BRYOATT

Attributes of British and Irish Mosses, Liverworts and Hornworts

With Information on Native Status, Size, Life Form, Life History, Geography and Habitat

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NERC Centre for Ecology and Hydrology
and Countryside Council for Wales

2007

Designed by Paul Westley, Norwich

Printed by The Saxon Print Group, Norwich

ISBN 978-1-85531-236-4

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Cover photograph: Bryophyte-dominated vegetation by a late-lying snow patch at Garbh Uisge Beag, Ben Macdui, July 2007 (courtesy of Gordon Rothero).

Published by Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE28 2LS.

Copies can be ordered by writing to the above address until Spring 2008; thereafter consult www.ceh.ac.uk

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Introduction

In recent years the availability in electronic form of 'attribute data' for all British vascular plant species has greatly enhanced our ability to interpret distribution patterns, and in particular to interpret changes in those patterns in response to environmental pressures. Whereas in the past plants tended to be grouped simply by broad habitat, such as woodland or calcareous grassland, they can now usefully be grouped by attributes that indicate additional features such as the life-form of species, their pH preferences and their shade-tolerance. Attributes thus allow many of the individual factors which together comprise the autecology of a species to be identified, and then allow species sharing particular traits to be grouped together even though they may grow in very different broad habitats. Thus a number of recent studies have shown a marked tendency for species characteristic of nutrient-rich places to have been more successful than those that grow in nutrient-poor habitats, and this is true over a range of broad habitats, time periods and spatial scales (e.g. Braithwaite *et al.*, 2006; Haines-Young *et al*., 2000; Walker & Preston, 2006).

This compilation is a sequel to *PLANTATT* (Hill, Preston & Roy, 2004), presenting for bryophytes similar attribute information to that which we presented for vascular plants. Just as for *PLANTATT*, we have assembled the information over a period of years, either for our own use or for particular projects. However, previously compiled information for bryophytes is much less plentiful than for vascular plants. Dierssen (2001) and Düll (1991) present data on the habitats and indicator values of European bryophytes. Neither of these is ideal for British users. Dierssen's comprehensive compilation is not available in database form and uses a rather complex typology of vegetation types and units of geographical range. Düll's indicator values do not agree well with experience in Britain and lack values for nitrogen. There was therefore a need for a similar compilation to *PLANTATT*.

The dataset presented here as *BRYOATT* is mainly new (Table 1). We have incorporated taxonomic information and data on geographical elements from existing sources. Ellenberg values were drawn from an existing set of values calculated for an unpublished report (Hill, Roy & Preston, 2005). Other data have been compiled from research papers, books and personal communications, or calculated from existing datasets. In a few cases they have simply been added from personal experience.

The BRYOATT dataset is published as a book, which may be downloaded as a pdf file from the Biological Records Centre website (http://www.brc.ac.uk). The spreadsheet of data (which includes some columns which are not published in the printed document) may also be downloaded from the BRC website, and we will update this spreadsheet from time to time with additions and corrections to the data published here.

Table 1
Attributes, codes and names listed as columns in BRYOATT.

Column name	Abbreviation	Source or other comment
(a) Taxonomic & status		
Taxon name		Name, mostly as in Blockeel & Long (1998)
Moss, liverwort or hornwort	ML	M moss, L liverwort, H hornwort
Order	Ord	Order; mosses from Goffinet & Buck (2004), liverworts from Forrest *et al.* (2006)
Native status	Stat	Our own opinion, using criteria from Crundwell (1985)
(b) Size and life history		
Length	Len	Length of shoot or thallus (or diameter of rosette)
Perennation	Per	Perennation (annual or perennial)
Life form	LF1, LF2	Life form; categories modified for BRYOATT
Tubers	Tub	Frequency of tubers, either on rhizoids (mosses) or thallus (liverworts)
Gemmae	Gem	Gemma frequency on leafy plant or thallus, not on protonema
Bulbils	Bul	Bulbil frequency
Deciduous branchlets	Bra	Deciduous branchlet frequency
Deciduous leaves	Lvs	Deciduous leaf frequency
Sex organs	Sex	Sexuality, whether monoecious or dioecious
Fruit	Fr	Occurrence and frequency of sporophytes
Spore size	Sp1, Sp2	Spore size minimum and maximum
(c) Geography		
Presence in parts of British Isles	E, W, Sc, IR, NI, CI	From Blockeel & Long (1998) and additional vice-county records up to 2006
Element	Elem	Element, from Hill & Preston (1998)
GB hectad number	GBno	Number of 10-km squares in GB + Man 1950 onwards
Irish hectad number	IRno	Number of 10-km squares in Ireland 1950 onwards
CI hectad number	CIno	Number of 10-km squares in Channel Islands 1950 onwards
January mean temperature	TJan	Mean January temperature of hectads where found
July mean temperature	TJul	Mean July temperature of hectads where found
Annual precipitation	Prec	Mean precipitation (mm) of hectads where found
Maximum altitude	Alt	Max altitude (m) in Britain and Ireland
(d) Habitat		
Ellenberg indicator value	L, F, R, N, S, HM	Compiled for an unpublished report (Hill *et al.*, 2005)
Substrate	14 categories	Compiled for BRYOATT; see Table 18
EUNIS habitat	32 categories	Compiled for BRYOATT; see Table 19

Taxonomy and native status

Species and orders

In the main tabulation, codes H, L and M are used to denote hornworts, liverworts and mosses respectively. The list of 1057 species comprises 4 hornworts, 297 liverworts and 756 mosses (Table 2). In addition, we include data on 36 species aggregates (mostly species *sensu lato*), 13 subspecies and 85 varieties. The orders are those recognized by Forrest *et al.* (2006) for liverworts and Goffinet & Buck (2004) for mosses. The largest orders are Hypnales and Jungermanniales each with about 200 members. At the other extreme, three liverwort orders, namely Blasiales, Haplomitriales and Pleuroziales and three moss orders, Archidiales, Diphysciales and Oedipodiales, have each only a single member in the British and indeed in the European flora.

Taxonomy and nomenclature

Our taxonomy and nomenclature follow the British Bryological Society's *Census Catalogue*, published as a book by Blockeel & Long (1998) and recently updated on the internet (Blackstock, Rothero & Hill, 2005). We depart from this nomenclature by retaining *Grimmia sessitana* for the plant listed as *G. ungeri* in the updated *Census Catalogue* and adopting the name *Bryum moravicum* for the plant referred to there as *B. laevifilum*. We have added eight taxa recently identified in Britain, *Anastrophyllum alpinum*, *Bryum valparaisense*, *Conocephalum salebrosum*, *Ephemerum hibernicum*, *Hypnum cupressiforme* var. *heseleri*, *Lophocolea brookwoodiana*, *Thamnobryum maderense* and *Tortella bambergeri*, and have deleted *Brachythecium appleyardiae*, *Didymodon mamillosus*, *Fissidens exiguus* and *Pictus scoticus*, which are no longer thought to be good taxa. We have treated the segregates of *Barbula convoluta* as var. *convoluta* and var. *sardoa*. Within *Seligeria trifaria* s.l. we have provided data (albeit very incomplete data) for just one of the two segregates, *S. patula*; data for *S. trifaria* s.str. are lacking. We have not included a separate treatment for the varieties of *Amblystegium serpens*, *Bryum capillare*, *Campylopus pyriformis*, *Ditrichum zonatum*, *Hygrohypnum luridum*, *Hypnum lacunosum*, *Orthotrichum cupulatum*, *Pterigynandrum filiforme*, *Tortella flavovirens*, *Tortula muralis* and *Trichostomum tenuirostre*, all of which are recognized by the updated *Census Catalogue*, and we have also excluded *Campylopus atrovirens* var. *gracilis*, *Ctenidium molluscum* var. *fastigiatum*, *Ephemerum serratum* var. *praecox*, *Fontinalis antipyretica* var. *cymbifolia* and var. *gigantea*, *Palustriella commutata* var. *sulcata*, *Polytrichum commune* var. *humile* and *Tortula subulata* var. *subinermis.*

Thirty-six species aggregates are included (Table 3) because data such as counts of grid squares may be unavailable or very incomplete for the segregates, so that sometimes aggregates have to be included in numerical analyses.

Table 2
Bryophyte orders and main groups. Counts are of the number of taxa in each group.

Code	Groups and orders	Species	Infraspecific	Aggregates
H	**Hornworts**	**4**	**0**	**1**
Anth	Anthocerotales	4		1
L	**Liverworts**	**297**	**12**	**8**
Blas	Blasiales	1		
Foss	Fossombroniales	14		1
Hapl	Haplomitriales	1		
Jung	Jungermanniales	202	7	5
Lepi	Lepicoleales	4		
Marc	Marchantiales	9	3	1
Metz	Metzgeriales	16		1
Pleu	Pleuroziales	1		
Pore	Porellales	27	2	
Radu	Radulales	6		
Ricc	Ricciales	14		
Sphae	Sphaerocarpales	2		
M	**Mosses**	**756**	**86**	**27**
Andr	Andreaeales	10	4	
Arch	Archidiales	1		
Brya	Bryales	118	11	2
Buxb	Buxbaumiales	2		
Dicr	Dicranales	109	4	6
Diph	Diphysciales	1		
Enca	Encalyptales	6		
Funa	Funariales	11		
Grim	Grimmiales	74	4	5
Hedw	Hedwigiales	3	2	1
Hook	Hookeriales	5		
Hypn	Hypnales	189	26	4
Oedi	Oedipodiales	1		
Orth	Orthotrichales	31	4	1
Poly	Polytrichales	16	4	
Pott	Pottiales	123	21	4
Rhiz	Rhizogoniales	2		
Sphag	Sphagnales	35	6	4
Spla	Splachnales	13		
Tetr	Tetraphidales	3		
Timm	Timmiales	3		
	Byophyte total	**1057**	**98**	**36**

Table 3
Composition of aggregate species in *BRYOATT*; the abbreviation s.l. is short for the Latin *sensu lato* ('in the broad sense').

Group	Aggregate	Component segregates
H	*Phaeoceros laevis* s.l.	*P. laevis*, *P. carolinianus*
L	*Anastrophyllum joergensenii* s.l.	*A. alpinum*, *A. joergensenii*
L	*Calypogeia neesiana* s.l.	*C. integristipula*, *C. neesiana*
L	*Chiloscyphus polyanthos* s.l.	*C. pallescens*, *C. polyanthos*
L	*Conocephalum conicum* s.l.	*C. conicum*, *C. salebrosum*
L	*Fossombronia pusilla* s.l.	*F. maritima*, *F. pusilla*
L	*Metzgeria fruticulosa* s.l.	*M. fruticulosa*, *M. temperata*
L	*Plagiochila asplenioides* s.l.	*P. asplenioides*, *P. britannica*, *P. porelloides*
L	*Plagiochila spinulosa* s.l.	*P. killarniensis*, *P. spinulosa*
M	*Aloina aloides* s.l.	*A. aloides*, *A. ambigua*
M	*Bryum caespiticium* s.l.	*B. caespiticium*, *B. kunzei*
M	*Bryum dichotomum* s.l.	*B. dichotomum* (including *B. dunense*), *B. dyffrynense*, *B gemmiferum*, *B. gemmilucens*
M	*Ceratodon purpureus* s.l.	*C. conicus*, *C. purpureus*
M	*Cratoneuron filicinum* s.l.	*C. filicinum*, *Callialaria curvicaulis*
M	*Dichodontium pellucidum* s.l.	*D. flavescens*, *D. pellucidum*
M	*Dicranum fuscescens* s.l.	*D. flexicaule*, *D. fuscescens*
M	*Ditrichum flexicaule* s.l.	*D. flexicaule*, *D. gracile*
M	*Drepanocladus revolvens* s.l.	*D. cossonii*, *D. revolvens*
M	*Fissidens pusillus* s.l.	*F. gracilifolius*, *F. pusillus*
M	*Fissidens viridulus* s.l.	*F. gracilifolius*, *F. limbatus*, *F. pusillus*, *F. viridulus*
M	*Grimmia donniana* s.l.	*G. arenaria*, *G. donniana*
M	*Hedwigia ciliata* s.l.	*H. ciliata*, *H. stellata*
M	*Hymenostylium recurvirostrum* s.l.	*H. insigne*, *H. recurvirostrum*
M	*Microbryum starckeanum* s.l.	*M. davallianum*, *M. starckeanum*
M	*Pseudoleskeella catenulata* s.l.	*P. rupestris*, *P. catenulata*
M	*Racomitrium canescens* s.l.	*R. canescens*, *R. elongatum*, *R. ericoides*
M	*Rhynchostegiella tenella* s.l.	*R. litorea*, *R. tenella*
M	*Schistidium apocarpum* s.l.	*S. apocarpum*, *S. atrofuscum*, *S. confertum*, *S. crassipilum*, *S. dupretii*, *S. elegantulum*, *S. flaccidum*, *S. frigidum*, *S. papillosum*, *S. pruinosum*, *S. robustum*, *S. strictum*, *S. trichodon*
M	*Schistidium rivulare* s.l.	*S. platyphyllum*, *S. rivulare*
M	*Seligeria trifaria* s.l.	*S. patula, S. trifaria*
M	*Sphagnum denticulatum* s.l.	*S. denticulatum*, *S. inundatum*
M	*Sphagnum imbricatum* s.l.	*S. affine*, *S. austinii*
M	*Sphagnum recurvum* s.l.	*S. angustifolium*, *S. fallax*, *S. flexuosum*
M	*Sphagnum subsecundum* s.l.	*S. denticulatum*, *S. inundatum*, *S. subsecundum*
M	*Syntrichia ruralis* s.l.	*S. ruraliformis*, *S. ruralis*
M	*Ulota crispa* s.l.	*U. bruchii*, *U. crispa*

Native/alien status

Species of uncertain status are classified as 'Native or alien'. Introduced species have been classified as archaeophytes or neophytes (Preston, Pearman & Hall, 2004). Both archaeophytes and neophytes are introduced species which are present in the wild as naturalized populations, that is they are spreading vegetatively or reproducing effectively by spores. An archaeophyte is a plant that became naturalized before AD 1500. A neophyte is one that became naturalized after that time.

Compared with vascular plants, among which introduced species are much more numerous than native species, the number of alien bryophytes is very low (Table 4). Only the two *Sphaerocarpos* species have been indicated as archaeophytes. This is because they seem to have been present in Britain for a long time, but can hardly have existed before agriculture opened up suitable habitat. Other archaeophytes will, in the absence of any evidence, either be classified as 'Native or alien', or, if there is currently no evidence that they are introductions, simply as 'Native'.

Table 4
Bryophyte native status in main groups; values are the number of species in each group, excluding varieties and subspecies.

Code	Explanation	Hornworts	Liverworts	Mosses	Total
AN	Alien neophyte		8	13	21
AR	Archaeophyte		2		2
N	Native	2	283	724	1009
NA	Native or alien	2	4	19	25
Total		**4**	**297**	**756**	**1057**

Size and life history attributes

Length

Every bryophyte taxon has a length measurement, which is to some extent an indication of size. Typically, the length is the height of the leafy shoot in acrocarpous mosses or the length of the shoot or thallus in pleurocarpous mosses and liverworts. For liverworts with roughly circular thalli, such as *Sphaerocarpos* spp., *Petalophyllum ralfsii* and some *Riccia* spp., the 'length' is in reality a diameter. For mosses that lack a stem, such as *Acaulon* spp. and *Ephemerum* spp., the length refers to the height of the plant when viewed from the side, including the leaves. (A similar problem arises with many ferns, the plant height in *PLANTATT* being deemed to be roughly equal to leaf length.) With *Buxbaumia*, it was not really possible to measure the length of the leafy shoot, and, for that genus only, the length refers to the length of the capsule. In *Tetrodontium brownianum*, the length refers to the length of the protonemal flaps, which normally overtop the perichaetial leaves.

The great majority of lengths were derived from floras, especially the standard floras by Paton (1999) and Smith (2004). Paton (1999) provides measurements for almost all liverworts, but Smith (2004) sometimes omits lengths, especially for the pleurocarpous species. Where measurements were lacking from British and Irish floras, they were taken especially from those for Italy (Cortini Pedrotti, 2001, 2006 [2005]), the Netherlands (Touw & Rubers, 1989) and European Russia (Ignatov & Ignatova, 2003, 2004). The published volumes for Spain (Guerra, Cano & Ros, 2006) and Sweden (Hallingbäck *et al.*, 2006) were also consulted, together with notices of newly-found species such as *Anastrophyllum alpinum* (Long *et al.*, 2006), *Conocephalum salebrosum* (Szweykowski, Buczkowska & Odrzykoski, 2005), *Cinclidotus riparius* (Blockeel, 1998) and *Tortella bambergeri* (Bosanquet, 2006).

Published measurements for some species varied widely between authors. Some of the differences can no doubt be attributed to the plants growing better in some environments than others. However, a commoner source of difference is the tendency to select extreme measurements in some cases and not in others. When William Wilson (1855) gave measurements for *Fissidens polyphyllus* he said that the stems are 'from three inches [8 cm] to a foot [30 cm] or more in length'. The upper limit is very rarely achieved, and is not the normal maximum size of the species. Smith (2004) gave a limit of 20 cm but Störmer (1969) had never found it longer than 13.5 cm in Norway. In this case, we have given 15 cm as the limit, suspecting that Störmer, who had made a special effort to measure the plant, examined specimens of more typical size. In many other cases, we have given an average of the lengths quoted by several authors.

Although values for length are inevitably somewhat vague, they are unlikely to be wrong by more than a factor of 1.5. Given that they vary from 0.9 mm (*Microbryum rectum*) to 500 mm (*Fontinalis antipyretica*), they do undoubtedly give an indication of size.

Table 5
Size and life history attributes. Species counts exclude aggregates and infraspecific taxa; counts of primary life-form are in the column N1=, counts of secondary life-form are in N2=.

Attribute or code	N1=	N2=	Explanation
(a) Length	**Len**		Length or diameter, mm (plant height if stemless)
(b) Annual or not	**Per**		Primary and secondary type of perennation
A	42		Annual; includes regeneration from tubers etc.
AP	30		Annual or perennial, more often annual
PA	50		Perennial or annual, more often perennial
P	935		Perennial
(c) Life form	**LF1**	**LF2**	Primary and secondary life form
Ac		4	Aquatic colonial (formless loose colonies)
At	10	8	Aquatic trailing (attached to substrate)
Cu	104	6	Cushion (dome-shaped colonies)
De	7	3	Dendroid (with stolons and erect shoots)
Fa	7	8	Fan (branches in plane on vertical substrate)
Le	3		Lemnoid (floating on the water)
Mr	98	31	Mat, rough (creeping, lateral branches erect)
Ms	196	43	Mat, smooth (creeping, branches lying flat)
Mt	24	6	Mat, thalloid (creeping, thalli forming a layer)
Sc	22	46	Solitary creeping (creeping solitary shoots)
St	19	5	Solitary thalloid (rosette forming patch not mat)
Tf	292	131	Turf (vertical stems with little or no branching)
Thread	5	4	Thread (solitary thread-like creeping stems)
Tp	19	6	Turf, protonemal (persistent protonema)
Ts	49	33	Turf, scattered (scattered vertical shoots)
Tuft	114	37	Tuft (loose cushions, not dome-shaped)
We	88	31	Weft (intertwining branched layers)

Annuals and perennials

Four categories are recognized, annual, perennial, and two intermediate categories (Table 5). No distinction is made between annuals regenerating from spores and those regenerating from vegetative propagules, including dormant buds, tubers, gemmae or bulbils. The essence of annuality is that species should regenerate from a propagule or perennating organ that is much smaller than the growing plant. Thus a bryophyte annual can in principle be rather like a vascular hemicryptophyte. A few bryophytes such as *Gongylanthus ericetorum* do indeed regenerate in this way.

Most strictly annual bryophytes are plants of disturbed ground, regenerating from spores. However, many normally annual bryophytes can be facultatively perennial if the ground is not disturbed; these are indicated as AP (annual or perennial), meaning that they are normally annual but sometimes perennial. Plants that are normally perennial but can complete their life cycle in a year are indicated PA (perennial or annual). The large majority of bryophytes are perennial.

The standard floras give some indication of whether or not bryophytes are annuals. Paton (1999) gives information on this for some genera (e.g. *Riccia, Fossombronia*) in which case her attribution is followed. Smith (2004) indicates annuals as 'ephemeral', but gives this information only for a few obviously annual genera or species (e.g. *Ephemerum, Funaria, Fissidens exilis*).

Life-form

A system of life-forms was set out by Mägdefrau (1982) and has been developed and used by various authors, especially by Bates (1998) and by Kürschner and his co-workers (Kürschner & Parolly, 1998; Kürschner, Tonguc, & Yayintas, 1998; Kürschner, 2002). Bates (1998) distinguished life-forms from growth-forms, using the criterion that the life-form is about the organization of shoots into colonies. He did not include the open-turf life-form of short-lived bryophytes (the 'annuals' of Mägdefrau, 1982), which include *Acaulon, Buxbaumia, Diphyscium* and *Ephemerum*, on the grounds that they represent a life-strategy in which little resource is invested into long-term colony organization. We have not followed him in this, because we required a scheme that could include all species.

In total, 17 life-forms are recognized in *BRYOATT* (Tables 5, 6). For the purposes of *BRYOATT*, size does not need to be categorized within life-form, because shoot length is given as a separate column. Thus tall turfs do not need to be distinguished from short turfs, nor small cushions from large ones.

The primary life-form is listed in column LF1. Many species (about 40%) have secondary life-forms which are listed in column LF2. In general the secondary life-form is less frequent than the primary one. However, in some species, they may be equally frequent – for example in *Plagiochila porelloides*, which has turf-like shoots growing out of a matted weft.

Vegetative propagules

The occurrence and frequency of vegetative propagules is given for tubers, gemmae, bulbils, deciduous branches and leaves (Table 7). Information on the occurrence of tubers is taken from Preston (2004), with some updating. Details of the other organs are taken from the standard floras and other relevant publications. 'Branches' includes both caducous but otherwise unmodified branches (as in *Campylopus introflexus* and *Microlejeunea ulicina*), and branches which are morphologically modified (*Dicranum flagellare, Pellia endiviifolia*). Similarly, 'leaves' includes the presence of caducous but otherwise unmodified leaves (*Dicranodontium denudatum, Frullania fragilifolia*), modified leaves (*Campylopus fragilis, Syntrichia laevipila*) and fragmenting leaves, including species such as *Dicranum tauricum* which shed their leaf tips. The table excludes three aquatic species which spread vegetatively by fragmentation of the whole plant (*Riccia fluitans, R. rhenana* and *Ricciocarpos natans*) and *Gymnocolea inflata*, which has caducous perianths.

Table 6
Life-forms in BRYOATT; abbreviations follow Table 4.

Name	Description	Examples
Shoots not forming part of an organized colony		
Solitary creeping (Sc)	Solitary or scattered, crawling over or through substrate; if more crowded would generally be a mat	*Calypogeia suecica*, *Fossombronia wondraczekii*
Solitary thalloid (St)	Solitary thalloid rosette, forming a small patch rather than the more extensive growth of a thalloid mat	*Anthoceros agrestis, Cryptothallus, Petalophyllum*, *Riccia glauca*
Turf, protonemal (Tp)	Scattered vertical shoots from persistent protonema; can approach turf form if dense	*Buxbaumia*, *Ephemerum, Pogonatum aloides* (usually), *Tetrodontium brownianum*
Turf, scattered (Ts)	Scattered vertical shoots, normally lacking protonema; can approach turf form if dense	*Acaulon*, *Aloina, Haplomitrium*, *Pterygoneurum*, *Seligeria*
Thread	Thread-like, with thread-like, variously-oriented stems that crawl through or over substrate or vegetation	*Blepharostoma* (usually), *Cephaloziella* spp. (usually), *Platydictya*
Lemnoid (Le)	Floating on the water and budding	*Ricciocarpos*, *Riccia fluitans*
Shoots forming part of an organized colony		
Turf * (Tf)	Many loosely or closely packet vertical stems with limited branching	*Atrichum*, *Barbula, Fissidens*, *Polytrichum*, *Sphagnum* (mostly)
Tuft	Tufts, forming loose cushions not necessarily of central origin	*Aulacomnium androgynum*, *Splachnum*, *Tortula subulata*
Cushion (Cu)	Dome-shaped colonies formed by variously-oriented shoots with a central origin	*Andreaea*, *Dicranoweisia*, *Grimmia*, *Gymnomitrion*, several *Orthotrichum* spp.
Dendroid (De)	Sympodially branching shoots with stolons from which spring erect main shoots bearing branches above	*Climacium*, *Isothecium alopecuroides*, *Thamnobryum alopecurum*
Mat, rough (Mr)	Shoots creeping substratum, having numerous erect lateral branches	*Brachythecium velutinum*, *Homalothecium sericeum*
Mat, smooth (Ms)	Shoots that creep over substratum, having leafy branches that generally lie flat	*Frullania dilatata*, *Plagiothecium*, *Pseudotaxiphyllum elegans*
Mat, thalloid (Mt)	Shoots that creep over substratum, composed of a layer of thalli	*Conocephalum conicum*, *Metzgeria furcata*, *Reboulia*
Weft * (We)	Loosely intertwining, usually richly branched layers	*Hylocomium*, *Pleurozium*, *Ptilidium*, *Trichocolea*
Fan (Fa)	Shoots arising from vertical bark or rock, branching repeatedly in horizontal plane	*Homalia*, *Leptodon smithii*, *Neckera complanata* (usually), *Porella platyphylla* (usually)
Aquatic trailing (At)	Aquatic attached to substrate and trailing in the water	*Cinclidotus*, *Fontinalis*, *Porella pinnata*
Aquatic colonial (Ac)	Aquatic, forming rather formless loose colonies not anchored to the substrate (a secondary life-form)	*Drepanocladus aduncus*, *Sphagnum cuspidatum*, *S. denticulatum* (when aquatic)

* Many liverworts have a weft-like base from which shoots appear as a turf; thus *Plagiochila porelloides* is classified as LF1=Tf, LF2=We.

In many mosses, protonema-gemmae are frequent or abundant, but information on their occurrence and frequency is inadequate and so we have not included them in this compilation. They are undoubtedly much more common than the early review by Whitehouse (1987) had suggested.

Table 7
Occurrence and frequency of vegetative propagules.

Attribute or code	N=	Explanation
(a) Tubers	**Tub**	
F	37	Frequent or common
O	6	Occasional
R	6	Rare
U	18	Found in GB or Ireland, frequency unknown
X	15	Not in Britain or Ireland but found elsewhere
(b) Gemmae	**Gem**	
F	131	Frequent or common
O	20	Occasional
R	15	Rare
X	7	Not in Britain or Ireland but found elsewhere
(c) Bulbils	**Bul**	
F	17	Frequent or common
O	2	Occasional
R	1	Rare
(d) Branches	**Bra**	
F	24	Frequent or common
O	12	Occasional
R	3	Rare
X	2	Not in Britain or Ireland but found elsewhere
(e) Leaves	**Lvs**	
F	23	Frequent or common
O	9	Occasional
R	2	Rare

Sexual reproduction and spores

The column labelled *Sex* gives information on whether species are monoecious or dioecious, or (in a few cases) have not been observed to produce sex organs (Table 8). Data on the sexuality of liverworts were mostly taken from Paton (1999) and on mosses from Smith (1978; 2004).

The column labelled *Fr* gives information on sporophyte frequency and derives from the same main sources. For liverworts, Paton's (1999) 'fairly frequent' and 'fairly common' are counted here as 'frequent'; 'common' is sometimes counted as 'frequent' and sometimes as 'abundant', depending on our experience of the species. We describe a species as fruiting abundantly if most well-grown colonies in the majority of the British and Irish range can be expected to fruit in most years. Most mosses indicated by Smith (1978; 2004) as fruiting commonly were coded as 'A' but some were coded as 'F'. Again, we have applied our own experience in making the distinction.

The months when sporophytes mature are indicated in columns *Spbeg, Spend* (not included in the printed version of BRYOATT). For a species with a single fruiting season, the first and last months of that season are indicated in these two columns. If there are 1-2 months without a record of mature sporophytes between the first and last dates, these are included in the recorded span. Thus a species found fruiting in May, June, July and September will be shown as fruiting in one period, between May and September. However, species with a gap of 3 or more months is treated as having two fruiting periods, so that a species in which mature fruit has been recorded in March, April, May, October and November is treated as March-May, October-November. For the second period, the columns *Spbeg2* and *Spend2* are used.

For liverworts, dates of sporophyte maturity have been taken from Paton (1999) and Holyoak (unpublished manuscript flora of Cornwall). For mosses, dates were taken from Hill (1988), Holyoak (*op. cit.*) and Paton (1969). Dates from Bates (1995) have been accepted for liverworts and *Sphagnum*, but not for mosses unless capsules were described as 'ripe' or 'dehiscing'. We have also added unpublished data from our personal recording in Cambridgeshire.

Minimum and maximum spore sizes are indicated in columns *Sp1* and *Sp2*. Where an approximate size such as '*c.* 15 µm' is given, 15 is given as both minimum and maximum. Where only a minimum or a maximum value is known, only this value is cited, so that a species with spores known to be 'up to 75 µm' has 75 listed as a maximum value. The dimensions of elliptical spores are those of the longer axis. If spores are released both singly and in tetrads (e.g. *Fossombronia incurva*) the dimensions of the single spores are given; where spores are always permanently united in tetrads (e.g. *Cryptothallus, Sphaerocarpos*), the dimensions of the tetrads are given

Dimensions of liverwort spores are taken from Paton (1999) for those genera for which she gives spore measurements; for other genera we have largely followed Damsholt (2002) and Schuster (1966-1992). Spore sizes of mosses are from Smith (1978; 2004) and Nyholm (1986-1998). In filling gaps we have used a range of other publications, of which Crum & Anderson (1981) and Cortini Pedrotti (2001, 2006 [2005]) have been the most useful. The most serious remaining gap is for the species of Lejeuneaceae, for which we have failed to find an informative source.

Table 8
Sexuality, sporophytes and spore size.

Attribute or code	N=	Explanation
(a) Oeciousness	**Sex**	
D	609	Dioecious
D(M)	4	Normally dioecious, rarely monoecious
MD	25	Monoecious or dioecious
M(D)	8	Normally monoecious, rarely dioecious
M	395	Monoecious
Nil	16	Gametangia not known
(b) Sporophytes	**Fr**	
A	265	Abundant
F	189	Frequent
O	140	Occasional
R	248	Rare
X	151	Not in Britain or Ireland but found elsewhere
Nil	64	Sporophytes not known
(c) Ripe sporophyte [Incomplete data, not in printed version]	**Spbeg**	Month beginning of ripe sporophyte
	Spend	Month end of ripe sporophyte
	Spbeg2	Month beginning of second period
	Spend2	Month end of second period
(d) Spore diameter	**Sp1**	Minimum spore size (µm)
	Sp2	Maximum spore size (µm)

Geographic attributes

Occurrence in Britain, Ireland and the Channel Islands

The British Bryological Society, through its vice-county recording scheme, keeps a record of the occurrence of bryophyte species in vice-counties (Blockeel & Long, 1998). For each vice-county, a species may either be not recorded, recorded but not since 1949, or recorded from 1950 onwards. Counts of species in territories of the British Isles (Table 9) can be derived directly from these records. For these counts, Wales consists of vice-counties 35 and 41-52. Scotland consists of vice-counties 72-112. England and the Isle of Man comprise the remaining British vice-counties. Northern Ireland consists of the six counties H33 and H36-40; the remaining Irish vice-counties are in the Republic.

Table 9

Numbers of bryophyte species recorded in territories of the Britain, Ireland and the Channel Islands. Values are the number of species in each group, excluding varieties and subspecies. For the purposes of this enumeration, Isle of Man records have been included with those for England.

Territory	Code	Hornwort	Liverwort	Moss	Total
(a) Records 1950 onwards					
England	E	4	249	630	883
Wales	W	4	217	561	782
Scotland	S	4	259	643	906
Irish Republic	IR	3	220	531	754
Northern Ireland	NI	3	175	409	587
Channel Islands	CI	1	75	212	288
(b) Not recorded since 1949					
England	(E)		1	19	20
Wales	(W)		4	18	22
Scotland	(S)			20	20
Irish Republic	(IR)		3	15	18
Northern Ireland	(NI)		2	45	47
Channel Islands	(CI)	1	1	20	22

European distributions – biogeographic elements

The categorization of taxa to biogeographic elements (Table 10) follows Hill & Preston (1998), with additions for newly recognized taxa. The element is made up of two components, E1 and E2. Non-native species have also been assigned to elements, based on their geographical distribution in Europe about the year 2007. We are well aware that elements may change if the species subsequently expand to new limits.

The Hyperoceanic eastern limit 0 is used only in the combinations 70 (Hyperoceanic Temperate) and 80 (Hyperoceanic Southern-temperate). Species categorized as 80 occur in Macaronesia; those categorized as 70 have similar distributions in Europe but are absent from Macaronesia. The Mediterranean-Atlantic major biome appears only in the combinations 91 (Mediterranean-Atlantic) and 92 (Submediterranean-Subatlantic).

European natives can be expected to change their distributions as a result of warmer winters. Indeed, there is already some penetration of oceanic species such as *Lepidozia cupressina* and *Orthotrichum pulchellum* to new localities in central Europe (Frahm & Klaus, 2001). We have not attempted to alter any categories as a result of these recent changes, but they may present difficulties in future unless distributions are characterized by climatic limits rather than by geographical ones.

Table 10
Major biomes and eastern limits used to specify biogeographic elements in Europe.

Attribute and codes	N=	Explanation
(a) E1		**Biogeographic element, major biome**
1	72	Arctic-montane (main distribution in tundra or above tree-line in temperate mountains)
2	131	Boreo-arctic montane (in tundra and coniferous forest zones)
3	23	Wide-boreal (from temperate zone to tundra)
4	205	Boreal-montane (main distribution in coniferous forest zone)
5	171	Boreo-temperate (in conifer and broadleaf zones)
6	18	Wide-temperate (from Mediterranean region to coniferous forest zone)
7	225	Temperate (in broadleaf forest zone)
8	115	Southern-temperate (in Mediterranean region and broadleaf forest zones)
9	97	Mediterranean-Atlantic (in Mediterranean region, and extending north in Atlantic zone of temperate Europe)
(b) E2		**Biogeographic element, eastern limit category**
0	58	Hyperoceanic, with a western distribution in atlantic zone
1	137	Oceanic (in atlantic zone of Europe, not or scarcely reaching east to Sweden, Germany or S Spain)
2	145	Suboceanic (extending east to Sweden, C Europe or Italy)
3	262	European (extending to more continental parts of Europe but not to Siberia)
4	18	Eurosiberian (eastern limit between 60°E and 120°E)
5	14	Eurasian (extending across Asia to east of 120°E)
6	423	Circumpolar (in Europe, Asia and N America)

Counts of occurrence in 10-km squares in Britain and Ireland

For each taxon, the number of 10-km squares (hectads) in Britain, Ireland and the Channel Islands is enumerated (Table 11). Only squares with post-1949 records have been counted, so that *Helodium blandowii* and *Paludella squarrosa*, not found in Britain since the 19th century, have a zero count there; *P. squarrosa* has a recent record from Ireland, where it has a count of 1. Counts were based on data in the database of the British Bryological Society at the Biological Records Centre in July 2007.

Climatic means

Climatic values for plants were calculated as the mean climate of the 10-km squares where they occur in Britain, Ireland and the Channel Islands, averaging over the squares enumerated for the counts. For these means, as for the counts, only post-1949 records were included. Climate data for 10-km squares were taken from baseline climate summaries of the UK Climate Impacts Programme (Hulme & Jenkins, 1998). These baseline summaries were constructed by interpolation of daily weather measurements from individual met stations, averaged over the 30-year period 1961-1990 (Barrow, Hulme & Jiang, 1993).

Table 11
Counts of squares, means of temperature and precipitation, and maximum altitudes.

Attribute	Min	Max	Explanation
(a) Counts			Counts of 10-km squares
GB	0	2351	Great Britain and Isle of Man
IR	0	416	Ireland
CI	0	11	Channel Islands
(b) Climatic means			Mean values for 10-km squares
Tjan	-1.9	8.0	January mean temperature (°C)
Tjul	9.9	16.7	July mean temperature (°C)
Prec	638	2748	Annual precipitation (mm)
(c) Maximum altitude			Maximum in Britain and Ireland
Alt	0	1344	Maximum altitude (m)

Maximum altitude

It would have been preferable to give separate maximum altitudes for Britain and Ireland. However, there was not enough information to do this for many species in Ireland, and maximum altitudes are for both islands taken together. Maximum altitudes were drawn from several sources, notably the database of the British Bryological Society, Paton's (1999) flora (liverworts), manuscript lists by M.F.V. Corley, D.G. Long and G.P. Rothero, and personal observations, especially by S.D.S.B. Wherever possible, we have attempted to support our maxima with an actual record, complete with finder and date. However, for 175 species, the maximum altitude is taken from the most recent BBS atlas (Hill, Preston & Smith, 1991-1994). These records have a locality, but details of the finder and date were not collected. Likewise for about 100 liverworts, the maximum altitude given by Paton (1999) does not have a supporting locality.

One species, *Timmia megapolitana*, is recorded from the lowest maximum altitude of 0 m, where it is regularly inundated by tidal fresh water. Five species, *Andreaea rothii, Brachythecium rutabulum, Ceratodon purpureus, Kiaeria blyttii* and *Racomitrium sudeticum*, are recorded from the maximum possible altitude, 1344 m, at the top of Ben Nevis. A further 19 species are recorded from nearby at 1340 m. The biogeographic elements of all of these except for *B. rutabulum* are in major biomes that include the boreal or arctic zones. The occurrence of *B. rutabulum* at this altitude is anomalous.

Habitat indicator values

Ellenberg indicator values

Ellenberg defined seven major scales, of which five are presented here. The two that are omitted, T (temperature) and K (continentality), correspond quite closely to the major biome and eastern limit categories used for European distributions by Hill & Preston (1998) and incorporated here in the biogeographic elements. The five remaining scales have values defined in the tables that follow. The values are based on those of Ellenberg *et al.* (1991), as modified by Hill *et al.* (1999). A few example species are given for each value, by way of explanation.

Indicator values for bryophytes found in plant communities with vascular plants were calculated by a computer program called INDEXT (Hill *et al.*, 2000). Starting with the indicator values of vascular plants associated in quadrats, we calculated a mean value for each quadrat, and then used regression to suggest new values for bryophytes.

This process gave initial values for only the 361 bryophytes recorded with vascular plants in at least five quadrats. For the remainder, it was necessary to use published associates. Associates were obtained especially from Paton (1999) for liverworts and Hill, Preston & Smith (1991-1994) for mosses. Other important sources were Paton (1969) and Wigginton (1995). With newly-reported species, the original notice in the British literature was used.

The main difficulty in building up a set of bryophyte indicator values was that many species are found on rocks, bark or rotten wood. These typically have few associates that occur in terrestrial habitats along with vascular plants. Thus they are poorly connected with Ellenberg values. Calculated values for the 361 species with enough occurrences in quadrats were treated as ‘anchor values’. For the remainder, an iterative process was needed, first fitting values for those species whose listed associates had anchor values and then moving on to the others. At the end of the process, values were critically reviewed in the light of personal experience and compared with unpublished Dutch values supplied by Dr Henk Siebel. Values were adjusted if necessary, and finally put forward for publication here.

We have also included a column to indicate the tolerance of species to heavy metals. There has been little systematic study of bryophytes on sites in Britain or Ireland that are rich in heavy metals. Our classification is therefore a first attempt and one which we expect could be improved with further fieldwork. Our main sources of data have been the floras of areas with old heavy-metal mines, notably the Isle of Man (Paton, 1971), North Wales (Hill, 1988) and Carmarthenshire (Bosanquet, Graham & Motley, 2005). D.T. Holyoak’s draft accounts of the Cornish bryophytes have been particularly useful, and we have also been fortunate in having access to unpublished lists compiled by N.G. Hodgetts for Halkyn Mountain (one of the few lists available for sites that are both rich in heavy metals and highly calcareous) and by R.D. Porley for polluted river gravels in Northumberland. We have also consulted lists of species growing in the *Festuca ovina–Minuartia verna* plant community (Rodwell, 2000) and associated with *Ditrichum plumbicola* (Crundwell, 1976). S.D.S.B. has added some observations from sites in South and Mid Wales. We have, unfortunately, been unable to find any studies of the bryophytes of disused lead mines in Derbyshire and Yorkshire.

Light values (L)

The range of Ellenberg values for light (Table 12) is extended to allow for *Cryptothallus mirabilis,* which lives in darkness.

Table 12
Ellenberg values for light (L).

Code	N=	Explanation
0	1	Plant in darkness (*Cryptothallus mirabilis*)
1	8	Plant in deep shade (*Calypogeia arguta*, *Fissidens serrulatus*, *Gyroweisia tenuis*, *Schistostega pennata*)
2	27	Between 1 and 3 (*Aphanolejeunea microscopica*, *Scapania umbrosa*, *Eucladium verticillatum*, *Plagiothecium latebricola*, *Seligeria calycina, Tetrodontium brownianum*)
3	67	Shade plant, mostly less than 5% relative illumination, seldom more than 30% illumination when trees are in full leaf (*Calypogeia fissa*, *Conocephalum conicum*, *Saccogyna viticulosa*, *Fissidens viridulus*, *Heterocladium heteropterum*, *Plagiothecium nemorale*, *Thamnobryum alopecurum*)
4	106	Between 3 and 5 (*Cephalozia bicuspidata*, *Lejeunea cavifolia*, *Plagiochila porelloides*, *Atrichum undulatum*, *Fissidens taxifolius*, *Polytrichum formosum*, *Rhynchostegium confertum*)
5	154	Semi-shade plant, rarely in full light, but generally with more than 10% relative illumination when trees are in leaf (*Diplophyllum albicans*, *Lophocolea bidentata*, *Radula complanata*, *Anomodon viticulosus*, *Bryoerythrophyllum recurvirostrum*, *Dicranoweisia cirrata*, *Leucobryum glaucum*, *Plagiomnium undulatum*, *Rhytidiadelphus loreus*)
6	238	Between 5 and 7 (*Cololejeunea minutissima*, *Fossombronia pusilla*, *Leiocolea turbinata*, *Brachythecium rutabulum*, *Dicranum scoparium*, *Eurhynchium hians*, *Orthotrichum affine*, *Polytrichum commune*, *Sphagnum squarrosum*)
7	283	Plant generally in well lit places, but also occurring in partial shade (*Anthelia julacea*, *Gymnocolea inflata*, *Marchantia polymorpha*, *Riccia sorocarpa*, *Andreaea rupestris*, *Barbula convoluta*, *Funaria hygrometrica*, *Racomitrium lanuginosum*, *Sphagnum capillifolium*, *Weissia controversa*)
8	156	Light-loving plant rarely found where relative illumination in summer is less than 40% (*Cladopodiella fluitans*, *Odontoschisma sphagni*, *Aloina aloides*, *Bryum pseudotriquetrum*, *Campylium stellatum*, *Grimmia pulvinata*, *Polytrichum juniperinum*, *Sphagnum papillosum*)
9	17	Plant in full light, found mostly in full sun (*Petalophyllum ralfsii, Bryum algovicum, Grimmia laevigata, Hennediella heimii, Polytrichum piliferum, Tortella flavovirens*)

Moisture values (F)

Moisture (F from the German *Feuchtigkeit*) is on a scale of 1 to 12 (Table 13).

Table 13
Ellenberg values for moisture (F).

Code	N=	Explanation
1	20	Indicator of extreme dryness, restricted to situations that often dry out for some time (*Grimmia donniana*, *G. laevigata*, *G. pulvinata*, *Hedwigia stellata*, *Syntrichia intermedia*)
2	31	Between 1 and 3 (*Campyliadelphus chrysophyllus*, *Campylopus pilifer*, *Pleurochaete squarrosa*, *Racomitrium fasciculare*, *R. heterostichum*, *Tortula muralis*)
3	47	Dry-site indicator, more often found on dry substrata than on moist places (*Aloina aloides*, *Andreaea rothii*, *Brachythecium albicans*, *Didymodon vinealis*, *Homalothecium sericeum*, *Microbryum davallianum*, *Syntrichia ruralis*)
4	108	On well-drained terrestrial substrata (*Barbula convoluta*, *Ceratodon purpureus*, *Fissidens dubius*, *Trichostomum crispulum*) or on bark or rock with some shelter (*Cololejeunea minutissima*, *Metzgeria furcata*, *Radula complanata*, *Orthotrichum affine*, *Rhynchostegiella tenella*)
5	229	On moderately moist soils (*Barbilophozia floerkei, Bryum bicolor, Dicranum scoparium, Hypnum jutlandicum, Rhytidiadelphus squarrosus*) or on bark or rock in moderately humid places (*Frullania tamarisci, Metzgeria fruticulosa, Anomodon viticulosus, Cryphaea heteromalla, Ulota bruchii*)
6	228	On moist soils (*Diplophyllum albicans*, *Lophocolea bidentata*, *Atrichum undulatum*, *Brachythecium rutabulum*, *Dicranum majus*, *Polytrichum formosum*, *Sphagnum quinquefarium*) or rock or bark in humid places (*Colura calyptrifolia*, *Plagiochila porelloides*, *Scapania gracilis*, *Homalia trichomanoides*, *Isothecium myosuroides*, *Racomitrium aquaticum*, *Tetraphis pellucida*)
7	135	On constantly moist or damp, but not permanently waterlogged substrata (*Calypogeia fissa*, *Conocephalum conicum*, *Fossombronia pusilla*, *Scapania nemorea*, *Bryum pallens*, *Fissidens adianthoides*, *Polytrichum commune*, *Sphagnum capillifolium*)
8	132	Between 7 and 9 (*Cephalozia connivens*, *Hygrobiella laxifolia*, *Odontoschisma sphagni*, *Pellia epiphylla*, *Brachythecium rivulare*, *Campylopus atrovirens*, *Pohlia wahlenbergii*, *Sphagnum palustre*)
9	102	In waterlogged sites, either in streams and flushes (*Chiloscyphus polyanthos*, *Trichocolea tomentella*, *Bryum pseudotriquetrum*, *Dicranella palustris*, *Philonotis fontana*, *Rhynchostegiella teneriffae, Sphagnum teres*) or on bogs (*Cladopodiella fluitans*, *Kurzia pauciflora*, *Mylia anomala*, *Sphagnum denticulatum*, *S. fallax*)
10	18	In pools and by streams that may intermittently lack water (*Nardia compressa*, *Scapania undulata*, *Calliergon cordifolium*, *Rhynchostegium riparioides*, *Sphagnum cuspidatum*, *S. pulchrum*)
11	4	On surface of still water (*Ricciocarpos natans*) or regularly submerged in running water, though sometimes at or above normal water level (*Amblystegium fluviatile*, *Rhynchostegium alopecuroides*)
12	3	Normally submerged (*Fontinalis* spp., *Octodiceras fontanum*)

Reaction (R)

Reaction (Table 14) refers to environmental acidity, typically measured by pH.

Table 14
Ellenberg values for reaction (R).

Code	N=	Explanation
1	30	Indicator of extreme acidity, never found on weakly acid or basic substrata (*Calypogeia neesiana*, *Gymnocolea inflata*, *Odontoschisma sphagni*, *Riccardia latifrons*, *Campylopus brevipilus*, *Sphagnum austinii*, *S. compactum*, *S. tenellum*)
2	141	Between 1 and 3 (*Barbilophozia floerkei*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Mylia taylorii*, *Scapania gracilis*, *Andreaea rothii*, *Campylopus atrovirens*, *Grimmia donniana*, *Polytrichum commune*, *Racomitrium fasciculare*, *R. heterostichum*, *Rhytidiadelphus loreus*, *Sphagnum fallax*)
3	137	On acid substrata, often on base-poor mineral soils or in acid flushes (*Calypogeia fissa*, *Marsupella emarginata*, *Saccogyna viticulosa*, *Aulacomnium palustre*, *Calliergon stramineum*, *Dicranum majus*, *D. scoparium*, *Hedwigia stellata*, *Orthodontium lineare*, *Sphagnum palustre*)
4	122	Between 3 and 5 (*Calypogeia arguta, Frullania tamarisci, Lophocolea bidentata, Pellia epiphylla, Scapania undulata, Calliergon cordifolium, Dicranella palustris, Dicranoweisia cirrata, Isothecium myosuroides, Philonotis fontana*)
5	163	On moderately acid soils (*Anthoceros* spp., *Fossombronia pusilla*, *Trichocolea tomentella*, *Atrichum undulatum*, *Fissidens bryoides*, *Pleuridium* spp., *Rhytidiadelphus squarrosus*) or rock or bark (*Lejeunea lamacerina*, *Metzgeria furcata*, *Pohlia cruda*, *Schistidium rivulare*, *Ulota bruchii)*
6	163	On basic soil (*Conocephalum conicum, Brachythecium rutabulum, Bryum pseudotriquetrum, Eurhynchium hians, Plagiomnium undulatum*) in basic waters (*Fontinalis antipyretica, Rhynchostegium riparioides*) or on basic rock or bark (*Frullania dilatata, Plagiochila porelloides, Radula complanata, Cryphaea heteromalla, Isothecium alopecuroides, Orthotrichum affine*)
7	198	On strongly basic substrata, sometimes on siliceous rocks or soil (*Lunularia cruciata*, *Pellia endiviifolia*, *Amblystegium serpens*, *Barbula convoluta*, *Bryum bicolor*, *Calliergonella cuspidata*, *Ctenidium molluscum*, *Didymodon fallax*, *Fissidens taxifolius*, *Homalothecium sericeum*, *Microbryum davallianum*)
8	70	Between 7 and 9 (*Leiocolea turbinata, Porella platyphylla, Aloina aloides, Anomodon viticulosus, Campyliadelphus chrysophyllus, Didymodon rigidulus, D. vinealis, Grimmia pulvinata, Palustriella commutata* var. *commutata*, *Orthotrichum anomalum, Syntrichia intermedia, Tortula muralis*)
9	33	On substrata with free calcium carbonate, mainly chalk and limestone (*Cephalozia baumgartneri*, *Eucladium verticillatum*, *Pleurochaete squarrosa*, *Seligeria calcarea*, *Tortella nitida*)

Nitrogen (N)

Nitrogen values (Table 15) are in fact a general indication of fertility. N values for vascular plants are on a scale from 1 to 9, but the two highest values, 8 and 9, correspond to conditions where bryophytes are crowded out by vascular plants.

Table 15
Ellenberg values for nitrogen (N).

Code	N=	Explanation
1	152	Indicator of extremely infertile sites; almost all are calcifuges (*Cephaloziella connivens*, *Diplophyllum albicans*, *Mylia anomala*, *Nardia compressa*, *Odontoschisma sphagni*, *Andreaea rothii*, *Campylopus atrovirens*, *Grimmia donniana*, *Hedwigia stellata*, *Polytrichum piliferum*, *Racomitrium fasciculare*, *R. heterostichum*, *Sphagnum papillosum*), but there are a few exceptions (*Anthelia* spp., *Aloina brevirostris*, *Blindia acuta*)
2	403	Indicator of infertile sites; these include calcifuges (*Barbilophozia floerkei*, *Cephalozia bicuspidata*, *Scapania gracilis*, *S. undulata*, *Dicranum scoparium*, *Sphagnum denticulatum*, *S. palustre*), middling species (*Aneura pinguis*, *Porella obtusata*, *Campylium stellatum*, *Pterogonium gracile*, *Thuidium delicatulum*) and calcicoles (*Cololejeunea calcarea*, *Campyliadelphus chrysophyllus*, *Ctenidium molluscum*, *Fissidens dubius*, *Homalothecium lutescens*)
3	184	Indicator of moderately infertile sites; N=3 species, like N=2 species, include a range of calcifuges (*Calypogeia fissa*, *Dicranum tauricum*, *Isothecium myosuroides*, *Philonotis fontana*, *Polytrichum formosum*), middling species (*Radula complanata*, *Brachythecium albicans*, *Bryum pseudotriquetrum*, *Weissia controversa*) and calcicoles (*Aloina ambigua*, *Didymodon fallax*, *Neckera crispa*, *Trichostomum crispulum*)
4	170	Between 3 and 5; these plants are found mainly in the lowlands, but include calcifuges (*Fossombronia pusilla*, *Pellia epiphylla*, *Orthodontium lineare*, *Mnium hornum*, *Pseudotaxiphyllum elegans*) as well as species of more basic substrates (*Cololejeunea minutissima*, *Plagiochila porelloides*, *Grimmia pulvinata*, *Homalothecium sericeum*, *Rhytidiadelphus squarrosus*, *Syntrichia ruralis*, *Ulota bruchii*)
5	88	Indicator of moderately fertile sites; these are almost without exception lowland species, with a few calcifuges (*Atrichum undulatum*, *Calliergon cordifolium*, *Fissidens bryoides*, *Plagiothecium curvifolium*, *P. denticulatum*), but most are tolerant of basic conditions (*Conocephalum conicum*, *Barbula convoluta*, *Brachythecium rivulare*, *Fissidens taxifolius*, *Orthotrichum affine*, *Plagiomnium undulatum*)
6	48	Between 5 and 7; these are mostly plants of eutrophic lowlands (*Riccia cavernosa*, *R. glauca*, *Amblystegium serpens*, *Brachythecium rutabulum*, *Bryum rubens*, *Dicranella staphylina*, *Leskea polycarpa*, *Pohlia melanodon*, *Tortula acaulon*), but Splachnaceae are on upland dung and carcases (*Splachnum* spp., *Tetraplodon* spp.)
7	12	Plant often found in richly fertile places (*Lunularia cruciata*, *Bryum argenteum*, *B. bicolor*, *Eurhynchium speciosum*, *Funaria hygrometrica*, *Leptodictyum riparium*)

Salt tolerance (S)

Values for salt tolerance (Table 16) start at zero, corresponding to no tolerance of salt.

Table 16
Ellenberg values for salt tolerance (S).

Code	N=	Explanation
0	1013	Absent from saline sites; if in coastal situations, only accidental and non-persistent if subjected to saline spray or water (96% of the flora)
1	19	Slightly salt-tolerant species, rare to occasional on saline soils but capable of persisting in the present of salt (includes dune and dune-slack species where the ground water is fresh but where some inputs of salt spray are likely) (*Fossombronia maritima, Frullania dilatata, F. microphylla, F. tamarisci, Petalophyllum ralfsii, Porella obtusata, Radula lindenbergiana, Riccia glauca, Brachythecium mildeanum, Bryum algovicum, B. dyffrynense, Campylopus fragilis, Ceratodon purpureus, Drepanocladus lycopodioides, D. sendtneri, Eurhynchium praelongum, Microbryum starckeanum, Scleropodium tourettii, Syntrichia ruraliformis, Tortula acaulon* var. *pilifera*)
2	12	Species occurring in both saline and non-saline situations, for which saline habitats are not strongly predominant (*Cololejeunea minutissima*, *Fossombronia angulosa*, *Frullania teneriffae*, *Amblystegium serpens*, *Archidium alternifolium*, *Bryum mamillatum*, *Campyliadelphus elodes*, *Drepanocladus aduncus*, *Glyphomitrium daviesii*, *Myurium hochstetteri*, *Tortula modica*, *Trichostomum brachydontium*)
3	6	Species most common in coastal sites but possibly or certainly capable of occurring in sites that do not receive salt spray (*Bryum warneum*, *Drepanocladus polygamus*, *Sanionia orthothecioides*, *Tortula wilsonii*, *Ulota phyllantha*, *Weissia perssonii*)
4	5	Species of salt meadows and upper saltmarsh, subject to at most only very occasional tidal inundation, or of cliffs receiving some salt spray (*Bryum calophyllum, Bryum marratii, Tortella flavovirens, Tortula atrovirens, Tortula viridifolia*)
5	2	Species of the upper edge of saltmarsh and obligate halophytes of cliffs receiving regular salt spray (*Hennediella heimii, Schistidium maritimum*)

Heavy-metal tolerance (HM)

Values for metal tolerance (Table 17) start at zero, corresponding to no tolerance of heavy metals.

Table 17
Indicator values for heavy-metal tolerance (HM).

Code	N=	Explanation
0	916	Species that are absent from substrates with moderate or high concentrations of heavy metals (87% of the flora)
1	71	Species that are recorded on substrates with moderate or high concentrations of heavy metals but only rarely. They are much more frequent elsewhere and may have occurred on rocks or soil that were locally lacking high metal content. Many are very common plants *(Lophocolea bidentata*, *Barbula convoluta*, *Bryum capillare*, *Calliergonella cuspidata*, *Eurhynchium praelongum*, *Hypnum cupressiforme*, *Mnium hornum*, *Plagiomnium undulatum*)
2	47	Species that are occasional or frequent on substrates with moderate or high concentrations of heavy metals, and within particular regions may be restricted to such sites, but do not occur as dominants over large areas and in British Isles as a whole they are much more frequent in other habitats. A few of the rarer species either definitely (*Grimmia donniana*) or probably (*Ditrichum lineare*, *Hymenostylium recurvirostrum*, *Microbryum starckeanum*) have tolerant genotypes, but many commoner ones may not (*Barbula unguiculata*, *Dicranella heteromalla*, *Dicranum scoparium*, *Didymodon fallax*, *Didymodon insulanus*, *Polytrichum juniperinum*, *Rhytidiadelphus squarrosus*, *Scleropodium purum*)
3	15	Species that are frequent and often abundant on substrates with moderate or high concentrations of heavy metals, sometimes occurring as dominants over large areas, but are also frequent in other habitats. The plants on polluted sites may be tolerant genotypes (*Cephaloziella integerrima*, *Cephaloziella stellulifera*, *Diplophyllum albicans*, *Gymnocolea inflata*, *Jungermannia gracillima*, *Nardia scalaris*, *Scapania compacta*, *Bryum pallens*, *Ceratodon purpureus*, *Dicranella varia*, *Dicranoweisia cirrata*, *Pohlia annotina*, *P. nutans*, *Schistidium crassipilum*, *Weissia controversa var. controversa*)
4	2	Species that are much more frequent on substrates with moderate or high concentrations of heavy metals than on unpolluted substrates, but are sometimes present on non-polluted sites (*Bryum pallescens*, *Pohlia andalusica, Weissia controversa* var. *densifolia*)
5	6	Species that in the British Isles are confined to substrates with moderate or high concentrations of heavy metals (*Cephaloziella massalongi*, *Cephaloziella nicholsonii*, *Ditrichum cornubicum*, *D. plumbicola*, *Grimmia atrata*, *Scopelophila cataractae*)

Substrates and habitats

Our treatment of the habitats of bryophytes departs in several ways from the corresponding section of *PLANTATT*. We have classified each bryophyte in two ways, recognising the major *habitat* such as coastal cliff, broad-leaved woodland or arable land, and the *substrate* on which the species occurs, such as rock, rotting wood or soil. Whereas substrates are relatively unimportant for British vascular plants, most of which are rooted in soil, they are clearly much more relevant to the ecology of a poikilohydrous group such as the bryophytes. Clearly both the habitat in our restricted use of the term and the substrate are part of the habitat of the species in its broadest sense.

To classify species into habitats, we have used the EUNIS habitat classification system (Davies, Moss & Hill, 2004; also available as http://eunis.eea.europa.eu/habitats.jsp). This is a hierarchical classification of European habitats and we have chosen to use level 2 of the hierarchy, so that coastal cliff is classified as habitat B3. B is the first level of the hierarchy and comprises coastal habitats; at level 2 it splits into three categories, B1 coastal dunes, B2 coastal shingle and B3 coastal rock cliffs, ledges and shores. On the whole the EUNIS system was not too difficult to apply to the bryophytes; a few cases of difficulty are discussed below. For substrates, we have devised our own simple substrate classification.

We have attempted to list all the habitats and substrates in which a species may be encountered, rather than (as in *PLANTATT*) simply the most characteristic habitat(s). We have used a simple scale to indicate the frequency with which they occur in each class (see below).

Substrate classes

Species have been allocated to one or more substrate classes (Table 18).

EUNIS habitat classes

Some of the EUNIS habitats are not represented in Britain or Ireland (e.g. F7, Spiny Mediterranean heaths and H6, Recent volcanic features) and others, although they occur in our area, do not support bryophytes (e.g. A5, Sublittoral sediment). We have also excluded some habitats which do support bryophytes but have a very strong overlap with others or are of rather marginal interest. The habitats classes we have used are listed in Table 19 and the excluded habitats in Table 20. The explanation of the habitat class concentrates on the features of relevance to the bryologist.

Table 18
Substrate classes.

Code	Name	N=	Notes
RH	Rock, hard	601	Includes drystone walls when made of hard rock
RS	Rock, soft	228	Includes chalk, soft sandstones and schists, tufa etc.
RW	Rock, worked	264	Includes building stone, roofing slates, brick, mortar, concrete, asphalt etc., but drystone walls built of unworked rocks and stones count as RH or RS
SR	Soil on rock	352	Thin layer of soil over rock; includes soil over natural, worked or artificial rock
SO	Soil	722	Includes mineral, sandy, gravelly, humus-rich and peaty soils; pure peats, sands and gravels are treated separately
PT	Peat	179	Includes relatively shallow peat over mineral soil
GS	Gravel or sand	275	
DW	Decorticated wood	203	Includes decorticated logs, rotting wood and worked wood (fence posts etc.)
DV	Decaying vegetation	105	Includes leaf litter, thatch, decaying vascular plant tussocks (e.g. *Carex paniculata*, *Molinia caerulea*) etc.
DA	Decaying animal	9	Decaying animal matter, including bones, dung etc.
BR	Bryophyte	79	Growing amongst or through other bryophytes (including *Sphagnum*)
EN	Epiphytic on non-woody substrates	23	Includes epiphytic occurrences on lichens, other bryophytes and fern fronds, and on the leaves of flowering plants
EW	Epiphytic on living wood	274	On bark on the trunks, branches, stems and exposed roots of vascular plants (including the trunks of tree ferns)
AQ	Floating on water	5	

Table 19
EUNIS habitat classes.

Code	Name	Explanation	N
A	**Marine habitats**		
A2	Littoral sediment	Saltmarshes in the intertidal zone	62
B	**Coastal habitats**		
B1	Coastal dunes and sandy shores	Sandy shores, shifting and stable sand dunes, moist and humid dune slacks, machair and grassland, heathland and woodland on dunes	185
B2	Coastal shingle	Includes scrub and woodland on shingle as well as open shingle	20
B3	Rock cliffs, ledges and shores	Includes rocky shores, rocky cliffs with halophytes and vegetated soft cliffs	269
C	**Inland surface waters**		
C1	Surface standing waters	Aquatic communities in lakes, reservoirs, ponds and canals; dune-slack pools; bog pools; wet phase of temporary ponds	25
C2	Surface running waters	Aquatic communities in rivers, springs, wet phase of temporary water-courses, films of water flowing over rocky watercourse margins	38
C3	Littoral zone of inland surface waters	The frequently inundated zone, including beds of emergents (*Glyceria fluitans*, *Phragmites* etc), low-growing amphibious vegetation (*Eleocharis acicularis*, *Littorella* etc), lake and river shingles, ephemeral vegetation of periodically inundated shores and areas in the spray zone of waterfalls; the occasionally flooded zone by rivers has been excluded	295
D	**Mires, bogs and fens**		
D1	Raised and blanket bogs		119
D2	Valley mires, poor fens and transition mires	Weakly to strongly acidic mires, often with *Calliergon, Drepanocladus* and *Sphagnum*, and soft water bryophyte springs with *Philonotis fontana* etc.	153
D4	Base-rich fens and calcareous spring mires	Base-rich mires, springs with calcareous or eutrophic water, basic montane flushes	97
E	**Grasslands and lands dominated by forbs, mosses or lichens**		
E1	Dry grasslands	Includes swards on rock debris, decomposed rock surfaces, rock edges with annuals and succulents, dry acidic and neutral grassland, inland dune grassland, calcareous grassland, grasslands rich in lichens and mosses on soils rich in heavy metals	178
E2	Mesic grasslands	Mesotrophic and eutrophic pastures, hay meadows, improved grassland, sports fields and lawns	22
E3	Seasonally wet and wet grasslands	Includes moist or wet eutrophic, mesotrophic and oligotrophic grasslands, and *Juncus effusus* meadows	126
E4	Alpine and subalpine grasslands	Includes snow-patch grassland, moss- and lichen-dominated snow patch communities and exposed moss- and lichen-dominated mountain summits, ridges and plateaux as well as montane grassland	112

Code	Name	Explanation	N
E7	Sparsely wooded grasslands	Includes parkland	62
F	**Heathland, scrub and tundra**		
F3	Temperate scrub	Temperate thickets and scrub, including *Corylus, Crataegus, Prunus, Rubus fruticosus* and *Ulex* scrub	104
F4	Temperate shrub heathland	Wet and dry heaths, usually dominated by Ericaceae but including *Molinia caerulea*-dominated communities	245
F9	Riverine and fen scrubs	Includes willow carr, fen scrub with *Rhamnus*, *Frangula* etc. and boreo-alpine willow scrub	110
FA	Hedgerows		143
G	**Woodland, forest habitats and other wooded land**		
G1	Broadleaved deciduous woodland	Includes semi-natural broadleaved woodland, poplar plantations and orchards, including species growing on rocks in woodland but excluding woodland rides	410
G1R	Rides in broadleaved deciduous woodland	Rides and forest roads in G1	94
G3	Coniferous woodland	Includes conifer plantations and semi-natural Caledonian pine forests, including species growing on rocks in such woodland but excluding woodland rides	126
G3R	Rides in coniferous woodland	Rides and forest roads in G3	47
H	**Inland unvegetated or sparsely vegetated habitats**		
H2	Screes		195
H3	Inland cliffs, rock pavements and outcrops	Includes sea-cliffs free from saline influence, inland cliffs, limestone pavements and disused quarries	650
H5	Miscellaneous inland habitats with very sparse or no vegetation	Includes block slopes, clay, silt, sand, gravel and rocky soils, including open or bryophyte-dominated soil banks by tracks or well above the water level on the sides of ditches, streams and rivers, inland dunes and burnt and trampled areas	271
I	**Regularly or recently cultivated agricultural, horticultural and domestic habitats**		
I1	Arable land and market gardens	Includes cultivated fields and fallow and recently abandoned arable land	110
I2	Cultivated areas of parks and gardens	Includes actively cultivated and recently abandoned parks and gardens	95
J	**Constructed, industrial and other artificial habitats**		
J1	Buildings of cities, towns and villages		52
J2	Low density buildings	Includes scattered residential buildings, agricultural buildings, fences, field walls and rural churchyards	315
J3	Extractive industry sites	Active mines and opencast sites, including sand and gravel workings, and recently abandoned extraction sites and quarries	282
J4	Transport networks and other constructed hard-surface areas	Roads, railways (including railway ballast), car parks and pavements	61

Excluded EUNIS habitats

The following habitats (Table 20) are represented in Britain and have associated bryophytes but are not sufficiently significant to be reported on.

Table 20
Main EUNIS habitat classes occurring in Britain or Ireland and supporting bryophytes but excluded from the dataset.

Code	Name	Comment
A1	Littoral rock and other hard substrata	Includes rocks within the splash zone; can be accommodated in B3
D5	Sedge and reed beds, normally without free-standing water	Bryologically rather insignificant
E5	Woodland fringes and clearings and tall forb habitats	Includes subalpine *Cicerbita alpina* etc. tall-herb communities, herbaceous woodland-edge communities, bracken fields and lowland tall-herb communities in eutrophic places and on abandoned land, a heterogeneous group of habitats with few bryophytes and those well represented in other habitats
F2	Arctic, alpine and subalpine scrub habitats	Includes areas of snow-patch dwarf willow scrub in Scottish Highlands, and dwarf or prostrate wind-pruned ericaceous vegetation, dwarf juniper and *Dryas* heaths; only occurs over restricted areas and bryophytes can be accommodated in other habitats (e.g. E4)
FB	Shrub plantations	Includes low-stem orchards and vineyards; bryologically insignificant
G2	Broadleaved evergreen wood	Represented by small areas of bryologically insignificant *Ilex aquifolium* woodland in Britain
G4	Mixed deciduous and coniferous woodland	A frequent and bryophyte-rich habitat, but we have treated the broadleaved and coniferous components separately
G5	Lines of trees, small anthropogenic woodlands, recently felled woodland, early stage woodland and coppice	Includes regrowth stages of coppice woodland without standards, early stages of plantations, Christmas tree and other tree nurseries, *Arctium*, *Rubus* and scrub communities in clearings, clear felled and burnt areas, a bryologically heterogeneous set of habitats which are covered by other classes
J5	Highly artificial man-made waters and associated structures	Bryophyte-poor habitats with all species also occurring under C, Inland surface waters
J6	Waste deposits	Includes habitats such as rubbish tips which are bryologically insignificant

Difficulties in applying the EUNIS classification

One of the major difficulties arises from the structural complexity of woodland habitats. We have arbitrarily chosen to code species on rocks in woodland as occurring in the woodland habitat G1 or G3, although in practice almost all are also coded as growing on inland rocks H3 as well, but we have invented our own subcategories of G1 and G3 for species on rides, tracks and non-metalled roads in woodland. Species growing on scattered trees (such as those in lines along a riverbank but above the flood level, on the edge of a gorge, or along a driveway) are also difficult to deal with and have tended to be coded as woodland, hedgerow or parkland species (if they also occur in these habitats).

The second major difficulty has been the treatment of the many bryophytes that occur on open soil on crumbling banks, such as ditch, stream and river banks above the water level, trackside and laneside banks and small banks in pastures. These have been coded under H5 which we have probably interpreted more broadly than the authors of the EUNIS classification intended.

Frequency classes

The occurrence in habitats and on substrates has been scored using the frequency classes in Table 21.

Table 21
Frequency classes used for substrates and habitats.

Class	Explanation
1	A rare habitat or substrate for the species
2	An occasional habitat or substrate for the species
3	A normal habitat or substrate for the species

Class 1 includes numerous chance or casual occurrences, and when using *BRYOATT* for analyses it is probably best to disregard occurrences at frequency class 1.

Sources of habitat and substrate information

The information on habitat and substrates was initially compiled from Hill *et al.* (1991) and Paton (1999) for liverworts and Hill *et al.* (1992; 1994) for mosses; data for mosses not treated in the latter were taken from Smith (2004). We then consulted a number of floras which were published after the compilation of the accounts in the *Atlas of Bryophytes*, notably Bates (1995), Bosanquet *et al.* (2005), Rothero (2002), Wigginton (1995) and D.T. Holyoak's draft accounts of the habitat of Cornish bryophytes. We have also amended some of the entries in the light of our own field experience.

Acknowledgements

We are grateful to several bryologists who helped to us to compile the data in this book. Jean Paton kindly gave us permission to extract data from *The Liverwort Flora of the British Isles*, which has been our main source for data on liverworts and which proved a joy to use because of the orderly and consistent way in which data are presented for each species. Other published works are acknowledged in the text but none has been used to the same extent as *The Liverwort Flora*. Jean Paton also commented on the draft altitude list for liverworts, and supplied a number of new maxima. David Holyoak very generously allowed us to use a copy of his unpublished, draft accounts of Cornish bryophytes, which will eventually provide the basis for a new bryophyte flora of that county. In compiling the altitude data we were fortunately able to draw upon Gordon Rothero's unrivalled knowledge of the Scottish mountains; we also incorporated information provided earlier for the *Atlas of Bryophytes* by Martin Corley and David Long. At Monks Wood, Marjorie King did much of the initial extraction of morphological data into spreadsheets. The Ellenberg values for bryophytes were developed under a project on Nitrogen Impacts on Biodiversity funded by Defra. For this, we relied on quadrat data in electronic form, and are grateful to Richard Alexander (Natural England), John Birks (Bergen), Dave Horsefield (Scottish Natural Heritage) and Ian Strachan (Joint Nature Conservation Committee). Dr Henk Siebel supplied Dutch indicator values for comparison. We thank Simon Smart for his encouragement for this part of the project and for supplying the Key Habitats dataset. We also thank Ron Porley for help in tracing sources of information on the bryophytes of sites rich in heavy metals.

Three of us work at the Biological Records Centre where the compilation of *BRYOATT* forms part of an agreed programme of work financed by the Centre for Ecology and Hydrology and the Joint Nature Conservation Committee; the Countryside Council for Wales also agreed to allow Sam Bosanquet to spend some of his working hours on this project. Finally, this compilation would have been impossible without the recording activities of members of the British Bryological Society, whose contributions to the recording schemes and publications run by the Society form the basis of much of the data summarized here.

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