Budding, breaking and spreading: asexual propagules

△Fig. 1. *Syntrichia papillosa*, always gemmiferous but never fruiting in Europe. S. Pilkington.

Sharon Pilkington looks at the wide range of ways in which bryophytes reproduce vegetatively

In the plant world, bryophytes are remarkable for the range of specialised asexual propagules produced by liverworts and acrocarpous mosses (Figs 1, 2). Many also possess the highly unusual ability to reproduce vegetatively from fragments of almost any part of the gametophyte.

Asexual propagules (synonym: brood bodies) are of two main kinds. Gemmae (Figs 3–5) are small, unicellular or more commonly multicellular structures with undifferentiated cells. Other propagules, e.g. bulbils and deciduous branchlets, are typically larger and comprise differentiated cells (Fig. 6).

Many British species rarely or never produce spores and so must rely on asexual means of reproduction. This is fundamental to the expansion of local populations and the dispersal of the species further afield, although other than species with very small gemmae most asexual propagules are significantly heavier than spores and do not disperse very far away from the parent.

However, the production of asexual propagules also enables certain bryophytes to colonise habitats that vascular plants cannot, including bare rock, bark and steep cliffs, and to take advantage of short-lived habitat niches such as cultivated ground or eroding banks. They are also important to mobile species needing to move rapidly between patchily distributed habitat niches, including trees or decaying fallen wood.

Gemmae and other small propagules are often

△Fig. 2. *Lophozia incisa* reproduces by both gemmae and spores. S. Pilkington.

carried away from the parent by wind or rain. Water, in the form of raindrops or splashing, may also play a major role in the dispersal of heavier propagules of the kind produced by *Lunularia cruciata.* Less commonly, species of riparian habitats employ running water as a vector for dispersal over sometimes considerable distances.

Birds also assist in the movement of asexual propagules as they forage and collect nest material, providing an important means of dispersal for e.g. certain epiphytes. Wild and domesticated mammals are also known to inadvertently pick up and disperse fragments of bryophyte, a process known rather tongue-twistingly as epizoochorous transport.

Use in identification

For the bryologist, the presence and appearance of asexual propagules can be helpful and is sometimes essential in confirming the identification of a species. Many small and short-lived mosses of arable land, including species of *Bryum* and *Dicranella*, characteristically possess rhizoidal gemmae whose colour, shape and size are distinct to each species. For further information *Arable Bryophytes* by Ron Porley (published 2008) is recommended.

Certain of the leafy liverwort genera also have distinctive gemmae, the presence of which can be important in identification. For example, *Lophozia* gemmae are usually pigmented and angular or stellate, *Radula* gemmae are smooth, thin and disc-like and in *Calypogeia* they are borne in clusters on specialised gemmiferous shoots.

Mosses

Rhizoidal gemmae (also known as tubers) are most commonly produced by acrocarpous mosses when there is no sporophyte. Many British species disperse solely by rhizoidal gemmae in open/disturbed habitats, but where plants are also able to produce viable spores, such propagules typically – though not always – become scarce.

Examples of mosses that produce rhizoidal gemmae: *Bryoerythrophyllum ferruginascens, Bryum klinggraeffii, B. ruderale* (Fig. 3), *Dicranella staphylina*, *Pohlia lutescens*.

Gemmae also occur on the leaves of some acrocarpous mosses and as they are small and easily dispersed by wind or water, they are usually found on the upper lamina, leaf tips or in the

Fig. 3. Rhizoidal tuber of *Bryum ruderale*. C. Halpin.

leaf axils. In a few species, clusters of gemmae are borne at the shoot tips.

Examples of mosses that produce gemmae on leaves and in leaf axils: *Bryum moravicum*, *Orthotrichum lyellii* (Fig. 4), *Syntrichia papillosa* (Fig. 1), *S. latifolia*, *Ulota phyllantha*, *Zygodon* spp.

Examples of mosses that bear gemmae clusters at shoot tips: *Aulacomnium androgynum, Tetraphis pellucida.*

Bulbils are tiny deciduous vegetative propagules, typically found in the leaf axils of certain acrocarps. They are often, but not always, stalked and club-shaped (clavate); *Pohlia annotina* bulbils for example may be vermicular (literally, worm-shaped) or clavate (club-shaped) depending on their position on the stem, the age of the plant and its habitat.

Examples of mosses that produce bulbils in leaf axils: *Bryum dichotomum*, *B. gemmiferum*, *Pohlia annotina* (Fig. 6), *P. camptotrachela*, *P. drummondii*.

Leaf fragments are produced by many mosses: the unistratose leaf lamina of many species becomes brittle when dry and disturbance events such as poaching or wind action in exposed places can fragment the leaves and disperse them. Each fragment has the ability to develop individually into a genetic clone of its parent.

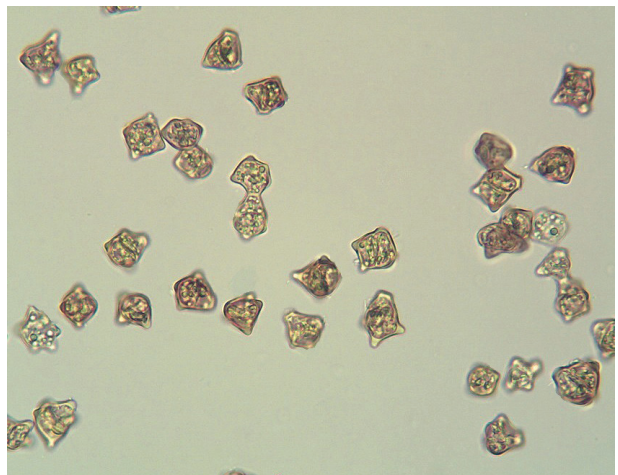
Deciduous leaves and branchlets function in the same way as leaf fragments and are particularly important in dispersal to species in genera such as *Campylopus*. Vegetative

Fig. 4. Gemmae of *Orthotrichum lyellii*. S. Pilkington.

reproduction is also important in *Sphagnum*, especially as many British and Irish species rarely produce sporophytes. New plants readily develop from broken-off branches, stem fragments and even damaged leaves and this ability has been successfully employed to 're-seed' areas of damaged peat with *Sphagnum* moss in moorland restoration projects.

Examples of mosses thought to disperse by means of leaf fragments: *Dialytrichia saxicola*, *Dicranum tauricum, Tortella nitida*.
Examples of mosses that produce deciduous leaves and branchlets: *Campylopus fragilis*, *C. pyriformis*, *Dicranodontium denudatum*, *Platygyrium repens, Pseudotaxiphyllum elegans*.

▽Fig. 5. Gemmae of *Lophozia sudetica*. S. Pilkington.



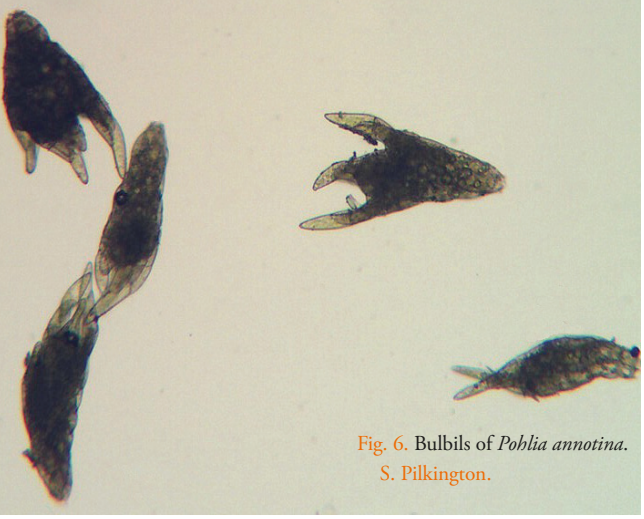


Fig. 6. Bulbils of *Pohlia annotina*. S. Pilkington.

Liverworts

Specialised asexual propagules are also frequently produced by many leafy liverworts. One or two-celled **gemmae** are often borne on leaf tips and margins near the tip of the shoot and certain species produce attenuated gemmiferous shoots to hold gemmae above the plants and promote dispersal.

In the thalloid liverworts the gemmae may be more complex structures. For example, flask-like structures on the surface of *Blasia pusilla* produce small, stalked ovoid gemmae. However, larger, stellate gemmae are also produced by the thallus surface. Small, two-celled gemmae form within the thallus tissue of some species of *Riccardia* and are released when the mother cell ruptures. Large, multicellular gemmae bud off from the thallus margins of *Metzgeria* species and their location on the plant can be useful for identification purposes.

In our largest thalloid liverworts, asexual reproduction is uncommon. When it does occur, gemmae are normally large and disc-like and produced by specialised structures that resemble cups on the thallus surface. These are nearly always present in certain species e.g. *Lunularia cruciata* and may represent the primary form of dispersal. *Marchantia polymorpha* is relatively unusual in producing gemmae from cup-like structures on the surface of the thallus as well as its distinctive umbrella-like male and female receptacles.

Examples of leafy liverworts that produce gemmae: *Barbilophozia attenuata, Calypogeia arguta*, *Diplophyllum albicans*, *Lophozia incisa* (Fig. 2), *L. sudetica* (Fig. 5), *Scapania nemorea*.

Examples of thalloid liverworts that produce gemmae: *Lunularia cruciata, Marchantia polymorpha, Metzgeria consanguinea*, *Riccardia palmata*.

Leafy liverwort **brittle stems and leaf fragments** can grow into a new plant. Certain species take brittleness to extremes; for example, the leaf lobules of *Frullania fragilifolia* have a tendency to be strongly caducous, detaching readily from the plant and earning it the common name of Spotty Fingers.

In thalloid liverworts, **branches** can also break off and disperse and their production may be promoted by adverse growing conditions or damage to the thallus.

Hornworts

None of the hornworts in the British Isles produce gemmae but some species are known to produce tuber-like perennating structures from the thallus; when these are produced in number and late in the season, they can behave as asexual propagules. Like liverworts, hornworts can also regenerate clonally from fragments of thallus.

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