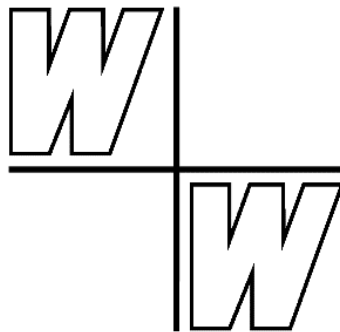


Data Collection on Intergeneric Hybrids and Basic Types: **BRYOPHYTA s. l.**

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version 2 01.10.2026



Studiengemeinschaft Wort und Wissen
<https://www.wort-und-wissen.org/artikel/data-collection-basic-types/>

„BRYOPHYTA s. l.“

mosses, hornworts and liverworts

= Laubmoose, Hornmoose und Lebermoose

Systematics according to en.wikipedia 2025. The taxonomy has been intensively changed in the last years! What formerly had the rank of a division Bryophyta s. l. is now divided into 3 divisions:

Anthocerotophyta (hornworts): 2 classes, 5 orders, 5 families, 214 species

Marchantiophyta (liverworts): 3 classes, 15 orders, 46 families, 9000 species

Bryophyta s. str. (mosses): 8 classes, 45 orders, 127 families, 12000 species

Hybrids are only known in division Bryophyta s. str.

In all mosses the diplophase is restricted to the zygote and the sporogon which often lacks conspicuous differences between related taxa. Therefore it is rather difficult to detect hybrids. See the literature below, e.g. Natcheva & Cronberg 2004, where all known (natural) interspecific and intergeneric hybrids up to 2004 are listed.

Summary

14 intergeneric hybrids., found in 7 families.

3 preliminary basic types:

Bryales 5 families 35: 1000. **2 IG** (incl. 1 IF)

Funariaceae 14: 300. **4 IG**

Sphagnaceae 2: 200. **0 IG**

Abbreviations:

° = taxa actually not accepted in the rank of a genus, e.g. *Cerasus*° (= *Prunus* p. p.)

10: 50 etc. The numbers behind the names of families etc. refer to extant genera and species

IS = interspecific hybrid. **IG** = intergeneric hybrid. **IST** = intersubtribal hybrid.

IT = intertribal hybrid. **ISF** = intersubfamilial hybrid. **IF** = interfamilial hybrid.

EC = embryo culture or ovule culture

SO = somatic hybrid by cell fusion; normally these hybrids are asymmetric

AS = asymmetric hybrids, they do not equally express maternal and paternal features

HY = assumed intergeneric hybridogeneous origin of a taxon.

nat. hyb. = natural hybrid **art. hyb.** = artificial hybrid

Colors within the crosses:

Red letters: intergeneric hybrids (incl. former IG).

Violet letters: multigeneric = plurigeneric hybrids.

Gray letters: hybridity unconfirmed or erroneous.

Green letters: notes on tribes, subfamilies etc. involved in the hybridization.

Yellow shaded: Notes concerning basic types.

General references on Bryophyta:

Anderson LE (1980) Cytology and reproductive biology of mosses. p. 37–76 in: Taylor RJ & Leviton AE (eds.) The mosses of North America. San Francisco: Pacific Div. Amer. Assoc. Adv. Sciences.

Ignatov MS et al. (2018) Hybridization in mosses, how distant it can be. Zhurnal Obshchei Biologii (= J. Gen. Biol.) 79 (2), 159–166. [In Russian]
https://elementy.ru/genbio/abstracts/551/Hybridization_in_mosses_how_distant_it_can_be Not yet analyzed. In the summary the existence of interfamilial hybrids is mentioned

Klinggraff H von (1889) Über die Bastarde bei Farnen und Moosen. Schriften Naturforsch. Ges. Danzig N. F. 7 (2), 172–178.

Natcheva R & Cronberg N (2004) What do we know about hybridization among bryophytes in nature? Can. J. Bot. 82, 1687–1704. Including putative gametophytic hybrids, not listed here

Liu Y et al. (2019) Liu Y et al. (2019) Resolution of the ordinal phylogeny of mosses using targeted exons from organellar and nuclear genomes Nature Communications. <https://doi.org/10.1038/s41467-019-09454-w>

Sanio C (1887) Bryologische Fragmente. III. Hedwigia 26, 194–214.

Timm R (1927) Über Moosbastarde, insbesondere über die Kreuzungen und Mittelformen zwischen *Pogonatum aloides* (Hedw.) PB. und *nanum* (Schreb.) PB. Hedwigia 67, 1–44.

Wyatt R et al. (1988) Hybrid origin of polyploid moss *Plagiomnium medium*. p. 22 in: Sixth Meeting Central East European Bryol. Working Group (Liblice, Czechoslovakia).

Division

BRYOPHYTA s.str. = MUSCI

8 classes, 45 orders, 127 families, 650 genera, 12000 species

mosses = Laubmoose

Arrangement of families according to the order.

8 classes:

Andreaeopsida: 1 family, 1: 100 species

Andreaebryopsida: 1 family, 1: 1

Bryopsida: 7 subclasses, 37 orders, 118 families, 11500 species

Oedipodiopsida: 1 family, 1:1

Polytrichopsida: 1 family, 20: 220

Sphagnopsida: 1–2 extant orders, 2–3 families, 4: 150–300

Takakiopsida: 1 family, 1: 2

Tetraphidopsida: 1 family, 2: 4

Bryales 5 families 35: ca. 1000 (class Bryopsida, subclass Bryidae)

5 families:

Bryaceae 17, Leptostomataceae 1, Mniaceae 15, Phyllodrepaniaceae 1,

Pulchrinodaceae 1.

Basic type **order Bryales** (35: 1000): 4 of the 5 families and all genera except one genus are directly or indirectly linked by hybridization, see the figure below.

Bryales: Bryaceae 17: 660. 2 IG (incl. 1 IF)

Brachymenium, *Bryum*, *Rhodobryum*, ...

Pohlia has been transferred to Mniaceae.

Part of basic type Bryales.

IS: Natcheva & Cronberg (2004): *Bryum* 6 IS.

Brachymenium × *Bryum* Ochi 1954 (*Bra. exile* × *Bry. argenteum*)

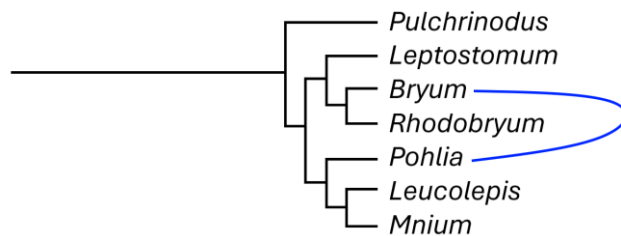
Bryum × *Pohlia* IF **Bryaceae** × **Mniaceae** (nat. hyb.) Ochi 1961 (*B. pallescens* × *P. crudoides*) v. Wettstein 1932 (*B. bicolor* × *P. melanodon*)

Bryales Mniaceae 15

Mnium, *Plagiomnium*, *Pohlia*, *Rhizomnium*, ...

Part of basic type Bryales. For *Bryum* × *Pohlia* see Bryaceae. *Pohlia* was formerly included in Bryaceae.

IS: Wyatt et al. (1988): *Plagiomnium*.



Bryales: hybridization in the phylogeny according to Liu Y et al. (2019). <https://doi.org/10.1038/s41467-019-09454-w>.

References on Bryales:

- Liu Y et al. (2019) Resolution of the ordinal phylogeny of mosses using targeted exons from organellar and nuclear genomes Nature Communications. <https://doi.org/10.1038/s41467-019-09454-w>
- Ochi H (1954) Notes on the mosses of Bryaceae in Japan, II. Intergeneric hybrid sporogone between *Bryum argenteum* var. *lanatum* (Palis) Bry. eur., and *Brachymenium exile*. J. Jpn. Bot. 29, 49–51.
- Ochi H (1961) Mosses of the Bryaceae in Japan and the adjacent regions, suppl. II. Possibly natural intergeneric hybrid (*Bryum pallescens* Schl. × *Pohlia crudoides* Broth.). Nikobia (Hiroshima) 2 (3), 179–184.
- Wettstein F von (1932) Genetik. In Manual of bryology. Ed. by F. Verdoorn. Hague, The Netherlands. pp. 233–272.
- Wyatt R et al. (1988) Hybrid origin of polyploid moss *Plagiomnium medium*. p. 22 in: Sixth Meeting Central East European Bryol. Working Group (Liblice, Czechoslovakia). see also Wyatt et al. (1988) <https://www.pnas.org/doi/epdf/10.1073/pnas.85.15.5601>

Dicranales 20 families (class Bryopsida, subclass Dicranidae)

Dicranales: Bruchiaceae 3–5: 120. 1 IG

Also treated as separate order.

Bruchia, *Eobrucia*, [*Pringleella*], *Trematodon*

Bruchia microspora × *Trematodon longicollis* (nat. hyb.) Rushing & Snider 1985, Natcheva & Cronberg 2004

References:

Rushing AE & Snider JA (1985) A natural hybrid between *Bruchia microspora* Nog. and *Trematodon longicollis* Michx. Monogr. Syst. Bot. Missouri Bot. Garden 11, 121–132.

Dicranales: Dicranaceae 24: 410

IS: *Campylopus flexuosus* × *C. fragilis* Natcheva & Cronberg 2004, *Dicranella cerviculata* × *D. heteromalla* Natcheva & Cronberg 2004

Dicranales: Ditrichaceae 25: 140. 1 IG

IS: *Astomopsis amblyocalyx* × *A. exserata* (Natcheva & Cronberg 2004)

Ditrichum × *Pleuridium* (→ × *Pleuriditrichum*)(nat. hyb., *D. pallidum* × *P. acuminatum*, *palustre*; *D. subulatum* × *P. subulatum*) Limpricht 1890 (Austria, Steiermark), Venturi 1881 (Portugal, Oporto), Andrews & Hermann 1959, Futschig & Kellner 1959 (Germany), Andrews 1960, Anderson & Snider 1982, Natcheva & Cronberg 2004

References:

Anderson LE & Snider JA (1982) Cytological and genetic barriers in mosses. J. Hattori Bot. Lab. (Nichinan) 52, 241–254.
Andrews AL (1960) Taxonomic notes. XV. The reciprocal hybrid of *Ditrichum-Pleuridium*. Bryologist 63, 179–181.
Andrews AL & Hermann FJ (1959) A natural hybrid in the Ditrichaceae. Bryologist 62, 119–122.
Futschig J & Kellner K (1959) Über Moosbastarde am natürlichen Standort. 1. Mitteilung: Ein neuer Bastard, *Pleuridium subulatum* (Schreb.) Lind. × *Ditrichum pallidum* (Schreb.) Hampe. Hess. Florist. Briefe 8 (93), 1–2.
Limpricht KG (1890) Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Leipzig: Kummer.
Venturi G von (1881) Une mousse hybride. Revue Bryol. 1881, 20–22.

Funariales 1family (class Bryopsida, subclass Funariidae)

Funariales: Funariaceae 14: 300. 4 IG

Funarioideae 13: 400 *Entosthodon* 85, *Funaria* 80, *Physcomitrella* 2, *Physcomitrium* 65, *Pyramidula* 1, ...

For compilations of hybrids and discussions, see von Wettstein 1924 a, b, 1925, 1940, Bauer & Brosig 1959, Fife 1985, Adler 1993, Natcheva & Cronberg 2004

Probably **basic type family Funariaceae** (14: 300): Adler 1993, 2025. Modern phylogenetic studies show that the most distant genera are connected by hybridization, see the figure below. – It is the only family of the order Funariales.

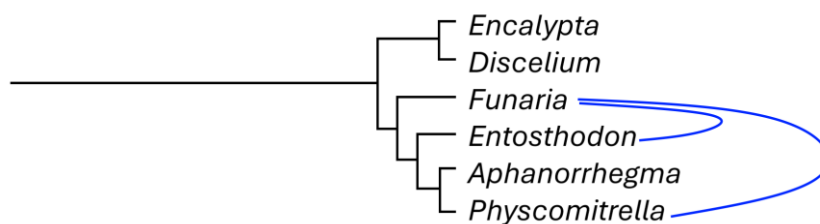
IS: *Funaria* 1 IS (*F. hygrometrica* × *F. muehlenbergi*, art. hyb. von Wettstein 1924, 1925), *Physcomitrium* 2 IS (*P. eurystomum* × *P. pyriforme*, art. hyb. von Wettstein 1924, 1925), *P. immersum* × *P. turbinatum* nat. hyb. Andrews 1942)

Entosthodon × *Funaria* (nat. hyb.) von Wettstein 1924 a, b, 1925 (*E. fascicularis* × *F. hygrometrica*), Natcheva & Cronberg 2004

Funaria × *Physcomitrella* (→ × *Funariophyscomitrella* F. Wettst.) (nat. + art. hyb., *F. hygrometrica* × *P. patens*) von Wettstein 1924 a, b, 1925, Natcheva & Cronberg 2004

Funaria hygrometrica × *Physcomitrium pyriforme* Bayrhammer 1849, von Wettstein 1924 a, b, 1925, Natcheva & Cronberg 2004

Physcomitrella × *Physcomitrium* (*P. patens* × *P. sphaericum*, *turbinatum* nat. hyb.) Amann 1893 (Switzerland), Andrews 1942, McDaniel et al. 2010, Natcheva & Cronberg 2004



Funariaceae: hybridization in the phylogeny according to Liu Y et al. (2019).

<https://doi.org/10.1038/s41467-019-09454-w>). – *Encalypta* and *Discelium* belong to separate families.

References:

- Adler M (1993) Merkmalsausbildung und Hybridisierung bei Funariaceen (Bryophyta, Musci). p. 67–70 in Scherer S (ed.) Typen des Lebens. Berlin: Pascal.
- Adler M (2025) Formation of characters and hybridization in the Funariaceae (Bryophyta, Musci). p. 89–94 in Sanders RW (ed.) Basic Types of Life. Tulsa, Oklahoma: Blyth Institute Press. [English translation of Adler 1993](#)
- Andrews AL (1942) Taxonomic notes II. Another natural hybrid in the Funariaceae. Bryologist 45, 179–181.
- Bauer L & Brosig M (1959) Zur Kenntnis reziproker Kreuzungen von Funariaceen. I. Die Bastarde *Funaria hygrometrica* × *Physcomitrium acuminatum* und reziprok. Z. Vererbungslehre 90, 400–408.
- Bayrhammer J (1849) Übersicht der Moose, Lebermoose und Flechten des Taunus. Jahrb. Nassau. Ver. Naturkd. 5, 101.
- McDaniel SF, Mark von Stackelberg M, Sandra Richardt S, Ralph S. Quatrano RS, Ralf Reski R & and Stefan A. Rensing SA (2010) The speciation history of the *Physcomitrium* - *Physcomitrella* species complex. Evolution 64, 217–231.
- Patel N, Medina R et al. (2023) Frequent allopolyploidy with distant progenitors in the moss genera *Physcomitrium* and *Entosthodon* (Funariaceae) identified via

subgenome phasing of targeted nuclear genes. *Evolution* 77, 2561–2575.

<https://biodiversity.uconn.edu/2023/12/02/new-publication-on-bryophytes-2/>

Wettstein F von (1924a) Morphologie und Physiologie des Formwechsels der Moose auf genetischer Grundlage I. *Z. Indukt. Abstammungs- Vererbungslehre* 33, 1–236.

Wettstein F von (1924 b) Gattungskreuzungen bei Moosen. *Z. Indukt. Abstammungs- Vererbungslehre* 33, 253–257.

Wettstein F von (1925) Genetische Untersuchungen an Moosen (Musci und Hepaticae). *Bibliographia Genetica* (The Hague) 1, 1–38.

Wettstein F von (1940) Experimentelle Untersuchungen zum Artbildungsproblem II. Zur Frage der Polyploidie als Artbildungsfaktor. *Ber. Deutsch. Bot. Ges.* 58, 374–388.

Grimmiales 4 families (class Bryopsida, subclass Dicranidae)

Grimmiales: Grimmiaceae 10: 330

IS: *Grimmia* 4 IS, *Racomitrium* 1 IS (*R. heterostichum* × *macrocarpum* Natcheva & Cronberg 2004)

Orthotrichales 1 family (class Bryopsida, subclass Bryidae)

Orthotrichales: Orthotrichaceae 32

IS: *Orthotrichum* 1 IS (see references)

References on Orthotrichaceae:

Hedderson TA (1986) A naturally occurring moss hybrid between *Orthotrichum gymnostomum* and *O. obtusifolium* from Newfoundland, Canada. *Bryologist* 89, 165–167.

Polytrichales 1 family (class Polytrichopsida)

Polytrichales: Polytrichaceae 20: 220 + some extinct genera. 2

IG

IS: *Pogonatum* 1 IS see Natcheva & Cronberg (2004):

Pogonatum × *Polytrichastrum* Derda et al. 2000 **HY** (arguments for the intergeneric hybridogeneous origin of some species of *Polytrichastrum* are given)

Polytrichum × *Polytrichastrum* Derda et al. 2000 **HY** (arguments for the intergeneric hybridogeneous origin of some species of *Polytrichastrum* are given)

References on Polytrichaceae:

Derda GS et al. (2000) Isozyme evidence regarding the origins of three allopolyploid species of *Polytrichastrum* (Polytrichaceae, Bryophyta). *Plant Syst. Evol.* 220, 37–53.

Timm R (1927) Über Moosbastarde, insbesondere über die Kreuzungen und Mittelformen zwischen *Pogonatum aloides* (Hedw.) PB. und *nanum* (Schreb.) PB. *Hedwigia* 67, 1–44.

Pottiales 4 or more families (class Bryopsida, subclass Dicranidae)

Pottiales: Pottiaceae 83: 1500. 3 IG

IS: *Pottia* 2 IS, *Weissia* 3 IS (see Natcheva & Cronberg 2004)

Phascum cuspidatum × *Pottia intermedia* Ulychna 1977, Natcheva & Cronberg 2004

Tortella („*Trichostomum*“) *flavovirens* × *Weissia longifolia* („*crispa*“) Nicholson 1910, Natcheva & Cronberg 2004

Weissia (*Astomum*°) *ludovicianum*, *muehlenbergianum* × *Weissia controversa* **IS** (now interspecific) (nat. hyb.) Nicholson 1931, Khanna 1960, Reese & Lemmon 1965, Williams 1966, Anderson & Lemmon 1972

References:

Anderson LE & Lemmon BE (1972) Cytological studies of natural hybrids and their parental species in the moss genera, *Astomum* and *Weissia*. *Ann. Missouri Bot. Garden* 59, 382–416. <http://biostor.org/reference/11983>

Nicholson WE (1910) A new hybrid moss. *Rev. Bryol.* 37, 23–24.

Nicholson WE (1931) Hybridity among the bryophytes. *Revue Bryol. N. S.* 4, 138–140.

Khanna KR (1960) Differential evolutionary activity in bryophytes. *Evolution* 18, 652–670.

Reese WD & Lemmon BE (1965) A natural hybrid between *Weissia* and *Astomum* and notes on the nomenclature of the North American species of *Astomum*. *Bryologist* 68, 277–283.

Ulychna KO (1977) Hybrid sporogones in *Phascum cuspidatum*, Pottiaceae, Musci. *Ukr. Bot. Zh.* 34, 155–158.

Williams C (1966) A natural hybrid in the genus *Weissia*. *Bryologist* 69, 361–365.

Sphagnales 3 families (class Sphagnopsida)

Sphagnales: Sphagnaceae 2: 200

Possibly **basic type family Sphagnaceae** due to its isolated position. Attention: Some authors distinguish 2–3 families in this order.

IS: see the references below.

References:

Cronberg N & Natcheva R (2002) Hybridization between the peat mosses, *Sphagnum capillifolium* and *S. quinquefarium* (Sphagnaceae, Bryophyta) as inferred by morphological characters and isozyme markers. *Plant Systematics and Evolution* 234, 53–70.

Flatberg KI (1988) *Sphagnum angustifolium* (Russ.) C. Jens. × *S. pulchrum* (Braithw.) Warnst., a gametophytic hybrid. *Lindbergia* 14, 4–7.

Splachnales 2 families (class Bryopsida, subclass Bryidae)

Splachnales: Splachnaceae 6: 70. 1 IG

2 subfamilies:

Splachnoideae 4 *Aplodon* 1, *Splachnum* 11, *Tetraplodon* 9, *Voitia* 2.

Tayloroideae 2 *Moseniella* 2, *Tayloria* 47.

Tetraplodon mnioides × *Voitia hyperborea* **Splachnoideae** (nat. hyb.) v. Wettstein 1932

References:

Wettstein F von (1932) Genetik. In: F. Verdoorn (ed.) *Manual of bryology*. Hague, The Netherlands, pp. 233–272.