa for which axenic *in vitro* cultures have been successfully established to date is provided in Table 1.

These patterns reflect broader global trends in moss diversity, where orders such as Hypnales and Bryales are commonly dominant in terms of species richness due to their wide ecological amplitude and adaptability to various substrates and moisture conditions (Geffert *et al.* 2013). The prevalence of Pottiales and Dicranales further suggests a significant representation of taxa adapted to drier or more open habitats (Vitt *et al*. 2014). The predominance of Sphagnaceae may be attributed to their significant ecological roles and potential applications (Shaw *et al.* 2016; Turetsky *et al.* 2025). Altogether, the taxonomic structure highlights a diverse and ecologically representative moss flora spanning a broad range of ecological niches.

Liverworts. Liverworts accounted for 151 of the revised taxa (nomenclature), representing 25.1% of the total number. Overall, 13 orders and 46 families of liverworts have been included in axenic *in vitro* cultivation to date. The most abundant orders were Jungermanniales (40.4%), Porellales (19.9%), and Marchantiales (19.2%) (Fig. 2A). Among families, Frullaniaceae emerged as the most frequently represented, comprising 12.6% of the cultivated liverwort taxa (Fig. 2B). The list of liverwort taxa for which axenic *in vitro* cultures have been successfully established to date is provided in Table 2.

The relatively high representation of the order Jungermanniales is not unexpected, as it is the most species-rich order among liverworts (Söderström *et al.* 2016). Although numerous species within this group have been successfully cultivated *in vitro*, most are represented by only one or two publications. Similarly, the predominance of the Frullaniaceae family suggests that leafy species within this group are either more commonly encountered in nature or more amenable to manipulation under axenic conditions compared to thallose forms. Despite the overall dominance of studies on leafy liverworts, one of the established model liverworts is thalloid species *Marchantia polymorpha,* which has been frequently investigated over time.

Hornworts. Only ten hornwort species (representing 1.7% of the total taxa) have been successfully cultivated under axenic *in vitro* conditions to date. These belong to two orders and two families, each comprising five species (Table 3).

The limited number of hornwort species successfully cultivated in axenic *in vitro* conditions reflects their overall low taxonomic diversity in nature (Villarreal *et al.* 2010). Furthermore, hornworts often exhibit specialized ecological requirements and slower growth rates, which may present additional challenges for axenic propagation compared to mosses and liverworts (Gunadi *et al.* 2022; Lafferty *et al.* 2024).

Table 1. Moss taxa checklist with corresponding order and number of publications. Entries marked with an asterisk (*) contain multiple taxa (original entry) which belong to a single revised taxon name.

Taxa (species/entry)	Ordo	N of references
Acaulon triquetrum (Spruce) Müll. Hal.	Pottiales	1
Aloina aloides (Koch ex Schultz) Kindb.	Pottiales	3
Amblystegium serpens (Hedw.) Schimp.	Hypnales	3
Anacamptodon latidens (Besch.) Broth.	Hypnales	1
Andreaea alpestris (Thed.) Schimp.	Andreaeales	1
Andreaea rupestris Hedw. *	Andreaeales	2
Anisothecium molliculum (Mitt.) Broth.	Dicranales	1
Anisothecium spirale (Mitt.) Broth.	Dicranales	1
Anoectangium stracheyanum Mitt.	Pottiales	1
Anoectangium thomsonii Mitt.	Pottiales	3
Anomobryum concinnatum (Spruce) Lindb. *	Bryales	2
Anomobryum julaceum (Schrad. ex P.Gaertn. et al.) Schimp.	Bryales	1
Anomodon giraldii Müll. Hal.	Hypnales	1
Anomodon pseudotristis (Müll. Hal.) Kindb.	Hypnales	1
Aphanorhegma serratum (Wilson & Hook.) Sull.	Funariales	1
Aplodon wormskioldii (Hornem.) *R. Br.*	Splachnales	1
Archidium ohioense Schimp. ex Müll. Hal.	Archidiales	1
Atrichum angustatum (Brid.) Bruch & Schimp.	Polytrichales	1
Atrichum undulatum (Hedw.) P. Beauv.	Polytrichales	28
Aulacomnium androgynum (Hedw.) Schwägr.	Rhizogoniales	3
Aulacomnium palustre (Hedw.) Schwägr.	Rhizogoniales	2
Aulacopilum trichophyllum Ångstr.	Dicranales	1
Barbula unguiculata Hedw.	Pottiales	4
Bartramia halleriana Hedw.	Bartramiales	1
Bartramia hampeana Müll. Hal.	Bartramiales	1
Bartramia ithyphylla Brid.	Bartramiales	1
Bartramia pomiformis Hedw. *	Bartramiales	3
Bartramia stricta Brid.	Bartramiales	1
Bartramia subulata Bruch & Schimp.	Bartramiales	1
Bartramidula bartramioides (Griff.) Wijk & Margad.	Bartramiales	1
Brachymenium capitulatum (Mitt.) Kindb.	Bryales	1
Brachymenium exile (Dozy & Molk.) Bosch & Sande Lac.	Bryales	1
Brachymenium pulchrum Hook.	Bryales	1
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	Hypnales	2
Brachythecium buchananii (Hook.) A. Jaeger	Hypnales	1
Brachythecium coreanum Cardot.	Hypnales	1
Brachythecium novae-angliae (Sull. & Lesq.) Austin	Hypnales	1
Brachythecium rutabulum (Hedw.) Schimp.	Hypnales	3

Braunia secunda (Hook.) Bruch & Schimp.	Hedwigiales	1
Brotherella henonii (Duby) M. Fleisch.	Hypnales	1
Brotherella recurvans (Michx.) M. Fleisch.	Hypnales	1
Bruchia vogesiaca Nestl. ex Schwägr.	Dicranales	1
Bryowijkia ambigua (Hook.) Nog.	Hypnales	1
Bryoxiphium japonicum (Berggr.) E. Britton	Bryoxiphiales	1
Bryum argenteum Hedw.	Bryales	25
Bryum atrovirens Brid.	Bryales	2
Bryum aubertii (Schwägr.) Brid.	Bryales	1
Bryum dunense A.J.E. Sm. & H. Whitehouse	Bryales	2
Bryum dyffrynense Holyoak	Bryales	1
Bryum radiculosum (Schwägr.) Mitt.	Bryales	1
Bryum riparium I. Hagen	Bryales	1
Bryum ruderale Crundw. & Nyholm	Bryales	2
Bryum sauteri Bruch & Schimp.	Bryales	1
Bryum schleicheri DC.	Bryales	1
Bryum sp.	Bryales	1
Bryum stellituber Arts	Bryales	1
Buxbaumia viridis (Moug. ex DC.) Brid. ex Moug. & Nestl.	Buxbaumiales	2
Callicladium haldanianum (Grev.) H.A.Crum	Hypnales	1
Callicostella belangeriana (Besch.) A. Jaeger	Hookeriales	1
Calliergon giganteum (Schimp.) Kindb.	Hypnales	1
Calohypnum oldhamii (Mitt.) Jan Kučera & Ignatov	Hypnales	1
Calymperes afzelii Sw.	Dicranales	1
Calymperes erosum Müll. Hal.	Dicranales	2
Calymperes spp.	Dicranales	1
Campylophyllopsis sommerfeltii (Myrin) Ochyra	Hypnales	1
Campylophyllum halleri (Hedw.) M. Fleisch.	Hypnales	1
Campylopus fragilis (Brid.) Bruch & Schimp.	Dicranales	1
Campylopus introflexus (Hedw.) Brid.	Dicranales	1
Campylopus oerstedianus (Müll.Hal.) Mitt.	Dicranales	1
Campylopus paradoxus Wilson	Dicranales	1
Campylopus richardii Brid.	Dicranales	1
Ceratodon purpureus (Hedw.) Brid.	Dicranales	19
Codonoblepharon forsteri (Dicks.) Goffinet	Orthotrichales	1
Chionoloma tenuirostre (Hook. & Taylor) M. Alonso, M.J. Cano & J.A. Jiménez	Pottiales	1
Cinclidotus aquaticus (Hedw.) Bruch & Schimp.	Pottiales	1
Cinclidotus fontinaloides (Hedw.) P. Beauv.	Pottiales	2
Cryphaea heteromalla (Hedw.) Brid.	Hypnales	1
Ctenidium hastile (Mitt.) Lindb.	Hypnales	1
Dawsonia superba Grev.	Polytrichales	1
Dicranella cerviculata (Hedw.) Schimp	Dicranales	1

Dicranella heteromalla (Hedw.) Schimp	Dicranales	3
Dicranella varia (Hedw.) Schimp.	Dicranales	1
Dicranoweisia cirrata (Hedw.) Lindb. ex Milde	Dicranales	3
Dicranoweisia crispula (Hedw.) Milde	Dicranales	1
Dicranum japonicum Mitt.	Dicranales	1
Dicranum scoparium Hedw.	Dicranales	5
Dicranum spurium Hedw.	Dicranales	1
Dicranum tauricum Sapjegin	Dicranales	1
Didymodon glaucus Ryan	Pottiales	1
Didymodon rigidulus Hedw.	Pottiales	1
Didymodon tomaculosus (Blockeel) M.F.V.Corley	Pottiales	1
Diphyscium foliosum (Hedw.) D. Mohr	Diphysciales	1
Diphyscium fulvifolium Mitt.	Diphysciales	1
Discelium nudum (Dicks.) Brid.	Disceliales	2
Distichium capillaceum (Hedw.) Bruch & Schimp.	Dicranales	1
Ditrichum cornubicum Paton	Dicranales	3
Ditrichum heteromallum (Hedw.) E. Britton	Dicranales	1
Ditrichum lineare (Sw.) Lindb.	Dicranales	1
Ditrichum pallidum (Hedw.) Hampe	Dicranales	1
Ditrichum plumbicola Crundw.	Dicranales	2
Ditrichum pusillum (Hedw.) Hampe	Dicranales	1
Dolichomitriopsis diversiformis (Mitt.) Nog.	Hypnales	2
Dozya japonica Sande Lac.	Hypnales	1
Drepanocladus lycopodioides (Brid.) Warnst.	Hypnales	2
Drummondia sinensis Müll.Hal.	Orthotrichales	1
Encalypta streptocarpa Hedw.	Encalyptales	1
Entodon challengeri (Paris) Cardot	Hypnales	1
Entodon flavescens (Hook.) A. Jaeger	Hypnales	1
Entodon macropodus (Hedw.) Müll.Hal.	Hypnales	1
Entodon myurus (Hook.) Hampe	Hypnales	1
Entosthodon muhlenbergii (Turner) Fife	Funariales	2
Entosthodon duriaei Mont.	Funariales	1
Entosthodon hungaricus (Boros) Loeske	Funariales	8
Entosthodon pulchellus (H. Philip.) Brugués	Funariales	1
Ephemerum cohaerens (Hedw.) Hampe	Pottiales	1
Ephemerum hibernicum Holyoak & V.S.Bryan	Pottiales	1
Ephemerum recurvifolium (Dicks.) Boulay	Pottiales	1
Ephemerum serratum (Hedw.) Hampe	Pottiales	1
Ephemerum sessile (Bruch) Müll.Hal.	Pottiales	1
Ephemerum spinulosum Bruch & Schimp.	Pottiales	1
Ephemerum spp.	Pottiales	1
Epipterygium tozeri (Grev.) Lindb.	Bryales	1

Erythrodontium julaceum (Schwägr.) Paris	Hypnales	1
Eucladium verticillatum (With.) Bruch & Schimp.	Pottiales	1
Eurhynchium striatum (Hedw.) Schimp.	Hypnales	1
Exsertotheca intermedia (Brid.) S. Olsson, Enroth & D. Quandt	Hypnales	1
Fissidens bryoides Hedw.	Dicranales	1
Fissidens dubius P. Beauv.	Dicranales	1
Fissidens flaccidus Mitt.	Dicranales	1
Fissidens incurvus Starke ex Röhl.	Dicranales	1
Fissidens sp.	Dicranales	1
Fontinalis antipyretica Hedw.	Hypnales	6
Fontinalis dalecarlica Bruch & Schimp.	Hypnales	2
Fontinalis duriaei Schimp.	Hypnales	1
Fontinalis squamosa Hedw.	Hypnales	1
Forsstroemia humilis (Mitt.) Enroth	Hypnales	1
Forsstroemia yezoana (Besch.) S. Olsson, Enroth & D. Quandt	Hypnales	1
Funaria hygrometrica Hedw.	Funariales	64
Funariella curviseta (Schwägr.) Sérgio	Funariales	1
Garckea phascoides Müll. Hal.	Dicranales	1
Gemmabryum coronatum (Schwägr.) J.R. Spence & H.P. Ramsay	Bryales	7
Gemmabryum dichotomum (Hedw.) J.R. Spence & H.P. Ramsay *	Bryales	4
Gemmabryum gemmiferum (R. Wilczek & Demaret) J.R. Spence	Bryales	1
Gemmabryum klinggraeffii (Schimp.) J.R. Spence & H.P. Ramsay	Bryales	2
Gemmabryum violaceum (Crundw. & Nyholm) J.R. Spence	Bryales	1
Goniomitrium seroi Casas	Funariales	1
Grimmia decipiens (Schultz) Lindb.	Grimmiales	1
Grimmia dissimulata E. Maier	Grimmiales	1
Grimmia elatior Bruch ex Bals. & De Not.	Grimmiales	1
Grimmia funalis (Schwägr.) Bruch & Schimp.	Grimmiales	1
Grimmia orbicularis Bruch ex Wilson	Grimmiales	1
Grimmia pilifera P. Beauv.	Grimmiales	1
Grimmia pulvinata (Hedw.) Sm.	Grimmiales	3
Grimmia trichophylla Grev.	Grimmiales	1
Hamatocaulis vernicosus (Mitt.) Hedenäs	Hypnales	1
Hedwigia ciliata (Hedw.) P. Beauv.	Hedwigiales	4
Hedwigidium integrifolium (P. Beauv.) Dixon	Hedwigiales	1
Hennediella gemmascens (P.C. Chen) W. A. Kramer	Pottiales	1
Hennediella heimii (Hedw.) R. H. Zander	Pottiales	6
Hennediella stanfordensis (Steere) Blockeel	Pottiales	1
Herzogiella seligeri (Brid.) Z. Iwats.	Hypnales	1

Homalia trichomanoides (Hedw.) Brid.	Hypnales	2
Homaliadelphus targionianus (Mitt.) Dixon & P.de la Varde	Hypnales	1
Homalothecium sericeum (Hew.) Schimp.	Hypnales	1
Homomallium connexum (Cardot) Broth.	Hypnales	1
Homomallium incurvatum (Schrad. ex Brid.) Loeske	Hypnales	1
Hookeria acutifolia Hook. & Grev.	Hookeriales	1
Hydrogonium gregarium (Mitt.) Jan Kučera	Pottiales	3
Hydrogonium orientale (F. Weber) Jan Kučera	Pottiales	1
Hylocomium splendens (Hedw.) Schimp.	Hypnales	2
Hymenoloma antarcticum (Müll.Hal.) Ochyra	Dicranales	1
Hymenostylium recurvirostrum (Hedw.) Dixon	Pottiales	1
Hyophila involuta (Hook.) A.Jaeger	Pottiales	1
Hyophila propagulifera Broth.	Pottiales	1
Hyophilla nymaniana (M.Fleisch.) M.Menzel	Pottiales	3
Hypnum cupressiforme Hedw.	Hypnales	6
Hypopterygium japonicum Mitt.	Hypopterygiales	1
Imbribryum alpinum (Huds. ex With.) N.Pedersen	Bryales	1
Imbribryum muehlenbeckii (Bruch & Schimp.) N.Pedersen	Bryales	1
Imbribryum subapiculatum (Hampe) D.Bell & Holyoak	Bryales	2
Imbrybryum tenuisetum (Limpr.) D.Bell & Holyoak	Bryales	4
Insomniella plumiformis (Wilson) Hedenäs, Schlesak & D.Quandt	Hypnales	2
Isopterygium albescens (Hook.) A.Jaeger	Hypnales	1
Isopterygium tenerifolium Mitt.	Hypnales	1
Isothecium alopecuroides (Lam. ex Dubois) Isov.	Hypnales	1
Isothecium subdiversiforme Broth.	Hypnales	1
Jirivanaea cuspidifera (Mitt.) U.B.Deshmukh & Rathor	Hypnales	1
Jochenia pallescens (Hedw.) Hedenäs, Schlesak & D.Quandt	Hypnales	1
Kindbergia arbuscula (Broth.) Ochyra	Hypnales	1
Kindbergia praelonga (Hedw.) Ochyra *	Hypnales	3
Leptobryum pyriforme (Hedw.) Wilson	Bryales	6
Leptodictyum riparium (Hedw.) Warnst. *	Hypnales	3
Leptodon longisetus Mont.	Hypnales	1
Leptodontium gemmascens (Mitt.) Braithw.	Pottiales	2
Leptotrichella brasiliensis (Duby) Ochyra	Dicranales	2
Lescuraea saxicola (Schimp.) Molendo	Hypnales	1
Leucobryum antillarum Schimp. ex Besch.	Dicranales	1
Leucobryum crispum Müll. Hal.	Dicranales	1
Leucobryum juniperoideum (Brid.) Müll.Hal.	Dicranales	1
Leucodon canariensis (Brid.) Schwägr.	Hypnales	1
Leucodon nipponicus Nog.	Hypnales	1
Leucodon sciuroides (Hedw.) Schwägr.	Hypnales	2
Lewinskya speciosa (Nees) F.Lara, Garilleti & Goffinet	Orthotrichales	1

Lindbergia brachyptera (Mitt.) Kindb.	Hypnales	1
Loeskeobryum cavifolium (Sande Lac.) M.Fleisch. ex Broth.	Hypnales	1
Macromitrium gymnostomum Sull. & Lesq.	Orthotrichales	1
Merceyopsis cataractae (Mitt.) Brinda, Ignatov & Fedosov *	Pottiales	4
Micromitrium tenerum (Bruch & Schimp.) Crosby.	Dicranales	1
Mielichhoferia bryoides (Harv.) Wijk & Margad.	Bryales	1
Mielichhoferia elongata (Hoppe & Hornsch. ex Hook.) Hornsch.	Bryales	2
Mnium hornum Hedw.	Bryales	4
Mnium lycopodioides Schwägr.	Bryales	1
Mnium spinulosum Bruch & Schimp.	Bryales	1
Mnium stellare Hedw.	Bryales	1
Molendoa hornschuchiana (Hook.) Lindb. ex Limpr.	Pottiales	1
Myuroclada maximowiczii (G.G. Borshch.) Steere & W.B. Schofield	Hypnales	1
Neckera cephalonica Jur. & Unger	Hypnales	1
Neckera pennata Hedw.	Hypnales	2
Neckera pumila Hedw.	Hypnales	1
Neckeropsis disticha (Hedw.) Kindb.	Hypnales	1
Nyholmiella gymnostoma (Bruch ex Brid.) Holmen & E. Warncke	Orthotrichales	1
Nyholmiella obtusifolia (Brid.) Holmen & E. Warncke	Orthotrichales	2
Octoblepharum albidum Hedw.	Dicranales	3
Oedipodiella australis (Wager & Dixon) Dixon	Gigaspermales	2
Oedipodium griffithianum (Dicks.) Schwägr.	Oedipodiales	1
Okamuraea hakoniensis (Mitt.) Broth.	Hypnales	1
Oreas martiana (Hoppe & Hornsch.) Brid.	Dicranales	1
Orthodontium gracile (Wilson ex Hook.) Schwägr. ex Bruch & Schimp.	Bryales	3
Orthodontium lineare Schwägr.	Bryales	4
Orthotrichum cupulatum Hoffm. ex Brid.	Orthotrichales	1
Orthotrichum handiense F. Lara, Garilleti & Mazimpaka	Orthotrichales	1
Orthotrichum pallens Bruch ex Brid.	Orthotrichales	1
Orthotrichum pumilum Sw. ex anon.	Orthotrichales	1
Oxyrrhynchium hians (Hedw.) Loeske	Hypnales	1
Palustriella decipiens (De Not.) Ochyra	Hypnales	1
Pelekium gratum (P. Beauv.) Touw	Hypnales	1
Philonotis falcata (Hook.) Mitt.	Bartramiales	1
Philonotis fontana (Hedw.) Brid.	Bartramiales	1
Philonotis hastata (Duby) Wijk & Margad.	Bartramiales	1
Philonotis lancifolia Mitt.	Bartramiales	1
Philonotis thwaitesii Mitt.	Bartramiales	1
Philonotis turneriana (Schwägr.) Mitt.	Bartramiales	3
Physcomitrium eurystomum Sendtn.	Funariales	4

Physcomitrium japonicum (Hedw.) Mitt.	Funariales	1
Physcomitrium patens (Hedw.) Mitt. *	Funariales	108
Physcomitrium pyriforme (Hedw.) Brid. *	Funariales	12
Physcomitrium sphaericum (C.F.Ludw. ex Schkuhr) Brid.	Funariales	2
Plagiobryum zieri (Dicks. ex Hedw.) Lindb.	Bryales	1
Plagiomnium acutum (Lindb.) T.J. Kop.	Bryales	1
Plagiomnium affine (Blandow ex Funck) T.J.Kop. *	Bryales	2
Plagiomnium cuspidatum (Hedw.) T.J. Kop. *	Bryales	4
Plagiomnium undulatum (Hedw.) T.J.Kop. *	Bryales	2
Plagiomnium vesicatum (Besch.) T.J. Kop.	Bryales	1
Plagiothecium nemorale (Mitt.) A.Jaeger	Hypnales	1
Platygyrium repens (Brid.) Schimp.	Hypnales	2
Plenogemma phyllantha (Brid.) Sawicki, Plášek & Ochyra	Orthotrichales	1
Pleuridium acuminatum Lindb.	Dicranales	2
Pleurozium schreberi (Willd. ex Brid.) Mitt.	Hypnales	2
Podperaea krylovii (Podp.) Z. lwats. & Glime	Hypnales	1
Pogonatum contortum (Menzies ex Brid.) Lesq.	Polytrichales	1
Pogonatum inflexum (Lindb.) Sande Lac.	Polytrichales	1
Pogonatum marginatum Mitt.	Polytrichales	1
Pogonatum pensilvanicum (Bartram ex Hedw.) Paris	Polytrichales	1
Pogonatum urnigerum (Hedw.) P.Beauv.	Polytrichales	2
Pohlia annotina (Hedw.) Lindb.	Bryales	1
Pohlia bulbifera (Warnst.) Warnst.	Bryales	2
Pohlia camptotrachela (Renauld & Cardot) Broth.	Bryales	2
Pohlia drummondii (Müll.Hal.) A.L.Andrews	Bryales	4
Pohlia elongata Hedw. *	Bryales	2
Pohlia flexuosa Harv.	Bryales	1
Pohlia lescuriana (Sull.) Ochi	Bryales	1
Pohlia lutescens (Limpr.) Lindb.	Bryales	1
Pohlia melanodon (Brid.) A.J. Shaw	Bryales	1
Pohlia nutans (Hedw.) Lindb.	Bryales	5
Polytrichum commune Hedw.	Polytrichales	6
Polytrichum formosum Hedw. *	Polytrichales	4
Polytrichum juniperinum Hedw.	Polytrichales	6
Polytrichum strictum Menzies ex Brid.	Polytrichales	1
Pottia bryoides (Dicks.) Mitt.	Pottiales	1
Pseudobraunia californica (Lesq.) Broth.	Hedwigiales	1
Pseudocrossidium replicatum (Taylor) R.H. Zander	Pottiales	3
Pseudoleskeella nervosa (Brid.) Nyholm	Hypnales	1
Pseudotaxiphyllum elegans (Brid.) Z. Iwats.	Hypnales	1
Pseudotaxiphyllum pohliicarpum (Sull. & Lesq.) Z. Iwats.	Hypnales	1
Pterobryon arbuscula Mitt.	Hypnales	1

Pterygoneurum compactum M.J. Cano, J. Guerra & Ros	Pottiales	1
Pterygoneurum sibiricum Otnyukova	Pottiales	1
Ptychomitrium indicum (Willd. ex Schrad.) A. Jaeger	Pottiales	1
Ptychostomum calophyllum (R. Br.) J.R. Spence	Bryales	1
Ptychostomum capillare (Hedw.) Holyoak & N. Pedersen	Bryales	8
Ptychostomum cernuum (Hedw.) Hornsch.	Bryales	1
Ptychostomum compactum var. *rutheanum* (Warnst.) Holyoak & N. Pedersen	Bryales	1
Ptychostomum cyclophyllum (Schwägr.) J.R. Spence	Bryales	1
Ptychostomum donianum (Grev.) Holyoak & N. Pedersen	Bryales	1
Ptychostomum imbricatulum (Müll. Hal.) Holyoak & N. Pedersen	Bryales	2
Ptychostomum knowltonii (Barnes) J.R. Spence	Bryales	1
Ptychostomum marratii (Hook. & Wilson) J.R. Spence	Bryales	1
Ptychostomum pallens (Sw.) J.R. Spence	Bryales	1
Ptychostomum pallescens (Schleich. ex Schwägr.) J.R. Spence	Bryales	5
Ptychostomum pseudotriquetrum (Hedw.) J.R.Spence & H.P. Ramsay *	Bryales	3
Ptychostomum rubens (Mitt.) Holyoak & N. Pedersen	Bryales	2
Ptychostomum schleicheri (DC) J.R. Spence var. *latifolium* (Schwägr.) D. Bell & Holyoak	Bryales	1
Ptychostomum torquescens (Bruch & Schimp.) Ros & Mazimpaka	Bryales	1
Ptychostomum warneum (Schwägr. ex Steud.) J.R. Spence	Bryales	1
Ptychostomum weigelii (Biehler) J.R. Spence	Bryales	1
Pulvigera lyellii (Hook. & Taylor) Plášek, Sawicki & Ochyra	Orthotrichales	1
Pylaisia polyantha (Hedw.) Schimp.	Hypnales	1
Pylaisia selwynii Kindb.	Hypnales	4
Pylaisiadelpha yokohamae (Broth.) W.R. Buck	Hypnales	2
Pylaisiella brotheri (Besch.) Z. Iwats. & Nog.	Hypnales	1
Pyramidula tetragona (Brid.) Brid.	Funariales	1
Pyrrhobryum dozyanum (Sande Lac.) Manuel	Rhizogoniales	1
Racomitrium canescens (Hedw.) Brid.	Grimmiales	1
Racomitrium lanuginosum (Hedw.) Brid.	Grimmiales	1
Racopilum africanum Mitt.	Hypnodendrales	1
Racopilum sp.	Hypnodendrales	1
Rhacocarpus purpurascens (Brid.) Paris	Hedwigiales	1
Rhizomnium magnifolium (Horik.) T.J.Kop.	Bryales	1
Rhizomnium parvulum (Mitt.) T.J.Kop.	Bryales	1
Rhizomnium pseudopunctatum (Bruch & Schimp.) T.J.Kop.	Bryales	1
Rhizomnium punctatum (Hedw.) T.J. Kop. *	Bryales	2
Rhizomnium tuomikoskii T.J. Kop.	Bryales	1
Rhodobryum giganteum (Schwägr.) Paris	Bryales	1
Rhodobryum roseum (Hedw.) Limpr.	Bryales	1
Rhynchostegium murale (Hedw.) Schimp.	Hypnales	2

Rhynchostegium pallidifolium (Mitt.) A. Jaeger	Hypnales	1
Rhynchostegium riparioides (Hedw.) Cardot	Hypnales	2
Rhynchostegium rotundifolium (Scop. ex Brid.) Schimp.	Hypnales	1
Rhytidiadelphus loreus (Hedw.) Warnst.	Hypnales	1
Rhytidiadelphus squarrosus (Hedw.) Warnst.	Hypnales	1
Rhytidiadelphus triquetrus (Hedw.) Warnst.	Hypnales	1
Rosulabryum billarderii (Schwägr.) J.R. Spence	Bryales	1
Rosulabryum bornholmense (Wink. & R. Ruthe) J.R. Spence	Bryales	1
Rosulabryum densifolium (Brid.) Ochyra	Bryales	1
Rosulabryum flaccidum (Brid.) J.R. Spence	Bryales	2
Rosulabryum moravicum (Podp.) Ochyra & Stebel	Bryales	1
Saelania glaucescens (Hedw.) Broth. *	Pottiales	2
Sanionia uncinata (Hedw.) Loeske *	Hypnales	2
Schistostega pennata (Hedw.) F. Weber & D. Mohr	Dicranales	2
Sciuro-hypnum plumosum (Hedw.) Ignatov & Huttunen	Hypnales	3
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen	Hypnales	1
Scopelophila ligulata (Spruce) Spruce	Pottiales	1
Scorpiurium circinatum (Brid.) M. Fleisch. & Loeske	Hypnales	1
Seligeria carniolica (Breidl. & Beck) Nyholm	Grimmiales	1
Sematophyllum subpinnatum (Brid.) E. Britton	Hypnales	1
Sphagnum angustifolium (Russow) C.E.O. Jensen	Sphagnales	3
Sphagnum balticum (Russow) C.E.O. Jensen	Sphagnales	2
Sphagnum capillifolium (Ehrh.) Hedw. *	Sphagnales	4
Sphagnum centrale C.E.O. Jensen	Sphagnales	2
Sphagnum compactum DC.	Sphagnales	2
Sphagnum contortum Schultz	Sphagnales	2
Sphagnum cuspidatum Ehrh. ex Hoffm.	Sphagnales	5
Sphagnum denticulatum Brid. *	Sphagnales	2
Sphagnum fallax (H.Klinggr.) H.Klinggr.	Sphagnales	6
Sphagnum fimbriatum Wilson	Sphagnales	4
Sphagnum fitzgeraldii Renauld ex Lesq. & James	Sphagnales	1
Sphagnum fuscum (Schimp.) H. Klinggr.	Sphagnales	3
Sphagnum girgensohnii Russow	Sphagnales	1
Sphagnum imbricatum Hornsch. ex Russow	Sphagnales	3
Sphagnum inundatum Russcow	Sphagnales	1
Sphagnum isoviitae Flatberg	Sphagnales	1
Sphagnum lindbergii Schimp.	Sphagnales	2
Sphagnum macrophyllum Bernh. ex Brid.	Sphagnales	1
Sphagnum magellanicum Brid.	Sphagnales	4
Sphagnum medium Limpr. /*divinum* Flatberg & Hassel	Sphagnales	1
Sphagnum meridense (Hampe) Müll. Hal.	Sphagnales	1
Sphagnum palustre L.	Sphagnales	9

Sphagnum papillosum Lindb.	Sphagnales	3
Sphagnum platyphylloides Warnst.	Sphagnales	1
Sphagnum riparium Ångstr.	Sphagnales	1
Sphagnum rubellum Wilson	Sphagnales	2
Sphagnum russowii Warnst.	Sphagnales	1
Sphagnum squarrosum Crome	Sphagnales	5
Sphagnum subfulvum Sjörs	Sphagnales	1
Sphagnum subnitens Russow & Warnst.	Sphagnales	4
Sphagnum subsecundum Nees	Sphagnales	1
Sphagnum tenellum (Brid.) Bory	Sphagnales	1
Sphagnum torreyanum Sull.	Sphagnales	1
Sphagnum trinitense Müll. Hal.	Sphagnales	1
Sphagnum warnstorfii Russow	Sphagnales	2
Splachnum ampullaceum Hedw.	Splachnales	6
Splachnum sphaericum Hedw.	Splachnales	2
Stereophyllum radiculosum (Hook) Mitt.	Hypnales	1
Straminergon stramineum (Dicks. ex Brid.) Hedenäs	Hypnales	1
Syntrichia caninervis Mitt. *	Pottiales	3
Syntrichia laevipila Brid. *	Pottiales	3
Syntrichia latifolia (Bruch ex Hartm.) Huebener	Pottiales	1
Syntrichia norvegica F. Weber	Pottiales	1
Syntrichia pagorum (Milde) J.J.Amann	Pottiales	2
Syntrichia papillosa (Wilson ex Spruce) Spruce	Pottiales	1
Syntrichia princeps (De Not.) Mitt. *	Pottiales	2
Syntrichia ruralis (Hedw.) F. Weber & D. Mohr *	Pottiales	3
Syntrichia ruralis complex	Pottiales	1
Takakia lepidozioides S. Hatt. & Inoue	Takakiales	2
Taxiphyllum barbieri (Cardot & Copp.) Z. Iwats.	Hypnales	1
Taxiphyllum cuspidifolium (Cardot) Z. Iwats.	Hypnales	1
Taxiphyllum taxirameum (Mitt.) M. Fleisch.	Hypnales	1
Tayloria froelichiana (Hedw.) Mitt. ex Broth.	Splachnales	1
Tayloria lingulata (Dicks.) Lindb.	Splachnales	1
Tayloria rudolphiana (Garov.) Bruch & Schimp.	Splachnales	1
Tayloria splachnoides (Schleich. ex Schwägr.) Hook.	Splachnales	1
Tayloria tenuis (Dicks.) Schimp.	Splachnales	1
Tetraphis geniculata Girg. ex Milde	Tetraphidales	1
Tetraphis pellucida Hedw.	Tetraphidales	6
Tetraplodon mnioides (Hedw.) Bruch & Schimp.	Splachnales	1
Thamniopsis incurva (Hornsch.) W.R. Buck	Hookeriales	1
Thamnobryum alopecurum (Hedw.) Gangulee	Hypnales	1
Thamnobryum plicatulum (Sande Lac.) Z. Iwats.	Hypnales	1

Thamnobryum subseriatum (Mitt. ex Sande Lac.) B.C. Tan	Hypnales	1
Thuidium glaucinum (Mitt.) Bosch & Sande Lac.	Hypnales	1
Thuidium kanedae Sakurai	Hypnales	1
Thuidium sp.	Hypnales	1
Timmia austriaca Hedw.	Timmiales	1
Timmia megapolitana Hedw.	Timmiales	1
Timmiella anomala (Bruch & Schimp.) Limpr.	Pottiales	3
Tortella flavovirens (Bruch) Broth	Pottiales	1
Tortella humilis (Hedw.) Jenn.	Pottiales	1
Tortella inflexa (Bruch) Broth.	Pottiales	1
Tortella squarrosa (Brid.) Limpr.	Pottiales	3
Tortula acaulon (With.) R.H. Zander	Pottiales	1
Tortula caucasica Lindb.	Pottiales	2
Tortula cernua (Huebener) Lindb.	Pottiales	1
Tortula muralis Hedw.	Pottiales	5
Tortula subulata Hedw.	Pottiales	1
Trachycystis microphylla (Dozy & Molk.) Lindb.	Bryales	1
Trematodon ambiguus (Hedw.) Hornsch.	Dicranales	1
Trematodon brevicalyx Dixon ex L.N. Mathur	Dicranales	4
Trematodon longicollis Michx.	Dicranales	1
Trichodon cylindricus (Hedw.) Schimp.	Dicranales	1
Ulota crispa (Hedw.) Brid.	Orthotrichales	2
Vesicularia vesicularis (Schwägr.) Broth. *	Hypnales	2
Vesicularia vesicularis (Schwägr.) Broth. var. *vesicularis*	Hypnales	1
Weissia condensa (Voit) Lindb.	Pottiales	1
Weissia controversa Hedw.	Pottiales	2
Weissia levieri (Limpr.) Kindb.	Pottiales	1
Weissia squarrosa (Nees & Hornsch.) Müll.Hal.	Pottiales	1
Zygodon gracilis Wilson	Orthotrichales	1
Zygodon rupestris Schimp. ex Lorentz	Orthotrichales	1
Zygodon strictus Mitt.	Orthotrichales	1
Zygodon viridissimus (Dicks.) Brid.	Orthotrichales	1

Table 2. Liverwort taxa checklist with corresponding order and number of publications. Entries marked with an asterisk (*) contain multiple taxa (original entry) which belong to a single revised taxon name.

Taxa (species/entry)	Ordo	N of references
Acrolejeunea fertilis (Reinw., Blume & Nees) Schiffn.	Porellales	3
Anastrophyllum michauxii (F. Weber) H. Buch	Jungermanniales	1
Aneura pinguis (L.) Dumort. *	Metzgeriales	6
Apometzgeria pubescens (Schrank) Kuwah.	Metzgeriales	1

Asterella blumeana (Nees) Kachroo	Marchantiales	1
Asterella tenella (L.) P. Beauv.	Marchantiales	1
Asterella wallichiana (Lehm. & Lindenb.) Grolle	Marchantiales	1
Balantiopsis diplophylla (Hook. f. & Taylor) Mitt. *	Jungermanniales	2
Barbilophozia barbata (Schmidel ex Schreb.) Loeske	Jungermanniales	1
Biantheridion undulifolium (Nees) Konstant. & Vilnet	Jungermanniales	1
Blasia pusilla L.	Blasiales	3
Calypogeia azurea Stotler & Crotz	Jungermanniales	1
Calypogeia fissa (L.) Raddi. *	Jungermanniales	3
Calypogeia granulata Inoue	Jungermanniales	1
Calypogeia integristipula Steph.	Jungermanniales	2
Calypogeia sphagnicola (Arnell & J. Perss.) Warnst. & Loeske	Jungermanniales	1
Calypogeia suecica (Arnell & J. Perss.) Müll. Frib.	Jungermanniales	1
Cephalozia bicuspidata (L.) Dumort.	Jungermanniales	2
Cephalozia sp.	Jungermanniales	1
Cephaloziella hampeana (Nees) Schiffn. ex Loeske	Jungermanniales	1
Cephaloziella massalongoi (Spruce) Müll. Frib.	Jungermanniales	1
Cephaloziella nicholsonii Douin	Jungermanniales	1
Cheilolejeunea clypeata (Schwein.) W. Ye & R.L. Zhu	Porellales	1
Chiloscyphus sp.	Jungermanniales	1
Clevea pusilla (Steph.) Rubas. & D.G. Long	Marchantiales	1
Cololejeunea biddlecomiae (Austin ex Pearson) A. Evans	Porellales	1
Conocephalum conicum (L.) Dumort.	Marchantiales	8
Cryptomitrium himalayense Kashyap	Marchantiales	2
Diplophyllum albicans (L.) Dumort.	Jungermanniales	1
Diplophyllum apiculatum (A. Evans) Steph.	Jungermanniales	1
Exormotheca brevipedunculata (Kashyap) D.G. Long, Crand.-Stotl., L.L. Forrest & J.C. Villarreal	Marchantiales	2
Fossombronia alaskana Steere & Inoue	Fossombroniales	1
Fossombronia foveolata Lindb. var. *cristula* (Austin) R.M. Schust.	Fossombroniales	1
Fossombronia porphyrorhiza (Nees) Prosk.	Fossombroniales	1
Fossombronia pusilla (L.) Nees	Fossombroniales	3
Fossombronia spp.	Fossombroniales	1
Frullania asagrayana Mont.	Porellales	2
Frullania bolanderi Austin	Porellales	1
Frullania brittoniae A. Evans	Porellales	1
Frullania californica (M. Howe) A. Evans	Porellales	1
Frullania cobrensis Gottsche	Porellales	1
Frullania dilatata (L.) Dumort.	Porellales	2
Frullania donnellii Austin	Porellales	1
Frullania eboracensis Lehm.	Porellales	2
Frullania ericoides (Nees) Mont.	Porellales	1

Frullania franciscana M. Howe	Porellales	1
Frullania inflata Gottsche *	Porellales	2
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	Porellales	1
Frullania meyeniana Lindenb.	Porellales	1
Frullania nisquallensis Sull.	Porellales	1
Frullania oakesiana Aust.	Porellales	1
Frullania obcordata (Lehm. & Lindenb.) Lehm. & Lindenb.	Porellales	1
Frullania riojaneirensis (Raddi) Ångstr.	Porellales	1
Frullania squarrosa Dumort.	Porellales	1
Frullania tamarisci (L.) Dumort. subsp. *tamarisci*	Porellales	1
Fuscocephaloziopsis catenulata (Huebener) Váňa & L. Söderstr.	Jungermanniales	1
Fuscocephaloziopsis connivens (Dicks.) Váňa & L. Söderstr.	Jungermanniales	1
Fuscocephaloziopsis lunulifolia (Dumort.) Váňa & L. Söderstr.	Jungermanniales	1
Fuscocephaloziopsis pleniceps (Austin) Váňa & L. Söderstr.	Jungermanniales	1
Geocalyx graveolens (Schrad.) Nees	Jungermanniales	1
Gymnocolea inflata (Huds.) Dumort.	Jungermanniales	1
Haplomitrium blumei (Nees) R.M. Schust.	Calobryales	1
Haplomitrium mnioides (Lindb.) R.M. Schust.	Calobryales	1
Harpanthus scutatus (F. Weber & D. Mohr) Spruce	Jungermanniales	1
Heteroscyphus coalitus (Hook.) Schiffn.	Jungermanniales	2
Heteroscyphus planus (Mitt.) Schiffn.	Jungermanniales	1
Isotachis lyallii Mitt.	Jungermanniales	1
Jungermannia atrovirens Dumort.	Jungermanniales	1
Kurzia pauciflora (Dicks.) Grolle	Jungermanniales	1
Lepidolaena hodgsoniae Grolle	Porellales	1
Lepidozia reptans (L.) Dumort.	Jungermanniales	1
Liochlaena lanceolata Nees	Jungermanniales	1
Liochlaena subulata (A. Evans) Schljakov	Jungermanniales	6
Lophocolea bidentata (L.) Dumort.	Jungermanniales	1
Lophocolea heterophylla (Schrad.) Dumort.	Jungermanniales	3
Lophocolea hodgsoniae Hamlin	Jungermanniales	1
Lophocolea sp.	Jungermanniales	1
Lopholejeunea sp.	Porellales	1
Lophoziopsis excisa (Dicks.) Konstant. & Vilnet	Jungermanniales	1
Lunularia cruciata (L.) Dumort. ex Lindb.	Lunulariales	9
Marchantia emarginata Reinw., Blume & Nees	Marchantiales	1
Marchantia inflexa Nees & Mont.	Marchantiales	1
Marchantia linearis Lehm. & Lindenb.	Marchantiales	5
Marchantia paleacea Bertol. *	Marchantiales	10
Marchantia polymorpha L.	Marchantiales	62

Marchantia polymorpha L. subsp. *ruderalis* Bischl. & Boissel.-Dub.	Marchantiales	11
Marchantia spp.	Marchantiales	1
Marchantia quadrata Scop.	Marchantiales	1
Marchantia romanica (Radian) D.G. Long, Crand.-Stotl., L.L. Forrest & J.C. Villarreal	Marchantiales	1
Mesoptychia collaris (Nees) L. Söderstr. & Váňa	Jungermanniales	1
Microlepidozia setacea Jørg.	Jungermanniales	1
Moerckia hibernica (Hook.) Gottsche	Pallaviciniales	1
Monoclea gottschei Lindb. subsp. *elongata* Gradst. & Mues	Marchantiales	1
Neohodgsonia mirabilis (Perss.) Perss.	Neohodgsoniales	1
Neolepidozia patentissima (Hook. f. & Taylor) E.D. Cooper	Jungermanniales	1
Nowellia curvifolia (Dicks.) Mitt.	Jungermanniales	1
Odontoschisma denudatum (Mart.) Dumort.	Jungermanniales	1
Odontoschisma fluitans (Nees) L. Söderstr. & Váňa	Jungermanniales	1
Pachyglossa austrigena (Hook. f. & Taylor) L. Söderstr.	Jungermanniales	1
Pallavicinia lyellii (Hook.) Gray	Pallaviciniales	2
Pallavicinia subciliata (Austin) Steph.	Pallaviciniales	1
Pellia borealis Lorb.	Pelliales	2
Pellia endiviifolia (Dicks.) Dumort.	Pelliales	5
Pellia epiphylla (L.) Corda	Pelliales	5
Pellia neesiana (Gottsche) Limpr.	Pelliales	3
Plagiochasma appendiculatum Lehm. & Lindenb.	Marchantiales	1
Plagiochasma rupestre (J.R. Forst. & G. Forst.) Steph.	Marchantiales	1
Plagiochila asplenioides (L.) Dumort.	Jungermanniales	1
Plagiochila longispina Lindenb. & Gottsche	Jungermanniales	1
Plagiochila ovalifolia Mitt.	Jungermanniales	1
Plagiochila porelloides (Torr. ex Nees) Lindenb.	Jungermanniales	1
Plagiochila sp.	Jungermanniales	1
Plectocolea infusca Mitt.	Jungermanniales	2
Podomitrium phyllanthus (Hook.) Mitt.	Pallaviciniales	1
Porella cordaeana (Huebener) Moore	Porellales	1
Porella vernicosa Lindb.	Porellales	1
Ptilidium ciliare (L.) Hampe	Ptilidiales	1
Ptilidium pulcherrimum (Weber) Vain.	Ptilidiales	1
Radula complanata (L.) Dumort.	Porellales	3
Radula lindenbergiana Gottsche ex C. Hartm.	Porellales	1
Radula marginata Gottsche, Lindenb. & Nees	Porellales	1
Radula obconica Sull.	Porellales	1
Reboulia hemisphaerica (L.) Raddi	Marchantiales	6
Riccardia eriocaula (Hook.) Besch. & C. Massal.	Metzgeriales	1
Riccardia latifrons (Lindb.) Lindb.	Metzgeriales	1
Riccardia multifida (L.) Gray	Metzgeriales	1

Riccardia sp.	Metzgeriales	1
Riccia crystallina L.	Marchantiales	1
Riccia discolor Lehm. & Lindenb.	Marchantiales	1
Riccia fluitans L.	Marchantiales	4
Riccia frostii Austin	Marchantiales	2
Riccia sorocarpa Bisch.	Marchantiales	1
Riccia sp.	Marchantiales	1
Ricciocarpos natans (L.) Corda	Marchantiales	4
Riella helicophylla (Bory & Mont.) Mont.	Sphaerocarpales	2
Sauteria alpina (Nees) Nees	Marchantiales	1
Scapania nemorea (L.) Grolle	Jungermanniales	2
Scapania parvitexta Steph.	Jungermanniales	1
Scapania undulata (L.) Dumort.	Jungermanniales	1
Schistochila ciliata (Mitt.) Steph.	Jungermanniales	1
Schistochilopsis incisa (Schrad.) Konstant.	Jungermanniales	1
Solenostoma hyalinum (Lyell) Mitt.	Jungermanniales	1
Solenostoma schaulianum (Steph.) Váňa & D.G. Long	Jungermanniales	1
Sphaerocarpos donnellii Austin	Sphaerocarpales	2
Sphaerocarpos europaeus Lorb. *	Sphaerocarpales	7
Symphyogyna aspera Steph. ex F.A. McCormick	Pallaviciniales	1
Symphyogyna brongniartii Mont.	Pallaviciniales	1
Syzygiella autumnalis (DC.) K. Feldberg, Váňa, Hentschel & Heinrichs	Jungermanniales	3
Targionia hypophylla L.	Marchantiales	1
Trichocolea tomentella (Ehrh.) Dumort.	Jungermanniales	2
Tylimanthus viridis Mitt.	Jungermanniales	1

Table 3. Hornwort taxa checklist with corresponding order and number of publications. Entries marked with an asterisk (*) contain multiple taxa (original entry) which belong to a single revised taxon name.

Taxa (species/entry)	Ordo	N of references
Anthoceros agrestis Paton	Anthocerotales	8
Anthoceros angustus Steph.	Anthocerotales	1
Anthoceros formosae Steph.	Anthocerotales	2
Anthoceros punctatus L.	Anthocerotales	4
Folioceros fuciformis (Mont.) D.C. Bhardwaj	Anthocerotales	1
Notothylas javanica (Sande Lac.) Gottsche	Notothyladales	1
Notothylas khasiana Udar & D.K. Singh	Notothyladales	1
Notothylas orbicularis (Schwein.) Sull	Notothyladales	1
Phaeoceros carolinianus (Michx.) Prosk.	Notothyladales	1
Phaeoceros laevis (L.) Prosk. *	Notothyladales	2

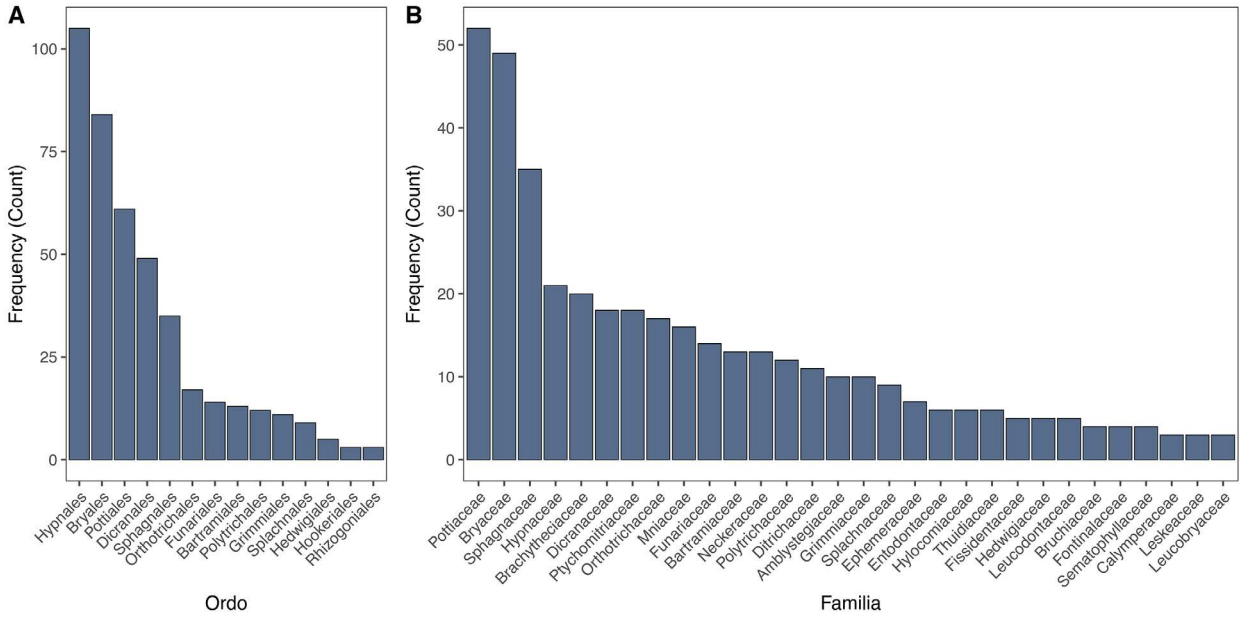

Fig. 1. Number of moss entries classified by order (A) and family (B). Only orders and families with more than two entries are presented.

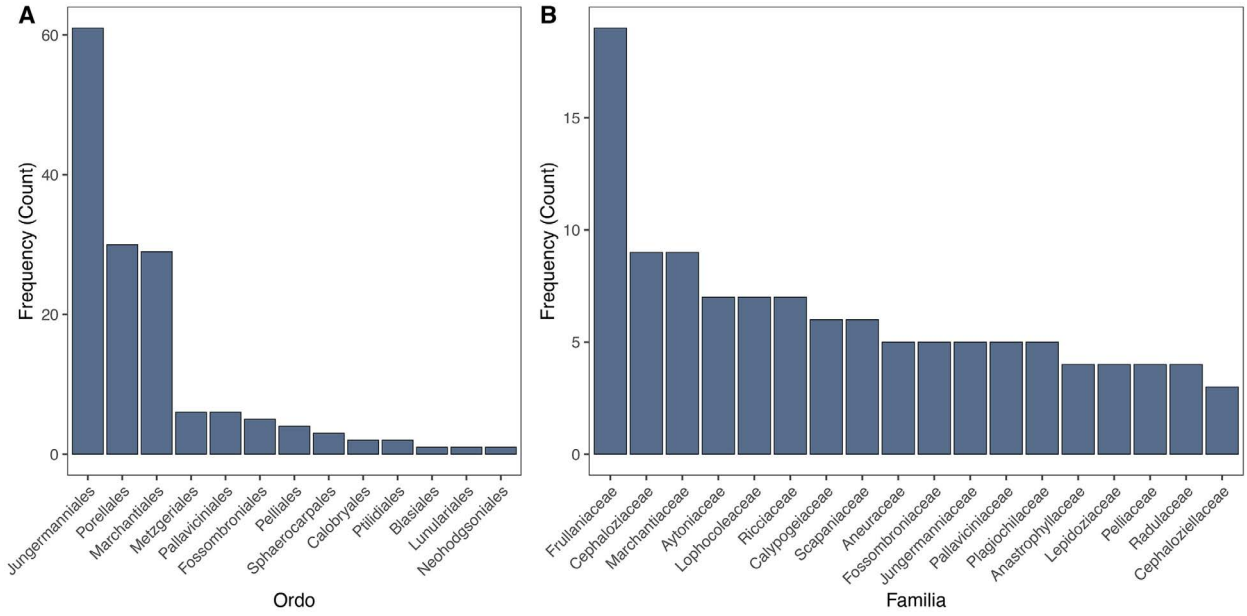

Fig. 2. Number of liverwort entries classified by order (A) and family (B). Only families with more than two entries are presented.

Emerging model bryophytes. Based on the defined selection criteria (section 2.3), several moss species emerge as promising models for future research. In addition to the well-established model *Physcomitrium patens*, which accounts for 108 publication occurrences (representing 11.3% of all moss taxa publication occurrences), other frequently studied species include *Funaria hygrometrica* (6.7%), *Atrichum undulatum* (2.9%), *Bryum argenteum* (2.6%), and *Ceratodon purpureus* (2%). Moreover, it is important to note that 72.4% of moss species are mentioned in only a single publication, indicating a lack

of in-depth studies. Nevertheless, many of these species are likely to possess unique or biologically interesting traits which could qualify them as potential model organisms in future research.

Regarding liverworts, the model species *Marchantia polymorpha* is dominant accounting for 23.3% (19.7 and 3.5% *M. polymorpha* and *M. polymorpha* subsp. *ruderalis*, respectively) of all liverwort taxa occurrences. Emerging models also include *M. paleacea* (3.2%), *Lunularia cruciata* (2.9%), *Conocephalum conicum* (2.5%), and *Sphaerocarpos europaeus* (2.2%). Interestingly, a greater number of publications have focused on the axenic cultivation of thalloid liverworts, whereas comparatively fewer studies have investigated leafy liverworts. As a result, no model species have been proposed from the latter group. This is paradoxical, given that our analysis indicates that leafy liverworts, particularly those from the family *Frullaniaceae*, are the most frequently represented (Fig. 2). This predominance appears to be driven by both the number of publications and the diversity of *Frullania* species used in axenic cultivation. In many instances, multiple species were included within a single study, yet these taxa were not subsequently investigated in further research. Notably, 75.1% of liverwort species in our dataset are cited in only one publication, consistent with this observation. The prevailing focus on thalloid species to date may reflect the availability of established cultivation protocols or the more extensively studied chemical properties of these taxa.

In hornworts, besides the well-established model *Anthoceros agrestis* (eight publications or 36.4% of all hornwort taxa occurrences), *Anthoceros punctatus* emerges as a potential model with four publication occurrences (18.2%). Interestingly, the majority of investigated species have each been mentioned in only a single publication to date, accounting for 60% of all species cited.

CONCLUSION

A comprehensive checklist of bryophyte species successfully cultivated under axenic conditions represents a valuable resource for both fundamental and applied research. It provides a reference framework guiding the design of comparative studies across ecological, physiological, and evolutionary contexts. It also facilitates the identification of knowledge gaps and highlights those taxa which remain unexplored or underrepresented in cultivation studies. Moreover, by making reliable cultivation protocols accessible, this resource supports *ex situ* conservation of rare and threatened species and helps mitigate long-term pressure on natural populations. Ultimately, the existence of this resource serves to enhance reproducibility and accelerate progress in bryophyte biology and biotechnology.

Acknowledgments – We thank the Serbian Ministry of Science, Technological Development and Innovations, contracts no: 451-03-65/2024-03/200178 and 451-03-66/2024-03/200178 and the Grant Agency of the Ministry of Education, Science, Research, and Sport of the Slovak Republic (VEGA 1/0768/25).

REFERENCES

Abay G, Karakoç ÖC, Tüfekçi AR, Koldaş S & Demirtas I. 2012. Insecticidal activity of *Hypnum cupressiforme* (Bryophyta) against *Sitophilus granarius* (Coleoptera: Curculionidae). *Journal of Stored Products Research* **51**: 6–10. http://dx.doi.org/10.1016/j.jspr.2012.05.005

Asakawa Y, Toyota M, von Konrat M & Braggins JE. 2003. Volatile components of selected species of the liverwort genera *Frullania* and *Schusterella* (Frullaniaceae) from New Zealand, Australia and South America: a chemosystematic approach. *Phytochemistry* **62**(3): 439–452.

Commisso M, Guarino F, Marchi L, Muto A, Piro A & Degola F. 2021. Bryo-activities: a review on how bryophytes are contributing to the arsenal of natural bioactive compounds against fungi. *Plants* **10**(2): 203. https://doi.org/10.3390/plants10020203

Ćosić MV, Božović DP, Jadranin BZ, Vujičić MM, Sabovljević AD & Sabovljević MS. 2025. Axenic cultivation of bryophytes: growth media composition. *Plant Cell, Tissue and Organ Culture* **160**: 50. http://dx.doi.org/10.1007/s11240-024-02957-5

Drobnik J & Stebel A. 2021. Four centuries of medicinal mosses and liverworts in European ethnopharmacy and scientific pharmacy: a review. *Plants* **10**: 1296. https://doi.org/10.3390/plants10071296

Duckett JG, Burch J, Fletcher PW, Matcham HW, Read DJ, Russel AJ & Pressel S. 2024. *In vitro* cultivation of bryophytes: a review of practicalities, problems, progress and promise. *Journal of Bryology* **26**: 3–20. http://dx.doi.org/10.1179/037366803235001742

Dziwak M, Wróblewska K, Szumny A & Galek R. 2022. Modern use of bryophytes as a source of secondary metabolites. *Agronomy* **12**(6): 1456. https://doi.org/10.3390/agronomy12061456

Geffert JL, Frahm JP, Barthlott W & Mutke J. 2013. Global moss diversity: spatial and taxonomic patterns of species richness. *Journal of Bryology* **35**(1): 1–11. https://doi.org/10.1179/1743282012Y.0000000038

Gunadi A, Li FW & Van Eck J. 2022. Accelerating gametophytic growth in the model hornwort *Anthoceros agrestis*. *Applications in Plant Sciences* **10**(2): e11460. https://doi.org/10.1002/aps3.11460

Hodgetts N & Lockhart N. 2020. *Checklist and country status of European bryophytes – update 2020. Irish Wildlife Manuals, No. 123*. National Parks and Wildlife Service, Department of culture, Heritage and the Gaeltacht, Ireland.

Horn A, Pascal A, Lončarević I, Marques RV, Lu Y, Miguel S, Bourgaud F, Thorsteinsdóttir M, Cronberg N, Becker JD, Reski R & Simonsen HT. 2021. Natural products from Bryophytes: from basic biology to biotechnological applications. *Critical Reviews in Plant Sciences* **40**: 191–217. https://doi.org/10.1080/07352689.2021.1911034

Lafferty DJ, Robison TA, Gunadi A, Schafran PW, Gunn LH, Van Eck J & Li FW. 2024. Biolistics-mediated transformation of hornworts and its application to study pyrenoid protein localization. *Journal of Experimental Botany* **75**(16): 4760–4771. https://doi.org/10.1093/jxb/erae243

Longton RE. 1992. The role of bryophytes and lichens in terrestrial ecosystems. In: Farmer AM & Bates JW (eds.), Bryophytes in a changing environment, pp. 32–76, Calerndon Press, Oxford.

Rowntree JK, Pressel S, Ramsay MM, Sabovljevic A & Sabovljevic M. 2011. *In vitro* conservation of European bryophytes. *In Vitro Cellular and Developmental Biology – Plant* **47**(1): 55–64. http://dx.doi.org/10.1007/s11627-010-9326-3

Sabovljević M, Vujičić M, Pantović J & Sabovljević A. 2014. Bryophyte conservation biology: *in vitro* approach to the ex situ conservation of bryophytes from Europe. *Plant Biosystems* **148**(4): 857–868. https://doi.org/10.1080/11263504.2014.949328

Sabovljević MS, Ćosić MV, Jadranin BZ, Pantović JP, Giba ZS, Vujičić MM & Sabovljević AD. 2022. The conservation physiology of bryophytes. *Plants* **11**(10): 1282. https://doi.org/10.3390/plants11101282

Saxena D & Harinder. 2004. Uses of bryophytes. *Resonance* **9**(6): 56–65.

Shaw A, Schmutz J, Devos N, Shu S, Carrell A & Weston D. 2016. The *Sphagnum* genome project: a new model for ecological and evolutionary genomics. *Advances in Botanical Research* **78**: 167–187. https://doi.org/10.1016/bs.abr.2016.01.003

Söderström L, Hagborg A, Konrat M, Bartholomew-Began S, Bell D, Briscoe L, Brown E, Cargill DC, Costa D, Crandall-Stotler B, Cooper E, Dauphin G, Engel J, Feldberg K, Glenny D, Gradstein S, He X, Heinrichs J, Hentschel J, Ilkiu-Borges AL, Katagiri T, Konstantinova NA, Larraín J, Long DG, Nebel M, Pócs T, Puche F, Reiner-Drehwald E, Renner MAM, Sass-Gyarmati A, Schäfer-Verwimp A, Moragues JGS, Stotler RE, Sukkharak P, Thiers BM, Uribe J, Váňa J, Villarreal JC, Wigginton M, Zhang L & Zhu RL. 2016. World checklist of hornworts and liverworts. *PhytoKeys* **59**: 1–828. http://dx.doi.org/10.3897/phytokeys.59.6261

Turetsky MR, Weston DJ, Cox WD, Petro C & Shaw AJ. 2025. The challenging but unique eco-evolutionary aspects of *Sphagnum* moss. *New Phytologist* **247**: 1608–1621. https://doi.org/10.1111/nph.70233

Vanderpoorten A & Goffinet B. 2009. *Introduction to bryophytes*. Cambridge University Press. https://doi.org/10.1017/CBO9780511626838

Villarreal JC, Cargill DC, Hagborg A, Soderstrom L & Renzaglia KS. 2010. A synthesis of hornwort diversity: patterns, causes and future work. *Phytotaxa* **9**: 150–166. https://doi.org/10.11646/phytotaxa.9.1.8

Vitt DH, Crandall-Stotler B & Wood A. 2014. Bryophytes: survival in a dry world through tolerance and avoidance. In: Rajakaruna N, Boyd R & Harris T (eds.), *Plant ecology and evolution in harsh environments*, pp. 267–295, Nova Publishers.

COMPREHENSIVE PLANT BIOLOGY

REZIME

Aksenične kulture briofita: lista gajenih vrsta

Djordje P. Božović, Marija V. Vesović, Bojana Z. Jadranin, Nikolina A. Matić, Aneta D. Sabovljević i Marko S. Sabovljević

Briofite predstavljaju drugu najveću grupu recentnih kopnenih biljaka i igraju ključne ekološke uloge u kolonizaciji, regulaciji vodnog režima i formiranju staništa. Pored svog ekološkog značaja, oni su bogat izvor biološki aktivnih jedinjenja sa potencijalnom primenom u medicini, poljoprivredi i biotehnologiji. Međutim, briofite i dalje predstavljaju izazov za gajenje u kontrolisanim, posebno akseničnim uslovima zbog njihovog sporog rasta, uskih ekoloških zahteva i ograničenog znanja o njihovoj nutritivnoj i reproduktivnoj biologiji, posebno kod retkih vrsta. Kao rezultat, samo mali deo vrsta je uspešno održavan u akseničnoj kulturi, a informacije o metodama gajenja su sporadične i često zanemarene. Da bismo popunili ovu prazninu, sproveli smo detaljan pregled objavljene literature o aksenično gajenim briofitama, sastavili sveobuhvatnu listu sa referencama na originalne izvore i istakli potencijalne model vrste. Ova lista i literaturna baza podataka pružaju vredan resurs konsolidovanjem rasutog znanja i služi kao osnova za buduća istraživanja u biologiji i očuvanju briofita i kao platforma za proširenje njihovog biotehnološkog potencijala.

Ključne reči: mahovine, jetrenjače, rožnjače, *in vitro*, diverzitet, briofite