

## NOTES ON IDENTIFICATION OF SPECIES OF BRYACEAE

### (A) GENERAL HINTS

Not all specimens can be identified! Mature capsules are needed to determine some taxa, others may require bulbils or tubers to be present. Hence care should always be taken when collecting Bryaceae to represent well developed capsules and bulbils, if they occur. Specimens collected should be large enough for the range of variation in characters to be estimated and to allow sufficient material to be left intact for future study (e.g. 20 stems and 5 good capsules would be minimal; several inflorescences are desirable if they are present; bulbils or tubers should be represented by small samples when they occur).

Two or more Bryaceae species often grow intermixed and capsules of one species sometimes grow out of tufts composed largely of the gametophyte of another species. It is desirable therefore to take care during fieldwork to so far as possible avoid mixed gatherings, not least because by the time that capsules mature it is often found that leaves on the fertile stems are partly decayed. In these circumstances leaves on innovations or the rotted remains from the main stem should be checked. Study of leaves on adjacent stems risks muddles in mixed gatherings.

Even when 'good' specimens at the correct stage of development are obtained they may prove unidentifiable, especially if the material is non-fertile. In particular, growth in abnormally submerged, shaded, droughty, saline, or nutrient-enriched conditions may result in atypical gametophytes that can defy identification. Exposed conditions in the Arctic and high on mountains can result in dwarfing of gametophytes, poor development of leaf shape or leaf borders, and it has been claimed, cause variability in development of the peristome as well as in nearly every other diagnostic character.

Nevertheless, there is no need to be fearful of identifying Bryaceae since most species show consistent characters that allow reliable identifications. Admittedly Bryaceae specimens from harsh environments can be difficult or sometimes impossible to identify. Problems may arise due to the considerable number of coexisting species (e.g. on high mountains), dwarfing or poor development of gametophytic characters, frequent failure to ripen or even produce capsules and occasional interspecific hybridisation. The wet and cloudy climate of western Ireland apparently reduces the frequency of sporophytes and the regularity of capsule maturation in many Bryaceae, so that species needing mature capsules for identification such as *B. salinum* may be under-recorded there. Material from very dry regions such as Morocco and Egypt can also be stunted or otherwise poorly grown and troublesome if not hopeless to name.

**Interspecific hybrids** The literature contains various references to hybrids between European species of *Bryum s. l.* and these undoubtedly occur occasionally. Indeed, Wettstein created artificial hybrids between *Bryum* species in cultivation during the 1920s. Ochi (1954) recorded an 'intergeneric' hybrid involving *Brachymenium exile* and *Bryum argenteum*, which may well have been correctly identified, but his *Pohlia crudoides* x *Bryum pallescens* sporophyte (Ochi 1961) was surely misidentified.

The clearest circumstantial evidence of hybrids between Bryaceae species is of hybrid sporophytes, although if spores from such hybrids are fertile it would be expected that hybrid gametophytes ('recombinants' in the sense of Shaw 2000: 389) should occur and possibly lead to introgression between species. Hybrid sporophytes should be suspected when intermediates are found between coexisting species that cannot be explained as merely individual variants of either species, e.g. because their morphology is too divergent or because the sporophytes are clearly growing from gametophytes of the 'wrong' species. Some of the best examples of such hybrids found recently have been with *B. algovicum* and *B. archangelicum* in Co. Down. Other evidence of hybrids might be offered by variable spore size or presence of many abortive (infertile) spores,

but there are other explanations possible (see below). My own impression is that undoubted hybrids are rather infrequent in Bryaceae and that variability from other causes has often been uncritically assumed to result from hybridisation.

**Differences between Bryaceae and small Mniaceae** Small species of Mniaceae can be confused with Bryaceae. The widespread genus *Pohlia* (Mniaceae) differs in (1) usually having relatively longer, narrower leaf cells, (2) often having the upper half of the leaf  $\pm$  denticulate or toothed, (3) always lacking a leaf border of narrow cells, (4) the costa as seen in transverse section usually having several large median guide cells with stereids both above and below them (whereas Bryaceae lack large guide cells and typically show only a single band of stereids). One or another of those characters occurs in various species of Bryaceae, but rarely two or three together, except sometimes in *B. alpinum* which is one of the species of Bryaceae most prone to confusion with *Pohlia* spp., although it often differs from them in having strong red secondary pigmentation. Other characters helpful in separating *Pohlia* from Bryaceae are that the former genus has the costa ending in or below the leaf apex (whereas it is often excurrent in Bryaceae), perichaetial bracts longer compared to the length of upper leaves in many species, some species are paroicous (whereas no Bryaceae are truly paroicous), and cilia rudimentary to long but not appendiculate as in some Bryaceae.

**Mini-packets** When identification of herbarium material is based on detailed study of a small part of the specimen (e.g. on peristomes or diaspores) it is good practice to place the parts of the specimen that have been studied in separate *labelled* mini-packets kept within the main packet. Bits segregated in this manner can be reexamined easily in future, whereas permanent mounts on microscope slides are less convenient to store and they often deteriorate over the years. A slip of paper placed with the specimen and summarising the characters on which a determination has been based is also helpful for future workers.

## **(B) MORPHOLOGICAL CHARACTERS**

The following sections give a brief account of the morphology of Bryaceae, concentrating on features that differ among the European species. It also serves to define some of the terminology used in the keys that follow and to allow comparative discussion of variation in certain features.

**Life-forms** A classification of the life-forms of bryophytes is provided by Mägdefrau (1982), within which the European Bryaceae species correspond to:

[a] Annuals: Scattered plants growing erect as pioneers on open mineral soils; none of the Bryaceae entirely correspond to this category, but it is appropriate e.g. for *B. violaceum* when it grows as mainly immature plants on arable fields that are ploughed annually.

[b] Short turfs: Short shoots, hardly more than 10 mm high, stand close together and grow on after ripening of the sporogonia by means of (mostly sparsely and acrotonous) regenerative shoots. More or less closed, often very spreading turfs are thus formed which last for scarcely more than a few years. They grow on open mineral soils and on rocks. E.g. *B. argenteum*.

[c] Tall turfs: The upright shoots, which are not branched or only slightly so, form turfs of considerable height. The shoots grow on after gametangia formation or production of acrotonous regenerative shoots is continued. E.g. *B. pseudotriquetrum*.

[d] Cushions: Basal regenerative shoots are produced usually in considerable numbers on the upright shoots. The cushions therefore grow not only upwards but also extend sideways. If they are free-standing they are hemispherical in shape. If they are laterally inhibited (for instance in rock crevices), they become extraordinarily dense. E.g. *B. capillare* (sometimes), *B. schleicheri*.

Intermediate life-forms are common among Bryaceae. Populations of *B. dichotomum* or *B. warneum* may begin as Annuals but multiply to form Short turfs. Species such as *B. algovicum* or *B. pallescens* vary in height from Short turfs to Tall turfs. *B. capillare* sometimes forms rounded cushions, e.g. in rock cracks, but on soil it may spread to become a Short turf or Tall turf. A further complication arises because stems of some turf forming species such as *B. alpinum* may be more or less decumbent, so that its life form may then approach that of the 'Mat' more

characteristic of pleurocarpous mosses, especially if innovations are plentiful. Because of the tendency of life form to vary and difficulties in classifying intermediate conditions, it is not of great value in identifying Bryaceae species and the non-committal term 'tuft' is often used to categorise forms intermediate between Cushions and Short turfs or Tall turfs. Nevertheless, life-form can give useful pointers in identification, as with the often dense turfs of *B. caespiticium* or the laxer turfs of *B. pseudotriquetrum*.

**Stems** The colour of the stem may be helpful in identification, although details of its structure are not used. Immature stems as with immature leaves are often green in plants that gain a red or brown stem as they mature. The stem is fragile in some species of the genus (e.g. *B. marratii*, *B. pallens*), its breakage often resulting in deciduous propagules resembling large bulbils (e.g. in *B. marratii*). Other species such as *B. canariensis* have notably tough and wiry stems.

Arrangement of the leaves on the stem is often important in species identification. Two main trends exist: for leaves to be larger and tightly clustered in inflorescences at the stem apex (termed rosulate), or for leaves to be of approximately similar size and evenly spaced along the length of the stem (termed equidistant) although denser at inflorescences. *B. creberrimum* and *B. caespiticium* provide good examples of the rosulate arrangement (which reaches extreme development in *R. roseum*), whereas *B. argenteum*, *B. pallens* and *B. pseudotriquetrum* exemplify equidistant leaf arrangement. Such differences are most apparent with tall stems and they become almost or quite undetectable with low and stunted plants which may be of 'bud-like' form in many if not all species.

**Leaves** Characters of the leaves are usually important in identifying Bryaceae. The largest vegetative leaves of mature plants should be selected for study: from the upper parts of non-fertile stems but avoiding the youngest leaves, or from immediately below perichaetial or perigonal bracts just below the apices of fertile stems. Young leaves at the stem tips of mature plants, their lower leaves, leaves from innovations or leaves of young plants, should all be avoided (or interpreted with caution) because they commonly have less well developed characters than the mature upper vegetative leaves. Even then, since immature plants and mature plants that have grown under unfavorable or atypical conditions commonly have leaf characters that are poorly developed or absent, it is good practice to rely for identification only on positive characters that can be demonstrated convincingly and to place much less reliance on negative (absence) characters. Thus presence of e.g. a strong border, bistratose border, recurved leaf margin, decurrent leaf base or prominent teeth on upper part of leaf are likely to be important for identification, whereas absence of such characters may not be.

Leaf shape provides identification characters for some species, the often rather subtle difference between leaves widest at or near the base (e.g. *B. algovicum*, *B. caespiticium*) and widest at or just above mid-leaf (*B. capillare* and related species) being especially important. Leaf shape is best judged on a sample of leaves pulled from the stem. Decurrent leaf margins are characteristic of some species, these being strikingly developed in *B. weigeli* and often prominent in *B. pseudotriquetrum*. The decurrent bases remain on the stem when leaves are pulled away, so they are best examined *in situ* on the stem, using a low-power stereo-microscope. The decurrent bases are generally best developed on tall stems with widely spaced leaves and least developed or even absent on short densely leafy stems.

Development of the leaf border of narrow cells is an important character that may be hard to judge. It is best investigated around mid-leaf. Leaf margins are often recurved, so care is needed to ensure that the rows of cells along the leaf edge are fully visible. Hence, leaf sections are often necessary to establish the details of the border and virtually essential to demonstrate that it is bistratose in certain species (*B. arcticum*, *B. pallens*) or 2-3 stratose (*B. donianum*). The literature refers to leaves as 'bordered' only when several marginal rows of narrower, longer (and commonly more incrassate) cells differ *sharply* from those of the adjacent lamina. However, there is continuous variation within the genus in the number of marginal rows of narrow cells as well as

in their width, length, cell-wall thickness and the abruptness of transition to the lamina cells. Patient study of several leaves may be needed to determine the character of the border in individual specimens, and this often reveals variability even among leaves from the same stem. Immature plants or those from shaded, very wet or eutrophicated habitats often have a narrower border than usual, or one that is unistratose in species where it is usually bistratose (e.g. *B. pallens*). Growth in open sunny habitats prone to drought may result in forms with very wide borders, notably the '*platyloma*' and '*rufifolium*' forms of *B. capillare* which have often been recognised taxonomically.

The strength of the costa (nerve) and its length (evanescent = lost beneath apex, percurrent, or excurrent to form a short or long awn) is characteristic of many Bryaceae species and important in their identification. Examples include the weak usually evanescent costa in *B. marratii*, a strong costa ending in or just below the apex of *B. alpinum*, the shortly excurrent costa of *B. mildeanum*, the short but stout mucro of *B. donianum* and the rather long excurrent costa (awn) of *B. capillare*. Upper vegetative leaves should be examined, since the costa is commonly less excurrent on the lower leaves and sometimes more or less so on the perichaetial bracts. Unfortunately other species are much more variable, and strikingly so in *B. dichotomum* which includes very different looking forms that range from plants with the costa disappearing well below the apex (formerly regarded as part of '*B. bicolor*') to forms with the costa long-excurrent (formerly regarded as '*B. versicolor*' and '*B. dunense*'). Variation in certain other species is less extreme, but still sufficient for there to be a risk of confusion, as when the costa of *B. pseudotriquetrum* varies from its usual shortly excurrent condition to more longly excurrent, so the plants are superficially more similar to e.g. *B. pallescens*.

Colour of the leaves often provides useful characters, particularly when pink or red coloration (secondary pigmentation) is present (due to anthocyanins in the cell sap). Leaves of a few species lack any pink or red coloration (notably *B. cyclophyllum*, *B. dichotomum* and *B. mildeanum*), or have it only in inflorescences (*B. marratii*). Others are usually pink over much of the leaf (*B. weigeli*), usually red (*B. cryophilum*), often red but sometimes green (*B. alpinum*) or vary from green to bright pink or red (*B. pallens*). In species showing variable development of pink or red leaf coloration it is usually best developed in plants growing in open, sunny sites that are prone to dry out, whereas it may be absent in plants of wet, shaded places, sometimes varying in different parts of a single tuft. Some species but not others develop red coloration that is restricted to the basal cells of mature leaves that are otherwise green, providing a useful identification character. This localised red coloration is conspicuous e.g. in *B. archangelicum*, *B. algovicum*, *B. intermedium* and *B. pseudotriquetrum*, but absent e.g. in *B. cyclophyllum*, *B. pallens* and *B. warneum*. However, some *B. warneum* may develop brownish coloration of similar extent in a few perichaetial bracts. Pink or red coloration appears to persist even in old dried herbarium specimens, whereas the green coloration due to chlorophyll disappears within a few years after death of the plants.

**Rhizoids** Many Bryaceae have papillose rhizoids, but even in these species the papillae are only well developed on the larger rhizoids. Other species have smooth or only weakly papillose rhizoids. Rhizoid colour (as seen by transmitted light) may differ between species, being distinctively purple or violet in *Bryum violaceum* and (usually!) *B. ruderale*, but brown in most species. Within each species, the smaller rhizoids are paler than the larger ones and the smallest are often almost colourless. Notes on papillosity and colour of rhizoids therefore invariably refer to the large rhizoids. Care is sometimes needed to distinguish rhizoids from protonemal filament systems (caulonemata and chloronemata).

**Diaspores** Several different types of diaspores serve for vegetative reproduction in Bryaceae, and more than one type may be present in a single species or even on the same plant. Older literature used the term gemmae indiscriminately for a variety of structures on rhizoids, protonemata and in leaf axils that are given separate names in the keys below. Following Duckett & Ligron (1992), a distinction is made between structures that have specific liberation

mechanisms (abscission cells) and those which do not. The diaspores with abscission cells are still termed **gemmae**, whereas those lacking them are now termed **tubers**.

**Tubers** (rhizoid gemmae of Risse 1987) mostly occur on subterranean rhizoids but they may also occur above the soil surface in leaf axils on stems, e.g. in *B. rubens*, albeit that the elevated tubers are still borne on very short axillary rhizoids or rhizoid-initial cells. Such rhizoidal tubers in Bryaceae are typically spherical, subspherical or pyriform, multicellular, stipitate (on short rhizoid branch) and yellow, orange, red or brown by transmitted light when mature (but often translucent or whitish when immature). Identification of species within the '*Erythrocarpa*' (i.e. the former '*B. erythrocarpum*' aggregate) relies heavily on study of the size, shape, distribution (on short or long rhizoids, clustered or not), cell-size, and to a lesser extent colour of these rhizoidal tubers. Similar rhizoidal tubers occur in various other Bryaceae species, including *B. alpinum* and *B. capillare* and it has been confirmed that the '*Erythrocarpa*' share similarities due to convergent evolution rather than close relationship (Holyoak & Pedersen 2007).

For Belgian *B. dichotomum* (as *B. bicolor* and *B. barnesii*) Wilczek & Demaret (1978, 1980) described (a) 'typical' spherical to ovoid rhizoidal tubers, which as they mature develop into (b) often much larger irregular tubers on lateral rhizoids; also recorded were (c) peculiar small tubers of 1-5 large cells that terminate some rhizoids (these might result from fungal infection: see below). Quite different tuber-like thickening of stem bases (type (d)) has also been described from *B. dichotomum* (as *B. bicolor*) from the Kuwaiti desert by El-Saadawi & Zanaty (1990). The same authors also describe smaller spherical rhizoidal tubers (= type (a)) in these plants along with larger more irregularly shaped tubers terminating rhizoids that combine features of the large 'stem tubers' (d) with those of the rhizoidal tubers (these appear to match type (b), but apparently differed in being developed 'on very short lateral branches at stem bases' and at the apices of stout rhizoids). Detailed studies may show that a similarly wide range of tuber types also occurs in other species. In the meantime, the information from *B. dichotomum* warns us that species identification within the '*Erythrocarpa*' should only be based on plants with well characterised rounded to pyriform rhizoidal tubers that match those characteristic of particular species.

Examination of rhizoidal tubers can prove troublesome because of adhering soil particles. Repeated irrigation of specimens on a microscope slide helps free them of sandy or silty soil, but clays are more tenacious. Use of an ultrasonic bath or dispersing agents such as Calgon may help remove clays, but manipulation of specimens soon results in most of the finer rhizoids with attached tubers breaking off. Repeated transfer of specimens from Hoyer's Mountant to water and back again is probably the most effective way of removing fine mineral particles but routine use of Hoyer's Mountant has been abandoned because of its toxicity as a carcinogen, so it should only be used in a laboratory fume-hood. A sample of unattached tubers can usually be obtained by breaking the soil beneath specimens into fragments and searching the fractured edges of the (moist) soil using a stereo microscope (magnification x20-30) and picking off tubers and rhizoid fragments using fine forceps. However, in mixed gatherings it is frequently essential but often difficult to be certain which tubers are associated with which leafy stems: colour and papillosity of rhizoids often helps, but as a last resort plants may be grown from individual tubers placed on agar. Unfortunately, however, tubers of plants grown on artificial substrata such as agar may differ appreciably from those grown by the same plants on natural soils.

Enlargement of the apical cell of rhizoid branches in 2 out of >50 gatherings of *B. capillare* and one gathering of *B. pseudotriquetrum* was attributed to fungal parasitism (Martínez-Abaigar *et al.* 2005). Swollen apical cells noted in *B. dichotomum* (see above) and other species might have the same cause.

Specialised propagules with abscission cells (= **gemmae**) may occur on leaves (**foliar gemmae**), in leaf axils (**axillary gemmae**) and on protonemata (**protonemal gemmae**). Foliar gemmae are uncommon in Bryaceae; Martin (2001) described cylindrical (filamentous) uniseriate gemmae occurring regularly on leaves in Canadian populations of *Bryum cf. flaccidum*; similarly, Pressel

*et al.* (2007 figs 3a, b, 4a) illustrated gemmiferous protonemata growing from the lamina of *Bryum aubertii* and a wild-collected leaf of *B. moravicum*. Axillary and protonemal gemmae are more widespread and again consist of cylindrical (filamentous) uniseriate structures. Occurrence of filiform axillary gemmae is restricted to a few species (*B. cyclophyllum*, *B. moravicum*, '*B. vermigerum*' and occasionally *B. pallens* and *B. pseudotriquetrum*), covered in key B4 below. However, Pressel *et al.* (2007) reported filiform protonemal gemmae from 33 species of Bryaceae, those for 20 species being described for the first time in their paper. For many of the species they recorded similar gemmae on plants from the wild to those grown *in vitro*. They failed to find protonemal gemmae in only a few species that were cultivated *in vitro* (*A. concinnatum*, *A. julaceum*, *B. calophyllum*, *B. marratii*, *B. riparium*, *P. zieri*). With few exceptions the protonemal gemmae varied little in gross morphology and afforded few identification characters, although SEM studies of gemmae surfaces revealed differences in surface ornamentation. Reports of 'filiform rhizoidal gemmae' (listed for *B. demaretianum*, *A. lusitanicum* and *B. tenuisetum* by Spence 2003) are probably referable to protonemal gemmae growing on brown chloronemata misinterpreted as rhizoids.

**Bulbils** differ from gemmae in possessing a well defined stem apex and (usually) leaf primordia. Although the primordia are rudimentary in *B. gemmilucens*, growth of its bulbils in culture occurs from a well defined stem apex (J.G. Duckett pers. comm.). Large bulbils such as those of some *B. dichotomum* often grade into deciduous branchlets or branches. Large deciduous buds or apices broken from fragile stems may also resemble bulbils.

**Brood cells** are clearly distinct from gemmae, tubers and bulbils and are a general feature of suboptimal conditions, such as prolonged *in-vitro* culture, desiccation, liquid cultures, etc. (Pressel *et al.* 2007). They have apparently not been reported in wild Bryaceae plants; their significance to the plants is unknown but perhaps low because they are thin-walled and presumably have low tolerance of desiccation (Pressel *et al.* 2007).

**Inflorescences** Determination of the arrangement of gametangia (the reproductive structures, consisting of male antheridia and female archegonia) is important in recognition of numerous species of Bryaceae. Female (and mixed) inflorescences are termed **perichaetia**; male inflorescences are termed **perigonia**. The specialised leaves associated with inflorescences are here termed **perichaetial bracts** and **perigonial bracts**, respectively.

The plants may be **monoicous** (antheridia and archegonia on the same plant) or **dioicous** (antheridia and archegonia on different plants). Whereas it can readily be *proved* that individual specimens are monoicous, it can generally only be *inferred* that they are dioicous after a good search of suitable specimens with archegonia fails to reveal antheridia, and *vice-versa*. Indeed, with apparently dioicous plants there is often a lingering doubt that study of more or better material might reveal the missing structures. Monoicous Bryaceae may be **synoicous** (antheridia in perichaetia with the archegonia) or **autoicous** (antheridia in separate perigonia that are terminal on branches arising beneath perichaetia). Crundwell & Syed (1973) showed that male plants of *B. torquescens* and related species often have additional antheridia in the axils of bracts close below perigonia.

Investigation of the arrangement of gametangia is best carried out on specimens that are in good condition with young or maturing capsules. With these, presence of one type of gametangia without the other is usually significant since in Bryaceae the archegonia and antheridia on individual stems usually mature at about the same time. However, errors in identification very commonly arise from misinterpretation of the sexual arrangement, especially when antheridia have decayed but archegonia persist, or where synoicous plants have few antheridia in only a small proportion of inflorescences.

The following sequence of steps is recommended for checking the sexual arrangement of specimens. (1) Search for perigonia (inflorescences containing only antheridia) at apices of

branches arising beneath perichaetia (i.e. base of setae if these have already developed). If these are present on at least a proportion of stems the population is probably autoicous. The perigonia must be on branches arising from the stem (not adjacent stems) and a sample of up to ten well developed stems may need to be checked if perigonia are scarce. (2) If plants are not autoicous, break a stem off just below a perichaetium, then holding the specimen by the seta and working upwards towards the base of the seta, strip away all but the few uppermost perichaetial bracts. (3) Transfer the seta with attached perichaetium to a small drop of clean water on a slide and, using a good stereo-microscope with  $\times 20-40$  magnification, carefully dissect off all remaining bracts then search among the outer paraphyses and unused archegonia for antheridia (if any). If antheridia are found the plant is synoicous (these inflorescences usually have far more paraphyses than are present in all-female inflorescences). If no antheridia are found in several inflorescences on good fresh material the plant is not synoicous, but beware that on old stems the antheridia may be decaying or decayed. In a few synoicous species (e.g. *B. longisetum*, *B. pallescens*) antheridia occur only in small numbers and a majority of inflorescences with setae may lack antheridia, so that five or even ten inflorescences may need to be dissected in order to confirm the synoicous sexuality. (4) If no antheridia have been found on a number of stems having female inflorescences it may be deduced that the plants are dioicous (female only). Evidence for this will be strengthened if the plants have capsules forming *and* similar stems close by are all-male (with perigonia, lacking archegonia), but these are often no longer recognisable (although they must of course have been present close by if fertilisation has occurred in all-female inflorescences).

By the time capsules have shed their spores the gametophytes bearing them have usually begun to decay, and those bearing old capsules may be too decayed for reliable recognition of antheridia. In general, antheridia decay earlier than paraphyses or unused archegonia, the initially reddish or brown antheridia commonly becoming translucent and colourless before disintegrating progressively from the apex downwards. Whenever antheridia or remnants of their bases are found in decaying perichaetia there is no doubt that a synoicous plant is at hand, but their apparent absence often needs to be confirmed using less decayed specimens.

Most Bryaceae species show consistently dioicous, synoicous or autoicous arrangement of the gametangia, so these differences have been used in taxonomy as well as for recognising species. Nevertheless, several species have variable arrangements of gametangia. In *B. torquescens* individual plants growing together may be dioicous, autoicous or synoicous (i.e. form a polyoicous population) yet show no other differences. Most *B. warneum* are autoicous but a few populations are synoicous, apparently without any other differences between them. *B. algovicum* has widespread coastal populations that are synoicous ('var. *rutheanum*') but localised alpine populations that are apparently similar except for being autoicous ('var. *algovicum*'). In *B. pseudotriquetrum* the dioicous (*B. pseudotriquetrum* s. str.) and synoicous (var. *bimum*) forms differ in other characters so that they seem best treated as separate taxa. These examples imply that the arrangement of the sexes has been subject to repeated rearrangements during evolution in Bryaceae and that we should therefore beware that atypical states might occur unexpectedly in other species.

**Capsules** The angle at which the mature capsule is held was traditionally used to distinguish *Brachymerium* (capsule erect) from *Bryum* (capsule typically inclined to pendulous, rarely horizontal). Nevertheless, although within *Bryum* s. str. and the segregate (sub-)genus *Ptychostomum* most species have the mature capsules pointing vertically downwards (pendulous) or nearly so (cernuous), it is very common to find a proportion of capsules that are horizontal or inclined and rare tufts may have most or all capsules suberect. A few species have most of their capsules held at less steep angles, notably *B. arcticum* which usually has horizontal or inclined to cernuous capsules. Although such differences are often mentioned in literature, it should be pointed out that Bryaceae often grow on vertical or steeply inclined substrata, so that angles of capsules judged from herbarium specimens may bear little relation to the conditions with the living plants.

Length and shape of the capsule is commonly characteristic of particular species, and helpful for making provisional determinations in the field, but it changes according to the state of spore maturation and is also prone to occasional variation (e.g. stunting on small plants) that necessitate use of additional characters to confirm identifications. Even with well grown plants, the normal variability of capsule shape within populations necessitates assessment of capsule shape from at least several capsules. The capsule shape (and measurements) described here as in most of the literature is that of the darkening capsule approaching maturity but not fully mature; very young capsules are narrower; capsules close to maturity often show marked shrinkage of the neck region. In a few species the empty capsules differ markedly in shape.

Long symmetrical capsules characterise *B. capillare* and related species and to a lesser extent *B. pallens*; *B. uliginosum* has a long asymmetrical capsule with an oblique mouth; *P. demissum* and *P. zieri* have strikingly asymmetrical (gibbous) capsules; *B. marratii* has a very short capsule with an almost globular theca that provides an immediate distinction from the longer ovoid capsule of *B. calophyllum*. Slightly asymmetrical capsules are typical of *B. intermedium*, whereas rather similar plants such as *B. archangelicum* and *B. algovicum* normally have symmetrical capsules. Small-mouthed capsules (and long setae) are characteristic of *B. knowltonii* and *B. warneum* and often provide useful recognition features since e.g. *B. algovicum* typically has wide-mouthed capsules, but this is not entirely reliable as an identification character because occasional populations of *B. warneum* have been recorded with wide-mouthed capsules ('*B. mamillatum*' of older floras) and of *B. algovicum* with narrow mouthed capsules. Very wide-mouthed (turbinate) empty capsules characterise *B. turbinatum*. Several other species typically have capsules somewhat narrowed below the mouth and this also occurs occasionally in atypical populations of others (e.g. *B. algovicum*). Three species (*P. demissum*, *B. wrightii* and *P. zieri*) have dry empty capsules that remain inflated, with none of the shrivelling or wrinkling of empty dry capsule walls occurring in most species. On the other hand, capsules of *B. argenteum* and *B. dichotomum* have thin-walled exothecial cells so they decay quickly. Many species may produce unusually short setae bearing small stunted capsules that are atypical in shape and which cannot be relied on at all for identification characters.

The operculum (lid) of the capsule varies from merely convex with no apiculus or a tiny apiculus (mamillate) to conical or rostellate. A very low convex operculum characterises several species, and the rostellate operculum of *B. marratii* provides another character differentiating that species from *B. calophyllum* in which the conical operculum has a shorter apiculus. However, operculum shape of most species falls between the extreme types and is somewhat variable, so at best it may provide rather subtle hints in species identification.

Immature capsules are green; as spores ripen in different species this turns to yellowish, brown, deep brown, red or almost black. Capsules of most species darken abruptly as the spores mature, those of some changing from yellowish or light brown to blackish-brown within a week or two. Bright red colour of mature capsules is an important identification character of a few northern species (*B. wrightii*, '*B. axel-blyttii*' = form of *B. calophyllum*), occurring also in the very common *B. argenteum* and some populations of *B. dichotomum*, and different shades of yellow to brown or chestnut may characterise some of the commoner species, although varying stages of capsule maturity and variability between populations limit their value as identification characters. Likewise, colour of the rims of ripe capsules may sometimes be useful for species identification (e.g. yellow to orange in *B. archangelicum* but red in *B. salinum*), although care needs to be taken to compare only fully mature capsules. The exothecial cells of capsules potentially provide numerous characters to differentiate species, but in practice they seem rather similar in many different species: small and incrassate just below the mouth, progressively larger and laxer for several rows beneath, then rectangular to somewhat irregular throughout the theca. However, size of the uppermost exothecial cells provides another useful distinction between *B. archangelicum* and *B. salinum*, and shape of cells in mid-theca differs in '*B. mamillatum*' and *B. warneum*, although perhaps only as a function of the difference in shape of the theca itself in these taxa which are now thought to be conspecific. The neck of the capsule has more or less numerous



stomata, but their precise number, size, shape and distribution is not known to provide any important features that are useful in species identification.

**Peristomes** The structure of the peristome provides important identification characters for numerous species in the Bryaceae, such that plants of certain species (particularly in (sub-)genus *Ptychostomum*) can only be determined with mature or almost mature capsules. The ideal material to study consists of capsules observed very soon after the operculum has been shed naturally, so that most of the spores are still present. Slightly immature or older but undamaged capsules can often also be used, but care is needed as immature or old and damaged peristomes are easily misinterpreted.

Living plants with nearly mature capsules can be kept alive for a few days until some opercula are lost naturally. Most or all peristomes on plants with old empty capsules are usually too badly damaged for them to be useful. Study of peristomes in dried herbarium material should be preceded by soaking a mature capsule (or several) for at least ten minutes in water to which a trace of soap or photographic wetting agent has been added. On dried specimens which have been soaked, undehisced capsules with the dark coloration implying they are nearly mature commonly have fully formed peristomes; a large hole made in the wall of the theca helps in wetting them from the inside as well as the outside; the operculum can be carefully picked off with a needle; it often comes away more easily following further soaking in dilute KOH solution.

A convenient procedure for study of the peristome is to place a well soaked capsule in a spot of water on a microscope slide, use a sharp scalpel to cut longitudinally through the middle of the upper half of the capsule and peristome, then cut transversely across the middle of the capsule to produce two apical halves of capsule each with half a peristome. These halves need to be handled carefully because peristomes are fragile. Most spores should be gently removed, which can be accomplished easily by dropping spots of undiluted Ethanol or Methylated Spirit onto the spore mass (or less easily, by repeated irrigation with water, aided if necessary by gentle brushing with a small soft brush). The capsule halves should then be placed in a spot of water, one with inner surface uppermost, the other with outer surface uppermost, before a cover slip is placed on top. Details of the outer surface of the exostome can be seen easily by microscopic examination of the peristome half with outer surface uppermost, and its inner surface can often be studied by focusing through the  $\pm$  translucent teeth. The endostome is thin and translucent and best studied by focussing carefully up and down on the peristome half with inner surface uppermost.

Most of the commoner species of Bryaceae, and nearly all those with small spores, have a 'perfect' peristome that consists of 16 strong outer peristome (**exostome**) **teeth** within which is a membranous and translucent inner peristome (**endostome**) with 16 **processes** arranged alternately with the exostome teeth and nearly as long as them. Between each of the processes of the endostome, the 'perfect' peristome has **cilia** in groups of three (sometimes two or four), each consisting of a slender filament with short branches (appendiculae, hence described as 'cilia appendiculate'). Other Bryaceae species have the cilia more or less reduced, such that the branches are indicated only by thickenings ('cilia nodulose') or the cilia are short, very short ('cilia rudimentary') or absent. In *B. caucasicum* and *B. wrightii* the endostome is still further reduced, with no processes or cilia and the basal membrane shorter than in other species.

Characters of the exostome teeth are important in identification of some species. In all Bryaceae the outer surface (OPL = outer peristome layer) of the lower part of each tooth consists of the remains of two ranks of cells meeting along a zigzag midline. A few species have small perforations along the midline, notably *B. calophyllum* and on at least some teeth in *B. salinum*. Fine structures ('ornamentation') of the OPL vary within a few species, e.g. *B. arcticum*.

Inner surfaces of exostome teeth (PPL = principal peristome layer) consist of the remains of only a single rank of cells, the thickened walls of which form transverse **lamellae** (or 'trabeculae'). A few species have additional oblique or vertical lamellae ('**cross walls**') on the PPL that link the

transverse walls (to form the '*Ptychostomum* type' of peristome of Amann 1918 and other early specialists). These form important identification characters and are especially abundant and easy to see in *B. algovicum*, typically present in smaller numbers in *B. arcticum* (and '*B. bryoides*') and *B. warneum*, but occur only as rare abnormalities in other Bryaceae species.

The few species with the '*Ptychostomum*-type' peristome also differ from other Bryaceae in having the basal membrane of the endostome adhering to the exostome. This is mainly apparent through delays in wetting of the adhering surfaces when a peristome is placed in water, so that their appearance with trapped pockets of air changes as the specimen gradually becomes wetter and the air is lost. This feature is most easily demonstrated in *B. algovicum*, whereas it is often less readily apparent in *B. warneum*, in which the thick and rather opaque lamellae also hinder searches for 'cross walls'. Care therefore needs to be taken in judging occurrence of 'cross walls' on the exostome PPL (a) because the slow wetting of peristomes with adherent endostome produces a risk of confusing edges of air-pockets with 'cross walls', but also (b) because the adhering outer surface of the endostome itself has remnants of PPL cell walls.

Recognition of endostome cilia as absent, rudimentary, short, nodulose or appendiculate is often important in identifying Bryaceae, but care needs to be taken to avoid confusing cilia that have merely broken off with those which were absent or rudimentary. Old empty capsules may already have lost most or all of their cilia, and even with good material there are risks of breaking off cilia when peristomes are cut, cleaned of spores, then manipulated on slides. Carefully studying outlines of cilia rudiments helps in this, as does prior experience of their shape. Even when an appendiculate cilium appears to be present, it should be scrutinised to ensure that it is attached to the basal membrane and bears the appropriate structural relationship to neighbouring endostome processes, since hurried examination can result in half of a split, perforate endostome process being misinterpreted as a cilium.

**Spores** Size and less often colour of spores may be important in identification of some Bryaceae species. Fungal spores and algal cells may be present in old capsules and these sometimes outnumber the few remaining spores. The spore colour described is that seen by transmitted light. Living spores contain chlorophyll giving a more or less greenish colour; in old specimens the chlorophyll degrades so that the spores become yellower or browner, much as with leaves and stems. Beware that filters on microscopes may give a misleading impression of colours.

Spore measurements are based on mature spores measured in water using an eyepiece graticule on a light microscope. Measurements consist of the greatest dimension measurable across each spore and with care and good equipment they can be reproducible to  $\pm 0.5 \mu\text{m}$ . It normally suffices to scan groups of spores and measure a few of the largest and a few of the smallest, since ranges of measurements obtained by methodically measuring samples (e.g. of 30 spores) take much longer to obtain and generally turn out to be almost the same. Great precision in using spore measurements is hardly possible under the usual conditions of study, since ovoid spores will not be orientated consistently on slides, pressure on the cover slip may flatten ('enlarge') spores, smaller spores may move differentially beneath cover slips, and germinating spores expand. Furthermore, mean size of spores sometimes differs markedly from one capsule to another within a population, so that important determinations or surprising spore sizes should be checked from several capsules.

Occasional gatherings of Bryaceae may have capsules with a considerable proportion of spores that abort and fail to grow to full size, these small spores often appearing to be empty with their walls  $\pm$  collapsed inwards. Failure of spores to develop fully might sometimes be due to hybridity but more mundane factors such as bad weather have been shown to have a similar effect in pollen grains. Also, Stark (2001) gives details of the abortion of large numbers of developing capsules in the moss *Grimmia orbicularis* due to bad weather and similar occurrences are probably widespread among mosses. Measurements cited in the keys do not take account of abortive (empty) spores. In *Cinclidium* (Mniaceae) it was shown by Mogensen (1978) that growing spores

increase in volume in a series of steps with relatively inactive periods between them. Similar episodic growth during spore maturation seems likely in Bryaceae, so that measurements of spores for identification purposes should ideally be made only on mature spores that are being shed naturally. Inference of the size of mature spores from those that are immature and smaller to some unknown extent is undoubtedly prone to error, especially from capsules too young to show the darkening typically associated with spore maturation.

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#### **(E) CORRECTIONS TO NAMES USED IN SMITH (2006)**

*Anomobryum julaceum* var. *concinatum* = *A. concinatum*, *Bryum mamillatum* = *B. warneum*, *B. lawersianum* = *B. arcticum*, *B. stirtonii* = *B. elegans*, *B. laevifilum* = *B. moravicum*, *B. subelegans* = *B. pallens*, *B. imbricatum* = *B. archangelicum*, *B. neodamense* = *B. pseudotriquetrum* var. *pseudotriquetrum*, *B. funkii* = *B. kunzei*.

## KEYS TO EUROPEAN AND MACARONESIAN BRYACEAE SPECIES

### (A) NOTES ON USE OF KEYS

The following points should be remembered when using the keys, most of them being explained in more detail in the preceding notes.

*Ensure* that leaf, rhizoid, tuber, bulbil and sporophyte characters are all assessed from the same plant. Because different Bryaceae species commonly grow closely intermixed it is only by demonstrating physical connections between say leaves, stems and tubers that one can be sure they are on the same plant.

*Avoid* basing records on very scanty material (e.g. single stem with few leaves, or plant with <5 tubers) or poor material (e.g. plants grown shaded or in water, as betrayed by weak, straggling growth with sparse leaves on long slender stems). Particular care to select good material is needed with difficult taxa such as *B. radiculosum* or *B. bornholmense*, but desperately stunted material of such typically larger species as *B. capillare*, *B. torquescens* or *B. alpinum* can resemble the species that are always of small stature.

*Beware* of *Pohlia* spp.: see notes above.

*Juvenile plants* of Bryaceae normally lack tubers and they never have well grown sporophytes, but they may develop axillary bulbils in certain species. Growing material on or a visit later in the season may offer the only hope of identifying immature plants.

*Leaf characters* are those of well grown upper leaves; the largest perichaetial bracts are  $\pm$  similar. Avoid using new growth, basal leaves, innermost perichaetial bracts, perigonal bracts, leaves from juvenile stems or leaves from slender innovations. *Rhizoid* characters should be judged from a sample of several rhizoids; papillae or roughness are most apparent on the largest rhizoids. Both small (translucent) and large (opaque) rhizoids should be checked in transmitted light of varying intensity when seeking mauve or violet coloration. Coloured filters in the light path of the microscope may produce misleading effects.

Separate terms are used here for (a) *Tubers*, (b) *Axillary bulbils* and (c) *Axillary gemmae* (mostly filamentous, i.e. uniseriate). Note that older literature uses term 'gemmae' for tubers. Buds (e.g. in *B. caespiticium*) can be confused with axillary bulbils, but buds are not deciduous and they are often more variable in size with leaf primordia beginning to grow into leaves.

Despite comments in some literature, interspecific hybrids fortunately seem to be infrequent.

In order to allow identification of as much material as possible, both traditional **B**ipartite keys (for fertile specimens using characters of sporophyte and gametophyte, and for non-fertile specimens using only gametophytic characters) and a **M**ultiple access key (mainly for fertile specimens) are provided below. The multiple-access key should be less prone than the bipartite keys to errors arising from misinterpretation of certain difficult but important characters. At any event, it may provide a useful alternative if the bipartite keys

fail with good fertile specimens. The keys using characters of the sporophyte (**B2** and **M**) are generally more reliable than the other keys. Ideally, identifications made from the keys should be checked against detailed descriptions, good illustrations, and correctly identified specimens in a herbarium.

## **(B) BIPARTITE KEYS**

The short general key B1 leads to a series of more detailed keys, distinguished as Keys B2 to B6.

Check the specimen for mature capsules, tubers on rhizoids, axillary gemmae and axillary bulbils, then use key B1 to select which bipartite key to use. If a specimen has e.g. mature capsules and axillary bulbils it should be possible to identify it using Key B2 (preferably), Key B5 or Key B6, since there is much duplication within the keys to allow for identification where practicable of non-fertile plants and those in which the usual tubers, gemmae or bulbils may not have developed. However, absence of good capsules, tubers, etc. may often preclude reliable species identification.

### **KEY B1: GENERAL KEY**

- |   |               |
|---|---------------|
| 1. Mature capsules present with ± intact peristomes and mature spores   | Keys B2 and M |
| - . Mature capsules absent  | 2             |
| 2. Rhizoidal tubers present   | Key B3        |
| - . Rhizoidal tubers absent   | 3             |
| 3. Filamentous <i>axillary</i> gemmae present (i.e. not bulbils for which see next couplet and not filamentous gemmae developed on protonemata) | Key B4        |
| - . Filamentous axillary gemmae absent  | 4             |
| 4. Axillary bulbils present   | Key B5        |
| - . Axillary bulbils absent   | Key B6        |

## KEY B2: PLANTS WITH MATURE CAPSULES AND SPORES

This key excludes species that have never been found c.fr. in Europe or Macaronesia.

1. Exostome considerably shorter than endostome; cilia rudimentary; capsules gibbous with long neck; leaves with lax areolation 2  
-. Exostome longer than or  $\pm$  equalling endostome; cilia absent, rudimentary or long; capsules gibbous or symmetrical; leaves with firm or lax areolation 3
2. Shoots not julaceous; leaves lanceolate to ovate-lanceolate, red-brown, with excurrent costa; spores adhering in tetrads at maturity *demissum*  
-. Shoots julaceous; leaves broadly ovate, whitish, with costa evanescent, percurrent or occasionally shortly excurrent; spores not adhering in tetrads at maturity *zieri*
3. Plants with underground stolons; leaves conspicuously rosulate, forming terminal rosette in which largest leaves  $> 5$  mm long *and* spatulate *and*  $\pm$  toothed above 4  
-. Plants lacking underground stolons; leaves rosulate or equidistant; leaves not forming terminal rosette *and*  $> 5$  mm long *and* spatulate *and* toothed above 5
4. 16-21 leaves in terminal rosette; leaf section with two rows of large dorsal cells below stereids *roseum*  
-. 18-52 leaves in terminal rosette; leaf section with one row of large dorsal cells below stereids *ontariense*
5. Cells in upper part of leaf vermicular, with incrassate cell walls; capsule with neck about as long as theca 6  
-. Cells in upper part of leaf not vermicular; cell walls incrassate or not; capsule with short or long neck 8
6. Stems julaceous, shoot tips often obtuse or rounded; leaves concave, ovate, with costa extending to apex or evanescent; cilia appendiculate *julaceum*  
-. Stems julaceous or not, shoot tips often pointed or cuspidate; leaves not or weakly concave; costa mostly percurrent to excurrent; cilia rudimentary or absent 7
7. Leaves not concave; costa percurrent or shortly excurrent; capsules frequent, inclined to cernuous; sometimes with uniseriate axillary gemmae, but clavate bulbils lacking; Portugal & W. Spain only *lusitanicum*  
-. Leaves slightly concave; costa most often percurrent; capsules very rare, erect; often with clavate bulbils but uniseriate axillary gemmae lacking; widespread species (but capsules recorded in Europe only from C. France) *concinatum*
8. Endostome absent or with low basal membrane ( $<100 \mu\text{m}$ ); processes absent or small and slender 9  
-. Endostome with basal membrane  $>100 \mu\text{m}$ ; processes well developed 13
9. Capsule inclined to cernuous or pendulous; species with mainly arctic range, or from Caucasus 10  
-. Capsule erect to horizontal (rarely inclined); species from Macaronesia or southern Balkans (*Brachymerium* spp.) 11

10. Capsule light brown when freshly mature; leaves lanceolate to oblong-lanceolate; in our region only in Caucasus *caucasicum*  
 -. Capsule red when freshly mature; leaves and larger perichaetial bracts ovate to broadly ovate; mainly in Arctic *wrightii*
11. Taxa recorded from Azores, Madeira or Canary Islands 12  
 -. Very poorly known moss recorded only from Macedonia *paradoxum*  
 (confused with *B. cellulare* in some literature; transferred from *Mielichhoferia* to *Brachymerium* by A.J. Shaw)
12. Small tufted moss with gametophytes suggestive of diminutive *Bryum alpinum* but without red coloration; leaves ovate-lanceolate to ovate-oblong; bulbils lacking; capsule subcylindrical to very narrowly pyriform; spores (12)13-18  $\mu\text{m}$ ; Azores, Madeira and Canary Islands *notarisii*  
 -. Small moss with gametophytes suggestive of *Bryum dichotomum*; leaves ovate to oblong-lanceolate; often with axillary bulbils; capsule narrowly pyriform; spores 11-12  $\mu\text{m}$ ; mainly tropical sp., recorded from Madeira *kikuyense*  
 (syn. *Brachymerium philonotula*)
13. Capsule erect or inclined with endostome lacking cilia; leaves ovate, concave, shortly pointed, with very large and wide mid-leaf cells and indistinct leaf border *cellulare*  
 -. Capsule rarely inclined, usually pendulous; endostome with or without cilia; lacking this combination of leaf characters 14
14. Inner surface of lower part of exostome teeth (usually) with oblique 'cross walls' joining at least some of transverse trabeculae; base of endostome often adhering to exostome; cilia short or rudimentary 15  
 -. Inner surface of lower part of exostome teeth normally lacking oblique 'cross walls' joining transverse trabeculae; base of endostome only rarely adhering to exostome; cilia rudimentary, short or long 17  
 (but, if spores  $>24 \mu\text{m}$ , leaves acuminate and lacking red at base and plants autoicous or synoicous check also couplet 16)
15. Leaves red at base (contrasting with green lamina); exostome with many oblique cross walls; air trapped between exostome and adherent endostome giving characteristic patchy appearance when peristome wetted; capsules mainly mature in spring or early summer *algovicum*  
 (var. *algovicum* is dioicous; var. *rutheanum* is synoicous)  
 -. Leaves not red at base (but sometimes brown at base); exostome with few oblique cross walls; distinctive patchy appearance lacking when peristome wetted; capsules mainly mature in summer or autumn 16
16. Usually autoicous, sometimes synoicous; many spores usually  $> 40 \mu\text{m}$ ; capsule broadly pyriform, symmetrical, pendulous *warneum*  
 -. Synoicous; spores (20) 25-36 (39)  $\mu\text{m}$ ; capsule narrowly pyriform to elongate-pyriform, slightly asymmetrical, inclined *arcticum*



17. Cilia short (less than half as long as endostome processes) or rudimentary; spores mainly  $> 24 \mu\text{m}$  18  
 -. Cilia long (more than half the length of endostome processes), nodulose or appendiculate; spores  $< 25 \mu\text{m}$  25
18. Capsule not much longer than wide; operculum rostellate; leaves blunt at apex, green without pink or red coloration; leaf border weakly developed or absent, always unistratose *marratii*  
 -. Capsule length usually much more than width; operculum conical or mamillate; leaves obtuse to acute at apex, often with pink or red coloration; leaf border weak to strong and often bistratose 19
19. Capsule elliptical or narrowly obovoid (rarely ovoid) with short neck; upper leaves ovate to broadly ovate, obtuse to acute; leaf border almost absent to well-defined but narrow (of 0-2 rows of narrow incrassate cells); autoicous *calophyllum*  
 -. Capsule narrowly ellipsoid to narrowly pyriform with neck at least  $\frac{1}{3}$  total length; upper leaves ovate to narrowly lanceolate, acute; leaf border weakly defined to well defined (of 2-3 rows of narrow incrassate cells); dioicous, autoicous or synoicous 20
20. Dioicous or autoicous; leaf base not red; leaf border often bistratose 21  
 -. Synoicous; leaf base red, contrasting with colour of cells above; leaf border unistratose 22
21. Dioicous; capsule straight to curved, slightly asymmetrical; spores 16-26 (42)  $\mu\text{m}$ ; cilia often appendiculate, sometimes all short *pallens*  
 -. Autoicous; capsule asymmetrical with oblique mouth; spores 22-30  $\mu\text{m}$ ; cilia always rudimentary *uliginosum*
22. Costa percurrent to only shortly excurrent; leaf border present but rather weakly defined *knowltonii*  
 -. Costa clearly excurrent; leaf border usually well defined 23
23. Spores mostly 40-50  $\mu\text{m}$ ; seta often but not always  $> 30 \mu\text{m}$  *longisetum*  
 -. Spores all or mainly  $< 40 \mu\text{m}$ ; seta rarely  $> 30 \mu\text{m}$  24
24. Some exostome teeth with small perforations along midline; capsule mouth usually red at maturity; exothecial cells of 3rd and 4th row down from capsule mouth mostly 30-40  $\mu\text{m}$  wide *salinum*  
 -. Exostome teeth without small perforations along midline; capsule mouth usually orange at maturity; exothecial cells of 3rd and 4th row down from capsule mouth mostly 20-25  $\mu\text{m}$  wide *archangelicum*
25. Leaf base longly and broadly decurrent; leaves equidistant, rather widely spaced on stem, ovate with apex obtuse to acuminate, pinkish throughout (without red basal cells), bordered; dioicous; capsules rare *weigeli*  
 -. Leaf base not longly decurrent, or if so leaf base red contrasting with lamina cells above 26

26. Leaves obovate to orbicular, plane, with obtuse to rounded apex; margins hardly bordered; leaves green throughout, without red basal cells; uniseriate axillary gemmae often present; capsules rare *cyclophyllum*  
 -. This combination of characters lacking 27
27. Leaves unbordered, usually lanceolate to narrowly lanceolate, straight and imbricate when dry; cells very long and narrow, 60-80 (112) × 8-12 (16) μm in mid-leaf; plants often red or reddish with metallic sheen *alpinum*  
 -. This combination of characters lacking 28
28. Cilia mainly nodulose (sometimes with some appendiculate cilia); capsule usually slightly asymmetrical with somewhat oblique mouth; spores 18-24 μm; synoicous; leaf margin revolute from base to apex with ill-defined border; leaf base reddish *intermedium*  
 -. This combination of characters lacking; cilia appendiculate 29
29. Leaf apices hyaline (achlorophyllose) so shoots whitish when dry; shoots julaceous when moist due to ovate or broadly ovate, imbricate leaves *argenteum*  
 -. Leaf apices not hyaline; shoots not whitish when dry; shoots julaceous or not 30
30. Larger leaves widest at or above mid-leaf; basal cells of leaf not red and differing conspicuously in colour from cells above 31  
 -. At least most of larger leaves widest below mid-leaf; basal leaf cells red (and differing in colour from cells above) or not red 40
31. Shoots julaceous when moist; leaves concave, imbricate; walls of cells in mid-leaf porose; at least some rhizoids with tall conical papillae *elegans*  
 -. Shoots not julaceous; leaves concave or not, imbricate or not; walls of cells in mid-leaf porose or not; rhizoids often papillose but lacking tall conical papillae 32
32. Leaf margin appearing unbordered (ill-defined border at mid-leaf largely concealed by recurved leaf margin), dentate above *canariense*  
 -. Leaf margin with border poorly to well developed, entire or denticulate above 33
33. Leaf border stout, (1) 2 or 3 stratose; leaves mucronate or costa shortly excurrent; dioicous 34  
 -. Leaf border unistratose; costa percurrent to shortly to longly excurrent; dioicous, autoicous or synoicous 35
34. Plants green without pink or red coloration; leaf border 2-3 stratose, often yellowish, confluent with short stout mucro formed by excurrent costa; spores 12-14 μm *donianum*  
 -. Plants often with at least some pink or red coloration; leaf border (1) 2 stratose, not obviously confluent with excurrent costa; spores 16-26 (42) μm *pallens*
35. Uniseriate gemmae present in axils of lower leaves *moravicum*  
 -. Uniseriate axillary gemmae lacking 36

36. Costa percurrent to very shortly excurrent; larger leaves bordered below with (3)4-6 rows of  $\pm$  linear cells with strongly thickened walls; dry plants with upper leaves spirally twisted when dry; known from Sardinia, S. France, Portugal and W. Spain

*minii*

- . Costa usually excurrent as short to long awn; larger leaves bordered below with 3 or more rows of elongate cells with walls weakly or strongly thickened; if upper leaves spirally twisted when dry the awn usually long

37

37. Small plants, stems 2-15 mm; longest leaves < 2.5 mm; capsules mainly < 2.5 mm long

38

- . Larger plants, stems 10-50 mm; longest leaves > 2.5 mm; capsules mainly > 2.5 mm long

39

38. Dioicous, autoicous or synoicous; costa 65-100  $\mu\text{m}$  wide at leaf base; tubers only on long rhizoids, orange-red or amber-coloured becoming brown with age, translucent, their cells thin-walled (1-2  $\mu\text{m}$ ) and (30) 45-60  $\mu\text{m}$  long, not or only slightly protuberant

*bornholmense*

- . Dioicous; costa 45-75  $\mu\text{m}$  wide at leaf base; tubers on long rhizoids and often also on very short rhizoids (so that they may appear to arise in axils of lower leaves), bright crimson, red or dark red (rarely pink or whitish; normally lacking orange or brown colours), almost opaque; tuber cells thick-walled (2-3  $\mu\text{m}$ ) and 30-35 (45)  $\mu\text{m}$  long, often strongly protuberant

*rubens*

39. Dioicous; leaves often strongly spirally twisted around stems when dry; tip of apical cell of male paraphyses rounded; rhizoidal tubers red-brown, less often brown or red

*capillare*

- . Usually synoicous (less often autoicous or dioicous); leaves not or weakly spirally twisted around stems when dry; tip of apical cell of male paraphyses pointed; rhizoidal tubers red

*torquescens*

40. Leaves with well defined border of 2 or more rows of narrow cells (check rhizoids for  $\pm$  spherical red or brown tubers, if these are present return to couplet 32 and also check *caespiticium* at couplet 45)

41

- . Leaves unbordered or with border only ill-defined

49

41. Plants synoicous (sometimes with very few antheridia at base of seta) or autoicous

42

- . Plants dioicous

44

42. Leaves equidistant, commonly with base longly decurrent; costa percurrent to shortly excurrent (occasionally longer excurrent)

*pseudotriquetrum* var. *bimum*

- . Leaves somewhat rosulate with base not or only shortly decurrent; costa excurrent >150  $\mu\text{m}$

43

43. Spores 14-16  $\mu\text{m}$ ; processes with perforations about as long as wide; synoicous

*creberrimum*

- . Spores 18-20 (22)  $\mu\text{m}$ ; processes with perforations 1-2 times as long as wide; synoicous (often with very few antheridia at base of seta) or autoicous

*pallescent*

44. Leaves with red basal cells contrasting in colour with cells above 45  
 -. Basal cells of leaf not differing in colour from cells above 47
45. Leaves rosulate; leaf margins strongly recurved with border ill defined; mid-leaf cells rather narrow (12-16  $\mu\text{m}$ ); spores 10-14  $\mu\text{m}$ ; plants often densely tufted; costa usually long-excurrent *caespiticium*  
 -. This combination of characters lacking; leaves  $\pm$  equidistant; costa only shortly excurrent 46
46. Larger plants, commonly 10-150 mm; mid-leaf cells 12-24 (30)  $\mu\text{m}$  wide; leaf border typically well developed *pseudotriquetrum* var. *pseudotriquetrum*  
 -. Smaller plants, commonly 5-25 mm; mid-leaf cells 8-16  $\mu\text{m}$  wide; leaf border ill defined *mildeanum*
47. Leaf border (1) 2 stratose, well defined; leaf margins recurved; capsule not turbinate when empty *pallens*  
 -. Leaf border 1-2 stratose, ill-defined or distinct; leaf margins plane or incurved below; capsule turbinate when empty 48
48. Large tumid plants, often 50-100 mm tall; leaves very concave and often cucullate; mid-leaf cells 20-40 (60)  $\mu\text{m}$  wide; leaf border well defined; leaf margin plane or incurved below; costa relatively thin *schleicheri*  
 -. Smaller plants, typically 4-30 mm tall; leaves less concave, not cucullate; mid-leaf cells 14-26(30)  $\mu\text{m}$  wide; leaf border often poorly defined; costa strong *turbinatum*
49. Leaves with red basal cells contrasting in colour with cells above 50  
 -. Basal cells of leaf not differing in colour from cells above 55
50. Leaves equidistant; costa evanescent, percurrent or only shortly excurrent 51  
 -. Leaves rosulate; costa excurrent to long-excurrent 53
51. Slender branches much taller than main stem present, the branch leaves shorter and blunter than those on main stem; stem leaves shortly pointed to obtuse; capsule broadly pyriform to ellipsoidal or ovate, red when newly mature 52  
 -. Slender branches much taller than main stem absent; branch leaves and stem leaves similar; stem leaves acuminate; capsule narrower (narrowly pyriform), light brown when mature *mildeanum*
52. Cells in the upper and middle parts of branch leaves narrower (mainly 6-9  $\mu\text{m}$  wide; length: width mainly 6.0-7.5); exostome teeth mainly 400-460  $\mu\text{m}$  long; usually on basic soils *blindii*  
 -. Cells in the upper and middle parts of branch leaves wider (mainly 12-15  $\mu\text{m}$  wide; length: width mainly 2.5-3.5); exostome teeth mainly 310-350  $\mu\text{m}$  long; usually on neutral or acidic soils *oblongum*
53. Costa long excurrent; leaf margins strongly recurved  $\pm$  throughout; leaves ovate to ovate-oblong, not strongly concave, often imbricate only in comal tuft *caespiticium*  
 -. Costa excurrent in short point; leaf margins plane or narrowly recurved below; leaves ovate to broadly ovate, concave, imbricate 54

54. Plants in dense tufts; costa in uppermost leaves/perichaetial bracts excurrent in awn 100-500 (605)  $\mu\text{m}$  long that is recurved in dry plants; costa 47-61  $\mu\text{m}$  wide just above leaf base; dry leaves not prominently keeled dorsally; mid-leaf cells longer and narrower, length:width 2.5:1 to 5:1; capsules rare *kunzei*  
 -. Plants scattered or in loose patches; costa in uppermost leaves/perichaetial bracts excurrent in mucro or awn < 200  $\mu\text{m}$  long that is not conspicuously recurved when dry; costa 65-119  $\mu\text{m}$  wide just above leaf base; dry leaves prominently keeled dorsally, along the prominent costa; mid-leaf cells shorter and wider, length:width 1:1 to 3:1; capsules common *funkii*
55. Mid-leaf cells usually > 20  $\mu\text{m}$  wide; leaf apex obtuse to acute 56  
 -. Mid-leaf cells usually < 20  $\mu\text{m}$  wide (but sometimes wider in *gemmiparum*: see couplet 57); leaf apex obtuse, acute or acuminate 57
56. Empty capsules not turbinate; leaves ovate, concave, with obtuse to acute apex *muehlenbeckii*  
 (N.B. forms of *B. alpinum* that have grown submerged can closely resemble this sp.)  
 -. Empty capsules turbinate; leaves ovate to ovate-lanceolate or narrowly triangular with acuminate apex *turbinatum*
57. Costa 75-100  $\mu\text{m}$  wide near leaf base; mid-leaf cells 12-18 (28)  $\mu\text{m}$  wide; axillary bulbils often present *gemmiparum*  
 -. Costa < 75  $\mu\text{m}$  wide near leaf base; mid-leaf cells < 20  $\mu\text{m}$  wide; axillary bulbils present or not 58
58. Rhizoidal tubers present See key B3  
 -. Rhizoidal tubers absent 59
59. Axillary bulbils present See key B5  
 -. Axillary bulbils absent 60
60. Rhizoids purple to violet 61  
 -. Rhizoids brown, brownish, red, reddish, yellow or yellowish 62
61. Larger rhizoids coarsely papillose *ruderae*  
 -. Larger rhizoids smooth, less often finely papillose *violaceum*
62. Main stem of fertile plants exceeded by 1-3 innovations with erect leaves and cuspidate tips; leaves dimorphic, those on innovations shorter and blunter than those on main stem; some leaves with shortly decurrent reddish-brown auricles; plant of sandy coastal habitats *dyffrynense*  
 -. This combination of characters lacking 63
63. Capsule ovoid to shortly cylindrical (length < 2.5  $\times$  width) with short neck; exothecial cells thin-walled, empty capsules decaying rapidly probably *dichotomum*  
 (this species sometimes lacks bulbils when c.fr. whereas *gemmiferum* apparently does not)  
 -. Capsule narrowly ovoid, narrowly ovoid-cylindrical or narrowly pyriform (length > 2.5  $\times$  width) with longer neck; exothecial cells thicker-walled, empty capsules more persistent 64

64. Plants synoicous *sauteri*  
 -. Plants dioicous 65

65. Highly branched protonemata developed from rhizoids (usually gemmiferous), giving impression of densely bunched rhizoids *radiculosum*  
 -. Highly branched protonemata not developed from rhizoids small  
 Bryaceae that usually have tubers but which are probably unidentifiable unless tubers are found (include *klinggraeffii*, some *radiculosum*, some *runderale*, some *sauteri*, *subapiculatum*, *tenuisetum*).

### KEY B3: PLANTS WITH RHIZOIDAL TUBERS

This key excludes *B. apiculatum* (tubers unknown in Europe), *B. dixonii* (tubers known only in cultivation) and *B. muehlenbeckii* (records of tubers perhaps based only on misidentified *B. alpinum*). *B. caespiticium* and *B. gemmiparum* are included because tubers are reported in much of the literature, although the author has seen them only on misidentified plants. Beware that some *Pohlia* species with tubers can be confused with small Bryaceae. *Pohlia lescuriana* has brown spherical tubers that somewhat resemble those of certain Bryaceae.

1. Leaves widest at or above middle of leaf (i.e. point midway between base and apex of lamina, excluding any excurrent costa or awn or decurrent leaf auricles) 2  
 -. Leaves widest below middle 6
2. Leaves with border of at least 2 rows of narrow cells 3  
 -. Leaves unbordered (leaves toothed towards apex; leaves tough and difficult to pull from stems; costa excurrent in cuspidate point; tubers red, spherical, 180-300  $\mu\text{m}$ , with non-protuberant cells) *canariense*
3. Leaves broadly ovate, very concave, imbricate so shoots appear julaceous; cells in mid-leaf porose; rhizoids with tall conical papillae (tubers rarely present, only on long rhizoids, brown, spherical, 90-200  $\mu\text{m}$ , with non-protuberant cells); leaf border weak to strong; costa often rather shortly excurrent *elegans*  
 -. Leaves lanceolate to oblong-spathulate or ovate, flat or slightly concave; shoots not julaceous; cells in mid-leaf not porose; rhizoids smooth to  $\pm$  rough with low papillae; leaves usually with prominent border and costa  $\pm$  long excurrent 4
4. Filamentous gemmae present in leaf axils; leaf base often decurrent (tubers often present on long rhizoids, brown in colour like the rhizoids, spherical, 65-120  $\mu\text{m}$ , with non-protuberant cells) *moravicum*  
 -. Filamentous axillary gemmae lacking; leaf base not or scarcely decurrent; gemmae brown to red, 65-270  $\mu\text{m}$  5

5. Leaves often strongly spirally twisted when dry; tubers brown to red-brown and similar in colour to rhizoids; dioicous (tubers scarce to abundant, spherical, 66-270 (440)  $\mu\text{m}$  diameter, or ovoid to irregular, cells not protuberant) *capillare*  
 -. Leaves not spirally twisted when dry; tubers red and often brighter in colour than brown to red rhizoids; usually synoicous, less often autoicous or dioicous (tubers often abundant on long to short rhizoids, spherical, 75-255  $\mu\text{m}$  diameter, cells not protuberant) *torquescens*
6. Mature leaves straight and imbricate when dry 7  
 -. Mature leaves at least slightly twisted or flexuose when dry, especially near leaf tips 9
7. Leaves ovate, very concave, with hooded apex; strong costa ends just below apex (tubers sometimes present on short rhizoids, orange-red, spherical *ca* 160  $\mu\text{m}$  diameter) *muehlenbeckii*  
 -. Leaves ovate-lanceolate to lanceolate,  $\pm$  concave but apex not hooded; costa strong, ending below apex to percurrent 8
8. Leaves lanceolate; mid-leaf cells long and narrow, mainly 8-12  $\mu\text{m}$  wide; plants commonly  $\pm$  red with metallic gloss, but sometimes green and dull; axillary bulbils lacking; tubers usually present on short rhizoids, purplish-red to brownish-red,  $\pm$  spherical, 120-200  $\mu\text{m}$  diameter *alpinum*  
 -. Leaves ovate-lanceolate to lanceolate; mid-leaf cells wider, mainly 12-18  $\mu\text{m}$  wide; plants mainly green, lacking pronounced metallic gloss; large axillary bulbils often present; tubers apparently lacking despite reports in literature *gemmaiparum*
9. Tubers 'flattened' (thickness much less than length or width), with ends of marginal cells projecting to form lobes or teeth (tubers on short rhizoids, reddish, 100-200  $\times$  75-150  $\mu\text{m}$ ; leaves distinctly bordered; costa shortly excurrent) *riparium*  
 -. Tubers spherical, ovoid, pyriform or  $\pm$  irregular, but not consistently 'flattened' 10
10. Axillary bulbils usually present (or developing at other seasons) on at least some plants in a population; tubers of several types sometimes present, including: (a) mainly large (110-220  $\mu\text{m}$ ), subspherical tubers, pale yellow to red-brown or dull dark brown, maturing into much larger irregularly shaped tubers, with notably small surficial cells, (b) peculiar club-shaped tubers up to 150-180  $\times$  75  $\mu\text{m}$  terminating a rhizoid and comprised of 1-5 very large (45-75  $\mu\text{m}$ ) thick-walled brown cells 11  
 -. True axillary bulbils absent (although buds occasionally have similar appearance); tubers similar to (a) or (b) in preceding couplet absent (tubers that are present may be spherical, ovoid, pyriform, or much less often irregular, their colour yellow, orange, red or brown-red, rarely dull brown with notably small surficial cells) 12
11. Axillary bulbils when present <7 per leaf axil, often only 1-3; bulbils often >200  $\mu\text{m}$  long; leaf form very variable *dichotomum*  
 -. Axillary bulbils >10 per leaf axil, often >20; bulbils <200  $\mu\text{m}$  long; costa usually shortly excurrent *gemmaiferum*

12. Upper leaves with costa usually excurrent  $>200 \mu\text{m}$ ; leaf margin strongly recurved at least below; usually forms dense tufts (tubers rare: inconspicuous and chocolate-brown, or small and red, perhaps recorded in error or only on hybrids); mid-leaf cells  $12\text{-}16 \mu\text{m}$  wide, 2-3 marginal rows narrower and forming ill-defined border *caespiticium*  
 -. This combination of characters lacking: upper leaves with costa usually excurrent  $<200 \mu\text{m}$  or merely percurrent; leaf-margin  $\pm$  recurved; in lax or dense tufts or growing as scattered plants (commonly with tubers) 13
13. Mean length of tubers  $<100 \mu\text{m}$  14  
 -. Mean length of tubers  $>100 \mu\text{m}$  17
14. Rhizoids mauve to violet, smooth or less often finely papillose; tubers with non-protuberant cells, red, mainly  $60\text{-}90 \mu\text{m}$  *violaceum*  
 -. Rhizoids yellowish, pale brown, brown or red brown, smooth to coarsely papillose; tubers yellow, brown or red, with cells protuberant or not 15
15. Tubers spherical or subspherical (length: width  $<1.3$ ), with protuberant cells, crimson-red to dull red or less often brown, mainly  $60\text{-}100 \mu\text{m}$  *klinggraeffii*  
 -. Tubers spherical to elongate pyriform (length: width  $1.1\text{-}>2$ ), with cells not or only slightly protuberant, yellow to brown or red-brown 16
16. Tubers pyriform (length: width mainly  $>1.5$ ), 3-5 cells long but only 1-2 cells wide, larger ( $60\text{-}100 \times 40\text{-}60 \mu\text{m}$ ), brown to red-brown *sauteri*  
 -. Tubers spherical to pyriform (length: width  $1.1\text{-}1.5$ ), 2-4 cells wide, often smaller ( $40\text{-}60 \times 30\text{-}40 \mu\text{m}$ , but length to  $40\text{-}80 \mu\text{m}$  in some populations), yellow to brown *valparaisense*
17. Tubers mainly  $\pm$  spherical (length: width  $<1.3$ ), on short or long rhizoids, or both, not in clusters 18  
 -. Tubers distinctly pyriform (length: width  $1.3\text{-}2.4$ ); many tubers in clusters or strings on short rhizoids close to base of stems (tubers  $100\text{-}150 \times 60\text{-}100 \mu\text{m}$ , bright orange, with cells only slightly protuberant; leaf border indistinct; mid-leaf cells  $15\text{-}20 \mu\text{m}$  wide) *demaretianum*
18. Mid-leaf cells  $14\text{-}20 \mu\text{m}$  wide; leaves distinctly bordered with several rows of markedly narrower cells 19  
 -. Mid-leaf cells  $10\text{-}16 \mu\text{m}$  wide; leaves not or scarcely bordered with narrower cells 20
19. Tubers only on long rhizoids, orange-red or amber-coloured becoming brown with age, translucent, their cells thin-walled ( $1\text{-}2 \mu\text{m}$ ) and (30)  $45\text{-}60 \mu\text{m}$  long, not or only slightly protuberant; costa  $65\text{-}100 \mu\text{m}$  wide at leaf base *bornholmense*  
 -. Tubers on long rhizoids and often also on very short rhizoids (so that they may appear to arise in axils of lower leaves), bright crimson, red or dark red (rarely pink or whitish; normally lacking orange or brown colours), almost opaque; tuber cells thick-walled ( $2\text{-}3 \mu\text{m}$ ) and  $30\text{-}35$  ( $45$ )  $\mu\text{m}$  long, often strongly protuberant; costa  $45\text{-}75 \mu\text{m}$  wide at leaf base *rubens*



20. Rhizoids deep violet (rhizoids strongly papillose; tubers red to purplish-red, 125-180 (200)  $\mu\text{m}$ ) *ruderales*  
 -. Rhizoids yellow or various shades of brown or red-brown 21
21. Tubers pale yellow or yellow, less often orange, their cells protuberant (tubers 120-180 (220)  $\mu\text{m}$ ; rhizoids yellow or brownish) *tenuisetum*  
 -. Tubers usually orange, red or brown-red (rarely whitish or pink); if tubers yellow, diameter mainly > 200  $\mu\text{m}$ ; tuber cells not or scarcely protuberant; rhizoids yellowish or brown to red-brown 22
22. Tubers usually 190-260  $\mu\text{m}$  diameter (but as small as 120-200  $\mu\text{m}$  in occasional populations); mid-leaf cells 10-16  $\mu\text{m}$  wide; basal cells of leaf rectangular; rhizoids papillose;  $\pm$  calcifuge *subapiculatum*  
 -. Tubers 120-180 (200)  $\mu\text{m}$  diameter; mid-leaf cells 10-12 or 10-14  $\mu\text{m}$  wide; basal cells of leaf  $\pm$  quadrate to rectangular; rhizoids  $\pm$  coarsely papillose; often calcicolous 23
23. Tubers red to purplish-red (occasionally orange) and often contrasting with deep dull brown of rhizoids; rhizoids coarsely papillose; costa weaker, shortly excurrent; mid-leaf cells 10-14  $\mu\text{m}$  wide; basal cells of leaf rectangular  
*ruderales* (atypical forms with brown rhizoids)  
 -. Tubers brown to red, often similar in colour to brown or red-brown rhizoids; rhizoids very coarsely papillose; costa stronger, often yellow,  $\pm$  long excurrent; mid-leaf cells 10-12  $\mu\text{m}$  wide; basal cells of leaf  $\pm$  quadrate *radiculosum*

#### KEY B4: TO PLANTS WITH FILAMENTOUS AXILLARY GEMMAE

1. Small julaceous plants with erect imbricate leaves 0.4-0.8 mm long; upper leaf cells long-oval to elliptical and vermicular (Portugal and W. Spain only) *lusitanicum*  
 -. Larger plants; not julaceous; leaves > 1 mm long, usually erecto-patent to spreading; upper leaf cells not vermicular 2
2. Leaf apices acute or acuminate; leaves often with pink, red or brown coloration 3  
 -. Leaf apices obtuse to rounded; leaves green, without pink, red or brown coloration *cyclophyllum*
3. Leaf margin with border of narrow cells; larger plants with longer capsules 4  
 -. Leaf margin unbordered; small northern plant with short capsules '*vermigerum*'
4. Leaves widest at or below middle, decurrent or not at base, with basal cells green, pink, brown or red; costa shortly excurrent; plants green, pink, red or brown; tubers lacking 5  
 -. Leaves widest at or above middle, decurrent at base, with green basal cells; costa percurrent to excurrent as short awn; plants green, lacking red or pink coloration; brown tubers sometimes present *moravicum*

5. Basal cells of leaf usually red, contrasting with cells immediately above; leaf base usually decurrent; lamina cells in mid-leaf often narrower, usually 10-22  $\mu\text{m}$ ; leaf border unistratose; mature stem often orange to red when leaves are green

*pseudotriquetrum*

(var. *pseudotriquetrum* is dioicous, var. *bimum* synoicous)

- Basal cells of leaf same colour as cells above; leaf base not or slightly decurrent; lamina cells in mid-leaf often wider, usually 15-30  $\mu\text{m}$ ; leaf border commonly bistratose; mature stem similar in colour to leaves

*pallens*

### KEY B5: TO PLANTS WITH AXILLARY BULBILS

Note that this key only includes species with deciduous bulbils in the leaf axils; other species may have buds in at least a few leaf axils that look similar but which are not deciduous. Several species have longer microphyllous branches that are fragile or caducous, these are not included here, although *Anomobryum concinatum* (with clavate bulbils grading into short leafy branches) is included. Several *Pohlia* species with axillary bulbils are superficially similar (see above).

1. Stem and branch leaves all erect, imbricate, flat or  $\pm$  concave; shoots often julaceous, whitish, pale green or light green 2

- Stem leaves erecto-patent to spreading, not or only weakly concave; branch leaves erect and imbricate to spreading; shoots julaceous or not, colour variable 6

2. Middle and upper leaf cells rhomboid-hexagonal to narrowly rhomboid-hexagonal or elongate-rectangular, not sinuose; plants commonly whitish or pale green 3

- Middle and upper leaf cells narrow, often  $\pm$  vermicular; plants pale green or light green; capsule narrowly pyriform with neck about half length of theca 4

3. Bulbils green (often absent); plants commonly whitish due to achlorophyllose leaf tips; capsule shortly ovoid with short neck; very common and widespread sp. *argenteum*

- Bulbils dark red-brown when mature, present in all gatherings; plants pale to light green; capsules unknown; rare sp. known only from eastern Alps *austriacum*

4. Leaves concave, apex obtuse or obtuse and apiculate; shoots julaceous; shoot tips often obtuse or rounded; peristome with appendiculate cilia *julaceum*

- Leaves not or weakly concave, apex acute or acuminate; shoots not or weakly julaceous; shoot tips  $\pm$  cuspidate; peristome greatly reduced, without cilia (or capsules unknown) 5

5. Leaf apex acuminate; costa mostly percurrent or shortly excurrent; axillary bulbils often >10 per leaf axil, mainly red-brown or brown, with green leaf primordia mainly arising in upper half *bavaricum*

- Leaf apex acute (often apiculate); costa most often percurrent or ending just below leaf apex; axillary bulbils <10 per leaf axil, mainly green with brown colour restricted to basal half; leaf primordia often arising in both basal and apical halves of bulbil *concinatum*

6. Costa < 75  $\mu\text{m}$  wide near leaf base, evanescent, percurrent or excurrent; leaves usually ovate to ovate-lanceolate; bulbils 100-985  $\mu\text{m}$  long 7

- Costa 75-100  $\mu\text{m}$  wide near leaf base, evanescent to percurrent; leaves ovate-lanceolate to lanceolate; bulbils 250-750  $\mu\text{m}$  long *gemmiparum*

7. Bulbils or gemmae lacking leaf primordia 8  
 -. Bulbils or gemmae with leaf primordia 9
8. Green or yellowish to brown gemmae lacking leaf primordia present on upper part of stem, mainly oval to subspherical, stipitate (stalk 33-132  $\mu\text{m}$ ), with body (77)93-176  $\times$  (77)99-132  $\mu\text{m}$ , in addition to fewer green bulbils with well developed leaf primordia and occasional intermediate structures *apiculatum*  
 (very variable tropical and subtropical sp. recorded from Cornwall and Tenerife)  
 -. "Gemmae" lacking leaf primordia mainly 120-200  $\mu\text{m}$  long, not obviously stipitate (these are bulbils with leaf primordia indistinct or absent); green bulbils with well developed leaf primordia absent *gemmilucens*  
 (*Pohlia camptotrachela* is rather similar, but with narrower, more widely spaced leaves and smaller bulbils)
9. Bulbils rarely more than 5(6) per leaf axil, 100-985  $\mu\text{m}$  long, with or without distinct leaf primordia; colour variable but not usually orange; leaf with costa evanescent, percurrent or excurrent 10  
 -. Bulbils (5) 20-30 per axil in upper leaves, 100-160 (200)  $\mu\text{m}$  long, with distinct leaf primordia, often yellowish or orange-tinged (rarely reddish?); leaf with excurrent costa *gemmiferum*
10. Plants lacking innovations taller than main stem; branch leaves not differing much from leaves on main stem; bulbils green to yellow-green, up to 480 (600)  $\mu\text{m}$  long *dichotomum*  
 (*B. kikuyense* known from Madeira has similar leaves and bulbils to *dichotomum*, although capsules differ markedly; small leaves from innovations of *kikuyense* are often rather broadly ovate with a longer excurrent costa than would occur in *dichotomum* when that species has broad leaves, giving some branches a distinctive character. Large leaves from the main stems of *kikuyense* also have the leaf border of narrow cells much better developed than in leaves of *dichotomum*)  
 -. Main stem of fertile plants exceeded by 1-3 innovations with erect or erecto-patent leaves; leaves dimorphic, those on innovations shorter and blunter than those on main stem; older bulbils red, red-brown or brown at base, some often > 600  $\mu\text{m}$  long 11
11. Innovations with erect leaves and cuspidate tips; bulbils single in leaf axils, with brown coloration spreading upwards from base as they mature; plant of sandy coastal habitats *dyffrynense*  
 -. Innovations with leaves erect to erect-spreading, tips not cuspidate; bulbils 1-4 per axil, lower half green to pale orange when young, red-brown to red when older; northern and montane plant *blindii*

## KEY B6: TO PLANTS LACKING MATURE CAPSULES, RHIZOIDAL TUBERS, FILAMENTOUS AXILLARY GEMMAE, OR AXILLARY BULBILS

This key offers a last chance for identification of some specimens which lack many of the usual diagnostic characters. Success in using it will be more likely for bryologists having some familiarity with the commoner European species of Bryaceae. It will usually not work with immature or poorly grown plants. The key separates species showing various  $\pm$  striking gametophytic characters, before ending with residues of species that appear to be inseparable from their morphology. Most identifications based on this key should therefore be carefully checked against descriptions, illustrations and correctly identified herbarium specimens! Inflorescences are often present on plants lacking sporophytes and they will invariably be present on material with immature, damaged or moribund sporophytes, so some use is made of the sexual condition (e.g. synoicous or dioicous) in the key. However, when other characters exist the sexual condition is subordinated to them because many gatherings will lack any inflorescences.

Some species are not mentioned or at least not treated in detail in this key because identification may require: (a) mature capsules (*paradoxum*), (b) capsules or bulbils (*kikuyense*), (c) tubers (*demaretianum*, *klinggraeffii*, *radiculosum*, *sauteri*, *subapiculatum*, *tenuisetum*, *valparaisense*), or (d) because mature plants apparently always have axillary bulbils (*austriacum*, *gemmaferum*, *gemmailucens*) or (e) axillary gemmae (*moravicum*). Some of the other species that are mentioned in the key can only be determined as members of species-groups, which cannot be subdivided e.g. in the absence of mature capsules (*archangelicum*/ *algovicum*/ *longisetum*/ *salinum*).

1. Moist shoots (or at least the innovations) julaceous, with erect, imbricate leaves 2  
- Moist shoots or innovations not julaceous; leaves  $\pm$  spreading, not imbricate 13
2. Mid-leaf cells elongate, vermicular 3  
- Mid-leaf cells rhomboid to elongate-hexagonal, not vermicular 4
3. Leaves concave; plants not conspicuously yellowish when dry; usually  $>5$  mm tall; widespread *julaceum*  
(n.b. *concinatum* is similar, but more slender, with shoots scarcely julaceous)  
- Leaves flat; plants conspicuously yellowish when dry;  $<5$  mm tall; Portugal and W. Spain only *lusitanicum*
4. Shoots whitish or pale grey; cells in upper part of leaf lacking chlorophyll 5  
- Shoots green or greenish, not whitish or pale grey; cells in upper part of leaf chlorophyllose 6
5. Shoots reddish basally; moist shoots with leaf apices recurved near shoot tips; mainly montane *zieri*  
- Shoots not reddish basally; moist shoots with leaf apices not recurved near shoot tips; lowland and montane; very common and very variable *argenteum*

6. Large plants, stems typically 5-10 cm tall, forming big swollen light green to pinkish cushions in wet habitats; leaves equidistant, crowded, imbricate, very concave and often cucullate; costa thin, ending in apex or as short reflexed apiculus; leaf base not red (sometimes brown) and not decurrent *schleicheri*  
 (these are the characters of well-grown plants of var. *latifolium*; forms with narrower leaves and young or poorly grown plants are much less distinctive and may need careful separation from similar forms of *B. pallens* or *B. turbinatum*)  
 -. This combination of characters lacking 7
7. Stem and branch leaves not much different; main stems julaceous with concave, imbricate leaves (shoots 'bud-like'); spreading leaves lacking 8  
 -. Stem and branch leaves different; only the innovations (which often overtop the main stem) julaceous with  $\pm$  concave, imbricate leaves (appearing  $\pm$  cylindrical rather than bud-like); stem leaves spreading, less concave 10
8. Leaf often with border of narrow cells; costa often excurrent as rather long, slender awn; mid-leaf cells porose; rhizoids with tall conical papillae; leaf base not red *elegans*  
 -. Leaf lacking border of narrow cells; costa excurrent as short or rather stout awn; mid-leaf cells not porose; rhizoids  $\pm$  papillose but lacking tall conical papillae; leaf base red 9
9. Costa excurrent as a short mucro or (mainly in uppermost leaves/ perichaetial bracts) an awn  $<200 \mu\text{m}$  long that is not recurved in dry plants; costa stouter (65-119  $\mu\text{m}$  wide just above leaf base); dry leaves obviously keeled dorsally along the prominent costa; growing as scattered plants or in loose patches; lamina cells shorter and wider (length: width mainly 1:1 to 3:1 at mid-leaf) *funkii*  
 -. Costa longer excurrent, forming an awn often  $>200 \mu\text{m}$  long that is commonly recurved in dry plants; costa weaker (47-61  $\mu\text{m}$  wide just above leaf base); dry leaves not obviously keeled dorsally along costa; growing as dense tufts; lamina cells longer and narrower (length: width mainly 2.5:1 to 5:1 at mid-leaf) *kunzei*
10. Larger stem leaves with 3-4 rows of narrower cells forming  $\pm$  well defined border and recurved leaf margin; mid-leaf cells of stem leaves 14-24  $\mu\text{m}$  wide; synoicous *knowltonii*  
 -. Stem leaves unbordered, plane or weakly recurved at margin; mid-leaf cells of stem leaves  $<15 \mu\text{m}$  wide; dioicous 11
11. Leaves frequently with brown auricles; overall size larger (branch leaves 1.0-1.3  $\times$  0.6-0.7 mm); known only from coastal sands *dyffrynense*  
 -. Leaves lacking brown auricles; overall size smaller (branch leaves 0.3-0.9 (1.3)  $\times$  0.2-0.5 mm); montane or northern plants, not coastal 12
12. Cells in the upper and middle parts of branch leaves narrower (mainly 6-9  $\mu\text{m}$  wide; length: width mainly 6.0-7.5); on basic soils *blindii*  
 -. Cells in the upper and middle parts of branch leaves wider (mainly 12-15  $\mu\text{m}$  wide; length: width mainly 2.5-3.5); on neutral or acidic soils *oblongum*

13. Mid-leaf cells elongate, vermicular; leaves erect and imbricate when dry; erect or spreading when moist 14  
 -. Mid-leaf cells rhomboid to elongate-hexagonal, not vermicular; leaves various, usually  $\pm$  spreading 16
14. Medium-sized to rather robust plants, often red; leaves commonly with metallic sheen when dry; leaves lanceolate to narrowly lanceolate, erect when dry, spreading when moist; shoots not julaceous *alpinum*  
 -. Slender yellow-green plants; leaves without metallic sheen when dry; leaves erect and  $\pm$  imbricate when moist and when dry; leaves of moist shoots often slightly julaceous 15
15. Leaf apex acuminate; costa most often percurrent or shortly excurrent *bavaricum*  
 -. Leaf apex acute or acute and apiculate; costa most often evanescent to percurrent *concinatum*
16. Plants with underground stolons; leaves conspicuously rosulate, forming terminal rosette in which largest leaves >5 mm long *and* spatulate *and*  $\pm$  toothed above 17  
 -. Plants lacking underground stolons; leaves rosulate or equidistant; leaves not forming terminal rosette *and* >5 mm long *and* spatulate *and* toothed above 18
17. 16-21 leaves in terminal rosette; leaf section with two rows of large dorsal cells below stereids *roseum*  
 -. 18-52 leaves in terminal rosette; leaf section with one row of large dorsal cells below stereids *ontariense*
18. Leaf base long-decurrent *and* leaves widest well below middle; leaf apex acute to blunt but not rounded 19  
 -. Leaf base not decurrent or only shortly decurrent; if base has longer decurrency leaves widest at or near mid-leaf; leaf apex acute, blunt or rounded 22
19. Cells at leaf base red or reddish, differing in colour from rest of leaf; plants variable in colour, often green, red, or reddish but rarely pink throughout; leaves ovate to lanceolate, distant to imbricate; leaf base with long decurrency that may be narrow or moderately wide 20  
 -. Cells at leaf base not differing in colour from rest of leaf; plants commonly pink throughout; leaves ovate, rather distant; leaf base with long, wide decurrency *weigeli*
20. Leaves rather closely imbricate when moist so most of stem is concealed; stem brownish; decurrent leaf bases long but narrow (mainly a single cell wide); flattened, lobed, red tubers normally present *riparium*  
 -. Leaves imbricate to rather distant, commonly exposing at least parts of stem; stem green to orange or reddish, less often brownish; decurrent leaf bases short to long, but not very narrow when long; variable species 21 (*pseudotriquetrum*)
21. Dioicous; mid-leaf cells typically averaging (16)20-24  $\mu\text{m}$  wide *pseudotriquetrum* var. *pseudotriquetrum*  
 -. Synoicous; mid-leaf cells typically averaging 12-16  $\mu\text{m}$  wide *pseudotriquetrum* var. *bimum*

22. Leaves of dried plants showing strong spiral imbrication (like thread of cork-screw); leaves widest at or above middle; leaf margin bordered; costa usually excurrent in long, slender awn; dioicous *capillare*
- . Leaves of dried plants showing little or no spiral imbrication; leaves widest at or above middle or nearer base; leaf margin bordered or not; costa excurrent in awn, percurrent or evanescent; dioicous, autoicous or synoicous 23
23. Apex of larger upper leaves rounded to broadly obtuse; costa usually evanescent to percurrent 24
- . Apex of larger upper leaves acuminate, acute, shortly acute or subacute; costa evanescent, percurrent, or excurrent as short or long awn 31
24. Leaves with red basal cells; leaves usually concave, cucullate, bordered with narrow cells, often rather distant; dioicous 'neodamense' phenotype of *pseudotriquetrum*
- . Leaves with basal cells not differing in colour from rest of leaf; leaves concave or not, cucullate or not, bordered or not, distant to imbricate; dioicous or autoicous 25
25. Leaves obovate to orbicular, plane, ± distant; costa weak, evanescent; plants green without red, pink or brown pigments; dioicous *cyclophyllum*  
(forms of other species such as *B. gemmiparum*, *B. alpinum* and *B. pseudotriquetrum* that have grown submerged may closely resemble the morphology of *B. cyclophyllum*, so great care is needed; filiform axillary gemmae are frequently developed by *B. cyclophyllum*, occasional in *B. pseudotriquetrum*, absent in *B. gemmiparum* and *B. alpinum*)
- . Leaves ± ovate, concave, crowded to rather distant; costa weak to strong; plants green or with red, pink or brown pigments; dioicous or autoicous 26
26. Leaf base decurrent; leaves ovate to rounded-ovate, bordered with narrow cells; growing as deep, swelling, often red tufts in wet places in the Arctic and in subarctic mountains; dioicous *cryophilum*
- . Leaf base not or only shortly decurrent; leaves ovate-lanceolate, ovate, rounded-ovate, obovate or oblong-ovate; rather weakly bordered or unbordered; not usually growing as deep, swelling tufts; wide-ranging species, some of them coastal; dioicous or autoicous 27
27. Dry leaves erect, ± imbricate and not shrunken; costa strong in lower part of leaf; leaves unbordered; dioicous 28
- . Dry leaves erect or not, not imbricate, ± shrunken; costa weak to moderately developed in lower part of leaf; leaves unbordered or weakly bordered; dioicous or autoicous 29
28. Mid-leaf cells broader (mainly 18-20 μm wide); leaf apex obtuse or blunt; leaves narrower, less concave, with relatively broad base; widespread montane plant *muehlenbeckii*  
(forms of *B. alpinum* that have grown submerged may closely resemble this sp.)
- . Mid-leaf cells narrower (ca 14 μm wide); leaf apex rounded to obtuse; leaves broader, more concave, with relatively narrow base; known in our region only from Faeroes *miniatum*

29. Largest leaves up to 1.6 mm long; mid-leaf cells 10-20  $\mu\text{m}$  wide; leaves unbordered or at most with few rows of narrower marginal cells forming weakly defined border; axillary bulbils commonly present; dioicous *dichotomum*  
 -. Largest leaves (1.0) 1.5-3.0 mm long; mid-leaf cells (12)14-30  $\mu\text{m}$  wide; leaves unbordered or narrowly bordered; axillary bulbils absent; autoicous 30
30. Upper leaves longer and relatively narrower (normally with length: breadth >2: 1); plants green, lacking any red or pink coloration except in inflorescences; larger leaves with blunt to broadly rounded apex; leaf border of narrow cells not or little developed; leaf margin not recurved below; costa extending less close to leaf apex *marratii*  
 -. Upper leaves shorter and relatively wider (normally with length: breadth <2: 1); plants often strongly tinged olive, tan, reddish or pinkish; leaves with acute to blunt apex; leaf border of narrow cells usually  $\pm$  developed; leaf margin often recurved below; costa extending nearer to leaf apex *calophyllum*  
 (non-fertile plants < 5 mm tall of *B. calophyllum* and *B. marratii* cannot be separated reliably from morphological characters, although they sometimes differ in colour)
31. Larger rhizoids purple 32  
 -. Larger rhizoids brown, yellowish, reddish, or purplish-brown 33
32. Largest rhizoids strongly papillose (diagnostic large tubers usually present) *rudemale*  
 -. Largest rhizoids smooth or only faintly papillose (diagnostic small tubers usually present) *violaceum*
33. Leaves widest at or above middle; leaf arrangement rosulate 34  
 -. Leaves widest below middle; leaf arrangement rosulate or equidistant 40
34. Leaves with well defined border of narrow cells; not or weakly toothed near apex 35  
 -. Leaves lacking well defined border of narrow cells; unbordered and often strongly toothed near apex *canariense*
35. Costa excurrent in short stout mucro; border 2-3 stratose in well developed leaves, extending to apex and confluent with mucro; plants usually lacking pink or red colouring *donianum*  
 -. Costa excurrent in short point or short to long awn; leaf border 1-2 stratose (if 2-stratose, plants often with stem and leaves pink or red  $\pm$  throughout) 36
36. Leaves widest around middle; leaf border often at least partly 2-stratose; plants with older parts of stem and mature leaves green, pink or red  $\pm$  throughout; costa  $\pm$  shortly excurrent; dioicous *pallens*  
 -. Leaves widest at or above middle; leaf border 1-stratose; plants with older parts of stems usually green, sometimes red; leaves seldom pink throughout; costa shortly excurrent or forming longer awn; dioicous, autoicous or synoicous 37



37. Larger plants, 10-30(50) mm tall; mid-leaf cells (12) 16-25  $\mu\text{m}$  wide; larger leaves usually widest well above middle; often growing in  $\pm$  dense tufts or cushions, on rock, bark or soil 38  
 -. Smaller plants, 5-16 mm tall; mid-leaf cells 16-20  $\mu\text{m}$  wide; larger leaves usually widest around middle; often growing as scattered plants or loose tufts, usually on soil 39
38. Dioicous; dry plants commonly with leaves spirally imbricate; tubers may provide additional characters probably *capillare*  
 Usually synoicous (infrequently dioicous or autoicous); dry plants with leaves not or slightly spirally imbricate; tubers may provide additional characters probably *torquescens*
39. Costa 65-100  $\mu\text{m}$  wide at leaf base; cell walls in leaf border thicker (2-3  $\mu\text{m}$ ); dioicous, or sometimes autoicous or synoicous; diagnostic tubers usually present in mature plants probably *bornholmense*  
 -. Costa 45-75  $\mu\text{m}$  wide at leaf base; cell walls in leaf border thinner (1-2  $\mu\text{m}$ ); dioicous; diagnostic tubers usually present in mature plants probably *rubens*
40. Leaf lamina with large lax cells (89-155  $\times$  20-31  $\mu\text{m}$  in larger leaves); leaf often bordered with several rows of long narrow cells; costa weak, usually ending just below or in the leaf apex; Mediterranean basin and Canary Is. *cellulare*  
 -. This combination of characters lacking 41
41. Small tufted moss; well developed lower leaves lanceolate to oblong-lanceolate; costa excurrent in long untoothed brown awn; mid-leaf cells moderately long (80-120  $\times$  9-15  $\mu\text{m}$ ); leaf border of narrow elongate cells; in our region known only in Caucasus *caucasicum*  
 -. This combination of characters lacking 42
42. Small tufted moss; leaves ovate-lanceolate to ovate-oblong (1.0) 1.1-1.8 (2.2)  $\times$  (0.35) 0.4-0.7 mm, sometimes brownish at base (not red); mid-leaf cells long-rhomboidal, (48) 52-71 (80)  $\times$  9-12.5 (13.5)  $\mu\text{m}$ ; marginal cells longer and narrower, with thick walls, forming broad but ill-defined border around mid-leaf; costa strong throughout, (55) 65-97  $\mu\text{m}$  wide at leaf base, shortly excurrent, in strong sharp mucro(45) 50-100 (130)  $\mu\text{m}$  long; Macaronesia only *notarisii*  
 -. This combination of characters lacking 43
43. Leaf arrangement equidistant 44  
 -. Leaf arrangement  $\pm$  rosulate 53
44. Base of leaf lamina red, differing in colour from rest of leaf; stem red or reddish; costa shortly excurrent 45  
 -. Base of leaf lamina not red (or whole leaf red and base not differing in colour); stem green, pink, red or brown; costa evanescent to shortly excurrent 47
45. Leaves with well defined border of narrow cells; upper leaves up to 2.0-3.0  $\times$  1.2 mm 46  
 -. Leaves with border of narrow cells weakly developed or absent; leaves 1.2-1.8  $\times$  0.4-0.8 mm (mean *ca* 1.5  $\times$  0.6 mm) *mildeanum*  
 (a species with few distinctive characters that is frequently misidentified; at least

one other unrecognised taxon from Austrian Alps has very similar morphology: H. Köckinger in prep.)

46. Mid-leaf cells usually 12-24  $\mu\text{m}$  wide; some leaf bases usually decurrent; microphyllous branches normally absent; larger rhizoids warty papillose; widespread species probably *pseudotriquetrum*  
(var. *pseudotriquetrum* is dioicous; var. *bimum* is synoicous)
- Mid-leaf cells 5.5-11  $\mu\text{m}$  wide; decurrent leaf bases lacking; microphyllous branches usually present on upper part of stem; larger rhizoids roughly papillose; known only from Austrian Alps *reyeri*  
(a rare species with stems 30-120 mm high, characteristic of spray-zones near waterfalls; see note under 45 above for smaller plants occurring among drier rocks in Austrian Alps)
47. Leaves with  $\pm$  well marked border of long narrow cells (often a bistratose border); whole plant often pink or red; mid-leaf cells rather broad (15-30  $\mu\text{m}$ ) and lax; stems similar in colour to leaves 48
- Leaves not or only weakly bordered; whole plant not pink or red; mid-leaf cells narrow to rather broad, not lax; stems green or brown to blackish below 50
48. Mainly in arctic; leaves few, ovate to broadly ovate (0.7-1.3  $\times$  0.3-0.6 mm), concave, shortly acuminate; perichaetial bracts similar but larger (up to 2.2  $\times$  1.3 mm); the bracts with well defined border which often partly bistratose, strong reddish-brown costa, mid-leaf cells 59.5-82.5  $\times$  19-24  $\mu\text{m}$ ; synoicous, capsules common *wrightii*
- This combination of characters lacking 49
49. Leaf margin recurved (except in very small plants); leaf border usually partly 2-stratose (except in very small plants) probably *pallens*
- Leaf margin plane; leaf border 1-2 stratose perhaps *turbinatum*
50. Leaves only shortly acute; leaves often concave; costa stout ( $>80$   $\mu\text{m}$  wide at leaf base) probably *gemmaiparum*  
(bulbils needed for reliable identification)
- Leaves acute; leaves concave to plane; costa narrower 51
51. Small plants (up to *ca* 10 mm tall); leaf margins plane; leaves imbricate when dry, erecto-patent when moist, concave, often brown or sometimes reddish at base, ovate and acute to ovate-lanceolate and acuminate; margin obscurely denticulate above; costa relatively thin, ending below apex to shortly excurrent; basal cells rectangular; cells in mid-leaf rhomboid-hexagonal, 10-16  $\mu\text{m}$  wide; 2-3 marginal rows of cells narrower but not forming border; Scotland only? *dixonii*
- Above combination of characters lacking 52
52. Plants reddish-brown or brown throughout, less often green or greenish; leaves lanceolate, weakly chlorophyllose, unbordered; margins plane or slightly recurved; dioicous alpine species, occurring at low altitudes only in Arctic perhaps *demissum*
- Above combination of characters lacking probably unidentifiable  
(renewed search for tubers or axillary bulbils may allow identification, as might collections at a different season if mature capsules are found)

53. Leaf base lacking band of red cells differing in colour from those of most of lamina (whole leaf sometimes pink or red) 54  
 -. Leaf base with band of red cells differing in colour from those of most of lamina (whole leaf sometimes red or reddish) 60
54. Leaf lacking well defined border of long narrow cells probably unidentifiable (includes *radiculosum*, *sauteri*, *subapiculatum*, etc.)  
 -. Leaf with well defined border of long narrow cells 55
55. Dry plants with slight spiral twisting of leaves at shoot tips; costa usually percurrent or shortly excurrent; dioicous; known only in Portugal, Spain, S. France and Sardinia *minii*  
 -. Dry plants without slight spiral twisting of leaves at shoot tips; costa usually shortly excurrent; synoicous, autoicous or dioicous; some species widespread 56
56. Dioicous species 57  
 -. Autoicous or synoicous species 58
57. Leaf margin recurved (except in very small plants); leaf border usually partly 2-stratose (except in very small plants) probably *pallens*  
 -. Leaf margin plane; leaf border 1-2 stratose perhaps *turbinatum*
58. Synoicous plants 59  
 -. Autoicous plants *uliginosum* or *warneum*
59. Leaf border often partly 2-stratose; plants often red or reddish throughout, sometimes green; in alpine or subalpine zone of mountains, only locally on coasts (of Baltic); species normally synoicous *arcticum*  
 -. Leaf border 1-stratose; plants not red or reddish; mainly coastal, less often by inland lakes or rivers, not alpine; species usually autoicous *warneum*
60. Leaf with well defined border of long narrow cells; synoicous, autoicous or dioicous 61  
 -. Leaf lacking well defined border of long narrow cells; dioicous 66
61. Synoicous plants 62  
 -. Autoicous plants 64  
 (probably *compactum* var. *compactum*, *creberrimum* or *pallescens*)
62. Costa percurrent or only very shortly excurrent; leaf border rather weakly defined perhaps *knowltonii*  
 (some arctic plants of *intermedium* share these characters but may have more strongly recurved leaf margins)  
 -. Costa shortly excurrent; leaf border well defined or weakly defined 63
63. Leaf margin revolute from base to near apex perhaps *intermedium*  
 -. Leaf margin  $\pm$  strongly recurved but not strongly revolute probably one of following: *algovicum* var. *algovicum*, *archangelicum*, *salinum*, some *pallescens*, *longisetum*: taxa usually inseparable without characters of mature capsules and spores

64. From mountains of C. Europe probably *algovicum* var. *algovicum*, *creberrimum* or *pallescens* (reliable identification requires characters of mature capsules and spores)  
-. From elsewhere in Europe or Macaronesia 65

65. Leaves rather broadly ovate perhaps *pallescens*  
(reliable identification requires characters of mature capsules and spores)

-. Leaves narrowly ovate to ovate-lanceolate *creberrimum* & some *pallescens*  
(reliable identification requires characters of mature capsules and spores; only *pallescens* appears to commonly grow on substrata rich in heavy metals)

66. Plants ± densely tufted; leaf margin recurved; costa excurrent in short to rather long awn probably *caespiticium*

-. Plants usually not densely tufted; leaf margin plane or slightly recurved; costa percurrent to excurrent in short awn probably unidentifiable  
(renewed search for tubers or axillary bulbils may allow identification, as might collections at a different season if mature capsules are found).

### (C) MULTIPLE-ACCESS KEY (MAINLY TO PLANTS WITH MATURE CAPSULES)

This key is mainly intended for use with fertile plants having mature capsules, since characters of the peristome and spores are used in addition to gametophytic characters. The first section lists single letter codes for each character state; the second section tabulates the character states for each species in alphabetical order of their code letters.

#### CHARACTERS

Sexuality – synoicous **A**, autoicous **B**, dioicous **C**;

Exostome – oblique cross-bars on inner surface linking transverse lamellae, present **D**, absent **E**;

Endostome cilia – lacking or rudimentary **F**, short **G**, long, appendiculate or nodulose **H**;

Spores with mean size – <16  $\mu\text{m}$  **I**, 16-20  $\mu\text{m}$  **J**, 21-30  $\mu\text{m}$  **K**, >30  $\mu\text{m}$  **L**; spores persistently adhering in tetrads marked\*;

Leaves – red at base (contrasting with colour of remainder of lamina) **M**, lacking red at base **N**;

Leaf apex – obtuse or rounded **O**, acute to acuminate **P**;

Costa of upper leaves – long excurrent (>200  $\mu\text{m}$ ) **Q**, shortly excurrent (<200  $\mu\text{m}$ ) **R**, percurrent or evanescent **S**;

Leaf-border – weak or absent **T**, well-developed, unistratose **U**, well-developed, 2-4 stratose **V**;

Leaf-shape – widest below middle **W**; widest at or just above mid-leaf **X**;

Leaf arrangement (excluding gametoecea) –  $\pm$  equidistant **Y**, rosulate **Z**.

#### MULTIPLE-ACCESS KEY

- = no data (capsules unknown); ? = character needs checking. [ ] = less common or rare character state. Where two or three character states occur both or all three are listed. See below for numbered notes. The poorly-known taxa '*geheebii*', '*pamirensis*', '*paradoxum*', '*savicziae*', '*vermigerum*' are excluded.

<i>algovicum s. str.</i>	C	D	FG	KL	M	P	R	U	W	Z
var. <i>rutheanum</i>	A	D	FG	KL	M	P	R	U	W	Z
<i>alpinum</i>	C	E	H	I	N	OP	S	T	W	Y
<i>apiculatum</i>	A	E	H	I	MN	P	R	T	WX	Y
<i>archangelicum</i>	A	E	FG	JKL	M	P	QR	TU	W	Z
<i>arcticum</i>	A	D	F	KL	N	P	RS	UV	X	Z
<i>argenteum</i>	C	E	H	I	N	P	QRS	T	X	Y
<i>austriacum</i>	C	-	-	-	N	P	Q	U	X	Y
<i>bavaricum</i>	C	-	-	-	N	P	QR	T	W	Y
<i>blindii</i>	C	E	H	I	M	O	S	T	W	YZ

<i>bornholmense</i>	ABC	E	H	I	N	P	QR	U	WX	Y?
<i>caespiticium</i>	C	E	H	IJ	MN	P	Q	T	W	Z
<i>calophyllum</i>	B	E	FG	KL	N	OP	RS	TUV	WX	Y
<i>canariense</i>	AB	E	H	I	M	P	QR	T	X	Z
<i>capillare</i>	C	E	H	I	M	P	Q	U	X	Z
<i>caucasicum</i>	C?	E	F	J	N	P	Q	U	W	Y
<i>cellulare</i>	C	E	F	IJK	N	P	RS	TU	WX	Y
<i>concinatum</i>	C	E	F	IJ	N	P	S	T	W	Y
<i>creberrimum</i>	A	E	H	I	M	P	R	U	W	YZ?
<i>cryophilum</i>	C	E	H	J	N	O	S	UV	WX	Y
<i>cyclophyllum</i>	C	E	H	I	N	O	S	T	X	Y
<i>demaretianum</i>	C	-	-	-	N	P	R	T	WX	YZ
<i>demissum</i>	C	E	F	L*	N	P	R	T	W	Y
<i>dichotomum</i>	C	E	H	I	N	OP	QRS	T	WX	Y
<i>dixonii</i>	?	-	-	-	M	P	RS	T	W	Y?
<i>donianum</i>	C	E	H	I	M	P	R	V	X	Z
<i>dyffrynense</i>	C	E	H	I	N	P	S	T	W	Y
<i>elegans</i>	C	E	H	I	M	P	RQ	TU	X	Z
<i>funkii</i>	C	E	H	J	M	P	R	T	WX	Z
<i>gemmiferum</i>	C	E	H	I	N	P	RS	T	W	Y
<i>gemmilucens</i>	C	-	-	-	N	P	S	T	W	Y
<i>gemmiparum</i>	C	E	H	I	N	P	S	T	W/X	Y
<i>intermedium</i>	AC	E	H	JK	M	P	QRS	TU	W	Z
<i>julaceum</i>	C	E	H	IJ	N	O	S	T	W	Y
<i>kikuyense</i>	C	D	F	I	N	P	QR	TU	W	Y
<i>klinggraeffii</i>	C	E	H	I	MN	P	RS	T	W	YZ
<i>knowltonii</i>	A	E	F	K	M	P	S	U	W	Z
<i>kunzei</i>	C	E	H	I	M	P	RQ	T	WX	Z
<i>longisetum</i>	A	E	FG	L	M	P	QR	U	W	YZ
<i>lusitanicum</i>	C	E	F	I	N	OP	RS	T	WX	Y
<i>marratii</i>	B	E	F	K	N	O	S	T	X	Y
<i>mildeanum</i>	C	E	H	I	M	P	R	T	W	Y
<i>miniatum</i> (1)	C	E	H	IJ	N	O	S	T	W	Y
<i>minii</i>	C	E	H	I	N	OP	RS	U	W	Z
<i>moravicum</i>	C	E	H	I	M	P	QRS	U	X	YZ?
<i>muehlenbeckii</i>	C	E	GH	IJ	N	OP	S	T	W	Y
<i>notarisii</i>	C	E	F	IJ	N	P	R	T	W	Y
<i>oblongum</i>	C	E	H	J	N?	OP	S	T	WX	Z?
<i>ontariense</i>	C	E	H	JK	N	P	RS	T	X	Z
<i>pallens</i>	C	E	FH	JK	N	P	RS	UV	X	YZ
<i>pallescens</i>	AB	E	GH	J	M	P	R	U	W	YZ
<i>pseudotriquetrum s. str.</i>	C	E	H	IJ	M	OP	RS	U	WX	Y
<i>var. bimum</i>	A	E	H	IJ	M	P	RS	U	WX	Y
<i>radiculosum</i>	C	E	H	I	N	P	QR	T	W	Y?
<i>reyeri</i>	C	-	-	-	M	P	RS	U	W	Y
<i>riparium</i>	C	-	-	-	M	P	R	TU	W	Y
<i>roseum</i>	C	E	H	JK	N	P	RS	T	X	Z
<i>rubens</i>	C	E	H	I	N	P	QR	U	WX	Y?
<i>ruderae</i>	C	E	H	I	N	P	R	T	W	Y?
<i>salinum</i>	AB	E	F	JK	M	P	R	U	W	Z
<i>sauteri</i>	ABC	E	GH	IJ	N	P[O]	R	T	W	Y
<i>schleicheri</i>	C	E	H	JK	N	P	RS	U	W?	Y
<i>subapiculatum</i>	C	E	H	I	N	P	R	T	W	Y
<i>tenuisetum</i>	AC	E	H	I	N	P	R	T	W	Y
<i>torquescens</i>	A[BC]	E	H	I	M	P	Q	U	X	YZ
<i>turbinatum</i>	C	E	H	J	N	P	R	UV	W	Y
<i>uliginosum</i>	B	E	G	K	N	P	RS	V	X	Y
<i>valparaisense</i> (2)	C	E	F	JK	N	P	RS	T	WX	Y
<i>violaceum</i>	C	E	H	I	N	P	R	T	W	Y
<i>warneum</i>	[A]B	DE	F	L	N	P	R	UV	WX	Y

<i>weigeli</i>	C	E	H	I	N	P	RS	U	X?	Y
<i>wrightii</i>	A	E	F	J	N	P	RS	UV	W	Y
<i>zieri</i>	C	E	F	L	N	OP	S	T	WX	Y

Notes: (1) Sporophytes unknown in Europe; characters of sporophytes based on N. American material;

(2) sporophytes unknown in Europe; their characters based on specimen from Chile.

D.T. Holyoak,  
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