Threatened bryophytes: *Leptodontium gemmascens* (thatch moss)

*Leptodontium gemmascens* (Mitt.) Braithw., commonly known as thatch moss because of its predilection for thatched roofs, is a unique moss in the British flora. It has a distinctive appearance, with gemmae clustered on the ends of its leaves, but it lacks sexual reproductive structures. Rare in Britain, it is scattered through western Europe and has isolated stations in the Southern Indian Ocean. It is closely associated with habitation, and in common with other members of its genus, grows on decaying vegetation.

**Description**

*L. gemmascens* (Fig. 1) is a small acrocarp, in the family Pottiaceae, up to 10 mm, but usually around 5 mm tall. It forms loose turfs that may coalesce into cushions or patches, or it occurs as scattered shoots. When dry, the leaves are appressed and weakly flexuose; when moist, they are spreading-recurved. The leaves are all similar (monomorphic) along the length of the stem. The basal laminal cells are shortly rectangular with sparse papillae and the hexagonal mid- to upper laminal cells have dense C-shaped papillae. A single marginal row of cells with obscure papillae, thicker walls and less dense cell contents forms a very faint, almost indiscernible border. The leaves taper gradually to an acuminate apex with an excurrent nerve and the upper leaf margins are coarsely but bluntly toothed.

Clusters of obovoid to claviform (2–)3(–4)-septate, multicellular, foliar gemmae form on the excurrent nerve of leaves from the stem apex to about three-quarters of the way down its length; such a feature is encountered in no other British moss. Gemmae of a similar morphology also occur in the leaf axils, attached to the stem, and on the basal, abaxial leaf lamina. There may be 15–40 gemmae in a spherical to cylindrical cluster on a nerve which is excurrent to 80 µm, and they range from 40 to 100 µm long and from 30 to 50 µm wide. Up to ten gemmae have been observed in a leaf axil, of a similar form and size to the gemmae on the excurrent nerve. A short stalk attaches both kinds of gemmae and liberation occurs by breakage along the lamella of the basal cell. Gametangia and sporophytes are unknown.

**British distribution**

In England, *L. gemmascens* has been recorded from a total of 19 vice-counties and 41 10-km squares (Fig. 2). In terms of its geographical cover, it has shown a decline, and since 2000 it is known from only six vice-counties and nine 10-km squares. *L. gemmascens* is extant at eight localities, although at two of these, Holnicote and Killerton Estates, it occurs on at least 13 and 7 roofs, respectively (Table 1). It is difficult to be sure whether the species was commoner in the past than it is now; intuitively the decline in thatch would suggest this to be the case, but we lack early records from grasslands where it is quite possible that it was overlooked. There is an east–west split in habitat occupation; in the south-west of England, which can be regarded as its current stronghold, it occurs on thatch, whereas in the east of England it occurs predominately in acidic grassland.

**European and world distribution**

*L. gemmascens* is currently known from six countries in mainland Europe: Belgium, Den-
Threatened bryophytes: Leptodontium gemmascens

Table 1. Post-1990 records of L. gemmascens in England

<table>
<thead>
<tr>
<th>Country</th>
<th>v.c.</th>
<th>Locality</th>
<th>Grid ref</th>
<th>Date</th>
<th>Designation</th>
<th>Habitat</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>West Cornwall</td>
<td>1</td>
<td>Hellfold</td>
<td>SW738262</td>
<td>2006</td>
<td>–</td>
<td>Thatch</td>
<td>1st record for Cornwall</td>
</tr>
<tr>
<td>South Devon</td>
<td>3</td>
<td>Pampool Cottage,</td>
<td>ST052031</td>
<td>2006</td>
<td>–</td>
<td>Thatch</td>
<td>Known since 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plymouth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>South Devon</td>
<td>3</td>
<td>Killerton Estate,</td>
<td>SS90</td>
<td>2006</td>
<td>–</td>
<td>Thatch</td>
<td>Confirmed on 7 roofs out of 33 examined</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(total thatch roofs 60–70)</td>
</tr>
<tr>
<td>South Somerset</td>
<td>5</td>
<td>Hobiscote Estate,</td>
<td>SS978480</td>
<td>2003</td>
<td>–</td>
<td>Thatch</td>
<td>Confirmed on 13 out of 28 roofs examined</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NT, Exmoor</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(total thatch roofs 52) – national stronghold</td>
</tr>
<tr>
<td>Dorset</td>
<td>9</td>
<td>Hardy’s Cottage,</td>
<td>SY72892S</td>
<td>2005</td>
<td>–</td>
<td>Thatch</td>
<td>1st found 1994 – abundant</td>
</tr>
<tr>
<td>Dorset</td>
<td>9</td>
<td>Briants Puddle,</td>
<td>SY19</td>
<td>1994</td>
<td>–</td>
<td>Thatch</td>
<td>No recent records</td>
</tr>
<tr>
<td>Dorset</td>
<td>9</td>
<td>Allinton House,</td>
<td>TY251029</td>
<td>2006</td>
<td>–</td>
<td>Thatch</td>
<td>Not seen in East Sussex for over 50 years – small population</td>
</tr>
<tr>
<td>East Sussex</td>
<td>14</td>
<td>Parson’s Heath</td>
<td>TL445257</td>
<td>1992</td>
<td>–</td>
<td>Grasland</td>
<td>Not found when searched in 2001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Fred Rumsey, pers. comm.)</td>
</tr>
<tr>
<td>Herefordshire</td>
<td>20</td>
<td>Parson’s Heath</td>
<td>TL74123</td>
<td>1996</td>
<td>–</td>
<td>Grasland</td>
<td>Not found when searched in 2001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Fred Rumsey, pers. comm.)</td>
</tr>
<tr>
<td>Herefordshire</td>
<td>20</td>
<td>Barnyard Mx Farm</td>
<td>TL160953</td>
<td>1996</td>
<td>–</td>
<td>Grasland</td>
<td>Not seen since 1st record 1996</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pond Woods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Fred Rumsey, pers. comm.)</td>
</tr>
<tr>
<td>East Suffolk</td>
<td>25</td>
<td>Dunwich Heath</td>
<td>TM482715</td>
<td>1998</td>
<td>–</td>
<td>Grasland</td>
<td>Not refused despite searches</td>
</tr>
<tr>
<td></td>
<td></td>
<td>NT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Fred Rumsey, pers. comm.)</td>
</tr>
<tr>
<td>West Suffolk</td>
<td>26</td>
<td>Barnhamcress Co.</td>
<td>TL865815</td>
<td>2002</td>
<td>–</td>
<td>Grasland</td>
<td>Large population</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Common</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>West Suffolk</td>
<td>26</td>
<td>Wortham LING</td>
<td>TM101795</td>
<td>2003</td>
<td>–</td>
<td>Grasland</td>
<td>Declined, small population</td>
</tr>
</tbody>
</table>

First reported L. proliferum from Marion Island in 1971, but this was re-determined as L. gemmascens by Zander (1971). The discovery of L. gemmascens in The Netherlands prompted van Zanten (1995) to hypothesize that the two taxa may be conspecific, on account of the apparent disjunct distribution. More recently, the report of L. gemmascens on Marion Island has been questioned (Church et al., 2004), suggesting that the plant was likely to be L. proliferum. However, the sub-Antarctic specimens of L. gemmascens match perfectly with European plants (Ryszard Ochrya, pers. comm.).

Ecology

L. gemmascens is primarily a plant of acidic, base-poor substrates, characteristically growing on decaying organic matter in well-lit to partially shaded sites. It is a lowland plant, from near sea level in Cornwall to a maximum altitude of 200m (Broadmoor, Surrey, 1946). Its main habitat in England is on weathered thatch; indeed the first record in England was from thatch, found by Mitten in 1845 although it was not published until 1868 (Hunt, 1868). It also occurs in semi-natural acidic grasslands, and more rarely on detritus in rot holes of trees, on wood and on rabbit droppings. It is interesting to speculate whether L. gemmascens moved from grasslands to thatch, or vice versa. The lack of early records from grassland does not necessarily imply this habitat was colonized later; indeed it is more likely to have migrated from grasslands to thatch. In other parts of the world, members of the genus also grow on decaying vegetation in natural habitats, and in some European countries where it does occur it is unknown on thatch. There is little or no information on the population dynamics of L. gemmascens, but it appears to behave as a pluriennial where a colony normally lasts a few years, and mortality

mark, Germany, Luxemburg, France and The Netherlands. There are suggestions that it may be spreading in central-western Europe, possibly in response to climate change (Frahm & Klaus, 1997). In Germany it is known from about 40 localities (Steffen Caspari, pers. comm.) in the western half of the country, all recorded from 1984 onwards (Schneider et al., 1998). The localities, concentrated in the mountainous areas of Saar-Nahe-Bergland, Eifel and Hunsrueck, link to the Luxemburg (Werner & Sauer, 1994) and Belgium Ardennes (Arts et al., 1992). It is known from about 13 localities in Luxemburg and five localities in Belgium. All occurrences in these three countries are in acidic grassland (thatched roofs are virtually unknown). L. gemmascens was discovered in The Netherlands in 1994 (van Zanten, 1995), and is now known in a total of three localities of which one is a recent discovery (2005) on thatch (Bart van Tooren & Hans Colpa, pers. comm.). (Thatch moss is the vernacular name given to L. flexifolium in The Netherlands). In Denmark it is known from about four or five localities, mostly on thatch, with only one from acidic, heathy grassland under Calluna, found in 2000 (Gert Steen Mogensen, pers. comm.). In France the three post-1990 records (Paris Basin and the Auvergne area) and all past records are from thatch (Vincent Hugonnier, pers. comm.).

Until 1971, L. gemmascens was regarded as a European endemic, but a robust form is known to occur on the sub-Antarctic Marion Island (Zander, 1971); in 2001 it was found on Prince Edward Island, and in 2006 on Ile Australia in the Kerguelen Province in the Southern Indian Ocean (Ryszard Ochrya, pers. comm.). This disjunct distribution pattern, with no obvious connection between the northern hemisphere localities, raises the possibility that man introduced it to these islands (Ochrya et al., 2003), perhaps by imported cattle feed or some similar route (Richard Zander, pers. comm.).

Hill & Preston (1998) classified L. gemmascens as belonging to the Suboceanic Temperate phytogeographical element. The identity of the Marion Island plant was still in doubt at the time of publication, but they commented that if it was correct, then the enigmatic L. gemmascens is likely to be a species of tropical origin, whose centre of distribution is not yet known.

Status in Britain and Europe

L. gemmascens is listed as Vulnerable in Britain (Church et al., 2004) and is on the revised UK BAP list (JNCC, 2007; Anonymous, 1995). It is listed as Rare (evaluated using old IUCN guidelines) in Europe (ECCB, 1995).

Taxonomy

There has been some confusion between L. gemmascens and the southern hemisphere taxon L. proliferum Herzog which has been reported from the Andes of Colombia and Bolivia, Mexico and southern Africa (Lesotho). Zanten

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is caused by competition or change of habitat. It shows some of the traits of a long-lived shuttle (During, 1992), and gemmae probably enable rapid population expansion during colonization episodes when conditions are favourable. On thatch and in grassland it has to tolerate extended periods of water deficit, and during the summer months it can be very difficult to find. A search for *L. gemmascens* gametophores on thatch in Sussex in May 2008 was unsuccessful, but a piece of weathered thatch removed and examined microscopically revealed a few typical gemmae. The study on Exmoor (Hedderson *et al.*, 2003a) did not show a correlation with aspect or pitch of the roof, although Exmoor is situated in a region of southern England that experiences high levels of precipitation. Further east, however, on the Killerton Estate in Devon and at Alfriston Clergy house in Sussex, where it is significantly drier, *L. gemmascens* is more or less restricted to north-facing aspects, only occasionally on west- or east-facing aspects. On Exmoor, *L. gemmascens* is most consistently found within a species-rich *Umbilicus rupestris* community (Hedderson *et al.*, 2003b). This community is characterized by low cover values for *Campylopus* species, so it is likely that exclusion factors are also operating. On many thatched roofs, *Campylopus introflexus* is the dominant bryophyte, often forming continuous cover and potentially denying space to other species, including *L. gemmascens*.

There is a wide range of bryophytes, lichens and vascular plants that have been recorded on thatch (Hedderson *et al.*, 2003b; Porley, 2006). Frequent cryptogram associates of *L. gemmascens* on thatch include *C. introflexus*, *Ceratodon purpurascens*, *Dicranoweisia cirrata*, *Dicranum scoparium*, *Hypnum cupressiforme* and, amongst the lichens, *Cladonia* (including *C. chlorophora*, *C. coniocraea*, *C. flerbeanum*, *C. macilenta* and *C. squamosa*), *Physcia tenella* and *Placynthiella icmalae*. Species associated with *L. gemmascens* in 10 cm² quadrats on the Killerton Estate (Porley, 2006) include *Brachythecium rutabulum*, *Bryum capillare*, *C. introflexus*, *D. cirrata*, *D. scoparium*, *Frullania dilatata*, *H. cupressiforme*, *Microcoleus ulicina*, *Cladonia spp.* and *Peligeria spp.*. Also of interest is the occurrence of *Leptodontium flexiformis* on thatch. On the Killerton Estate I found it on seven roofs (out of a total of 33 roofs surveyed) often in large quantity, but it never overlapped with *L. gemmascens*, always preferring more exposed positions, usually on south-facing aspects. On Alfriston Clergy house in Sussex, *L. gemmascens* occurs on north- and east-facing aspects that receive some shelter from an adjacent yew.

Although the presence of *L. gemmascens* on thatch is strongly correlated with age, colonization and establishment are dependent on many factors. On new thatch, a smooth cuticle on the straw or reed may reduce the likelihood of gemmae or other propagules attaining a toehold, particularly under conditions of rain run-off. On the Killerton Estate, and on Hardy’s Cottage, most occurrences are on the gable ends and eaves of roofs, or in valleys or chimney abutments, where rain run-off maintains higher moisture levels in the coat for longer periods. An alternative explanation for this local distribution pattern is that propagules are washed down and collect at such points. The effect of thatch ‘cluster’ size is probably also important in maintaining viable populations; Holnicote and Killerton are strongholds for *L. gemmascens* and both estates have many thatched properties in close proximity.
Acidic grasslands

The occurrence of *L. gemmascens* in acidic grassland was first reported by Driver (1982). It was discovered in 1980 growing on the rotting bases of grasses and rushes on Patmore Heath, Hertfordshire. It occurs in rather botanically dull, unmanaged *Festuca-Rumex* grasslands (NVC U1) (Fig. 5), growing on the decaying leaf bases of a number of grasses, often heavily shaded, including *Arrhenatherum elatius*, *Festuca rubra* and *Deschampsia cespitosa*, and at its coastal site near Dunwich it occurred on dead leaves of *Elphiahgia atherica* (Richard Fisk, pers. comm.). It has also been reported on the decaying basal stems of *Juncus effusus*, *Rumex acetosella* and on a burnt hawthorn stump (Driver, 1982), on stems of *Ulex europaeus* (Adams, 1982), and on *Carex arenaria* and on gorse litter at Barnham Cross Common (Fred Rumsey, pers. comm.). It is sensitive to heavy grazing as this prevents the development of decaying litter and detritus. Rabbits are a feature on most grasslands and are associated with grasslands dominated by *L. gemmascens*. It is occasionally found growing on rabbit droppings (Hill et al., 1992; Fred Rumsey, pers. comm.). Associated bryophytes in these grasslands include *Aulacomnium palustre*, *Bryum rubens*, *Campylopus pyriformis*, *Ceratodon purpureus*, *D. scoparius*, *Hypnum juniperinum*, *Lophocolea bidentata*, *Toluidia natans*, *Polystichum juniperinum* and *Ptilidium ciliare*.

In continental Europe, *L. gemmascens* occupies similar habitats, typically on decaying tussocks of *Festuca ovina* agg. and *Deschampsia flexuosa*, often on gentle south-west-facing slopes in anthropogenically disturbed grassy-heath sites succeeding to shrub-dominated communities, but it also occurs on *Festuca* tussocks dispersed around rock outcrops in more natural sites, often amongst widely scattered oak trees (Schneider et al., 1998; Werner & Sauer, 1994).

On the sub-Antarctic Marion Island, *L. gemmascens* is associated with grasslands dominated by *Poa coodeii*, where it grows on the decaying bases of tussocks. It is common in coastal areas, from sea level to about 100 m, in eutrophic sites that are strongly affected by birds (trampling by penguins, nesting petrels) and manuring by marine mammals (Ryszard Ochyra, pers. comm.).

Conservation

The decline of *L. gemmascens* in some parts of Britain has been noted, but it is more difficult to be equivocal about its rarity in the past compared with today, particularly in view of the lack of early records from grassland. It was known on thatch from Hurstpierpoint, Sussex, from 1845 (first British record) to 1906. At Amberley, Sussex, it was first reported in 1857 with a succession of records up to 1975, spanning a period of 119 years. It is possible that a decline in *L. gemmascens* records from thatch set in long before bryological recording began. There is evidence of thatch in the Neolithic, and eventually it became the most widespread roofing material on many types of structures, particularly during the medieval period. A general decline in thatch began in the late 18th century, and continued through the 19th and 20th centuries, all but collapsing in the late 1940s and 1950s as a result of shortages of good quality straw, rising labour costs, the availability of cheap alternatives, and loss of skilled craftsmen in two world wars (Letts, 2001). However, the thatching industry has not disappeared; it is estimated that about 24,000 listed buildings in England are thatched (English Heritage, 2000), and new thatched buildings are still being built, for example in Dorset. Thatching practises have also changed, particularly in recent times. There was a phase of replacing wheat straw with reed, although this is now discouraged, and the entire coat was replaced rather than the more traditional practise of repairing patches or strips. Today, thatched buildings are often isolated, with implications for the dispersal and establishment of *L. gemmascens*. Writing at the end of the 19th century, Braithwaite (1887) did not see any cause for concern: ‘Although it disappears with the removal of the thatch, when this has been renewed and is passing into decay, *L. gemmascens* is certain to reappear’. The reappearance or occurrence of *L. gemmascens* today is not so certain.

Today, many thatched buildings are owned and managed by the National Trust (NT) and thus they are key players in the conservation of thatch moss (only two buildings on which *L. gemmascens* is currently known to occur are not NT properties). In 2006, the NT became joint Lead Partners under the UK BAP with Natural England to ensure that thatch moss is taken into account when buildings need to be repaired. The Trust’s *Building Manual* states that surveys for thatch moss should wherever possible be incorporated into the quinquennial review building’s survey process. Where the moss occurs on private properties, there is limited scope to carry out survey or conservation action, other than persuasion. There are various instruments a Local Authority can use to ensure thatch on buildings is preserved, such as the Town and Country Planning (Listed Buildings and Conservation Areas) Act 1990, and advice within Planning Policy Guidance 15, Annex C29, which states, amongst other things, that re-thatching should normally be done in a form of thatch traditional to the region. However, these mechanisms are not aimed at conserving moss or biodiversity in general.

Management

The NT, in consultation with Master Thatcher and English Nature (now Natural England) has produced guidelines for the management of thatched properties, aimed at the conservation of *L. gemmascens*. Briefly, this advocates the traditional practise of repairing and patching, and re-thatching of the entire roof system should be avoided. It is recognized that the commonly held and recent perception that ‘good’ thatch consists of a uniform even-aged pristine coat is an issue that the NT in particular will need to handle carefully. The use of galvanized wire netting (but see above) and the pre-treatment...
of thatch material with fire retardants should also be avoided. Campylopus introflexus, which can become dominant on a roof, can be lightly raked off. This has been successful on Hardy’s Cottage (Fig. 3), where following raking off of this species, L. gemmascens increased, presumably from gemmae lodged in the thatch coat, although C. introflexus also eventually grew back. There is as yet no agreement as to whether a covering of moss on a thatched roof does more harm by retaining moisture than it does good by forming an extra coating to the thatch (English Heritage, 2000).

Semi-natural grasslands present a quite different challenge. Often such acidic, heathy grasslands are neglected, and the build up of litter then makes them vulnerable to damage by fire. Grazing is seldom practised on these sites, and if fire does not destroy the site, development of scrub soon shades out L. gemmascens. Extensive grazing is the ideal regime to attain the fine balance that allows some litter and detritus accumulation, whilst at the same time keeping scrub in check. Rabbits are beneficial, but control of their numbers and grazing pressure is notoriously difficult.

**Translocation**

There are occasions when it will be necessary to repair a thatched roof, or part of, and this may lead to the loss of L. gemmascens. Although it is the view of the statutory conservation agencies that the relocation of species is not an acceptable alternative to *in situ* conservation, it is recognized that species translocations can help to reverse declines of threatened species. Where damage is inevitable, translocation following established guidelines (IUCN, 1995; McLean, 2003) is seen as a legitimate conservation activity.

At Alfriston Clergy House, colonies of L. gemmascens were threatened by the necessary replacement of thatch on the north aspect, and the opportunity was taken to experiment with a translocation method (Porley, 2005). In October 2005, I, working closely with a thatching consultant and with the support of the NT, relocated seven discrete colonies of L. gemmascens from the north aspect (Fig. 6) to the east-facing hip end. An existing small colony on the east hip end confirmed that conditions were favourable.

Using iron hooks, sheathes of thatch were very carefully drawn from the donor coat with L. gemmascens attached to their butt ends. To accommodate the transplants, the hip end coat was opened with iron hooks and the intact thatch sheaths were fed into the gaps (Fig. 7). To act as ‘permanent’ markers for each transplant, microchips embedded in a plastic nail were driven into the ends of drilled willow rods, which were in turn fed into the coat along the lie of the thatch. Monitoring in November 2006 showed that all seven transplanted colonies of L. gemmascens had survived, although it will be necessary to monitor the outcome for a number of years to come. The technique, if successful, may be applied to other buildings where L. gemmascens is at risk; alternatively other translocation methods could be tested, such as using suspensions of gemmae or gametophytic material from *ex situ* cultures.

**Ex situ conservation and genetic variation**

L. gemmascens (from Wortham Ling and Barnham Cross Common) has been deposited in a cryopreservation facility at Royal Botanic Gardens Kew following the development of innovative methods for the initiation of *in vitro* axenic bryophyte cultures (Rowntree, 2006). In addition, DNA has been deposited in the RBG Kew DNA bank. This material provides a valuable resource for future re-introductions and investigations into the biology of L. gemmascens. RBG Kew has also applied AFLP genetic fingerprinting techniques to assess the genetic diversity present in material from Wortham Ling.
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Barnham Cross Common and Hardy’s Cottage. The results indicated a higher than expected level of diversity among and within the populations, and a UPGMA analysis of the AFLP data showed that samples from the same population group together and that the populations are differentiated from each other. Conservation of the species should therefore involve ex situ culture of samples from a range of populations to ensure the genetic diversity of L. gemmascens is captured (Smith et al., 2007).

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Leukotrien (Musci, Pottiaceae), nieuw voor de Belgische mooslfa. Dierwetens 50, 16–21.


This is a companion volume to PLANTATT, and provides for all British and Irish species a codified set of attributes for use in ecological analyses. These include information on native status, size, life form, life history, altitudinal and geographical range, and habitat of 1,057 British and Irish bryophyte species, and a further 134 aggregates and infraspecific taxa. Much of the information is newly compiled, or generated after this publication. Ellenberg values for light, moisture, nitrogen and salt tolerance are provided for all taxa. A new classification of the life forms is proposed and applied to all taxa. Their substrates and EUNIS habitats in Britain and Ireland are also tabulated.

The publication is now available to download in two parts on the CEH website at www.ceh.ac.uk/products/publications/bryoatt.html. The tables will be updated from time to time. For a full review of BRYOATT, see Journal of Bryology, vol. 30, part 1, p. 100.