Review

Asexual reproduction, habitat colonization and habitat maintenance in bryophytes☆

Wolfgang Frey [a],*, Harald Kürschner [b]

[a] Ortlerweg 39d, 12207 Berlin, Germany
[b] Freie Universität Berlin, Institut für Biologie, Altensteinstraße 6, 14195 Berlin, Germany

ARTICLE INFO

ABSTRACT

Asexual reproduction s. l. is widespread in plants and also a basic reproductive mechanism in bryophytes. Today, three types of asexual reproduction are recognized: (1) the asexual reproduction s. str. by regeneration from ± specialized caducous organs (leaves, leaf apices, shoots, branches, bulbils) and by production of specialized propagules (gemmae, protonemal brood cells, tubers), (2) fragmentation of plants, resp. part of plants into ± unspecialized fragments, and (3) clonal reproduction (cloning). The latter occurs in bryophytes by protonema decay, by disintegration of modules, resp. formation of ramets (dividuals, "daughter plants") that leads to self-cloning or forced-cloning of parts of the gametophyte (shoots, stoloniferous and rhizomatous axes, rhizoid wicks, basiscopic innovation plants). Clonal reproduction (cloning), in former time scarcely noted, gained great interest within the last decade mainly in vascular plants showing clonal growth. This reproduction mechanism is thought to be a keystone factor for asexual reproduction, habitat colonization and habitat maintenance. Species which reproduce clonally are able to colonize and maintain habitats in an effective way by the so-called "consequent vegetative multiplication". The review presents an overview of the current state of knowledge of asexual reproduction types in bryophytes, with a focus on fragmentation and clonal reproduction (cloning), the mechanisms of habitat colonization and habitat maintenance, which all are of important significance in the dynamic processes of development of bryophyte populations.

© 2010 Elsevier GmbH. All rights reserved.

Contents

Introduction

Sexual reproduction is based on new combination of the genetic material (cross-fertilization, inter-, intrachromosomal recombination), offering the possibility of high genetic variety and different genetic types. The latter often are well adapted to changing ecological conditions, thus stimulating evolution. However, in bryophytes,

sexual reproduction is limited, as more than 50% of the bryophytes are monoicous, leading to self-fertilization and excluding genetic recombinations. Longton and Miles (1982) for example have shown that of the 690 species of mosses in England, only about 50% regularly form sporophytes, and 18% never were found with sporophytes. Worldwide in 4% of the species sporophytes are unknown up to now. Asexual reproduction s. l. and the formation of asexual diaspores therefore is a remarkable feature and widespread in bryophytes. In nearly no other plant group asexual reproduction is so important than in bryophytes.

A great number of bryophyte species, especially dioicous ones, reproduce exclusively asexually. Reproduction by regeneration from ± specialized caducous organs (leaves, leaf apices, shoots, branches, bulbils) and by the production of specialized propagules (gemmae, protonemal brood cells, tubers) is well known, based on the fundamental studies of Correns (1899) for mosses and Degenkolbe (1937) for liverworts. Subsequent comprehensive treatments on this topic were given by Longton and Schuster (1983), Imura and Iwatsuki (1990), Imura (1994), Newton and Mishler (1994) and Laaka-Lindberg et al. (2003). Furthermore, asexual reproduction is a keystone factor in the life strategy concepts of During (1979, 2000), Frey and Kürschner (1991), and Frey and Lösch (2010).

Vegetation analyses of vascular plants indicate that fragmentation of plants, resp. parts of plants in ± unspecialized fragments and clonal reproduction (cloning) by self-cloning (due to endogenous mechanisms) or forced-cloning (by external influences) plays an important role in asexual reproduction, as well as in habitat colonization and local maintenance. Clonally growing plants often grow in distinct spatially discrete patches separated from each other or forming a continuous cover. Clonal reproduction produces ramets (dividuals, "daughter plants"; generally under aspects of genetic identity: "merigenets"), and by repeated vegetative multiplication species with such reproductive traits are able to colonize and maintain habitats in a highly effective way (e.g., Pfeiffer, 2005, 2007; Pfeiffer et al., 2008).

Also a great number of bryophytes show fragmentation of gametophytic parts or clonal growth with clonal reproduction. First combined morphological and molecular studies by Pfeiffer et al. (2006), Fritz (2010), and Lieske (2010) revealed the same mechanisms as in vascular plants, proving the formation of extensive clones by clonal reproduction and repeated "vegetative multiplication" [a term first introduced in bryophyte reproduction biology by Mickiewicz (1975), and later used by Longton and Schuster (1983)].

The results of such studies lead to a new evaluation and classification of asexual reproduction and a more detailed understanding of asexual reproduction mechanisms in population biology. In the following review an overview of the current knowledge on asexual reproduction s. l. in bryophytes is presented, focused on clonal reproduction, the ongoing mechanisms of vegetative multiplication, habitat colonization and habitat maintenance.

Methodical approaches in studies of clonal reproduction in bryophytes

Under natural conditions, the morphological relationships of merigenets were revealed in only a few cases. Molecular genetical fingerprinting techniques however, mainly the AFLP-technique (Amplified Fragment Length Polymorphism), allow statements on the affiliation of merigenets to a genet (clone), which arised by clonal (asexual) reproduction. Further applied techniques are the RAPD-technique (Random Amplified Polymorphic DNA), Microsatellite-analyses, and Iso(en)zyme analyses. A detailed overview of the morphological–anatomical and molecular techniques applied to bryophytes as well as to vascular plants is given,

e.g., in Pfeiffer (2007), Pfeiffer et al. (2006, 2008), Grundmann et al. (2008), Spagnuolo et al. (2009), Fritz (2010) and Lieske (2010). For specific terms used, cf. Malcolm and Malcolm (2006). The bryological nomenclature follows Frey et al. (2006), Frey and Stech (2009) and in few cases cited literature. "Leaf", "shoot", "rhizome", etc. are used in an analogous sense with the words describing the axes and their accessory organs in vascular plants.

Asexual reproduction types in bryophytes

Two basic types of **asexual reproduction sensu lato** are distinguished in literature: (1) **asexual reproduction sensu stricto** and (2) **clonal reproduction (cloning),** incl. fragmentation (Urbanska, 1992; Frey and Lösch, 1998, 2010; Pfeiffer, 2003). In the following review we use this concept but raise "**fragmentation**" to a reproduction type of its own and focus mainly on clonal reproduction. For an explanation of more fundamental aspects see Frey and Lösch (2010).

Asexual reproduction s. str. (with ± specialized propagula) (Fig. 1, Table 1)

Asexual reproduction s. str. is characterized by ± specialized caducous (syn. deciduous) organs (leaves, leaf apices, shoots, branches, bulbils) or by specialized propagules (e.g., protonemal brood cells, gemmae, tubers) and mitospores. The foundations of terminology are laid and examples of these reproductive types are given by Correns (1899 – mosses), Degenkolbe (1937 – liverworts), Schuster (1966 – liverworts) and Longton and Schuster (1983 – general). Further data are given by Pfeiffer (2003) and Schaumann (2005). In general, the asexual bryophyte propagules are relatively heavy and highly specialized, consisting of uni- to multicellular vegetative structures that separate from the parent plant (asexual diaspores). They do not resemble the mother plant and, by contrast to meiospores, have an high water content and often no accrustated cell walls. Mitospores s. str. are not present in bryophytes.

This type of asexual reproduction has been treated well in bryophyte literature (e.g., Imura and Iwatsuki, 1990; Laaka-Lindberg et al., 2003; Newton and Mishler, 1994; cf. Fig. 1, Table 1).

Within asexual reproduction s. str., the following three types can be distinguished:

- Regeneration from ± specialized caducous organs;
- Protonemal gemmae and tubers;
- "Asexual" spores (Newton and Mishler, 1994).

Regeneration from ± specialized, caducous organs

In this case, relatively heavy and specialized or determined asexual reproductive structures (leaves, leaf apices, shoots, branches, bulbils) are formed. Regeneration from detached leaves and defined shoot parts is frequent in mosses but rare or absent in liverworts.

– Leaves and leaf apices, caducous leaves (sensu Longton and Schuster, 1983), **incl. brood leaves** (sensu Correns, 1899). They include both, normal vegetative leaves and specialized diminutive leaves, also those ones with an abscission layer (brood leaves, "Brutblätter", "folia decidua", sensu Correns, 1899). In all cases these caducous organs become detached from the parent shoots. Examples in mosses with ± **normal caducous leaves** are *Hypopterygium didictyon*, *Pleurochaete squarrosa* (Giordano et al., 1996) and *Syntrichia caninervis*; with **brood leaves** *Aulacomnium androgynum*, *Campylopus fragilis*, *Dicranodontium longirostre*, and *Dicranum montanum*. Brood leaves often differ from normal leaves in shape and size and in the development of the costa (usually similar to that one of juvenile leaves). They may be reduced to minute, few celled
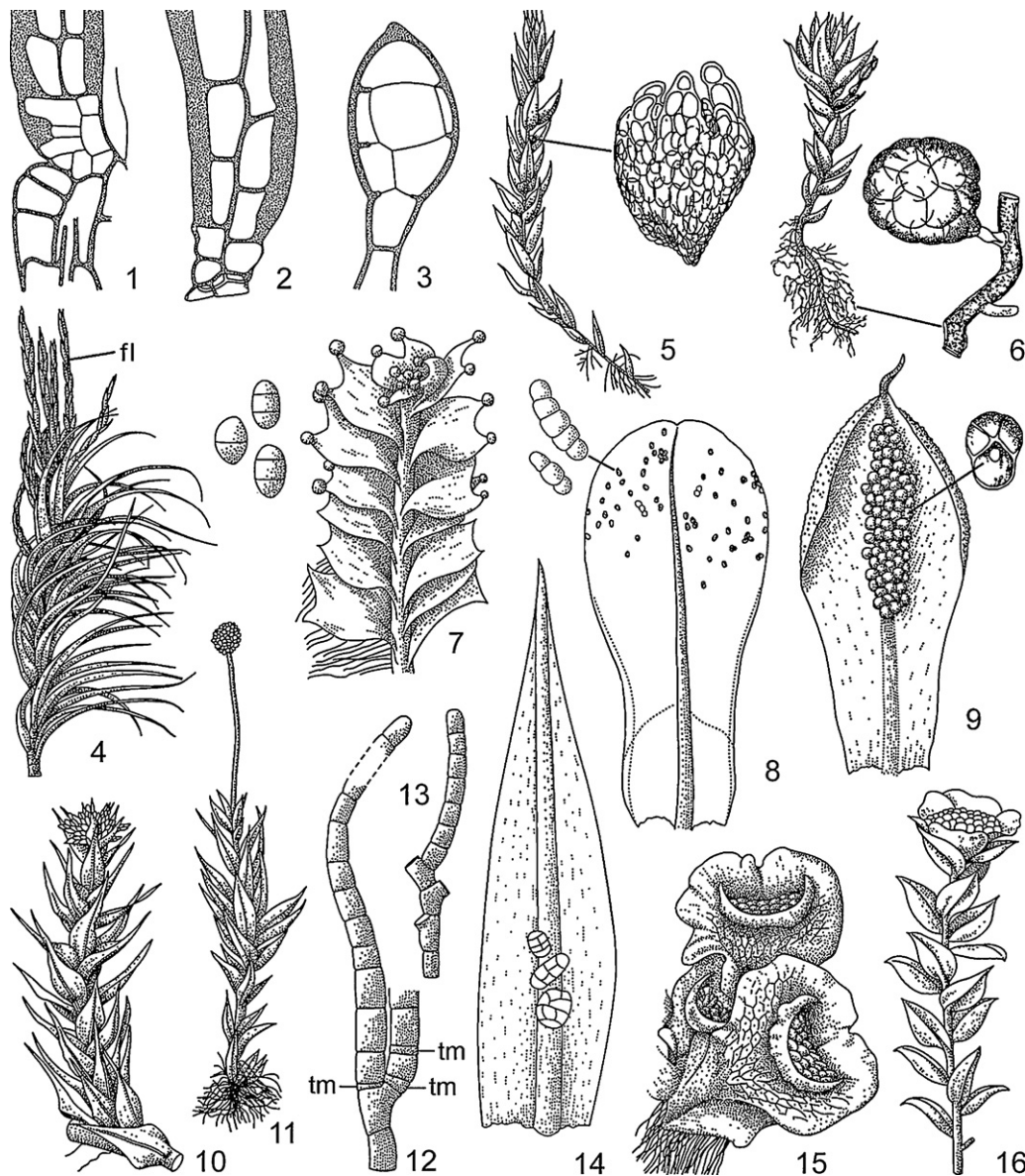
Fig. 1. Asexual reproduction s. str. by regeneration from ± specialized caducous organs (leaves, leaf apices, shoots, branches, bulbils) and production of specialized propagules. (1 and 2) *Dicranodontium longirostre.* Brood leaves ("Brutblätter" sensu Correns, 1899) with abscission zone; longitudinal section (orig. without size data). 3, 11. *Aulacomnium androgynum.* (3) Gemma (brood leaf sensu Correns, 1899) (ca. ×50); (11) Plant with gemmae on a pseudopodium (×5). (4) *Dicranum flagellare.* Shoot tip with caducous branchlets ("Bruchäste" sensu Correns, 1899) (×5). (5) *Pohlia bulbifera.* Plant, axillary bulbil (×6, resp. ×50). (6) *Bryum radiculosum.* Plant, rhizoidal gemma (×5, resp. ×60). (7) *Lophozia ventricosa.* Shoot, lateral leaves with clusters of gemmae (×8, resp. ×200). (8) *Syntrichia latifolia.* Leaf, leaf lamina with gemmae (×10, resp. ×200). (9) *Syntrichia papillosa.* Leaf with gemmae-bearing costa (×10, resp. ×200). (10) *Pseudoleskeella nervosa.* Branch with caducous branchlets in the axils of the upper leaves (×15). (12 and 13) *Encalypta streptocarpa.* Filamentous gemmae (×100). (14) *Grimmia torquata.* Leaf with endogenous gemmae (×10, resp. ×200). (15) *Lunularia cruciata.* Thallus with gemma cups; cups with gemmae (×2). (16) *Tetraphis pellucida.* Shoot with gemma cup; cup with gemmae (×2.5). fl flagellum, tm tmema (abscission) cell. ((1–3, 12 and 13) After Correns, 1899; (4, 11 and 16) Orig.; (5 and 6) after Touw and Rubers, 1989; (7 and 9–10, 15): after Frey et al., 1995; (8 and 14) after Mönkemeyer, 1927. Figs. redrawn.)

ovoid or clavate structures resembling gemmae, as it is the case, e.g., in *Aulacomnium androgynum* (Fig. 1(3) and (11)). Brood leaves possess a differentiated abscission layer ("Trenngewebe"). The cell walls in this layer are very thin and fragile, and the leaves are easily detached. A good example is *Dicranodontium longirostre* (Fig. 1(1) and (2)). Brood leaves are also often clustered on a condensed axis or "pseudopodium", e.g. in *Aulacomnium androgynum* (Fig. 1(3) and (11)) and *Syntrichia laevipila.* A critical revision of the caducous leaf types in mosses is needed, to separate especially those ones without a highly specialized abscission layer. New gametophytes (buds) originate directly from leaf cells, resp. the costa, or from a secondary protonema arising from leaf cells. Examples in liverworts are *Bazzania* spp. (e.g., *Bazzania nudicaulis*), Frullaniaceae, various Lejeuneaceae (e.g., *Ceratolejeunea caducifolia*, *Cheiloleje-*

unea decidua, *Drepanolejeunea propagulifera*), Plagiochilaceae (e.g., *Plagiochila corniculata*), Radulaceae.

– Leaves and leaf apices, caducous leaf apices. Upper parts of leaves may have regions with thin cell walls, where the leaf tip regularly breaks off. Examples in mosses are *Campylopus fragilis*, *Dicranum viride*, *D. tauricum*, *Tortella fragilis*, examples in liverworts *Acrobolbus ciliatus*, *Frullania microphylla*, *Plagiochila caduciloba* (fragmentation of the linear leaf lobes).

– Caducous shoot apices ("Brutknospen" sensu Correns, 1899**)** are apices of vegetative, only little modified shoot tips, which are regularly deciduous along an abscission layer.

An example in mosses is *Campylopus flexuosus* (cf. longitudinal section in Fig. 21 of Correns, 1899). In *Bryum argenteum*, in culture as well as in nature, secondary protonemata radiate from the original

Table 1
Synopsis of asexual reproduction s. l. modes in bryophytes [based on Correns (1899) and Longton and Schuster (1983), with data from Pfeiffer (2003), Schaumann (2005), and Lieske (2010)].

A Asexual reproduction s. str. (with ± specialized propagula)
  1 Regeneration from ± specialized caducous (syn. deciduous) organs
    1.1 Leaves and leaf apices
      - Caducous leaves (sensu Longton and Schuster, 1983), incl. brood leaves (sensu Correns, 1899)
      - Caducous leaf apices
    1.2 ±specialized caducous shoot apices, branches, branchlets (caducous defined shoot and thallus parts)
      - Caducous shoot apices ("Brutknospen" sensu Correns, 1899)
      - Caducous branches and caducous branchlets ("Brutäste", incl. "Bruchäste" sensu Correns, 1899), cladia
      - Caducous flagelliform shoots (flagella, flagelliform propagula)
      - Bulbils (s.str.)
    1.3 Caducous perianths
  2 Protonemal gemmae and tubers
      - Protonemal (chloronemal) gemmae (gemmiferous protonemata), incl. protonemal brood cells
      - Gemmae s. str. ("Brutkörper" sensu Correns, 1899) (Laminal gemmae, costal gemmae, cauline/axillary gemmae, endogenous gemmae, gametangial gemmae, rhizoidal gemmae)
      - Gemmae in thallose liverworts
      - Rhizoidal tubers, tubers
  3 "Asexual" spores
B Fragmentation of gametophytes or part of gametophytes (leaves, shoots, thalli) into unspecialized (indeterminate) fragments
C Clonal reproduction (cloning)
  1 Production of numerous gametophytes (buds) on protonema derived from a spore. [Cloning via independent gametophyte (bud) formation on protonema derived from a single spore.]
  2 Decay of older parts of the gametophyte (main axis, secondary axes) leading to the disintegration of younger parts and through subsequent growth of the fragments to new plants (dividuals)
  3 Formation of ramets (separated aerial shoots; daughter plants, dividuals) by decay, resp. disintegration of stoloniferous axes or rhizomatous (rhizome-like) subterranean axes
  4 Formation of ramets (separated aerial shoots; daughter plants, dividuals) by decay, resp. disintegration of the rhizoid system (rhizoid wicks) ("Rhizoidsprossung"). [Clonal reproduction (cloning) after decay, resp. disintegration of wicks by self-cloning, resp. forced-cloning]
  5 Formation of cauline basiscopic innovation plants ("Basitone stämmchenbürtige Innovationspflänzchen")

---

apices, and give rise to several hundred shoots. When detached and carried to favourable sites, these shoot apices continue their growth to a whole plant with development of rhizoids from their basal parts (Imura and Iwatsuki, 1990).

– Caducous branches and caducous branchlets (condensed and caducous branches in leaf axils) ("Brutäste", incl. "Bruchäste" sensu Correns, 1899; Fig. 1(4) and (10)). These are condensed caducous branches and branchlets in leaf axils at branch tips, with reduced leaves and an abscission layer. Examples in mosses are *Leucodon sciuroides* (Ahrens, 2007), *Dicranum flagellare* (Fig. 1(4)), *Platygyrium repens*, *Pseudoleskeella nervosa*. Included in this type are also caducous branches with ± normal leaves, detached at the base of the branch, e.g., *Dicranum scoparium*. The development of new shoots starts from apex or basal parts of branchlets and via a secondary protonema (Imura and Iwatsuki, 1990). In liverworts such "Bruchäste" (Degenkolbe, 1937) occur in *Herbertus aduncus* subsp. *hutchinsiae* (Løe and Söderström, 2001), and in Lejeuneaceae, e.g., *Lejeunea laetevirens*, *L. cardoti* (Schuster, 1984, p. 849). Sometimes it is difficult to separate them from cladia (see below). So far, the thallus outgrowths of thallose liverworts that easily break-off (e.g., in *Pellia endiviifolia*) and the buds of *Conocephalum conicum* (winter buds) are included within this type; for *Metzgeria*, see "gemmae".

– Cladia (sensu Schuster, 1984; cf. Fig. 18 in Degenkolbe, 1937) are variously modified abbreviated axes ("brood branchlets"), which arise basitopic to leaves as collared branches ("Kragen"). They are caducous. Examples found in liverworts are some Lejeuneaceae (*Drepanolejeunea*, *Leptolejeunea*, *Odontolejeunea*). Cladia bear reduced primary underleaves that develop a conspicuous discoidal "holdfast", derived from rhizoids. In *Harpalejeunea ovata* and *Lejeunea cladiophora* the cladia are merely smaller-leaved caducous branches. Certain Plagiochilaceae produce also "leaf cladia", as in *Plagiochila aspleniformis* and *P. virginica* (Schuster, 1984, p. 849).

– Caducous flagelliform shoots are attenuate branches with vestigial leaves, located in leaf axils (flagella, flagelliform propagula). "Flagellae" are generally slender shoots bearing small (vestigial) leaves and are often produced in large numbers in leaf

axils of upper leaves on vegetative shoots. A good example in mosses is *Pseudotaxiphyllum elegans*. Production of secondary protonemata occurs mainly from leaf axils; shoots develop from the apex or from leaf axils. Observation of germinating flagella in the field and observation of direct shoot formation are recorded by Imura and Iwatsuki (1990).

The term flagellum is often used for stoloniform shoots with small leaves that provide a method of lateral growth but not for dispersal. A clarification with respect to asexual reproduction is necessary in Neckeraceae (*Neckera complanata*, *Porotrichum* spp.).

– Bulbils (s. str.: bud-like branches with leaf projections, usually in leaf axils). Bulbils are highly condensed, caducous, bud-like to thread-like branches with strongly reduced leaf primordia, occuring in axillary position, one to several per leaf (analogues to the bulbils of vascular plants). In mosses they are frequent in Bryaceae (*Bryum* spp., *Leptobryum pyriforme*, *Pohlia* spp. – Fig. 1(5)). When detached and carried to favourable sites, bulbils begin to "germinate". In most cases, a secondary protonemal phase precedes the production of leafy gametophytes. The secondary protonema extends mostly from the apical or basal part of the bulbils, rarely from the middle parts. Occasionally, new buds are formed directly from the reactivated apical cells (Imura and Iwatsuki, 1990).

– Caducous perianths are recorded only in *Chonocolea ruwenzorensis* and *Gymnocolea inflata* (liverworts).

Protonemal gemmae and tubers

– Protonemal (chloronemal) gemmae (gemmiferous protonema), incl. protonemal brood cells, are defined as one- to few (12)-celled propagules (protonemal gemmae) on above ground primary chloronemal filaments, possessing specific liberation mechanisms by abscission (tmema-cells, "Trennzellen", Brachytmema, Tmema and "Brutzellen" sensu Correns, 1899, p. 156; detailed for *Leptobryum pyriforme* by Duckett and Ligrone, 1992). More seldom are filamentous (moniliform), 3–6 cells long protonemal gemmae (e.g., in Bryaceae). When mature, the thin-walled abscission (tmema-) cells break easily and the gemmae are set free.

In gemmae, there is also an abscission at the middle lamellae of the basal cells, e.g. in *Dicranum montanum*. Gemmiferous protonemata occur in 20–30% of all mosses, especially in acrocarpous ones, particularly in *Bryum* spp. (Pressel et al., 2007), Dicranales, *Mittenia* (Mitteniaceae), Pottiales (with schizolytic separation), and Schistostegaceae. Protonemal gemmae are remarkably rare in pleurocarpous taxa, occurring, however, e.g., in *Orthotrichum obtusifolium*, *Oxyrrhynchium hians*, and *Pseudotaxiphyllum elegans*. Andreaeidae, Buxbaumiales (see below), Fissidentales, Grimmiales, Polytrichales, and Sphagnidae are principally without protonemal gemmae. Protonemal gemmae function in increasing the potential for initial establishment and localized dispersal of the plant, especially in situations where sporophytes are rarely produced. At present, they have been reported only from mosses. For specialized literature see Duckett and Matcham (1995) and Pressel et al. (2007).

– Protonemal brood cells, specifically, are produced by redifferentiation of ageing chloronema cells. They are not well known at present and in need of clarification, but proposed to be separated from protonemal gemmae. Tmema (abscission) cells are missing in these structures. Protonemal brood cells occur in mosses, e.g. in *Diphyscium foliosum* (tips of the protonema branches are transformed into clusters of long-lived, desiccation-tolerant, caducous, spherical brood-cells) and in *Aloina* spp. (brood cells on the protonema, surviving dry seasons).

– Gemmae s. str. (singular: gemma) ("Brutkörper" sensu Correns, 1899**)** are common in mosses and liverworts (Fig. 1(7–9 and 12–16)). They are one to multicellular asexual propagules, ranging from unicellular bodies to filaments or globose structures. They are born on protonema (see above), on various parts of the gametophyte, i.e., on leaves (laminal, costal), on thalli, stems (cauline), rhizoids, in leaf axils (axillary), endogenous, on specialized non-deciduous gemmiferous shoots or in leafy or thallose (gemmae-bearing) gemma cups (e.g., *Lunularia cruciata*, Fig. 1(15), *Tetraphis pellucida*, Fig. 1(16)).

Gemmae are lacking an apical cell (some species have a protonemal initial cell, e.g. *Tetraphis pellucida*) and projections resembling leaves or leaf primordia (cf. bulbils). In mosses a protonemal phase precedes the production of the shoots developing from gemmae. In leafy liverworts, gemmae often germinate directly to leafy plants.

– Laminal gemmae ("Blattgemmen") arise directly from leaf cells (laminal, from the border or from apices, respectively). They are 1–2-celled to multicellular, spherical, discoidal, clavate, filamentous, or lamelliform. Examples to be found in mosses are *Grimmia trichophylla*, *Orthotrichum tenellum*, and *Syntrichia latifolia* (Fig. 1(8)). Regeneration by buds from leaf (costa) cells via a secondary protonemal stage is reported from *Oedopodiella australis* (Rushing and Mueller, 1986).

Foliose liverworts show a great variety of laminal gemmae [Calypogeiaceae, Cephaloziaceae, Frullaniaceae, e.g., *Frullania parvistipula* (leaf border), Lophoziaceae, e.g., *Lophozia ventricosa* (Fig. 1(7)), Scapaniaceae].

– Costal gemmae ("Rippengemmen") arise directly from costal cells. They are spherical, clavate or filamentous in shape, and get formed on the costa at the apex, middle, or basal part of leaves, both, on ventral or dorsal side. Those formed at base may be difficult to separate from cauline gemmae. Examples in mosses: *Syntrichia papillosa* (Fig. 1(9)), *Syrrhopodon* spp. (leaf apices), *Ulota phyllantha*.

– Cauline/axillary gemmae (formed from stem cells, "Stämmchengemmen") are tuberous, clavate or filamentous, and apparently originate from cortical cells on the stem surface or in leaf axils. A classification according to stem/leaf position is often difficult. Examples in mosses: *Anomobryum julaceum*, *Dicranoloma billardieri*, *Didymodon rigidulus*, *Encalypta streptocarpa*, (Fig. 1(12 and 13)), *Isopterygiopsis muelleriana*, *Plagiothecium nemorale*, *Pterigynandrum filiforme*.

– Endogenous gemmae ("Endogene Gemmen"). In a few cases asexual diaspores (gemmae) are produced endogenously within an initial cell. This case is reported from Grimmiaceae, e.g., *Grimmia torquata* (Fig. 1(14)), *G. trichophylla*, and *Racomitrium vulcanicola*. In *G. torquata*, the endogenous stalked gemmae develop above the leaf base out of cells on the ventral side of the costa (Fig. 1(14)). In liverworts, ovoid or ellipsoidal 2-celled endogenous gemmae occur in *Bazzania kokowana*, the Fossombroniaceae, in *Jungermannia caespiticia*, and *Riccardia* spp. (Metzgeriidae).

– Gametangial gemmae are discoid or ovoid, stalked multicellular gemmae, often present in leaf axils together with antheridia. They were recorded from *Oedipodium griffithianum* (Oedopodiaceae).

– Rhizoidal gemmae originate from subterranean rhizoids and lack an apical cell. They occur as uniseriate or often branched filaments, or several-celled, spherical or club-shaped bodies. Germination to leafy shoots occurs solely via a secondary protonema (Imura and Iwatsuki, 1990). Examples in mosses: *Bryoerythrophyllum ferruginascens, Bryum radiculosum* (Fig. 1(6)), *Dicranella staphylina*, and *Leptobryum pyriforme* (Risse, 1987).

Rhizoid gemmae are part of the asexual diaspore bank of bryophytes (During, 2001). They are to a high degree able to survive unfavourable conditions (drought, cold), much better than shoots.

– Gemmae in thallose liverworts. Multicellular gemmae are known from *Cavicularia densa*, discoid and thallose gemmae from *Metzgeria* spp. The latter originate from the thallus margins (e.g., *M. temperata*), and are called also brood branches. In *Blasia pusilla* two types of multicellular parenchymatous gemmae exist.

– Rhizoidal tubers, tubers ("Knöllchen"). In mosses, rhizoidal tubers are spherical to ellipsoidal, pyriform, thick-walled, with an apical cell with two or three cutting faces. They are composed of 10 to more than one hundred cells, usually reddish brown to dark brown in colour when mature, and are borne on usually subterranean rhizoids. Two different types of germination are reported from rhizoidal tubers: (1) the tubers develop directly into a leafy shoot, when the apical cell is reactivated (e.g., *Bryum capillare*, *B. rubens*). (2) The diaspore produces secondary protonemata and forms moss plants indirectly, when the apical cell is not reactivated (Imura and Iwatsuki, 1990). Rhizoidal tubers are observed in many moss species, and in particular widely distributed in acrocarpous mosses, especially Bryaceae, Dicranaceae, Ditrichaceae, Fissidentaceae, and Pottiaceae (cf. Preston, 2004). In Grimmiaceae (e.g., *Grimmia pulvinata*, Meusel, 1935, p. 181) rhizoidal tubers develop after decay of shoots. Tubers are long-lived and possess larger amounts of nutritive substances than spores. As rhizoidal gemmae, they are part of the asexual diaspore bank. Rhizoidal tubers and rhizoidal gemmae are able to survive unfavourable environmental conditions (e.g., drought and cold) in high amount and remain viable for a long time. They are typical for taxa which propagate almost entirely asexual and are associated with the colonists strategy; these taxa colonize habitats in a short time in a very effective way.

In liverworts, tubers occur almost exclusively in *Fossombronia*, *Petalophyllum* and *Sewardiella* (Fossombroniales), in *Geothallus tuberosus* (Sphaerocarpales), *Riccia* spp., (e.g., *R. gougetiana*), typically as an adaptation to arid environments. In hornworts, several *Anthoceros* and *Phaeoceros* spp., (e.g., *P. laevis*), have swollen, small thallus cells with reduced vacuoles, covered by an epidermis (="inner tubers", Ligrone and Lopes, 1989). They include cyanobacteria that belong to the hornwort symbiosis. After decay of the thallus these tubers survive long dry periods and re-colonize the former habitat. *P. bulbiculosus* shows stalked tubers on the ventral thallus side, which function as asexual diaspores and perennating organs.

In general, asexual propagula in bryophytes are often, due to their mass, at the maximum limit of short-range dispersal. With

increasing mass the probability of transport by air streams in vegetated areas decreases significantly, and transport by air streams usually results in dispersal over only short distances, especially in closed forests (e.g., *Anastrophyllum hellerianum*, 0–10 m from the source colonies: Pohjamo et al., 2006). Asexual reproduction will therefore mainly contribute to local colonization and habitat maintenance.

"Asexual" spores (Newton and Mishler, 1994)

"Asexual" spores function as spores in the alteration of generations, but have the genetic identity of asexual diaspores. They may arise through: (1) **Selfing**: on the same physical individual of monoicous species are different arrangements of gametangia possible, leading to formation of genetically identical zygotes. (2) **Asexual clone selfing**: sporophyte and spore production occur on different physical individuals which are derived from one single germination event and have become separated at the periphery of a spreading clone. (3) **Spore clone selfing**: different physical individuals can originate from spores of one capsule ("haploid sibs") that are genetically identical because the capsule arose from selfing. An apparent process of dioicous or monoicous outbreeding between such individuals will be in fact comparable to a selfing event. Such a process might occur, e.g., in phyllodioicous species.

Fragmentation of gametophytes or parts of gametophytes (leaves, shoots, thalli) into unspecialized (indeterminate) fragments (Fig. 3(6), Table 1) – (Frey and Hensen, 1995; Longton and Schuster, 1983).

In bryophytes nearly all gametophyte cells retain the capacity for re-growth from detached vegetative fragments forming new gametophytes (Correns, 1899; During, 1990; Frey and Hensen, 1995; Kreh, 1909). Fragmentation of leaves and shoots is very common, fragmentation of thalli is more seldom. In most cases the new plants (dividuals, see below) are established via formation of a secondary protonema.

Fragmentation of leaves (fragile leaves, "folia fragilia", "Bruchblätter" sensu Correns, 1899) is widespread in mosses and leafy liverworts. It occurs along predetermined lines of weakness in leaf cell arrangement into random fragments of individual cells, resp. cell complexes. Examples in mosses: *Dicranoloma billardieri*, *Dicranum viride*, *Syntrichia fragilis* (Fig. 3(6)) and *Trichostomum brachydontium*. In liverworts (Jungermanniidae) fragmenting of leaves ("leaf fragments") is not thoroughly investigated, but can be observed as a widespread mechanism of asexual reproduction maintaining regional populations. Examples are *Bazzania pectinata*, *B. pseudovittata*, *B. spiralis* (SE Asia), *Plagiochila caduciloba* (endemic in the Appalachian Mountains) and *P. cuneata* (Neotropics). Often large sterile populations are formed by leaf fragments (e.g., in *Herbertus* spp., Appalachian Mountains). Reduction to a single sex or to sterile populations that reproduce solely asexually is a prevailing phenomenon in foliose liverworts.

In mosses fragmentation of shoots is not rare, but till now not systematically investigated. However, in *Andreaea crassinervia*, *Dicranoloma billardieri*, *Dicranum scoparium*, *Leucodon sciuroides* (see also "caducous branches"), *Philonotis rigida*, and *Pseudoleskea catenulata* shoots break very often into unspecialized fragments. Løe and Söderström (2001) have shown that in *Herbertus stramineus* subsp. *hutchinsiae,* where sporophytes are unknown, the shoots are likely to be very long-lived and re-growth after fragmentation occurs (see also "caducous branches"). Contrary, in foliose liverworts clonal reproduction (cloning) by shoot fragmentation (e.g., in *Pycnolejeunea* sp., Degenkolbe, 1937, p. 43, *Lejeunea laetevirens*, Reiner-Drehwald, 2010) is much rarer than in mosses. In thallose liverworts simple fragmentation of the thallus can occur (e.g., in *Plagiochasma appendiculatum*). In hornworts some *Megaceros* spp.
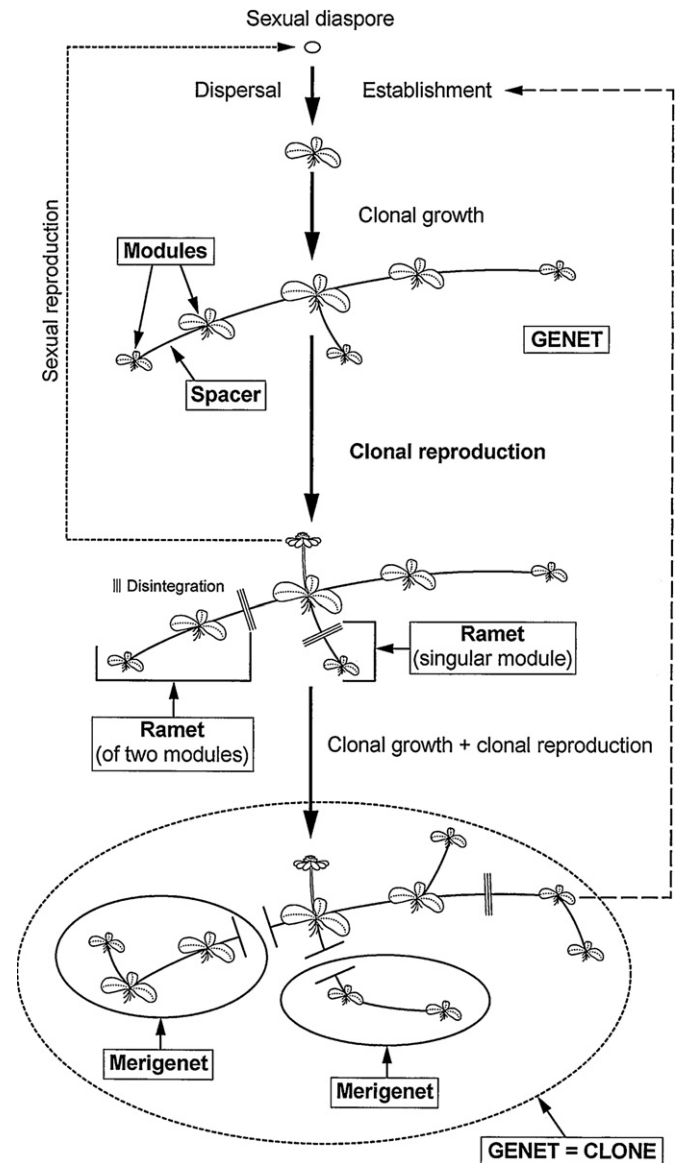

Fig. 2. Clonal reproduction (cloning) and habitat colonization of clonal plants; schematic drawing with the terms applied to the respective structures. For explanation see text. (After Pfeiffer, 2005.)

with curly thallus margins show limited reproduction by fragmentation of the thallus border.

Fragments seems to play a considerable role in dispersal ecology of bryophytes (Heinken et al., 2007; Heinken, 2000; McDaniel and Miller, 2000), and are documented even from Pleistocene deposits (Miller, 1985).

Clonal reproduction (cloning) (Figs. 2–6, Table 1)

Clonal reproduction (cloning) is known from plants with clonal growth, i.e., plants with spatial growth by repeated formation of modules, leading to successful establishment and habitat expansion. In general, clonal reproduction means the division of a genetic individual (genet; derived from a zygote via sexual diaspores) into ± similar parts (ramets, dividuals), that are capable to live independently from each other after separation (Frey and Lösch, 1998, 2010; Urbanska, 1992).

The mechanism of cloning for a model plant with clonal growth is illustrated in Fig. 2 exemplarily (Pfeiffer, 2005). First, a seedling is
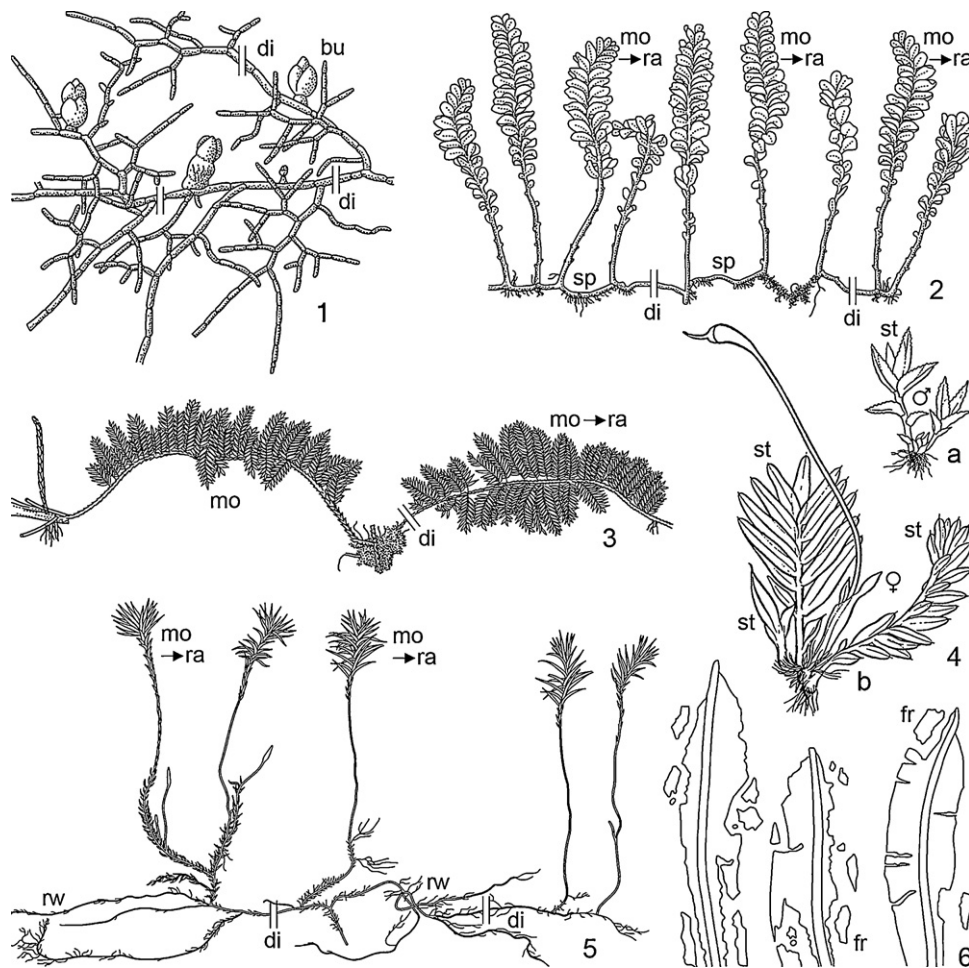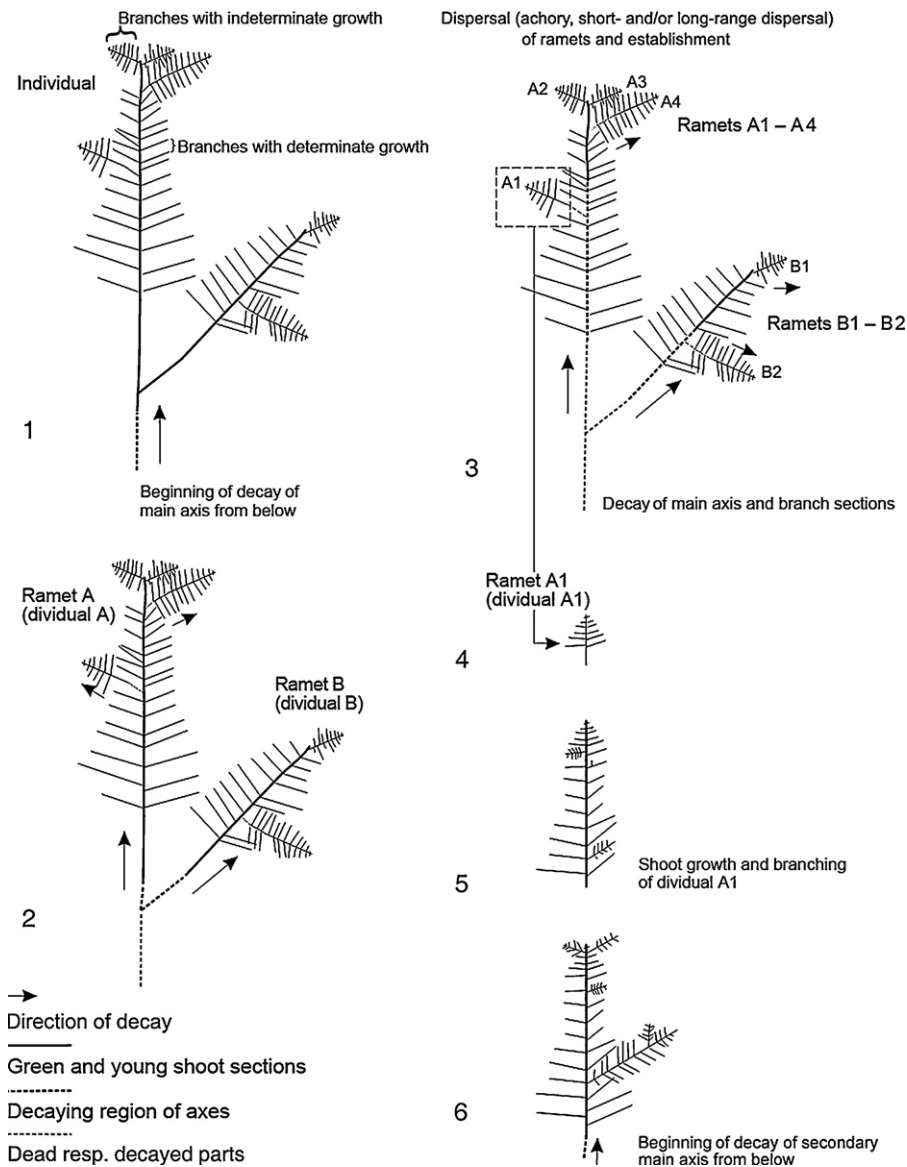
Fig. 3. Clonal reproduction (cloning). (1) Decay of a moss protonema and formation of dividuals (buds, young gametophytes) (×100). (2) *Tylimanthus saccatus.* Disintegration of modules (leafy aerial axes) by self-cloning or forced-cloning of the primary creeping rhizomatous axis (spacers) and formation of ramets (×0.5). (3) *Thuidium laeviusculum.* Curved main shoot with modules and disintegration of modules, resp. ramets (×0.4). (4) *Fissidens taxifolius.* (a) Young plant with male primary shoot, basiscopic with female and sterile shoot. (b) Basiscopic innovation system with female and sterile shoots. (5) *Polytrichum juniperinum.* Subterranean rhizoid wicks with erect aerial shoots, leading after decay, resp. disintegration to the formation of several ramets (×0.5). (6) *Syntrichia fragilis.* Fragile (fragmenting) leaves ("Bruchblätter") (×40). bu bud, di disintegration, fr fragment, mo module, ra ramet, rw rhizoid wick, sp spacer, st sterile shoot. ((1–3 and 6) After Frey and Lösch, 1998, 2010; (4 and 5) after Meusel, 1935; redrawn and altered.)

established by germination of a sexual diaspore. The arising clonally growing plant with **leaf modules**, connected by **spacers**, represents just like the preceding seedling a genetic individual (**genet**). **Decay** or **disintegration** of spacers by self-cloning or forced-cloning leads to morphological and physiological independent **ramets** (**dividuals**) with one, two or more modules, respectively. Thus, ramets derived by division of a genetic individual, represent dividuals and are asexual diaspores in terms of dispersal ecology. The terminus "ramet" could be used in a broader sense, including specialized propagula, fragments and ramets s. str., in case of bryophytes the latter ones comparable to those in vascular plants. Each ramet continues growing clonally. Further decay, resp. disintegration and continuation of clonally growth of ramets lead to "secondary" and "tertiary" ramets, called "**merigenets**". In total, the merigenets derived from a genetic individual altogether form a **genet = clone**. Apart from somatic mutations, which seldom occur, all dividuals of a clone are genetically identical.

The mechanism of repeated clonal reproduction, combined with continued clonal growth of the dividuals, is called "**consequent vegetative multiplication**" (Longton and Schuster, 1983; Mickiewicz, 1975; Pfeiffer, 2007). Species with such vegetative multiplication are able to colonize and maintain habitats in an effective way.

Types of clonal reproduction (cloning)

– Production of numerous gametophytes (buds) on protonema derived from a spore (Fig. 3(1), Table 1 1) = clonal reproduction (cloning) via independent gametophytes (bud) formation on protonema derived from a single spore. This form of clonal growth is typical for mosses with decaying or persistent protonema. Non-persisting protonemata decay after formation of buds. From a single spore several up to numerous buds (gametophytes), i.e., daughter plants (dividuals) are generated (Fig. 3(1)). Persistent protonemata (e.g, in *Pogonatum* spp., *Dichelyma capillaceum*, *Zygodon forsteri*) may divide by self-cloning or forced-cloning. In *Sphagnum* spp. (exception *S. girgensohnii*) and hornworts, each protonema produces one bud only and gives rise to one single mature gametophyte. Therefore clonal reproduction from a protonema is not realized in these bryophytes. In most liverworts and in hornworts, clonal reproduction via formation of independent gametophytes from a protonema which derived from a single spore, is very rare. Only in some liverwort taxa (e.g., *Chiloscyphus* spp., *Lophocolea* spp.) branched filamentous protonemata exist, and here all branches are potentially capable to produce a bud (gametophyte). Sporadically this also occurs in more advanced taxa (e.g. *Perssoniella*) (Longton and Schuster,

Fig. 4. Clonal reproduction (cloning). Example: *Abietinella abietina* (Lieske, 2010). Cloning by decay of older shoots (main axes; secondary, tertiary axes) [division of a genetic individual (1–3), resp. dividual (6)], leading to the disintegration of branches of indeterminate growth (younger parts or branches loose contact, e.g., ramet A1), dispersal of the diaspores (e.g., ramet A1), and subsequent growth of the ramets to new plants [dividuals, "daughter plants" (6)]. (1–3) Stages of decay of main axis and side branch axes, leading to ramets A1–A4 and B1–B2, (4–6) stages of ramet growth to a new plant (dividual, "daughter plant") and (6) beginning of decay of main axis of the dividual. A1–4, B1–2 ramets. (After Lieske, 2010, redrawn and altered.)

1983). If protonemata decay, subsequent asexual reproduction mechanisms derived from asexual diaspores (e.g., gemmae, fragmentation, decay of older parts of the gametophyte) can lead to a great number of gametophytes. In hornworts, the short-lived protonemal stage usually gives rise to one single mature thallus.

– Decay of older parts of the gametophyte (main axes, secondary axes) leading to the disintegration of younger parts and by subsequent growth of the fragments to new plants (dividuals) (Figs. 4 and 6; Table 1). Clonal reproduction is frequent in many mosses (both acrocarpous and pleurocarpous ones, e.g., *Leucobryum* spp., *Abietinella abietina*), in *Sphagnum*, and in a great number of foliose liverworts (e.g., *Bazzania* spp., *Schistochila* spp.). They often form by this way extensive clones (especially in species with rare sexual reproduction). Clone formation seems to be important in maintaining habitats where sexual reproduction is impossible.

Many pleurocarpous mosses (Figs. 4 and 6) produce longer branches of indeterminate growth (main axes and a limited number of side branches) and more frequent numerous short branches of determinate growth (most of the side branches). The dominant mode of clonal reproduction is the decay of older parts of the gametophyte (shoots, axes of side branches) from below, so that the younger parts loose the contact with the main axis and disintegrate subsequently. These gametophytic parts are thereafter ramets. Each ramet represents a new daughter plant (dividual) with the same basitonic decaying potential. This continuing process leads to large, extended, genetically uniform stands (clones) (mats, turfs of wefts with intertwining shoots), a phenomenon first described by Correns (1899, p. 328) and Meusel (1935) for mosses. In mosses, morphologically well investigated examples are, e.g., *Tortula muralis* (Longton and Miles, 1982) and *Pleurozium schreberi* (Longton and Schuster, 1983). In *Tortula muralis* "...many branches are initiated as innovations arising below terminal 'inflorescenses' – causing the colony to develop as an expanding cushion of shoots radiating from a central point. In the population studied young branches developed rhizoids at the base and the connection between branches and their parents
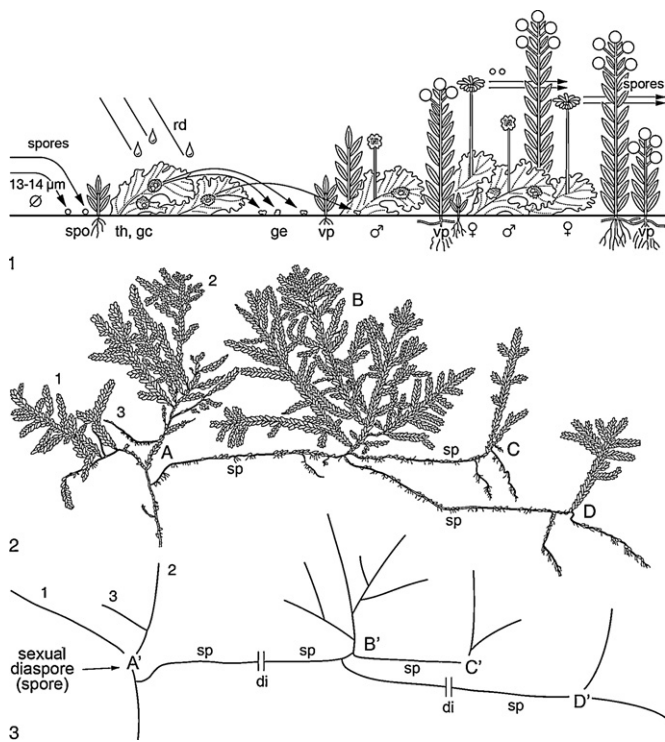
Fig. 5. Asexual reproduction, "consequent vegetative multiplication", habitat colonization and habitat maintenance. (1) *Marchantia polymorpha*. Asexual reproduction s. str. by gemmae and habitat colonization. (2 and 3) *Metaneckera menziesii*. Clonal growth, clonal reproduction, vegetative multiplication and habitat colonization. (2) *M. menziesii*. Habit of a clonally growing plant (individual), with stoloniferous main axis and modules A–D. (3) *M. menziesii*. Disintegration of the individual plant (genet) in ramets A', B'–C' and D' (dividuals, "daughter plants", merigenets), schematic. 1–3 branches, A–D modules, after the disintegration of the ramets (dividuals), di disintegration by self-cloning or forced cloning, gc gemma cup with gemmae, ge gemma, rd rain drop, sp spacer, spo spore, th thallus with gemma cups, vp vascular plant, ♂ male plant with antheridiophore, ♀ female plant with archegoniophore. ((1) After Frey and Lösch, 1998, redrawn; (2) after Meusel, 1935, (3) orig.)

broke down within approximately two years ..." (Longton and Schuster, 1983, p. 389f). Recently evidence of clonal reproduction, respectively the formation of extensive genetically uniform stands (clones, patches), has been given based on molecular data in the acrocarpous moss *Pleurochaete squarrosa* (Grundmann et al., 2008), and in the pleurocarpous mosses *Abietinella abietina* (Fig. 4), *Homalothecium lutescens* (Lieske, 2010), *Pleurozium schre-*

Fig. 6. Asexual reproduction, vegetative multiplication, habitat colonization and habitat maintenance. *Hypnum cupressiforme*. Decay of an individual weft (genet) – arrows – on wood into main and secondary axes (photo: W. Frey, near Klais, Bavaria).

beri and *Pseudoscleropodium purum* (Fritz, 2010), and *Rhytidium rugosum* (Pfeiffer et al., 2006). AFLP-fingerprinting indicated that extensive stands of these mosses are of clonal origin. In leafy liverworts (examples cited above) clonal reproduction seems to occur commonly by decaying of older parts of the gametophyte after branching of mature plants. This leads to the formation of large, genetically uniform stands, presumably most often derived from one single spore or a ramet (frequently in unisexual taxa).

– **Formation of ramets (separated aerial shoots; daughter plants, dividuals) by decay, resp. disintegration of stoloniferous axes or rhizomatous (rhizome-like) subterranean axes** (Figs. 3(2) and (3); 5(2) and (3); Table 1). Clonally growing bryophytes with primary creeping axes (stoloniferous axes, rhizomatous axes; During, 1990) and with secondary erect aerial axes (shoots) show a disintegration of modules by self-cloning or forced-cloning, leading to ramets (dividuals) and establishment of new daughter plants. Up to now, decay resp. disintegration is not often proved in case studies, neither morphologically, nor by molecular techniques. It can be assumed, however, that this reproduction mechanism is present in bryophytes as well as in vascular plants. It may occur in mosses with clonal growth [e.g., *Anomodon* spp., *Canalohypopterygium tamariscinum*, *Climacium dendroides*, *Hypopterygium* spp., *Metaneckera menziesii* (Fig. 5(2) and (3)), Polytrichaceae, Thuidiaceae], and other clonally growing species, and in clonally growing liverworts with prostrate subterranean axes [e.g., *Haplomitrium*, *Hymenophyton*, *Plagiochila gigantea*, *Symphyogyna*, *Tylimanthus* (Fig. 3(2))]. Clonal growth leads to a lateral expansion of an individual, following "consequent vegetative multiplication" to extensive stands. Based on molecular evidence, only a few reliable data on this item are found in literature (Pfeiffer, 2003; Schaumann, 2005). However, this reproduction type is known from the earliest "shoot" (telom)-bearing land plants, such as *Aglaophyton major*, *Horneophyton lignieri*, and *Nothia aphylla* ("clonal individuals derived from asexual reproduction", Daviero-Gomez et al., 2005) and should have been developed quite early in the parallel evolution of the bryophyte branch of land plants as well.

– **Formation of ramets (separated aerial shoots; daughter plants, dividuals) by decay, resp. disintegration of the rhizoid system (rhizoid wicks) ("Rhizoidsprossung")**. (Fig. 3(5), Table 1). Formation of separate aerial shoots from disintegrating rhizoid wicks is at present known only from mosses, occurring primarily in Polytrichaceae and Pottiaceae (Fig. 3(5)), but not from liverworts. In members of these families often numerous erect shoots are formed on subterranean rhizoid wicks. The latter comprise a central broad rhizoid filament and narrower branch filaments, which coils tightly around the central filament (up to 200 μm in Ø); the aerial shoots are budded off at intervals (Wigglesworth, 1947). This may be a special form of clonal growth in bryophytes. By decay, resp. disintegration of the rhizoid wicks the aerial shoots become ramets ("daughter plants", dividuals). The derived solitary plants develop, and form new rhizoid wicks with new aerial shoots. This leads to a rapid colony expansion [e.g., *Atrichum* spp., *Bryum argenteum*, *Phascum cuspidatum* (new shoots on strong rhizoids), *Polytrichum piliferum* (extended turfs in sandy areas); cf. Figs. 1 and 27 in Meusel (1935), p. 135, 172; Longton and Schuster (1983)]. Whether this mode of proliferation possibly also occurs in liverworts, has still to be investigated; promising groups for such a phenomenon are, e.g., Schistochilaceae, Vetaformaceae.

Rhizoids can function also as asexual diaspores and perennating organs. Short-lived bryophytes (short-lived shuttle species, fugitives) are characterized by almost only sexual reproduction (spores), lacking asexual diaspores. They survive harsh environmental conditions (dry phases, winter times) with spores. However, it turned out that also perennating subterranean rhizoids can function as asexual diaspores. In *Acaulon triquetrum* the surviving rhizoids produce new chloronemata and gametophytes

(Ahrens, 2003). The rhizoids from *Ditrichum plumbicola* are highly desiccation-tolerant, allowing the moss to endure extreme environmental conditions (Rowntree et al., 2007). This phenomenon may be common and widespread also in desert bryophytes.

    – Formation of cauline basiscopic innovation plants ("Basitone stämmchenbürtige Innovationspflänzchen") (Fig. 3(4), Table 1). The formation of cauline basiscopic sterile innovation plants that represent dividuals ("daughter" plants) after disintegration is observed in *Fissidens* spp. (Fig. 3(4)). However, the process is still poorly investigated.

Asexual reproduction, "consequent vegetative multiplication", habitat colonization and habitat maintenance – examples (Figs. 5 and 6)

    Reproduction by asexual diaspores and dispersal of them are thought to be of high significance in maintenance of regional populations, in habitat colonization and habitat maintenance of bryophytes. Two examples will demonstrate the interacting strategies.

    Marchantia polymorpha (Fig. 5(1)) is a colonist with sexual and asexual reproductive effort, characterized by long-range dispersal of the spores and short-range dispersal of the asexual diaspores (gemmae). Typically it grows at humid sites. In addition, it can colonize ruderal or disturbed sites, such as old burnt patches. The spores are relatively small (Ø 13–14 μm) and are produced in large amounts. With these small spores nearly all potential habitats can be reached by long-range dispersal in air streams ("chance dispersal"). The spores germinate on open, earthy sites, and soon the thalli occur. On the dorsal surface of the thalli, roundish gemmae-cups with ovoid gemmae are produced, which will be splashed-off from the cups by falling rain-drops (splash-cup mechanism). Due to their heavy mass, the gemmae disperse only within short distances (short-range dispersal). They grow to new thalli with gemmae cups ("consequent vegetative multiplication"), and the asexual life cycle may start again. Within a first succession phase new thalli with gemmae cups, established via gemmae, are produced regularly. By this mode, *M. polymorpha* is able to colonize a habitat successfully. Often, however, the habitats are limited in time and space (temporary habitat), and underlie a rapid succession. Therefore, *M. polymorpha* soon will be replaced by vascular pioneer plants. Before this happens, sexual reproduction (sporophyte development) in *M. polymorpha* becomes induced. The spores are released, dispersed by air streams, and new sites will be reached by "chance dispersal".

    A second example provides *Metaneckera menziesii* (Fig. 5(2 and 3); cf. also Fig. 2). At present, this example is more theoretical deserving still some confirmation, but may occur under natural conditions. *M. menziesii* is a perennial stayer with sexual and asexual reproductive effort, growing mainly on limestone rocks and, more rarely, on tree trunks. It is characterized by long-range dispersal with relatively small spores (Ø ca. 25 μm) and short-range dispersal by asexual diaspores (ramets). As other Neckeraceae, the species disposes a clonal lateral expansion by procumbent, stoloniferous main axes up to 15–20 cm in length; the aerial branches give the plant the typical imbricate appearance of a Neckeraceae ("Tapetenrasen").

    Further well investigated, outstanding examples for clonal reproduction by decaying axes and "consequent vegetative multiplication" for habitat colonization and habitat maintenance are the pleurocarpous mosses *Rhytidium rugosum*/Rhytidiaceae (Pfeiffer et al., 2006), *Abietinella abietina*/Thuidiaceae (Lieske, 2010) and *Pseudoscleropodium purum*/Brachytheciaceae (Fritz, 2010). An example for clonal reproduction via caducous leaves provides the arcrocarpous moss *Pleurochaete squarrosa*/Pottiaceae (Grundmann et al., 2008; Spagnuolo et al., 2009). In all these examples, clonal repro-

duction, respectively the genetical constitution of patches, was tested and proved with molecular techniques.

    Based on these (and other) examples pattern and process of the **"consequent vegetative multiplication"** can be generalized as follows (see Fig. 5(2) and (3)): A germinating spore generates a genetical individual. Modules A, B, C, D (together with axes of the "mother plant") are derived by clonal growth and are connected by spacers. Decay, resp. disintegration of spacers take place by self-cloning (e.g., decaying) or forced-cloning, e.g., between modules A–B and C–D, leading to the ramets A′, B–C′, and D′, now dividuals ("daughter plants"). Modules B and C are still connected and represent together a ramet (dividual). Dividuals A′, B–C′, and D′ grow now separately clonally, and produce creeping main axes with further modules. Disintegration of modules and generating of new ramets continue in each dividual, and new dividuals resp. merigenets evolve. This reproduction mechanism by "consequent vegetative multiplication" is a repeated clonal reproduction (cloning), causing mostly a short-range lateral dispersal. All merigenets evolve from a single spore and represent together a genetical individual (genet, clone). After sexual reproduction, new habitats can be reached by "chance dispersal" (short-range, respectively long-range dispersal of spores) and new genetical individuals are generated by subsequent germination of spores. However, if asexual diaspores (ramets, dividuals) are dispersed (mainly in a local scale), the further derived ramets (dividuals, respectively merigenets) belong to the "old" clone. By "consequent vegetative multiplication" species are able to colonize and maintain successfully a habitat, once reached by spores via short-range, respectively long-range dispersal.

Concluding remarks

    Extensive reproduction by asexually produced diaspores frequently occurs in dioicous species, related to the rarity or general absence of one sex within a population. But even if both sexes co-occur, to ensure fertilization male and female plants must grow close together due to the limited reach for liquid-based movement of the spermatozoids. As the spores are unisexual, male and female plants occur only randomly together after dispersal, and sexual reproduction is only possible, if the missing elter reach the clone randomly. During the last years it became evidenced, that especially local maintenance of populations of most bryophyte species seem to occur nearly exclusively by asexual reproduction, and often the formation of sporophytes in such populations is rare. The asexually formed diaspores function ecologically as "spores" and play a key role in dispersal ecology and habitat colonization and have a great significance in the dynamic processes of bryophyte communities. In addition, asexual diaspores provide possibilities for survival of unfavourable life conditions, and support re-establishment in an habitat after changes in the environmental conditions. Some of the asexual diaspores types, for example rhizoid gemmae or tubers, show a long germination capacity and longevity.

    The dispersal of unisexual spores, respectively asexual diaspores, to isolated habitats on, e.g., islands and mountain massifs can lead to the formation of unisexual populations which maintain the habitat for years or hundreds of years only by asexual reproduction. This is, e.g., the case with sterile female plants of *Herbertus aduncus* subsp. *tenuis* in the Appalachian Mts.: They reproduce asexually by leaves with brittle and caducous lobes. During the Pleistocene, the distribution of many north-hemispherical bryophyte species were limited to small refugia with favourable climatic conditions. Today, only sterile populations exist there which reproduce only asexual (Longton and Schuster, 1983). Further examples for such situations are, among others, *Drepanolejeunea appalachiana*

(Appalachian Mts., asexual reproduction by caducous propagula, bearing a pair of reflexed, elobulate leaves), the male populations of *Acrobolbus ciliatus* in Japan – whereas female populations of this species occur in the Appalachian Mts. (asexual reproduction by rhizoid-bearing leaves which are occasionally caducous): Schuster (1966, 1980). Also the male populations of *Plagiochila exigua* in Europe (asexual reproduction by caducous leaves) can be quoted, whereas female plants of this species occur rarely in eastern North America, where male plants are unknown (Paton, 1999).

Gemmae and brood leaves/caducous leaves are often formed under suboptimal ecological circumstances, for example during longer dry periods. Asexual reproduction typically increases in border- or transitional areas of the species distribution centre. *Tetraphis pellucida* (Fig. 1(16)), for example, regularly forms sporophytes in the higher mountainous areas, but in the lowland it mainly reproduces asexually by gemmae. The same can be observed in *Lunularia cruciata* that forms sporophytes within its Atlantic-Mediterranean distribution centre, but reproduces asexually by gemmae (Fig. 1(15)) after introduction to secondary habitats, like garden soil in glass-houses in Central Europe.

On the other hand, clonal reproduction is thought to be a keystone factor within the population biology of many species. It enables extended habitat colonization and maintenance by "consequent vegetative multiplication". This has been verified and proved by molecular techniques with several examples of vascular plants (Pfeiffer, 2007). It is functioning and confers comparable ecological advantages also in mosses (e.g., *Abietinella abietina*, *Pleurochaete squarrosa*, *Pseudoscleropodium purum*, *Rhytidium rugosum*; Pfeiffer et al., 2006; Grundmann et al., 2008; Spagnuolo et al., 2009; Lieske, 2010). Especially in species lacking sporophytes (unisexual ones) repeated asexual reproduction leads to widely distributed, however, genetic identical clones. Obviously asexual reproduction is balancing in such cases mating difficulties and compensates insufficient production of sexually different spores in dioicous species. By this way the existence of populations and species might be saved for some period of time. An increased amount of (in)dividuals would be beneficial if with changed environmental conditions or occasionally by chance sexual reproduction can take place keeping high the genetic heterogeneity within the entire population and by this way its versatility responding to variable habitat conditions.

Acknowledgements

References

Ahrens, M., 2003. Untersuchungen zum Lebenszyklus von *Acaulon triquetrum*. Herzogia 16, 239–274.

Ahrens, M., 2007. Wachstum und Reproduktion des epiphytischen Laubmooses *Leucodon sciuroides* in der nördlichen Oberrheinebene (Südwestdeutschland). Carolinea 65, 69–103.

Correns, C., 1899. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. Bryoph. Bibl. 7, 1–472.

Daviero-Gomez, V., Kerp, H., Hass, H., 2005. *Nothia aphylla*: the issue of clonal development in early land plants. Int. J. Plant Sci. 166, 319–326.

Degenkolbe, W., 1937 [1938]. Brutorgane bei beblätterten Lebermoosen. Ann. Bryol. 10, 43–96.

Duckett, J.G., Ligrone, R., 1992. A survey of liberation mechanisms and germination patterns in mosses. J. Bryol. 17, 335–354.

Duckett, J.G., Matcham, H.W., 1995. Gemmiferous protonemata; an overlooked dimension in the reproductive biology of mosses. Bull. Brit. Bryol. Soc. 65, 22–23.

During, H.J., 1979. Life strategies of bryophytes: a preliminary review. Lindbergia 5, 2–18.

During, H.J., 1990. Clonal growth patterns among bryophytes. In: Groenendahl, J.V., de Kroon, H. (Eds.), Clonal Growth in Plants: Regulation and Function. SPB Acad. Publ., The Hague, pp. 153–176.

During, H.J., 2000. Life history characteristics of threatened bryophytes. Z. Ökologie Natursch. 9, 19–26.

During, H.J., 2001. Diaspore banks. Bryologist 104, 92–97.

Frey, W., Hensen, I., 1995. Lebensstrategien bei Pflanzen: ein Klassifizierungsvorschlag. Bot. Jahrb. Syst. 117, 187–209.

Frey, W., Kürschner, H., 1991. Lebensstrategien von terrestrischen Bryophyten in der Judäischen Wüste. Bot. Acta 104, 172–182.

Frey, W., Lösch, R., 1998. Lehrbuch der Geobotanik. 1. Aufl. G. Fischer, Stuttgart, Jena.

Frey, W., Lösch, R., 2010. Geobotanik. 3. Aufl. Spektrum Akad. Verl., Heidelberg.

Frey, W., Stech, M., 2009. Marchantiophyta, Bryophyta, Anthocerotophyta. In: Frey, W. (Ed.), Syllabus of Plant Families. Part 3. Borntraeger, Berlin, Stuttgart, pp. 9–263.

Frey, W., Frahm, J.-P., Fischer, E., Lobin, W., 1995. Die Moos-und Farnpflanzen Europas. G. Fischer, Stuttgart, Jena, New York.

Frey, W., Frahm, J.-P., Fischer, E., Lobin, W., 2006. In: Blockeel, T.L. (Ed.), The Liverworts, Mosses and Ferns of Europe. Harley Books, Martins, Colchester.

Fritz, S., 2010. Vegetative reproduction and clonal diversity in three pleurocarpous mosses (*Pseudoscleropodium purum*, *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*; Bryophytina) of mesic habitats. Diss. Freie Universität Berlin.

Giordano, S., Alfano, F., Esposito, A., Spagnuolo, V., Basile, A., Castaldo Cobianchi, R., 1996. Regeneration from detached leaves of *Pleurochaete squarrosa* (Brid.) Lindb. in culture and in the wild. J. Bryol. 19, 219–227.

Grundmann, M., Ansell, S.W., Russell, S.J., Koch, M.A., Vogel, J.C., 2008. Hotspots of diversity in a clonal world – the Mediterranean moss *Pleurochaete squarrosa* in Central Europe. Mol. Ecol. 17, 825–838.

Heinken, T., 2000. Dispersal of plants by a dog in a deciduous forest. Bot. Jahrb. Syst. 122, 449–467.

Heinken, T., Rohner, M.-S., Hoppert, M., 2007. Red wood ants (*Formica rufa* group) disperse bryophyte and lichen fragments on a local scale. Nova Hedwigia Beihefte 131, 147–163.

Imura, S., 1994. Vegetative diaspores in Japanese mosses. J. Hattori Bot. Lab. 77, 177–232.

Imura, S., Iwatsuki, Z., 1990. Classification of the vegetative diaspores on Japanese mosses. Hikobia 10, 435–443.

Kreh, W., 1909. Über die Regeneration der Lebermoose. Nova Acta Leopoldina 90, 217–301.

Laaka-Lindberg, S., Korpelainen, H., Pohjamo, M., 2003. Dispersal of asexual propagules in bryophytes. J. Hattori Bot. Lab. 93, 319–330.

Lieske, K., 2010. Vegetative reproduction and clonal diversity in pleurocarpous mosses (Bryophytina) of xeric habitats. A combined molecular and morphoanatomical study in the three mosses *Abietinella abietina* (Hedw.) Fleisch. (Thuidiaceae), *Homalothecium lutescens* (Hedw.) Robins. (Brachytheciaceae) and *Homalothecium sericeum* (Hedw.) Schimp. (Brachytheciaceae). Diss. Freie Universität Berlin.

Ligrone, R., Lopes, C., 1989. Ultrastructure, development and cytochemistry of storage cells in the ,tubers' of *Phaeoceros laevis* Prosk. (Anthocerotophyta). New Phytol. 112, 317–325.

Løe, G., Söderström, L., 2001. Regeneration of *Herbertus* S.F. Gray fragments in the laboratory. Lindbergia 26, 3–7.

Longton, R.E., Miles, C.J., 1982. Studies on the reproductive biology of mosses. J. Hattori Bot. Lab. 52, 219–239.

Longton, R.E., Schuster, R.M., 1983. Reproductive biology. In: Schuster, R.M. (Ed.), New Manual of Bryology. 1. Hattori, Nichinan, pp. 386–462.

Malcolm, B., Malcolm, N., 2006. Mosses and other bryophytes. An illustrated glossary, 2nd ed. Micro-Optics, Nelson, New Zealand.

McDaniel, S.F., Miller, N.G., 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. Bryologist 103, 592–600.

Meusel, H., 1935. Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopoldina N.F. 3, 123–277.

Mickiewicz, J., 1975. Vegetative multiplication and regeneration of *Polytrichum commune* populations. Acta Soc. Bot. Poloniae 44, 15–24.

Miller, N.G., 1985. Fossil evidence of the dispersal and establishment of mosses as gametophyte fragments. Monogr. Syst. Bot., Missouri Bot. Gard. 11, 71–78.

Mönkemeyer, W., 1927. Die Laubmoose Europas. Akad. Verlagsges, Leipzig.

Newton, A.E., Mishler, B.D., 1994. The evolutionary significance of asexual reproduction in mosses. J. Hattori Bot. Lab. 76, 127–145.

Paton, J.A., 1999. The Liverwort Flora of the British Isles. Harley Books, Martins, Colchester.

Pfeiffer, T., 2003. Terricolous bryophyte vegetation of New Zealand temperate rain forests. Communities, adaptive strategies and divergence patterns. Studies in austral temperate rain forest bryophytes 14. Bryoph. Bibl. 59, 1–147, 14 appendices.

Pfeiffer, T., 2005. Clonal growth and clonal reproduction in *Asarum europaeum* L. subsp. *europaeum* (Aristolochiaceae) and their relevance for habit colonisation and maintenance. A morpho-ecological characterisation. Bot. Jahrb. Syst. 126, 187–202.

Pfeiffer, T., 2007. Vegetative multiplication and patch colonisation of *Asarum europaeum* subsp. *europaeum* L. (Aristolochiaceae) inferred by combined morphological and molecular study. Flora 202, 89–97.

Pfeiffer, T., Fritz, S., Stech, M., Frey, W., 2006. Vegetative reproduction and clonal diversity in *Rhytidium rugosum* (Rhytidiaceae, Bryopsida) inferred by morphoanatomical and molecular analyses. J. Plant Res. 119, 125–135.

Pfeiffer, T., Günzel, C., Frey, W., 2008. Clonal reproduction, vegetative multiplication and habitat colonisation in *Tussilago farfara* (Asteraceae): a combined morphoecological and molecular study. Flora 203, 281–291.

Pohjamo, M., Laaka-Lindberg, S., Ovaskainen, O., Korpelainen, H., 2006. Dispersal potential of spores and asexual propagules in the epixylic hepatic *Anastrophyllum hellerianum*. Evol. Ecol. 20, 415–430.

Pressel, S., Matcham, H.W., Duckett, J.G., 2007. Studies of protonemal morphogenesis in mosses. XI. Bryum and allied genera: a plethora of propagules. J. Bryol. 29, 241–258.

Preston, C.D., 2004. An updated list of British and Irish bryophytes from which tubers have been reported. Field Bryol. 83, 2–13.

Reiner-Drehwald, E.M., 2010. On *Lejeunea* subgenus *Nanolejeunea* (Lejeuneaceae, Jungermanniopsida). Nova Hedwigia, Beih. 38, 115–126.

Risse, S., 1987. Rhizoid gemmae in mosses. Lindbergia 13, 111–126.

Rowntree, J.K., Duckett, J.G., Mortimer, C.L., Ramsay, M.M., Pressel, S., 2007. Formation of specialized propagules resistant to desiccation and cryopreservation in the threatened moss *Ditrichum plumbicola* (Ditrichales, Bryopsida). Ann. Bot. 100, 483–496.

Rushing, A.E., Mueller, D.M.J., 1986. Regeneration from the leaves of *Oedopodiella australis* (Wag. & Dix.) Dix. Cryptogamie. Bryol. Lichénol. 7, 11–17.

Schaumann, F., 2005. Terricolous bryophyte vegetation of Chilean temperate rain forests. Communities, adaptive strategies and divergence patterns. Studies in austral temperate rain forest bryophytes. 26. Bryoph. Bibl. 62, 1–154, 3 appendices.

Schuster, R.M., 1966, 1980. The Hepaticae and Anthocerotae of North America. Columbia Univ. Pr., New York-London, 1, 1–1062; 4, 1–1334.

Schuster, R.M., 1984. Evolution, phylogeny and classification of the Hepaticae. In: Schuster, R.M. (Ed.), New Manual of Bryology. 2. Hattori, Nichinan, pp. 892–1070.

Spagnuolo, V., Terracciano, S., Giordano, S., 2009. Clonal diversity and geographic structure in *Pleurochaete squarrosa* (Pottiaceae): different sampling scale approach. J. Plant Res. 122, 161–170.

Touw, A., Rubers, W.V., 1989. De Nederlandse Bladmosses. Kon. Ned. Nat. Ver., Utrecht.

Urbanska, K.M., 1992. Populationsbiologie der Pflanzen. G. Fischer, Stuttgart, Jena.

Wigglesworth, G., 1947. Reproduction in *Polytrichum commune* L. and the significance of the rhizoid system. Trans. Brit. Bryol. Soc. 1, 4–13.