

THE NATURAL HISTORY OF  
SLAPTON LEY NATIONAL NATURE RESERVE  
XX : THE CHANGING BRYOPHYTE FLORA.

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ABSTRACT

An annotated list of 197 mosses and liverworts recorded in the Slapton Ley National Nature Reserve is given together with a description of the main features of bryological interest in the individual Reserve units. A further 29 bryophytes from neighbouring habitats are also mentioned. Bryophyte diversity at Slapton is high compared with other similar coastal sites due to considerable habitat diversity. The flora is rich in Mediterranean and Atlantic elements. Bryophyte indicators of ancient woodland are few indicating that the woodlands are all of recent origin; however, Burlestone Wood outside the Reserve is of exceptional conservation value. The study is based on two independent surveys performed at an interval of twenty years. An analysis of the changes occurring over this period indicates that woodland species have increased, probably due to scrub encroachment and extension of the carr areas, while some species of open habitats have declined. Two alien species, *Orthodontium lineare* and *Campylopus introflexus*, have invaded or increased greatly and the sand dune moss *Tortula ruralis* ssp. *ruraliformis* has colonised and spread on the shingle ridge over the past two decades.

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## INTRODUCTION

The aim of this paper is to provide an account of the bryophytes occurring in the Slapton Ley National Nature Reserve which will be useful to future visitors to the Field Centre. We also believe that detailed studies on the floras of small areas, in this case a locality in the extreme south of England, can be of value as 'samples' for assessing the effects of environmental conditions on plants at a larger scale. This study of the bryophyte flora is based on two surveys carried out with an interval between of approximately twenty years. In this paper, we describe the bryophyte flora and its ecological relationships and also give an assessment of changes which have occurred between the two surveys.

The bryophytes (Division Bryophyta) comprise two large groups of land plants, the mosses (Class Bryopsida) and the liverworts (Class Hepaticopsida), plus a very small group, the hornworts (Class Anthocerotopsida). There are estimated to be around 20,000 bryophyte species worldwide which makes them numerically superior to the living gymnosperms, ferns and lycopods but vastly inferior to the flowering plants. Corley & Hill (1981) list 689 species of mosses, 284 liverworts and 3 hornworts in the Britain Isles which, collectively, possess one of the richest bryophyte floras in Europe.

Bryophytes are characterised by a life cycle in which the dominant green plant, the gametophyte, gives rise by sexual reproduction to an attached and usually short-lived (long-lived in hornworts) spore-producing structure, the sporophyte. Water is critically important, both to facilitate fertilisation and also because most bryophytes are unable to exploit water stored in the soil (Proctor, 1981). Many species exhibit true desiccation tolerance and can resume metabolism rapidly when re-moistened after drought, whereas others are sensitive to desiccation and are restricted to permanently wet habitats (Proctor, 1981, 1982). A wide range of adaptations for water conservation occurs including microscopic and macroscopic capillary structures which trap water and the colonial organisation of shoots which retards evaporation from leaf surfaces (Proctor, 1982, 1984; During, 1990). Except in the case of peat bogs, where *Sphagnum* mosses may dominate, bryophytes generally form minor components of communities dominated by vascular plants. However, because they lack roots they can exploit hard substrata such as rock and bark which are generally unavailable to higher plants. Useful introductory texts on bryophytes have been provided by Richardson (1981) and Schofield (1985). Watson's (1981) *British Mosses and Liverworts* is an excellent flora for beginners and gives details on collection, microscopic examination and preservation of specimens. More advanced students will find the two floras by Smith (1978, 1991) invaluable. They may also wish to consult the *Journal of Bryology* which contains papers dealing with all facets of the subject.

Slapton Ley NNR lies approximately 8 km east of Kingsbridge in the South Hams District of South Devon (vice-county 3) and, with the other sites studied here, occupies 10-km square SX 84 of the British National Grid (Fig. 1). Mercer (1966) gave a morphological description of the Reserve and devised a system of recording units which has formed the framework for later studies (Fig. 2). The focal point of the 188 ha Reserve is a freshwater lake, Slapton Ley, which is separated from the sea by a shingle ridge. The lake is divided by a causeway and road bridge into the open Lower Ley and the smaller and largely overgrown Higher Ley. The Reserve also includes the lower slopes of the hinterland (to 99m altitude) and areas of woodland extending inland along the valleys of the lake's feeder streams. Much of the Reserve lies on slates belonging to

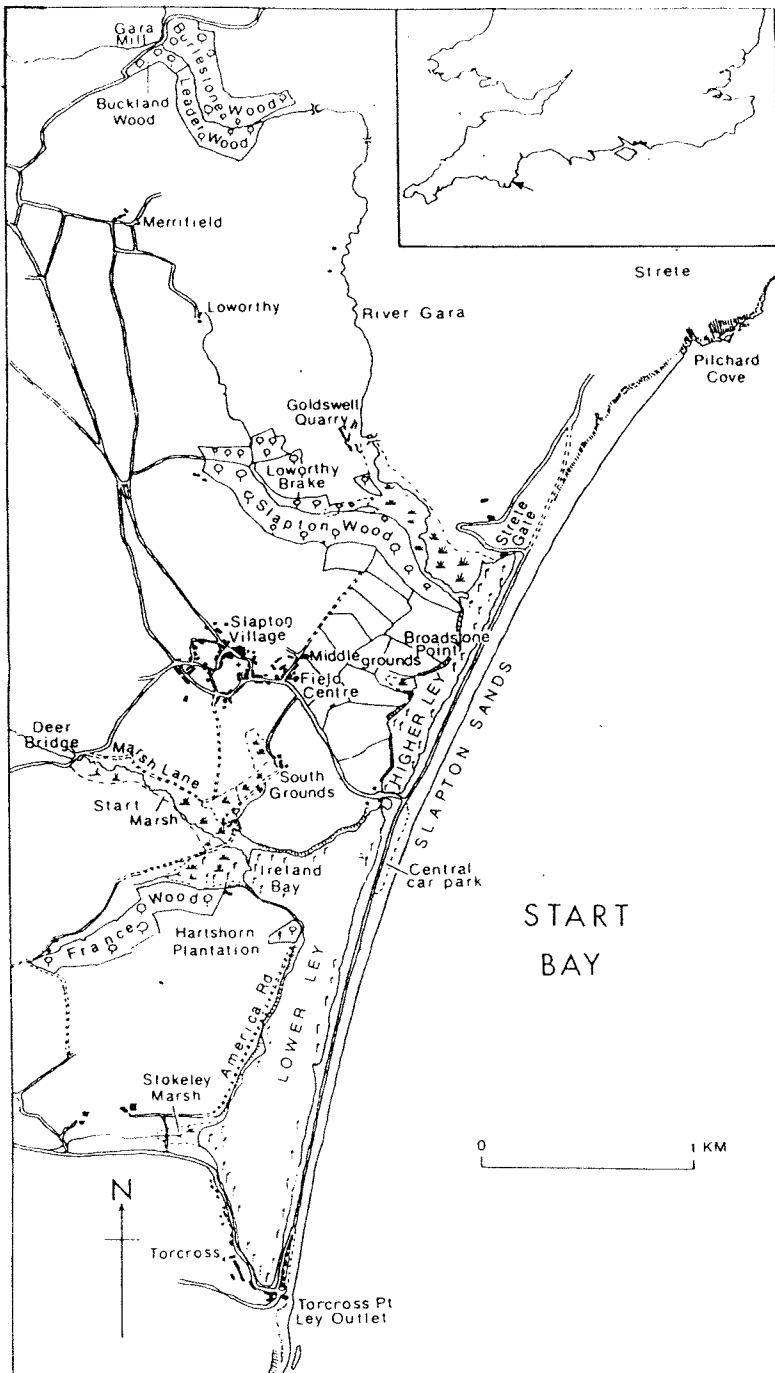


FIG. 1.

Map of Slapton Ley National Nature Reserve and of other sites mentioned in the text. Inset shows the position of Slapton (arrow) in southern Britain.

the Lower Devonian Meadfoot Beds, but an area of Permo-Triassic breccias and sandstones is exposed in Slapton village and forms the southern part of the inner shore of the Higher Ley and underlies South Grounds. The northern part of Slapton Wood lies on the Dartmouth Slates, also of Lower Devonian age. Low cliffs of periglacial 'head' and some harder rocks are exposed on the inland side of the Ley but there are no extensive rock outcrops in the Reserve. Trudgill (1983) described the soils of Slapton Wood, which are acid and nutrient poor with a high content of silt-sized particles and slate fragments. Brown earths predominate but brown podzolic soils occur on the north-facing slopes and are marked by the frequent occurrence of *Luzula sylvatica* (great woodrush). Soil pH values in Slapton Wood vary between 3.8 and 4.6, depending on type and horizon, but are higher (5.6–6.1) on alluvium in the valley bottom and values to pH 6.5 have been recorded in other parts of the Reserve (e.g. Brookes & Burns, 1969). Dolerite outcrops occur at Torcross Point just south of the Reserve and also form a series of basic cliffs and outcrops in the ravine of the River Gara at Burlestone and Leader Woods. The shingle ridge is composed mostly of gravel and coarse sand derived from acidic rocks and there is flint which must have come from East Devon or Dorset (Mercer, 1966). Numerous shell fragments are also present.

The climate at Slapton Ley, described by Ratsey (1975) from recordings made at the Field Centre from 1960–1973, appears to have a more equable temperature than other sites in South Devon. Mean air temperatures for the coldest month (February) and warmest month (July) were 5.7°C and 15.8°C, respectively. The proximity of the sea buffers the effects on temperature of low solar radiation in autumn and winter. Slapton is relatively frost free with air frosts recorded on an average of 22 occasions each year but on as few as 8 occasions in some years. High average temperatures in winter mean that the potential growth season (days when air temperature exceeds 6°C) lasts from early March until Christmas. The annual average rainfall is relatively high at 1056 mm and there are 135 wet-days (days with  $\geq 1$  mm) per annum on average. Precipitation is evenly spread throughout the year but tends to be heaviest in the winter. The most frequent winds are from the south-west (20.8%), west (20.5%) and north-east (15.9%). Mercer (1966) suggested that Slapton tended to experience fogs when adjacent areas were clear, however, Ratsey (1975) concluded that Slapton had little fog. Studies of the lichen flora by Hawksworth (1972) indicate that atmospheric pollution, at least by the highly phytotoxic sulphur dioxide, is insignificant.

Little bryological exploration was undertaken in the Slapton area until the opening of the Field Centre and there are no entries among the Devon bryophyte records of Barnes (1958). Records made in the late 1950s and early 1960s, principally by B. S. Brookes, Mrs. J. A. Paton, Dr. F. Rose, P. J. Wanstall and Dr. H. L. K. Whitehouse, are held on a card index at the Field Centre. Others, stored at the Biological Records Centre at Monks Wood Experimental Station, were made by bryologists participating in the British Bryological Society's Mapping Scheme. Some references to bryophytes, mainly common species, occur in earlier papers in this series, particularly Brookes & Burns (1969), Hawksworth (1972, 1986) and Ing (1976).

The present study is based on two separate surveys conducted by different personnel. The first detailed survey was undertaken by ARP during visits in 1965, 1966, 1967 and 1972 (hereafter called the earlier survey). The second was made by JWB, sometimes accompanied by MCFP, during short visits as follows: 11–13 March 1990, 25–27 October 1990, 24–26 March 1991, 18–20 September 1991, 4–7 March 1992. Additional records by MCFP were made during bryological courses held at the Field

Centre between August 1990 and August 1993. A detailed list of the records made in the 1990–1993 survey has been deposited at the Field Centre together with a comprehensive herbarium of bryophytes collected in the Nature Reserve and its environs.

#### DESCRIPTION OF HABITATS

The areas sampled for bryophytes (see Fig. 2) include the working units devised by Mercer (1966) and four habitat units (Causeway; Slapton village; Duck Marsh; Slapton churchyard) added by Hawksworth (1972). Some modifications were made to conform with current usage (Anon, 1988): South Grounds Marsh (G3) and South Grounds Meadow (O) partly replace Hawksworth's unit S, also, Duck Marsh is now usually referred to as Start Marsh and recoded G4 instead of DM. The wooded slope on the east side of South Grounds Marsh is separated as a discrete woodland unit: South Grounds Wood (SGW). Also, the masonry of Slapton Bridge, the roadbridge which separates the Higher and Lower Leys, is regarded as an additional mini unit (SB). For purposes of comparison of the bryophytes found in the Slapton Ley Nature Reserve with those in the surrounding landscape, two neighbouring habitat units are included: the Burlestone Wood Complex (BURL) and Goldswell Quarry (Q). Battleford Wood, an outlying Reserve unit, has not been covered in previous papers in this series and was not studied.

#### Shingle Ridge

No bryophytes occur on the mobile Seaward Face (A) of the shingle ridge; however, *Tortula muralis* grows sparingly on limestone blocks placed close to Torcross in about 1980 as part of the sea defences. These effectively extend the Crest to Torcross and the *Tortula* is best included in that unit.

The Crest (B) is a sparsely vegetated shingle platform lying entirely on the seaward side of the A379 road. Amongst low turf and on bare patches of fine shingle the only conspicuous mosses (particularly in winter when the vascular plants die back) are *Brachythecium albicans* and *Bryum capillare*. These are accompanied by smaller quantities of common species including *Barbula convoluta*, *B. unguiculata*, *Bryum argenteum*, *B. bicolor*, *Eurhynchium praelongum* and *Hypnum cupressiforme*. The dune moss *Tortula ruralis* ssp. *ruraliformis* occurs in scattered localities along the Crest whilst *Scleropodium tourettii* and *Barbula hornschurchiana* are rarer in trampled turf near the Slapton Bridge road junction. These plants must cope with severe summer desiccation. Rubble from the Royal Sands Hotel, accidentally blown-up during the D-Day training exercises, formerly provided a habitat for several bryophytes including *Pottia crinita* and *Trichostomum brachydontium* which have not been seen in the Reserve recently. The rubble was removed in 1971 when the central car park was extended. More recently a large quantity of red loam has been introduced to landscape the car park, and trampled patches bear the weedy species *Funaria hygrometrica* (formerly absent) and *Pottia truncata*.

The Backslope (C) extends inland from the A379 road to the reedswamp fringing the Higher and Lower Leys. In trampled areas on pathways, and where steeply banked against the road, the bare shingle carries a similar bryophyte flora to the Crest. *Scleropodium tourettii* grows in a few places but is uncommon. *Rhynchostegium megapolitanum* is known from its only site on the Reserve on heaped shingle midway between Slapton Bridge and Torcross. *Bryum dunense* was recently discovered here and



is also likely to occur on the Crest. The presence on the Backslope of *Riccia sorocarpa* and the abundance of *Barbula cylindrica* are perhaps indicative of a greater humus content and moisture retentiveness and a lower pH than on the more unstable shingle soils of the Crest. Elsewhere the Backslope is covered by tall herbaceous vegetation or scrub of *Rubus fruticosus* (bramble), *Prunus spinosa* (blackthorn), *Sambucus nigra* (elder) and young *Fraxinus excelsior* (ash) which is periodically cut. This is densest by the Lower Ley due east of Hartshorn Plantation where several bushes exceed 6 m height. Extensive patches of *Ulex europaeus* (gorse) scrub occur on ridges, presumably of leached shingle, south of Slapton Bridge. Several calcifuge bryophytes grow in low turf associated with these *Ulex* areas including *Ceratodon purpureus*, *Hypnum jutlandicum*, *Polytrichum juniperinum*, *Dicranum scoparium*, *Campylopus introflexus* and *Cephaloziella divaricata*. Lusher grassland, particularly where lightly shaded by the road embankment near to Strete Gate, supports *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus*, *Plagiomnium affine* and *Hypnum cupressiforme* var. *lacunosum* which are all rare or absent elsewhere on the Reserve. The ground below scrub, however, supports only the ubiquitous *Eurhynchium praelongum* and *Brachythecium rutabulum*. A reasonably rich epiphytic bryophyte flora clothes the more sheltered boles and branches of *Fraxinus* and especially *Sambucus* close to the Ley margin. *Tortula papillosa* and *T. laevipila* var. *laevipiliformis* are currently unknown elsewhere in the Reserve.

### Slapton Ley

Aquatic bryophytes are absent from the open waters of the Higher Ley (D) and the Lower Ley (E). However, several species are associated with the islands of *Salix cinerea* (common willow) carr in the Higher Ley or grow in the Ley-side fringes (D1–2; E1–6).

Information on the bryophytes of the Higher Ley islands is limited because of restricted access to boats, due mainly to the discontinuous nature of the open water areas. The bryophytes fall into two categories, species inhabiting the wet floor (peat, litter, mud) of the carr and epiphytes on the trunks and branches of the *Salix* trees. The first group includes bryophytes which are also common in the marshes, e.g. *Amblystegium riparium*, *Brachythecium rivulare*, *Eurhynchium speciosum*, *Plagiomnium ellipticum*, *Chiloscyphus polyanthos* and *Lophocolea bidentata* var. *bidentata*. The uncommon moss *Plagiothecium ruthei* is not infrequent here on rotten stumps and the thalloid liverwort *Riccardia chamedryfolia* is rare on bare peat. Neither species has been recorded elsewhere in the Reserve recently. *Sphagnum subnitens* was recorded here in 1972 but has not been found again. The *Salix* bushes on the islands support epiphytes which are generally common on the Reserve including *Hypnum cupressiforme* (vars. *cupressiforme* and *resupinatum*), *Ulota crispa*, *U. phyllantha*, *Zygodon viridissimus*, *Cololejeunea minutissima*, *Frullania dilatata* and *Lejeunea ulicina*. Several species are indicative of a sheltered and woodland-like environment (e.g. *Isoetecium myosuroides*, *Neckera complanata* and *Metzgeria temperata*) although they are growing only a few hundred metres from a relatively windswept coast. The flora of the northernmost Higher Ley islands is still completely unknown. As it is possible that the islands encapsulate a successional time-sequence, there is an argument for improving access to enable further exploration.

The shores of the Higher and Lower Ley are defined as the zone between the winter water mark and summer wading depth (Mercer, 1966). The presence of bryophytes depends, to a large extent, on the exposure to wave action which, in turn, controls the development of *Phragmites australis* (common reed). On exposed shores of the Lower

Ley lacking *Phragmites* reedswamp, bryophytes (e.g. *Amblystegium tenax*, *Scleropodium cespitans*) are largely limited to the surfaces of slate exposures, as in parts of E2 and E4. Generally, however, the emergent outcrops become covered in a mat of filamentous green algae which inhibits colonisation by mosses. Along most shores of the Higher Ley, and on many stretches of the Lower Ley, a dense reedswamp is established, e.g. D1 and E1, and few bryophytes have been discovered. An exception occurs where sallow carr has invaded and suppressed the growth of *Phragmites*. The Lower Ley Inner Shore (E4) and Torcross West Shore (E6) units are good examples and this habitat also extends along the Higher Ley Inner Shore (D2). The moss *Bryum pseudotriquetrum* grows on a peaty bank in the latter unit, its only locality in the Reserve. The common marshland species *Amblystegium riparium* thrives on the bare mud and is associated, on permanently wet tree roots and bases, with *A. serpens* and the similar and easily overlooked *A. varium*. A rich epiphyte flora occurs on the upper boles and branches of the *Salix* and resembles that of the marshes (see below). *Scleropodium cespitans* and *Leskea polycarpa* are local but particularly characteristic of the intermittently-flooded tree bases. They must tolerate periods of intense desiccation when the water level falls. The other epiphytes do not grow directly in the zone of fluctuating water level but, strictly, occupy a habitat unit not present in the Mercer (1966) scheme. Nevertheless, judging by their silt encrustations, some epiphytes (e.g. *Metzgeria fruticulosa*, *Zygodon conoideus* and *Isoetecium myosuroides*) tolerate inundation on the lower boles in winter when the water level rises.

### Marshes

Marshes have formed in bays on the landward side of Slapton Ley where streams or springs enter and deposit their silt load. From an ecological viewpoint large areas of the "marshes" are, technically, "carr" woodland which is dominated by sallow and *Alnus glutinosa* (alder) and frequently contains some ash. Tall tussocks of *Carex paniculata* (tussock sedge) commonly dominate the swampy floor of the carr. This community now dominates Slapton Wood Marsh and Carr (F1) in the delta of the Slapton Wood Stream and Little Marsh (F2) (contrast Mercer, 1966). Carr also occupies parts of France Wood Marsh (G1), Stokeley Marsh (G2), South Grounds Marsh (G3) and Start Marsh (G4). Elsewhere *Phragmites* reedswamp covers large areas (e.g. G4) or, where the water table is lower, *Oenanthe crocata* (hemlock water dropwort), *Epilobium hirsutum* (great hairy willow-herb) and other tall herbs form a rank vegetation cover (e.g. parts of G2). Bryophytes are normally absent from the latter type of community but occur sparingly in reedswamp and more abundantly in carr.

In reedswamp, the characteristic marshland bryophytes *Amblystegium riparium* and *Brachythecium rivulare* are the only frequent species. *Calliergon cordifolium*, *Plagiomnium ellipticum* and *Eurhynchium speciosum* are local in this habitat and *Drepanocladus aduncus* was recorded once on wooden boardwalk sleepers in F2. The marshland species are most abundant where *Salix* bushes are invading the reedswamp and create a "hole", at least in winter, in the dense *Phragmites* canopy. Most of the marshland species also grow on mud in carr where they are joined by species of tree bases (e.g. *Amblystegium varium*) and by those inhabiting rotten logs (e.g. *Rhizomnium punctatum*). A luxuriant epiphytic flora occurs on *Salix* in carr although it is clearly poorer in species and inferior in cover to the lichen flora. Common species include *Hypnum cupressiforme* var. *resupinatum*, *Orthotrichum diaphanum*, *O. tenellum*, *Rhynchostegium confertum*, *Frullania dilatata* and



*Metzgeria furcata*. *Ulotrichum phyllanthae* and *Cololejeunea minutissima* are particularly conspicuous in the more exposed areas such as Stokeley Marsh and France Wood Marsh. In more sheltered areas, *Cryphaea heteromalla*, *Lejeunea ulicina*, *Metzgeria fruticulosa* and *Radula complanata* achieve luxuriance and *Ulotrichum crispum* is most plentiful. *Orthotrichum lyellii* reaches greatest luxuriance in sheltered carr in G4 near Deer Bridge where it is associated with markedly acidophilous lichens.

The Causeway (CY) unit (Hawksworth, 1972) separates G4 and E3. In the past, the main interest was a line of mature *Populus* (poplar) trees but these have mostly vanished. The uncommon epiphytic moss *Pterogonium gracile* was seen here in 1967 but had gone by 1972. Only the commoner epiphytic bryophytes now grow on the predominating *Salix*. The moist grassy path is one of the few sites in the Reserve for *Calliergon cuspidatum* and *Rhytidiadelphus squarrosus*. The common marshland species grow on tree roots, litter and mud at the edges of the Causeway and *Riccardia chamedryfolia* formerly occurred. Old mortared stonework of the bridge parapet has *Bryum capillare*, *B. radiculosum*, *Rhynchostegiella tenella*, *Tortella nitida* and *Tortula muralis*. *Scleropodium cespitosum* fringes the base of one of the stone gateposts at the northern end of CY.

### Leyside Fringes

These comprise the low cliffs on the inland side of Slapton Ley. They are formed, in many places, from relatively soft 'head' deposits and, more locally, from solid slate, sandstone or breccia. The cliff profile varies considerably depending on the geology, and in a few places there are freshwater seepages. The steeper 'head' exposures are frequently too unstable for colonisation by bryophytes. Badger setts and other animal burrows create areas of disturbed soil and shaded niches which favour some bryophyte species. Dense scrub of bramble and blackthorn makes access to many areas difficult. Mature *Acer pseudoplatanus* (sycamore), *Quercus robur* (pedunculate oak) and ash occur on the cliff slopes or else overhang them in many places and, together with elders, support numerous epiphytes. Patches of bare earth and slaty rubble are common on the cliffs. Shaded soil pockets sometimes harbour *Bryum sauteri*, *Epipterygium tozeri*, *Calypogeia arguta*, *C. fissa*, *Fissidens bryoides*, *F. taxifolius* and *F. viridulus*. Woodland species, which grow where there is deeper shading by trees, include *Dicranella heteromalla*, *Eurhynchium praelongum*, *E. pumilum*, *Isopterygium elegans*, *Mnium hornum*, *Thamnobryum alopecurum*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Lejeunea lamacerina* and *Lophocolea heterophylla*. *Schistostega pennata* was discovered by virtue of its strikingly luminescent protonema ("goblin gold") in the entrance to an animal burrow in I3. *Fissidens incurvus* and *Brachythecium populeum* formerly grew on slate outcrops in I2 but have now disappeared, possibly due to overgrowth of the stones or greater shading.

The hard rock exposures do not support a rich flora of epilithic bryophytes because of their limited extent and the effects of shading. The only truly epilithic species is *Grimmia trichophylla* var. *subsquarrosa* on the sandstone slabs at Broadstone Point (H) but it has not been seen recently.

Few strongly desiccation-sensitive species inhabit the Leyside cliffs but *Pellia epiphylla* grows sparsely on flushed 'head' in I3. *Conocephalum conicum* and *Lunularia cruciata* extend upwards from the water level where vertical cliffs rise directly from the Higher Ley in H/D2. The cliffs comprise a drier habitat than the woodlands and probable summer drought damage of *Mnium hornum* and *Conocephalum conicum* has been observed in I2 and H/D2, respectively.

### Woodland

The comments of Mercer (1966) and Burton and Mercer (1978) indicate that none of the woods in the Reserve is likely to represent ancient woodland (*sensu* Rackham 1986). All occur on steep slopes and the important France Wood and Slapton Wood complexes also include streams and present a wealth of humid, bryophyte-rich habitats.

The Slapton Wood complex (J) houses a larger number of bryophyte species than any other Reserve compartment (see Table 6). The Main Wood (J1) is on a steep north to north-east facing slope. *Castanea sativa*, originally planted, still dominates but *Quercus robur* is numerous together with *Fagus sylvatica* (beech), *Fraxinus excelsior* and *Acer pseudoplatanus*. The ground flora is richest on steep banks of acidic slatey clay by tracks. Common species include *Atrichum undulatum*, *Dicranella heteromalla*, *Eurhynchium praelongum*, *E. pumilum*, *Fissidens bryoides*, *Isopterygium elegans*, *Mnium hornum*, *Plagiothecium nemorale*, *Pogonatum aloides*, *Polytrichum formosum* (local), *Thuidium tamariscinum*, *Calypogeia arguta*, *C. fissa*, *Pellia epiphylla* and *Plagiochila asplenoides*. The rare moss *Schistostega pennata* is frequent in deeply shaded earth niches by the upper ride and was also seen with sporophytes on vertical earth exposed where a tree had toppled downhill. Recently disturbed soil on uprooted tree roots experiences a succession of colonisation in which *Pogonatum aloides*, *Dicranella heteromalla* and *Atrichum undulatum* are early colonisers whilst *Hypnum jutlandicum*, *Isopterygium elegans* and *Polytrichum formosum* appear to be later arrivals. In moist areas, *Eurhynchium striatum*, *Hookeria lucens* and *Conocephalum conicum* are abundant while *Rhynchostegium riparioides* occurs on stones in a flush. Rotten logs support *Brachythecium rutabulum*, *Campylopus paradoxus* (rare), *Dicranum scoparium*, *Eurhynchium praelongum* var. *stokesii*, *Isopterygium elegans*, *Plagiomnium undulatum*, *Rhizomnium punctatum*, *Cephalozia lunulifolia*, *Lepidozia reptans*, *Lophocolea bidentata* and *L. heterophylla*. The invasive alien moss *Orthodontium lineare* has been known on logs here for over 30 years but remains scarce. The only recent record of *Plagiothecium undulatum* in the Reserve is from a log in J1. A few small slate outcrops occur in the eastern area and support many of the species of banks plus *Plagiothecium denticulatum* and *Lejeunea lamacerina*. The latter grows occasionally on stones, logs and tree boles. *Heterocladium heteropterum* var. *flaccidum* has only been seen on a stone on the lower boundary bank.

The semi-aquatic moss *Brachythecium plumosum* is only known in the Reserve from wet sloping stones on a steep track. The epiphytic flora is rather poorly developed due to the deep shade in summer but *Hypnum cupressiforme* var. *resupinatum*, *Metzgeria furcata*, *Neckera pumila*, *Ulota crispa* and *Frullania dilatata* are frequent and *Isothecium myosuroides* clothes the trunks of mature trees to a height of several metres. *Ulota phyllantha* was recorded on the upper trunk of a fallen ash. Well-lit elders on the western edge have luxuriant *Cryphaea heteromalla*, *Cololejeunea minutissima* and *Radula complanata*.

The most conspicuous development of bryophytes in the Reserve occurs in Valley Bottom Scrub (J2) particularly along the banks of the Slapton Wood Stream. Mature ash trees grow along the banks and in places provide a lighter shade than in the Main Wood. Several old elder bushes survive here together with *Corylus avellana* (hazel) but they are mostly overtopped by mature sycamore trees and the scrub-like nature of the unit is less apparent than formerly. Many woodland species also found in J1 luxuriate on the clay banks of the stream in association with *Eurhynchium swartzii*, *Isothecium myurum*, *Neckera complanata*, *Thamnobryum alopecurum* and *Lejeunea lamacerina* on tree bases and stones. *Hookeria lucens* and *Conocephalum conicum* are strikingly abundant; the

former often has sporophytes and the latter has occasionally been found with slender mushroom-like female receptacles bearing hanging capsules in spring.

Despite the high humidity, the moisture-demanding *Heterocladium heteropterum* var. *flaccidum* has only been seen in small quantity on a deeply shaded old stone wall by the stream. *Dicranum majus* and *Nowellia curvifolia* were recorded here on logs in the earlier survey; *Dimajus* still persists, *Nowellia* has been seen recently only in J1. Several bryophytes grow on stones in the stream or on concrete or gritty detritus at the edges including *Amblystegium tenax*, *Brachythecium rivulare*, *Fissidens crassipes*, *Rhynchostegium riparioides*, *Chiloscyphus polyanthos* and *Pellia endiviifolia*. Most of these species are indicative of moderate base enrichment of the water despite the predominantly acidic soils hereabouts. So too is *Aneura pinguis*; its only Reserve locality is a marshy clearing by the stream near the bottom of the compartment. The combination of shelter and moderately good illumination favours a luxuriant epiphytic flora in which *Neckera pumila*, *Ulota crispa* and its var. *norvegica*, and *Metzgeria* spp. are prominent and *Lejeunea lamacerina* is not infrequent on mossy bark. *Orthotrichum striatum* was once recorded here but has not been seen recently.

Loworthy Brake (J3) faces south-west and is one of the driest and most acidic compartments of Slapton Wood (soil pH 3.8). Mature *Castanea* and *Fagus* form the main canopy and there is only a poorly developed shrub layer. *Abies* sp. (fir) has been planted in the north-western part where previously *Pinus sylvestris* (Scots pine) was present (Brookes & Burns, 1969). The sparse ground flora contains a few common calcifuge and relatively drought-insensitive mosses including *Hypnum jutlandicum*, *Mnium hornum*, *Isoterygium elegans* and *Dicranella heteromalla*. The moss *Polytrichum formosum*, which has well-developed internal water conducting tissues, is more abundant here than elsewhere in the Reserve. One of the most interesting habitats is the steep bank of the upper ride where the above species are common and *Calypogeia* spp., *Diplophyllum albicans*, *Lepidozia reptans*, *Pellia epiphylla*, *Atrichum undulatum* and *Pogonatum aloides* are frequent. Shoots of *P. aloides* often became blackened here as a result of summer drought.

The most interesting plant in J3 is *Leucobryum juniperoides* whose conspicuous cushions occur sparingly on the steep woodland slope on logs and litter under *Castanea*, its only Reserve locality. *Leucobryum* species possess leaves in which the living photosynthetic cells are surrounded by large, dead, water-storing cells which give the plants some protection against drought. The closely related *L. glaucum* requires relatively warm conditions for growth (Bates, 1989a), a requirement amply met in J3 because of its southerly aspect.

The epiphyte flora of the *Castanea* trunks is poor and is dominated by *Isothecium myosuroides* and *Hypnum mammillatum*. *Lejeunea ulicina* occurs sparsely intermixed with the latter.

In the 1960s, Square Brake (J4) was an impenetrable scrub of blackthorn and *Euonymus europaeus* (spindle tree) with few bryophytes. It now consists of a more open woodland with hazel, mature ash, sycamore and *Ilex aquifolium* (holly). The bryophyte flora bordering the Slapton Wood Stream is a continuation of that found in identical situations in J2. Woodland bryophytes are frequent in the centre of the compartment and *Eurhynchium striatum* is particularly abundant. The epiphytic flora on ash and sycamore away from the stream includes *Cololejeunea minutissima*, *Radula complanata*, *Zygodon viridissimus* and abundant *Cryphaea heteromalla*.

Eastergrounds Brake (J5) is a very varied unit containing mature woodland, streamside and open scrub areas. A rich epiphytic flora occurs, particularly at the

western edge on elders. *Isoetecium myosuroides* grows to 1.5 m on exposed boles of sycamore here. *Neckera pumila* and *Cryphaea heteromalla* are abundant on sycamore boles in more sheltered parts. Fallen sycamore trunks support *Homalothecium sericeum* and *Brachythecium velutinum*. *Lejeunea lamacerina* is common on holly roots and stones on the northern boundary bank and by the Slapton Wood Stream. A ditch on the southern side contains several drought-sensitive species including *Conocephalum conicum*, *Pellia epiphylla*, *Plagiochila asplenioides*, *Epipterygium tozeri*, *Hookeria lucens*, *Plagiomnium undulatum*, *Rhizomnium punctatum* and *Thamnobryum alopecurum*. Many of these also grow by the main stream. Despite its small size, this is a bryologically rich unit with 68 taxa recorded.

The Gara Valley Triangle (J6) is an isolated unit on a north-east facing slope above the Gara valley. It is a steep rocky woodland with mature oak, sycamore and some ash, holly and elders, especially near the bottom of the slope. The main interest centres on small shaded slate outcrops which are mostly covered with *Isoetecium myosuroides*, *Mnium hornum* and *Eurhynchium praelongum*. Seedlings of the wall pennywort (*Umbilicus rupestris*) thrive on this mossy covering. *Isopterygium elegans* is abundant on soil in crevices. *Plagiothecium undulatum* occurred formerly but has not been found again. However, *Lejeunea lamacerina* and *Heterocladium heteropterum* var. *flaccidum*, previously unknown here, are now present.

France Wood (K) occupies a roughly north-west facing valley side with a stream (France Wood Stream) at its lower edge. *Castanea* is the dominant tree but many other species occur and *Fraxinus* and *Acer* are regenerating vigorously in gaps. The exposed eastern parts of the wood suffered badly from the severe storms in October 1987 and early 1990 when many over-mature *Castanea* fell. The increase in illumination has stimulated bramble growth to such an extent that access into the wood is virtually impossible in summer, a situation which is exacerbated by the negligible use currently made of this unit. Many of the bryophytes found in Slapton Wood also occur here but often in smaller quantities owing to the drier microclimate. Thus the moisture-loving *Pellia epiphylla*, *Plagiochila asplenioides*, *Hookeria lucens*, *Plagiomnium undulatum* and *Thamnobryum alopecurum* are scarce and *Thuidium tamariscinum* is absent. However, several of these species are locally plentiful on the clay banks of the stream where *Conocephalum conicum* and *Eurhynchium pumilum* are particularly abundant. *Pogonatum aloides* is noticeably commoner on the bank of the main ride in the lush western part of the wood than in the more exposed eastern section.

Several mosses, formerly recorded on banks by the main ride, now appear to be absent; these include *Bryum microerythrocarpum*, *Dicranella rufescens*, *D. schreberana*, *Ditrichum cylindricum*, *Pohlia lutescens* and *Pseudephemerum nitidum*. These species are probably dependent on the regular exposure of fresh soil surfaces and may, therefore, be victims of the current low management regime. Rotten logs abound and in moist areas near the stream *Nowellia curvifolia* occurs on decorticated logs together with *Lophocolea heterophylla*, *Cephalozia bicuspidata* and *Orthodontium lineare*. The latter appears to be a recent colonist here. *Isoetecium myurum* and *Neckera complanata* are frequent on living tree bases and newly fallen trunks. *Dicranum scoparium*, formerly unknown here, occurs on logs provided by the recent storms.

The epiphytic flora is not luxuriant owing to the high exposure, shade and scarcity of elders but the rare moss *Leptodon smithii* is perhaps more frequent here on mature *Acer* and *Fraxinus* than in any other Reserve unit.

Hartshorn Plantation (L) occupies a promontory overlooking the Lower Ley and is

fully exposed to sea breezes. It suffered considerable damage from American shelling during 1943 (Mercer, 1966). Today it is composed mainly of *Acer pseudoplatanus* with some *Castanea* and a few *Fagus* and *Fraxinus* trees. Old *Pinus sylvestris* and some recently planted saplings predominate at the top of the wood and mature *Sambucus* inhabits clearings between these. The small slate outcrops of this steep rocky woodland are mostly overgrown with *Hedera helix* (ivy) and support few woodland bryophytes. The same is true of the low cliff in the quarry near the bottom where, formerly, *Brachythecium populeum* grew. The site is now heavily shaded by mature *Acer*. *Lejeunea lamacerina* still survives here. *Hypnum cupressiforme* var. *resupinatum* and *Metzgeria furcata* are the only common epiphytes on the largely bare boles of the sycamores.

A richer epiphytic flora occurs on *Salix* in a marshy foreland continuous with the base of the wood and also on elders amongst the pines. The former includes abundant *Ulotrichum phyllanthae* and *Cololejeunea minutissima* plus *Orthotrichum lyellii* and *O. pulchellum* whilst *O. tenellum* is present on both host trees. Interestingly, elders growing directly beneath *Pinus*, a conifer with strongly acidic bark, support only a film of algae.

In this exposed site, the flora of rotten logs is limited and dominated by *Hypnum cupressiforme* var. *resupinatum* and *Lophocolea heterophylla*. However, one partially decomposed log yielded *Plagiothecium latebricola*, not known elsewhere in the Reserve, and *Orthodontium lineare*.

South Grounds Wood (SGW) lies within the Reserve and consists of a long strip of *Acer pseudoplatanus*-dominated woodland on a north-west-facing slope which is terminated by a quarry. The unit is not recognised in previous papers in this series but it is referred to in the Reserve management plan (Anon, 1988) and possesses an interesting woodland bryophyte flora. Most of the trees are immature and recent coppicing has been carried out in one area but the presence of old stumps indicates some continuity of woodland at this site. *Orthodontium lineare* on old stumps is more abundant here than elsewhere, and *Dicranum scoparium*, *Orthotrichum lyellii*, *Pogonatum aloides*, *Cephalozia bicuspidata* and *Diplophyllum albicans* are all present and infrequent in the Reserve.

The Burlestone Wood complex (BURL) lies 1.5 km north of the Reserve in the valley of the River Gara below Gara Mill. It is included as an example of a valley woodland with a rich ravine flora of a type not found in the Reserve woods but likely to be of considerable interest to bryologists visiting the Field Centre. The unit is composed of three privately owned woods: Burlestone Wood which is mainly south-west facing; Leader Wood which is mainly north-east facing; and Buckland Wood which is also north-east facing. The River Gara here flows through a ravine with cliffs largely of basic dolerite exposed on either bank.

The constantly humid microclimate and irrigated basic rock exposures enable a luxuriant development of common woodland bryophytes which surpasses anything seen in the Reserve. Also, several moisture-demanding and base-demanding species occur which are mostly absent from the Reserve flora. These include the liverworts *Frullania tamarisci*, *Lophocolea fragrans*, *Marchesinia mackaii*, *Plagiochila killarniensis*, *P. porelloides*, *Porella arboris-vitae*, *Saccogyna viticulosa* and the mosses *Bartramia pomiformis*, *Cynodontium bruntonii*, *Dicranum majus*, *Diphyscium foliosum*, *Fissidens cristatus*, *Grimmia hartmanii*, *Oxystegus tenuirostris* and *Rhytidiadelphus loreus*. The River Gara also supports *Fissidens rivularis* and *Porella pinnata* which are both absent from the Reserve. The flora is dominated by moderately base-demanding bryophytes and contrasts markedly with the type of flora found in upland valley woodlands around Dartmoor where calcifuges predominate (Proctor, 1964; see later discussion).

### Fields

The status of the small Reserve fields has changed considerably since they were first described by Mercer (1966).

Little Marsh Field (M) was once cultivated but now consists of rough grassland with recently planted broadleaf saplings. The old earth and stone hedgebank formerly supported *Cirriphyllum crassinervium* and *Tortula subulata* but is now rather overgrown and the most interesting species remaining is *Epipterygium tozeri*.

Among the Stokeley Fields (N), Ireland Field (N1) is now considerably overgrown with bramble and young sycamore and merges into France Wood. It is of negligible bryological interest. Hartshorn Fields (N2) were previously arable and usually barley was grown. On 19 August 1966 the arable weed flora recorded here on slatey clay soil (pH 6.3) included *Fossombronina pusilla*, *Barbula fallax*, *B. unguiculata*, *Bryum microerythrocarpum*, *Dicranella rufescens*, *D. schreberiana*, *D. varia* (possibly *D. staphylinia*), *Ditrichum cylindricum*, *Eurhynchium swartzii*, *Phascum cuspidatum* and *Pottia truncata*. These fields are now pasture and bryophytes are mainly limited to bare trampled patches where only *Brachythecium rutabulum*, *Bryum rubens*, *Ceratodon purpureus*, *Dicranella staphylinia*, *Eurhynchium praelongum* and *Pottia truncata* have been seen recently.

America Road and Fields (N3) was also previously arable land with barley as the usual crop and a small arable field bryophyte flora. It has long been abandoned and now consists of immature and rather impenetrable woodland with low bryological interest. Moist soil on and by the track and around the roots of fallen trees has produced *Riccia glauca*, *Bryum rubens*, *B. rudérale*, *Dicranella schreberiana*, *D. staphylinia*, *Fissidens viridulus*, *Funaria fascicularis*, *Pohlia carnea* and *Pottia truncata*. Some interest is provided by the trackside epiphytes on *Fraxinus*, *Sambucus* and *Salix* but *Leptodon smithii* and *Tortula laevipila* var. *laevipiliformis* have vanished with the loss of the elms.

Peasdish (N4) is the only remaining arable unit in the Reserve. In August 1966, *Barbula unguiculata*, *Bryum rubens*, *Dicranella schreberiana*, *Ephemerum serratum* var. *minutissimum*, *Fissidens bryoides* and *Pottia truncata* were present on soil under barley. Recently, bryophytes have only been observed among grass in the field gateway and include *Bryum violaceum*, not known elsewhere in the Reserve.

South Grounds Meadow (O) is a marshy meadow which grades into G3. It is dominated by tall vascular species including *Juncus*, *Epilobium*, *Equisetum* and grasses, and contains no bryophytes. Bryophytes on the bank by the footpath include *Pleuroidium acuminatum* and *Weissia controversa* which are uncommon elsewhere.

### Slapton Village

The ancient stone walls and rock cuttings exposed in the village, together with earth in gardens and by roads, provide habitats for several interesting bryophytes. On stone walls, the common species are *Amblystegium serpens*, *Barbula convoluta*, *B. tophacea*, *B. trifaria*, *B. unguiculata*, *Grimmia pulvinata*, *Homalothecium sericeum*, *Hypnum cupressiforme* var. *resupinatum*, *Orthotrichum anomalum*, *Rhynchostegiella tenella*, *Schistidium apocarpum*, *Tortella nitida*, *Tortula intermedia*, *T. muralis*, *Zygodon viridissimus* and *Porella platyphylla*. Much rarer are *Barbula revoluta* and *Scorpiurium circinatum* seen on the roadside wall on the south-east side of the Field Centre.

*Brachythecium rivulare*, *Conocephalum conicum* and *Lunularia cruciata* grow in village streamlets whilst *Amblystegium tenax* was found on stones under a fountain. *Grimmia trichophylla* var. *trichophylla*, seen on a slate wall top, is the only markedly calcifuge

species found on stone. These habitats have not been exhaustively explored and further additions are likely.

#### Slapton Church

The churchyard contains shaded grassland and a wealth of calcareous and some siliceous stone surfaces. The partly-shaded turf supports the grassland mosses *Pseudoscleropodium purum* and *Rhytidiadelphus squarrosus* which are uncommon in the Reserve.

Shaded calcareous stonework of the deep gutter around the church has *Barbula recurvirostra*, *B. rigidula*, *B. vinealis*, *Calliergon cuspidatum*, *Cirriphyllum crassinervium*, *Rhynchostegium confertum*, *Thamnobryum alopecurum*, *Zygodon viridissimus* and *Frullania dilatata*. *Tortella nitida*, *Tortula intermedia* and *Porella platyphylla* are more widespread and pick out the mortar between the slate stones. A large population of *Trichostomum crispulum* was observed on the cement coping of the retaining wall on the east side of the churchyard. *Dicranoweisia cirrata* is the only species restricted to siliceous stone.

#### Goldswell Quarry

This abandoned slate quarry lies 0.25 km north of J6. It has been excavated in the wooded east facing valley slope of the lower River Gara. The main reason for its inclusion is that a survey of its interesting bryophyte flora was made in 1966 and considerable changes have taken place since. A series of cliff terraces constitute the back of the quarry and much loose slate lies about in unstable scree-like heaps.

The quarry is now enveloped in woodland and contains a luxuriant woodland bryophyte flora in which *Eurhynchium striatum* and *Thuidium tamariscinum* are particularly abundant. The moist quarry walls are covered in growths of *Eurhynchium praelongum*, *Isopterygium elegans*, *Isothecium myosuroides*, *Thamnobryum alopecurum*, *Thuidium tamariscinum* and *Plagiochila asplenioides*. Where seepages occur, *Fissidens cristatus*, *Lejeunea lamacerina* and *Lophocolea bidentata* var. *bidentata* are frequent and *Isothecium myurum*, *Cirriphyllum crassinervium*, *Homalia trichomanoides* and *Hookeria lucens* are not infrequent. Very wet cliffs locally support *Rhynchostegium riparioides* and *Oxystegus sinuosus*.

The most interesting bryophytes are *Lophocolea fragrans*, which occupies a low and deeply shaded stretch of damp cliff, and *Metzgeria conjugata*, found in a single overhung cliff niche and not seen elsewhere in this survey. In the earlier survey, *Ctenidium molluscum*, *Dicranoweisia cirrata*, *Grimmia pulvinata*, *Polytrichum juniperinum* and *Ptychomitrium polyphyllum* were also reported. Most of these have probably been lost due to shading as the woodland canopy has developed. *Brachythecium populeum* and *Homalothecium sericeum* were recently found in the only remaining area of well-illuminated cliff.

## THE FLORA

The scientific names used and the order of the species follows Corley & Hill (1981) for mosses and Smith (1991) for liverworts. A natural arrangement has been preferred because many bryophyte orders have distinctive ecological features and useful information is lost if genera are alphabetically ordered (Bates, 1991).

A list of the habitat units in which the taxon was recorded follows the scientific name. An entry in italics (e.g. *J1*) indicates that the plant was not found in the most recent (1990–1993) survey; normal type (e.g. *J1*) means that the plant was seen recently but not during the earlier (1965–1972) survey; bold print (e.g. **J1**) denotes that it was found in both surveys. It should be noted that units CH, G3, O, SGW and SV were not examined in the earlier survey.

An asterisk precedes the name if the plant has not been recorded within the Reserve which, for this purpose, includes all units except Burlestone Wood and Goldswell Quarry. Sometimes records are listed for sites outside these units and the abbreviation ENV, for environs, is used. If a plant was formerly recorded in the Reserve but was not found again during the recent survey, the name is preceded by a dagger (†).

If a species has not been seen recently, or it is rare, the earliest record is given. In most cases, a brief general statement about status at Slapton is provided or, for uncommon taxa, a list of localities. This is based on the results of the 1990–1993 survey except where otherwise stated. If sporophytes were recorded, this is always mentioned.

## HEPATICOPSIDA

## Jungermanniales

*Lepidozia reptans* : **BURL**; *J1*, 2, 3; **K**.  
Scarce, forming large patches on rotting logs in sheltered woodland.

\**Calypogeia mulleriana* : **BURL**.  
Only in Burlestone Wood, no recent record.

*Calypogeia fissa* : **BURL**; *D*; *H*; **J1**, 2, 3, 5, 6; **K**; *Q*.  
Clay banks in woodland and soil-filled crevices in shaded cliffs; formerly on litter on an island in the Higher Ley.

*Calypogeia arguta* : **BURL**; *F2*; **H**; *I2*, 3; **J1**, 2, 3, 4, 5, 6; **K**.  
Frequent on clay in woodland, by tracks, on stream banks and in the entrances of animal burrows; also on 'head' cliffs by the Ley and on *Carex paniculata* tussocks in Little Marsh.

\**Trichocolea tomentella* : **BURL**.

Leader Wood, F. Rose, August 1959. Not found again in either survey.

*Cephalozia bicuspidata* : **BURL**; *H*; **J1**; **K**; *SGW*  
Infrequent on sheltered Ley-side cliffs, banks, paths and rotting wood in sheltered woodland where seen once with perianths and once with sporophytes.

*Cephalozia lunulifolia* : **BURL**; *J1*, 2, 3.  
Locally abundant on logs and stumps in humid woodland, twice seen with perianths.

*Nowellia curvifolia* : *J1*, *J2*; **K**.  
Very rare on decorticated rotting logs near streams in woodland. With perianths in Slapton Wood; with gemmae in France Wood.

*Cephaloziella divaricata* : **C**.  
In short turf and amongst *Campylopus introflexus* on trampled acid ground on Backslope south of Slapton Bridge.



*Jungermannia gracillima* : J1.

Clayey soil of path with *Calypogeia arguta* and *Cephalozia bicuspidata*. Male plants only.

*Diplophyllum albicans* : BURL; H; J1, 3, 5, 6.

Locally abundant on 'head' and sandstone cliffs by the Ley and on clay banks and rock outcrops in woodland. Sporophytes seen in Eastergrounds Brake and on a cliff in Buckland Wood.

*Lophocolea bidentata* var. *bidentata* :

BURL; C; CY; D; F1, 2; G1, 2, 4; H; J1, 2, 3, 4, 5, 6; K; L; M; N1; Q; SGW.

Common in woodland on rotten wood, soil (especially stream banks), rocks and tree bases. Also mixed with *Hypnum jutlandicum* in turf on Backslope. Only noted with sporophytes in humid woodland.

*Lophocolea bidentata* var. *rivularis* :

BURL; C; D; G1, 3, 4; J1, 5; K; Q. Formerly much confused with var. *bidentata* and, possibly, over-recorded in the earlier survey. Rare amongst grasses and on mud and litter in marshy places.

*Lophocolea heterophylla* : BURL; CY; D2; F1, 2; G2, 4; H; I2, 3; J1, 2, 3, 4, 5, 6; K; L; M; N3; SGW.

Abundant on rotting wood and frequent on shaded soil in woodlands. Also on *Salix* bark and on litter in marshes. Sporophytes common in spring.

\**Lophocolea fragrans* : BURL; Q.

Plentiful on shaded boulders and rock outcrops in Leader Wood (with perianths), less so in Burlestone Wood (with sporophytes); locally common on a moist and deeply

shaded cliff in Goldswell Quarry.

*Chiloscyphus polyanthos* : BURL; D; F1, 2; J2, 4, 5.

Attached to stones in Slapton Wood Stream and the River Gara; also on rotten wood, *Salix* bases and litter in marshes. Sporophytes observed once only.

\**Saccogyna viticulosus* : BURL.

Rare on shaded rocks by the River Gara, Leader Wood. In October 1990 young green shoots were regenerating from a mat of bleached shoots presumably injured by the 1990 summer drought.

\**Plagiochila killarniensis* : BURL.

Locally abundant on steep faces of dolerite outcrops in a ravine of the River Gara, Leader Wood and Burlestone Wood.

†*Plagiochila porelloides* : BURL; J?.

Unspecified compartment(s) of Slapton Wood, "M.S.F.", 1959; H.L.K. Whitehouse, 1960; J. A. Paton, 1961; not seen in later surveys. Frequent on cliffs and boulders in Burlestone Wood and Leader Wood.

*Plagiochila asplenoides* : BURL; F1; G3; J1, 2, 5, 6; K; Q.

Locally abundant on banks and streamsides in humid woodland; festooning wet cliffs in Leader Wood and Burlestone Wood.

*Radula complanata* : BURL; C; D, 2; E6; G1, 4; J1, 2, 4, 5; K; N3; SGW.

An infrequent epiphyte of *Salix*, *Corylus*, *Sambucus*, *Fraxinus* and, rarely, *Quercus* in sheltered woodland and carr; formerly on a slate wall in Duck Marsh. Occasionally with perianths. Locally abundant on

young *Acer* in Burlestone Wood where with sporophytes.

\**Porella arboris-vitae* : **BURL**.

Locally plentiful on shaded dolerite cliffs by the River Gara, Leader Wood; scarcer in Burlestone Wood.

*Porella platyphylla* : **BURL**; **CH**; **SV**.

Commonly forming large patches on mortared stone walls around the village; in stone gutter at base of the church wall.

\**Porella pinnata* : **BURL**.

Very rare, extensive colony on a large boulder in the River Gara, Burlestone Wood.

\**Frullania tamarisci* : **BURL**.

Occasional on *Corylus*, *Fraxinus*, mossy logs and rock in ravine, Burlestone Wood and Leader Wood, with perianths

*Frullania dilatata* : **BURL**; **C**; **CH**; **CY**; **D**, 1, 2; **E1**, 4, 6; **F1**, 2; **G1**, 2, 3, 4; **H**; **I1**, 2, 3; **J1**, 2, 3, 4, 5, 6; **K**; **L**; **N1**, 3; **O**; **SGW**.

An abundant epiphyte, particularly on *Acer* and *Salix*, but recorded on all common broadleaf species and *Ulex europaeus* in both sheltered woodlands and exposed situations. Also on a shaded stone wall of Slapton church. Often deep purple in well-lit conditions. Perianths abundant, sporophytes seen twice.

\**Lejeunea cavifolia* : **BURL**.

On well-lit dolerite outcrops near top of steep NE-facing slope, Leader Wood.

*Lejeunea lamacerina* : **BURL**; **F1**; **G4**; **H**; **I2**; **J1**, 2, 4, 5, 6; **L**; **Q**.

Locally abundant on deeply shaded stones, old walls and cliffs in humid

places. Also recorded on sticks, clay streambanks and the bark of *Ilex*, *Quercus*, *Ulmus*, *Fraxinus*, *Corylus* and *Acer* in woodland. Often associated with *Heterocladium heteropterum* var. *flaccidum*. Perianths frequent, sporophytes occasional.

*Lejeunea ulicina* : **BURL**; **CY**; **D**, 2; **E6**; **F1**; **G1**, 2, 4; **H**, **I3**; **J1**, 2, 3, 4, 5; **K**. Frequent on boles of *Salix*, *Castanea*, *Acer*, *Ilex*, *Sambucus*, *Prunus* and *Quercus*, often growing amongst other bryophytes. Mainly in woodland and more sheltered, landward parts of the Reserve.

*Cololejeunea minutissima* : **C**; **CY**; **D**, 1, 2; **E1**, 6; **F2**; **G1**, 3, 4; **H**; **I1**, 2, 3; **J1**, 4, 5; **K**; **L**; **SGW**.

A common and often abundant epiphyte on *Salix* and *Alnus* in exposed carr and margins of the Ley. Also on *Acer*, *Fraxinus*, *Sambucus*, *Prunus* and, formerly, *Ulmus* at exposed margins of woodland. Usually with perianths and with gemmae but rare or absent sporophytes observed.

\**Marchesia mackaii* : **BURL**.

Several colonies on a well-lit but north-east-facing dolerite cliff face at top of Leader Wood.

## Metzgeriales

*Fossombromia pusilla* : **G4**; **K**; **L**; **N2**; **SV**.

Formerly, on shaded clay in woodland and also in arable land and grass leys adjacent to the Reserve. Recently, only seen on damp soil in Marsh Lane and on an earth bank by Wood Lane. Sterile plants cannot be identified without spores but they will quickly produce capsules if kept moist on a cool window-ledge.

*Pellia epiphylla* : **BURL**; D; **F1**; G2, 4; **I3**; **J1**, 2, 3, 5; **K**.

Locally abundant on continuously moist clay, humus and peat in woodland and carr. Also scarce around seepages on 'head' cliffs by the Lower Ley. Sporophytes frequent in sheltered woodland, dehiscing in February/March.

*Pellia endiviifolia* : **BURL**; **F1**; G4; **J2**, 4, 5.

On stones in streams and on muddy streambanks in woodland.

*Aneura pinguis* : J2.

Unspecified compartment(s) of Slapton Wood: "M.S.F.", 1959; H. L. K. Whitehouse, 1960; J. A. Paton, 1961; unrecorded in earlier survey. Several large patches on gritty mud in open marshy area on north side of Slapton Wood Stream near bottom of J2.

*Riccardia chamedryfolia* : **CY**; D.

Very rare. Formerly on rotting stump in reedswamp by Causeway. Recently seen on a peat lump at the edge of an island in the Higher Ley.

<sup>†</sup>*Riccardia palmata* : J?.

Damp rotten trunk with *Rhizomnium punctatum*, Slapton Wood, P. J. Wanstall, 1964, new to South Devon. Not found again in either survey.

*Metzgeria furcata* : **BURL**; **C**; CH; **CY**; **D**, 1, 2; **E1**, 4, 6; **F1**, 2; **G1**, 2, 3, 4; **H**; **I1**, 2, 3; **J1**, 2, 3, 4, 5, 6; **K**; **L**; **N3**; O; Q, SGW.

An extremely abundant epiphyte, recorded on all common broadleaf tree species in woodland and in the open. Occasional on logs, cliffs and old stone walls, sometimes in deep shade, e.g. on a wall in Slapton churchyard.

*Metzgeria temperata* : **BURL**; C; D; **F1**; **I3**; J5.

Not distinguished from *M.*

*fruticulosa* until Paton (1977a) pointed out that both species occur in Britain. Infrequent on *Acer*, *Salix*, *Sambucus* and *Betula* (Burlestone Wood) in scrub, carr and woodland. Once found intermixed with *M. fruticulosa*.

*Metzgeria fruticulosa* : **BURL**; **C**; **CY**; **D2**; **E1**, 3, 6; **F1**, 2; **G1**, 2, 3, 4; **H**; **I1**, 3; **J1**, 2, 5, 6; **L**.

Records from the earlier survey might include *M. temperata*; however, *M. fruticulosa* is considerably more abundant, so there are probably few errors. Common as an epiphyte of *Salix*, *Sambucus* and, more rarely, *Quercus*, *Corylus*, *Populus* and *Ulmus* in carr and humid woodland. Sometimes very abundant where high humidity is combined with good illumination. Tolerates occasional immersion on *Salix* bases in the Ley-side fringes.

\**Metzgeria conjugata* : **BURL**; **Q**.

Very rare. On rocks, Leader Wood, F. Rose, March 1962; not found again here. Small quantity on shaded overhanging cliff, Goldswell Quarry.

## Marchantiales

*Lunularia cruciata* : **BURL**; **CY**; **D2**; **E4**; **F1**, 2; **G4**; **H**; **I1**, 3; J2; **K**; **N1**, 3; O; SGW; SV.

Frequent on wet soil, logs, tree roots and stones by streams, on Ley-side cliffs and on tracks. Male inflorescences seen twice in earlier survey only.

*Conocephalum conicum* : **BURL**; D, 2; **F1**; **G1**; **I2**; **J1**, 2, 4, 5; **K**; SV.

Common and locally abundant on mud, stones and wood by streams and ditches and on banks in humid woodland. Growing directly on peat surface of an island in the Higher Ley. Extending 50 cm up from the surface of the Higher Ley on 'head' cliffs south of Little Marsh but many thalli here blackened, perhaps by drought in the previous (1989) summer. Archegoniophores with ripe sporophytes observed by Slapton Wood Stream in March 1967 and 1992.

*Riccia sorocarpa* : C.

Scarce on trampled soil on Backslope, south of Slapton Bridge. Formerly in a field outside Reserve at Middlegrounds.

*Riccia glauca* : G4; M; N3.

Only seen recently on damp soil amidst thin grass on paths, with sporophytes.

## ANTHOCEROTOPSIDA

### Anthocerotales

\**Phaeoceros laevis* : ENV.

Damp soil on shaded side of the entrance to a badger's sett in a field near the eastern extremity of Slapton Wood, Middlegrounds, with sporophytes, March 1967. Not found again.

## BRYOPSIDA

### Sphagnales

†*Sphagnum subnitens* : D.

Two patches on island in the Higher Ley, 1972. Not found again.

### Polytrichales

*Polytrichum formosum* : BURL; J1, 2, 3, 5, 6.

Local in woodland on well-drained acidic soils; occasionally on rotten logs. The largest populations occur on slopes of southerly aspect in Loworthy Brake (with sporophytes) and Burlestone Wood.

*Polytrichum juniperinum* : C; Q.

Within the Reserve, only amongst low vegetation on the Backslope; formerly in Goldswell Quarry.

*Polytrichum aloides* : I3; J1, 3, 5; K; SGW.

Clayey and slatey banks in sheltered woodland; often on soil heaps raised on roots of fallen trees; once on a slate wall. Sporophytes frequent, maturing in winter or early spring.

*Atrichum undulatum* : BURL; CH; F1; G2, 4; H; I1, 3; J1, 2, 3, 4, 5, 6; K; L; N1; Q; SGW.

Common on soil and rarer on rotting logs in woodland, also in crevices of sheltered Ley-side cliffs and in shaded turf of Slapton churchyard. Sporophytes recorded twice only but perhaps overlooked.

### Buxbaumiales

\**Diphyscium foliosum* : BURL.

Formerly recorded in Burlestone Wood; not found again.

### Dicranales

*Pleuridium acuminatum* : C; I1, 3; J6; K; O.

Exposed stony soil on paths and cliffs, also amongst thin turf on Backslope, and on disturbed soil beneath an animal burrow and around roots of fallen trees. Sporophytes abundant.

*Pleuridium subulatum* : O.

Bare soil on bank beside path. Very rare. With sporophytes.

†*Pseudephemerum nitidum* : K.

Slatey bank (pH 5) in France Wood; not found again.

†*Ditrichum cylindricum* : G2; K; N2, 3.

Formerly uncommon on clayey-slatey banks in France Wood, under crops in arable land and in tussocky grassland of Stokeley Marsh. Not found again in recent survey.

*Ceratodon purpureus* : B; BURL; C; CH; D; 2; F2; G2; I1, 2, 3; N2; O; Q; SB.

In a variety of habitats but nowhere common: short trampled turf on shingle ridge; pasture; stony banks; chippings on a tomb; tarmac; wooden boardwalk in the Higher Ley. Sporophytes not recorded but possibly overlooked.

\**Cynodontium bruntonii* : BURL.

Very rare on sheltered, wet cliff by River Gara, Leader Wood.

*Dicranella schreberana* : K; N2, 3, 4.

Rare, only seen recently in Reserve on soil around roots of a fallen tree by America Road and, outside Reserve, in stubblefield and pasture at Middlegrounds and near Loworthy Brake.

†*Dicranella rufescens* : G2; I3; K; N2.

Formerly uncommon on clayey-slatey banks in France Wood, on Lower Ley cliffs under *Rubus*, among grass tussocks in Stokeley Marsh and in arable fields outside the Reserve, with sporophytes. No recent record.

*Dicranella varia* : C; G2; I1, 3; K; M; N2, 3, 4.

Records made in the earlier survey

probably mainly represent *D.*

*staphylina* which was first described by Whitehouse (1969). The earlier records were from: the Backslope; soil on banks, cliffs and in arable fields; rough hummocky grassland in Stokeley Marsh. Only seen recently on an earth cliff by the Lower Ley.

*Dicranella staphylina* : E6; N2, 3.

Described as a new species by Whitehouse (1969). Recorded in Reserve on trampled soil in pasture, a trackside and on soil dug out of drainage ditch. Found outside Reserve in stubblefield at Middlegrounds.

*Dicranella heteromalla* : BURL; G2, 4; H; I2, 3; J1, 2, 3, 4, 5, 6; K; L; M; SGW.

Common on well-drained banks and on rotting logs and stumps in woodland; also occasional on soil on shaded Ley-side cliffs. Sporophytes frequent.

*Dicranoweisia cirrata* : CH; D2; I1; Q.

Very rare. Formerly in Reserve on planking of old landing stage in Higher Ley. Recently seen on a siliceous graveslab in the churchyard (with sporophytes) and as a single cushion on *Crataegus* in I1, with gemmae.

*Dicranum scoparium* : BURL; C; F1; J1, 2, 6; K; L; SGW.

Locally abundant on thinly vegetated areas of the Backslope and occasional in woodland, usually on rotting *Castanea* logs, but also on cliff ledges in Leader Wood. Sporophytes only seen in Leader Wood.

*Dicranum majus* : BURL; J2.

Rare on rotting logs near Slapton

Wood Stream. Seen outside Reserve on roadside bank at edge of Buckland Wood.

*Campylopus paradoxus* : **BURL**; J1, 2.

Rare, on rotten logs and a boulder in humid woodland.

*Campylopus introflexus* : C.

A recent addition to the flora of the Backslope where short plants are locally abundant on trampled, leached ground south of Slapton Bridge. Luxuriant plants with sporophytes seen on a large decorticated log.

*Leucobryum juniperoides* : J3.

Earlier records of *L. glaucum* probably belong here. About 20 cushions observed on humus and rotting wood on south-facing slope under *Castanea*. Sterile; identification based on size of hyaline cells on upper surface of leaf (see Corley & Hill, 1981, for details).

## Fissidentales

*Fissidens viridulus* : G2, 4; H; I1, 3; J1, N3; Q.

Uncommon on clay and slate banks and on Ley-side cliffs. Sporophytes occasional, February / March.

†*Fissidens incurvus* : I2, 3; J5; N3.

Formerly, rare in crevices of shaded slate on Ley-side cliffs and shaded clay streambank in Eastergrounds Brake, with sporophytes. Not found again but possibly overlooked as it cannot be named if sporophytes are lacking.

*Fissidens bryoides* : **BURL**; F1; G2, 3, 4; H; I1, 2, 3; J1, 2, 4, 5, 6; K; L; M; N3, 4; O; Q; SGW; SV.

Common on shaded earth in woodland and on the Ley-side cliffs; once on a rotten log. Formerly recorded in arable land under barley, and in grassland. Sporophytes common, ripening over winter-early spring.

\**Fissidens rivularis* : **BURL**.

Abundant on boulders submerged in the River Gara. Sporophytes common, observed at point of dehiscence on 27th October 1990.

*Fissidens crassipes* : **BURL**; E6; J2.

Rare on stones in an unshaded stretch of Slapton Wood Stream, with sporophytes. Earlier noted in the River Gara and on root of a fallen tree in the Higher Ley.

*Fissidens exilis* : **BURL**; J6.

Only seen in the Reserve in a small quantity on bare soil around an animal burrow, with sporophytes.

*Fissidens taxifolius* ssp. *taxifolius* :

**BURL**; E6; F1; G4; H; I1, 2, 3; J1, 2, 3, 4, 5, 6; K; M; N3, O; Q; SGW. Common on shaded earth and slaty rubble in woods, by streams and on cliffs; rare in pasture. Sporophytes uncommon, January to April.

*Fissidens taxifolius* ssp. *pallidicaulis* : J2.

At water level on concrete V-notch weir, Slapton Wood Stream. New to Devon. Under-recorded in Britain (T. L. Blockeel, *personal communication*).

*Fissidens cristatus* : **BURL**; Q.

Earlier records of *F. adianthoides* probably belong here. Locally abundant on damp shaded cliffs in Leader Wood, Burlestone Wood and Goldswell Quarry.

**Pottiales**

*Tortula ruralis* ssp. *ruraliformis* : B.

Not seen in the earlier survey but unlikely to have been overlooked. Several patches recorded recently on bare shingle scattered along the Crest from near Strete Gate to a point south of the central car park where vascular vegetation peters out.

*Tortula intermedia* : C; CH; SB; SV.

Rare on mortared stonework, e.g. roadside wall by entrance to Field Centre; very rare on shingle heaped up against the A379 road on Backslope.

*Tortula laevipila* var. *laevipila* : C; CY; E1, 4, 6; G2, 4; H; I1, 3; J5; N3; SB.

Occasional on *Sambucus*, *Fraxinus* and *Acer*; formerly recorded on *Populus*, *Salix*, *Alnus* and *Ulmus*; also on masonry of Slapton Bridge and on siliceous slabs at Broadstone Point. Sporophytes frequent.

*Tortula laevipila* var. *laevipiliformis* : C; E6; G2; N3.

A gemmiferous form, doubtfully distinct from var. *laevipila*. Only seen recently on a decrepit *Sambucus* on Backslope south of Slapton Bridge. Earlier records were from *Ulmus* and *Salix*.

*Tortula muralis* : B; BURL; C; CH; CY; E6; G4; H; I1, 2, 3; O; SB; SV.

Common on concrete and mortared walls; occasional on slate outcrops; sparsely present on limestone blocks used as sea defences at boundary of Crest and Face near Torcross. Sporophytes common.

<sup>†</sup>*Tortula subulata* : M.

A small colony formerly occurred on a sheltered part of the slate boundary wall around Little Marsh Field. No recent record.

*Tortula papillosa* : C; E1, 4, 6; G2.

Only seen recently on three *Sambucus* bushes on Backslope but possibly overlooked elsewhere as *T. laevipila*. Earlier, small populations were found on *Salix*, *Fraxinus*, *Populus*, *Alnus* and *Ulmus*.

\**Desmatodon convolutus* : ENV.

On soil-covered top of old stone wall on the seacliffs, Torcross Point, with sporophytes.

<sup>†</sup>*Pottia crinita* : B; C; ENV.

Formerly uncommon, in closely-worn turf and path on Crest and Backslope. Only seen recently outside the Reserve in earth-filled crevices of sea cliffs near Lower Ley outlet, Torcross Point, with sporophytes.

*Pottia truncata* : B; C; G2, 4; H; I1, 3; J2; K; L; M; N2, 3, 4; O.

Frequent on bare earth on paths, in pastures and on imported red loam on Crest in the central car park. Formerly frequent in arable fields but recently only seen in this habitat in a wheat stubblefield at Middlegrounds. Sporophytes abundant, dehiscing in late autumn.

\**Pottia recta* : ENV.

On soil in recently sown grass ley outside the Reserve at Middlegrounds. Not seen recently.

*Phascum cuspidatum* : C; I1; N2, 3.

Rare on bare earth on paths and banks in the Reserve and in pastures and a stubblefield just outside the

Reserve. Formerly on clay soil (pH 6.3) under cereals in the Reserve fields.

*Barbula convoluta* var. *convoluta* : **B**; **BURL**; **C**; **E6**; G2, 4; H; **I1**, 2; **M**; **N3**; SV.

Frequent on soil, often on paths, and mortared walls; usually in well-lit situations. Sporophytes recorded once.

*Barbula convoluta* var. *commutata* : **CY**; **E5**, 6; H; **I1**; **J1**; **N4**; **O**; SV.

Probably only a habitat modification. Occasional, in similar habitats to var. *convoluta* but most often found on moist masonry.

*Barbula unguiculata* : **B**; **BURL**; **C**; **CY**; **E6**; G3, 4; **I1**; **N2**, 4; **O**; SV.

Frequent on bare soil and shingle, especially where trampled, and on mortared stone walls but not on natural slate outcrops. Formerly recorded in arable crops and grass leys. Sporophytes only found once.

*Barbula revoluta* : **E6**; SV.

Very rare. Formerly on brickwork of culvert at Torcross. Recently seen in small quantity on cement coping of roadside wall outside the Field Centre.

*Barbula hornschurchiana* : **B**.

Rare in short turf on Crest near Slapton Bridge; formerly also on rubble of Royal Sands Hotel ruins.

<sup>†</sup>*Barbula fallax* : **C**; **K**; **M**; **N2**, 3.

Formerly occurred in grasslands and under grass-clover leys, also on clayey rides in woodland and path on Backslope. No recent records.

*Barbula rigidula* : **B**; **BURL**; **CH**; **E6**; **I1**.

Rare, on moist, shaded masonry; formerly on ruins of the Hotel.

*Barbula trifaria* : **CH**; G3; **O**; SV.

Uncommon on damp masonry and rocky banks; there are no earlier records.

*Barbula tophacea* : **B**; **E6**; H; **I1**, 3; **K**; **Q**; SV.

Infrequent on moist stones in a variety of situations, also on shingle and flushed 'head' cliffs.

*Barbula vinealis* : **B**; **CH**; **J2**; SV.

Rare, on stones and masonry.

*Barbula cylindrica* : **B**; **C**; **CY**; **E2**, 5, 6; **H**; **I1**, 2, 3; **J1**; **M**; **N3**; **O**; **SB**; **SGW**.

Common on soil, particularly at sides of tracks and on shingle, slate rocks and walls. Rarer but luxuriant on prostrate boughs and boulders on shaded margins of the Lower Ley.

*Barbula recurvirostra* : **CH**.

Only seen on shaded stonework of deep gutter around the church, with sporophytes.

*Weissia controversa* : **E5**; G4; **I1**, 3; **O**.

Uncommon on earth in cuttings, hedgebanks and on cliffs, with sporophytes, February / March.

\**Weissia microstoma* : **ENV**.

Formerly recorded just outside the Reserve under recently-sown grass at Middlegrounds, with sporophytes. Not found again but possibly overlooked as sporophytes are required for identification.

\**Weissia multicapsularis* : **ENV**.

Formerly recorded outside the Reserve under recently sown grass



crop at Middlegrounds and in pasture at South Grounds, with sporophytes, February. No recent records.

\**Oxystegus sinuosus* : Q.

Very rare, among *Thamnobryum alopecurum* and *Eurhynchium praelongum* on steep, irrigated rock face, Goldswell Quarry.

\**Oxystegus tenuirostris* : **BURL**.

Recently, seen only on stone in bank of old mill leat, Burlestone Wood.

*Trichostomum crispulum* : CH.

Locally abundant on cement coping of wall on east side of churchyard.

†*Trichostomum brachydontium* : B.

Formerly on stone in ruins of the Hotel. Not found again.

\**Tortella flavovirens* : ENV.

Earth-filled rock crevices just outside the Reserve on sea-cliffs above the Lower Ley outlet, Torcross Point.

*Tortella nitida* : **BURL**; CH; **CY**; E6; **G4**; SB; SV.

Locally plentiful on mortared slate walls and bridge parapets. On the church wall it occupies both shaded and well-lit sites but noticeably picks out the mortar in preference to the slate stones.

## Grimmiales

\**Schistidium maritimum* : ENV.

Occurs sparingly just outside Reserve in rock crevices at 10-15 m above mean sea level on sea-cliffs above the Lower Ley outlet, Torcross Point, with sporophytes. Further afield, it is frequent on rocks above high tide mark around Prawle and Bolt Head.

*Schistidium apocarpum* : **BURL**; CH; SV.

Occasional on mortared walls and asbestos tiles. In the churchyard, it colonised fresh cement wall cappings ahead of the other common species. Sporophytes common.

*Grimmia pulvinata* : **BURL**; CH; I1; Q; **SB**; SV.

Occasional on mortared walls but rare on natural slate outcrops. Sporophytes common, ripening in late spring.

*Grimmia trichophylla* var. *trichophylla* : SV.

Rare, on top of slate wall between village post office and church.

†*Grimmia trichophylla* var. *subsquarrosa* : H.

Formerly, recorded on siliceous slabs at Broadstone Point, 1972. Outside the Reserve, it is not infrequent on coastal rock exposures above the spray zone, e.g. at East Prawle and Bolt Head.

\**Grimmia hartmanii* : **BURL**.

Very rare, recently recorded from a single sloping boulder in Burlestone Wood. Gemmae not recorded in either survey.

\**Ptychomitrium polyphyllum* : Q.

Formerly, recorded in Goldswell Quarry, but not found again recently; presumably lost due to woodland encroachment.

## Funariales

*Funaria hygrometrica* : B; **BURL**; C; CH; E6; G2; K; O; SV.

Scarce and probably sporadic, on bare or disturbed soil, only seen

once on an old bonfire site.  
Sporophytes common.

*Funaria fascicularis* : C; M; N3.

Now rare in the Reserve: on bare earth in a cutting and around roots of a fallen tree, with sporophytes in spring; abundant in a stubblefield outside the Reserve at Middlegrounds. Formerly more frequent, occurring in arable land and pasture.

<sup>†</sup>*Physcomitrium pyriforme* : F2; G2; J?.

Unspecified compartment of Slapton Wood, J. A. Paton, 1961. Formerly, infrequent in marshy ground, with sporophytes. No recent record but probably overlooked as sporophytes are required for identification.

<sup>†</sup>*Ephemerum serratum*

var. *minutissimum* : N4.

Formerly in arable fields within and just outside the Reserve, with sporophytes in March and immature in August. Not found again.

### Schistostegales

*Schistostega pennata* : I3; J1, 2; K.

Locally abundant in niches in steep clay bank by the upper ride in Slapton Wood, where it is often overhung by tussocks of *Luzula sylvatica* and probably does not receive much direct rainfall. Rare elsewhere in pockets in steep, well-drained clayey earth, e.g. in mouth of shaded animal burrow on Ley-side cliff. Sporophytes found once, ripe in March.

### Bryales

*Orthodontium lineare* : J1 & ?; K; L; SGW.

First recorded in an unspecified compartment of Slapton Wood, H.L.K. Whitehouse, 1960 but evidently remained rare there and was not seen in the earlier survey. It is still local and rare on rotten logs and stumps in woodland but was present on at least five stumps in SGW. Sporophytes frequent and recorded at all sites, ripening in late spring.

*Pohlia lutescens* : I1; J6; K; L; M.

Rare on slatey earth banks under trees.

*Pohlia carnea* : BURL; N3, 4.

Rare on bare earth of track cutting, among grass and on bank of the River Gara.

*Pohlia wahlenbergii* : J1; K; Q.

Recently, seen on well-lit but moist section of gritty upper ride in Slapton Wood. Previously, recorded on a ride in France Wood (soil pH 5) and from Goldswell Quarry. Its sudden appearance, in a previously well-explored site in Slapton Wood, may have been triggered by unusually wet conditions in late summer 1991.

*Epipterygium tozeri* : BURL; G2, 4; H; I1, 3; J5, 6; K; L; M; SGW; SV.

Frequent, and sometimes locally abundant, on moist, shaded earth in hedgebanks, Ley-side cliffs, ditches and streamsides but uncommon in the main woodland areas, perhaps due to lack of fresh, well-drained surfaces to colonise. Sporophytes very rare: a single capsule, France Wood, March 1967.

*Bryum*

Plants of this large and taxonomically difficult genus are

frequent on the dry shingle ridge Crest and Backslope but they only rarely produce the sporophytes which are essential for identification. Both synoecious and dioecious taxa occur and it is likely that further careful study would add to the list given here.

*Bryum capillare* : **B**; **BURL**; **C**; **CH**; **CY**; **D**, 2; **E5**, **6**; **F1**, 2; **G4**; **H**; **I1**, **3**; **J1**, 4, 5, 6; **L**; **M**; **N3**, 4; **O**; **SB**; **SV**.

Common, on soil, logs and decaying wooden structures, mortared stone walls, concrete, brickwork; now epiphytic on *Salix* and *Sambucus* only, but formerly noted on *Quercus*, *Populus*, *Fraxinus* and *Ulmus*. Locally plentiful on the shingle ridge. Sporophytes infrequent, only noted in moist or shaded habitats.

*Bryum pseudotriquetrum* : **D2**.  
Peaty bank of Higher Ley under *Salix*.

*Bryum caespiticium* : **B**; **CY**.  
Among turf on Crest and formerly on a slate wall on the Causeway, with sporophytes Non-fruiting dioecious plants with longly tapering leaves on the shingle ridge may largely belong here.

*Bryum bicolor* : **B**; **C**; **E6**; **G4**; **H**; **I1**, 2, 3; **N3**, 4; **O**; **SB**.  
Widely dispersed on soil, shingle, crevices in slate rocks, tarmac and silted concrete by water. Usually, in well-lit but moisture-retentive situations.

*Bryum dunense* : **C**.  
Known from *B. bicolor* by its longly excurrent nerve and larger, solitary bulbils in the leaf axils. Very rare on shingle, Backslope south of Slapton

Bridge, but perhaps overlooked elsewhere as *B. bicolor*.

*Bryum argenteum* var. *argenteum* : **B**; **C**; **CY**; **G2**; **H**; **I1**; **N3**; **SB**; **SV**.

Characteristic of man-made habitats, occasional on earth and shingle paths, disturbed soil, tarmac, masonry and once on a wooden footbridge. Formerly, under cereals in America Fields.

<sup>†</sup>*Bryum argenteum* var. *lanatum* : **I1**.  
Found once only: on an exposed slate outcrop on the shore of the Lower Ley in August 1966.

*Bryum radiculosum* : **CY**; **E6**; **SB**.  
Rare, or overlooked, on mortared parapets and concrete sluice of the Lower Ley outfall.

*Bryum rudemale* : **G4**; **J6**; **N3**; **O**.  
Uncommon on soil on tracks and paths, among grass and around an animal burrow.

*Bryum violaceum* : **N4**.  
Found once only: among grass in entrance to an arable field, Peasdish.

*Bryum sauteri* : **G2**; **I1**, 3; **K**; **M**.  
In small colonies on bare soil or mud, uncommon.

<sup>†</sup>*Bryum microerythrocarpum* : **G2**; **K**; **N2**, 3; **S**.  
Formerly, frequent under cereals and in grassland within and just outside the Reserve. No recent record.

*Bryum rubens* : **B**; **C**; **CY**; **G2**; **I1**; **K**; **N2**, 3, 4; **O**.  
Occasional on bare soil and shingle, especially where recently disturbed or on footpaths, e.g. soil lifted on roots of a fallen tree or in grazed turf.

*Mnium hornum* : **BURL**; **D**; **F1**, 2; *G2*, 3, 4; **H**; *I2*; **J1**, 2, 3, 4, 5, 6; **K**; **L**; **Q**; **SGW**.

Common on earth banks and, locally, on slate outcrops, mossy walls, logs and stumps in woodland and drier types of carr. Also on logs and peat on wooded islands in the Higher Ley and rare on shaded Ley-side cliffs. In France Wood, it is most abundant in the more-sheltered western area. Bleaching of a large patch of plants observed on Hartshorn Cliffs was probably due to summer drought. Sporophytes occasional in spring.

*Rhizomnium punctatum* : **BURL**; *E4*; **F1**, 2; *G2*, 4; **J1**, 2, 5.

Occasional on rotten logs, less often on soil, in marshes, flushes and on streamsides; usually in deep shade. Sporophytes very rare, August.

*Plagiomnium affine* : **C**; *G4*.

Very rare, amongst tall vegetation on Backslope and on a rotten log in Start Marsh.

*Plagiomnium ellipticum* : **CY**; **D**; *F1*, 2.

Rare, on rotten logs, silted planks of a boardwalk, on mud in marshes and on an island in the Higher Ley.

*Plagiomnium undulatum* : **BURL**; **CH**; **CY**; **F1**; *G2*, 3, 4; **J1**, 2, 4, 5; **K**; *N1*; **Q**.

Common in humid woodland, especially on rotten logs, streamsides and grassy rides; luxuriant on shaded cliffs in Leader Wood. Male inflorescences seen but no sporophytes found.

\**Plagiomnium rostratum* : **BURL**.

Formerly, recorded from Burlestone Wood but not found again.

\**Bartramia pomiformis* : **BURL**.

Only seen, recently, on a north-

facing cliff of acid schist by the River Gara, Buckland Wood, with sporophytes.

### Orthotrichales

*Zygodon viridissimus* : **BURL**; **C**; **CH**; **CY**; **D**, 1, 2; *E1*, 6; *G1*, 2, 4; **H**; **I1**, 2, 3; **J1**, 4, 5, 6; **K**; *M*; *N1*, 3; **O**; **SB**; **SV**.

A common epiphyte, frequent on *Sambucus*, *Fraxinus* and *Acer* and seen on several other common broadleaf trees. Occasional on concrete and mortared slate walls, e.g. abundant on the church wall, and formerly on siliceous slabs at Broadstone Point. Sporophytes noted four times, ripening spring-summer.

*Zygodon conoideus* : **C**; **CY**; *D2*; *E1*, 4; *G4*; **H**; *I3*; **J1**, 2, 5.

An infrequent epiphyte of *Salix*, *Sambucus* and *Acer*, formerly of *Ulmus*, and often intermixed with *Metzgeria fruticulosa*. Usually occurs in humid carr or woodland but present in exposed scrub on the Backslope. Sporophytes occasional, dehiscing February / March.

†*Orthotrichum striatum* : **BURL**; **J2**.

Formerly in the Reserve on *Corylus* twigs and boles, with sporophytes.

*Orthotrichum lyellii* : *G2*, 4; **J?**; **L**; **SGW**.

In an unspecified compartment of Slapton Wood, "M.S.F.", 1959; H.L.K. Whitehouse, 1960; found once only in earlier survey: rare on *Salix*, Start Marsh. Recently, seen sparingly on *Salix* and *Acer* in four localities; most abundant on *Salix* in dense, sheltered carr near Deer Bridge.

*Orthotrichum affine* : **BURL**; C; CY; D; E1; F1; G1, 4; I2, 3; J1, 2, 5, 6; K; N1.

Has evidently increased since the earlier survey when it was recorded as an epiphyte of *Corylus* and *Sambucus* only. Recently seen also on *Salix*, *Fraxinus* and *Acer* but commonest on *Sambucus*.

Sporophytes common, ripening in spring. As in many of the Orthotrichales, the empty capsules from the previous year persist while the new ones develop.

*Orthotrichum anomalum* : **BURL**; H; **SB**; SV.

Rare, on mortared walls and, formerly, on a siliceous slab at Broadstone Point, with sporophytes, ripening in spring.

*Orthotrichum tenellum* : **BURL**; C; D; 2; E1, 4, 6; G1, 2, 3, 4; **H**; I1, 3; J5; L; **N3**; **SB**.

A common epiphyte of *Fraxinus*, *Sambucus* and *Salix*, also on *Acer*, *Corylus* and, formerly, *Alnus* and *Ulmus*. Found once on sawn logs and previously on the masonry of Slapton Bridge. Sporophytes common, dehiscing late spring-summer.

*Orthotrichum diaphanum* : C; CY; E1, 3, 4, 6; F2; **G2**, 4; **H**; I1, 2, 3; J1, 5; K; L; N1, 3; O; **SB**; **SGW**; **SV**.

A common epiphyte of *Sambucus*, much less frequent on *Salix*, *Fraxinus*, *Acer* and *Prunus* and, formerly, on *Populus* and *Ulmus*. Characteristic of open habitats rather than closed woodland. Occasional on masonry, brickwork and slate outcrops. Sporophytes common, ripening in the spring.

*Orthotrichum pulchellum* : **BURL**; C; CY; D2; F2; G2; 4; I1; J5; L; N1.

Formerly, frequent on *Ulmus*, *Salix* and *Sambucus* in a variety of humid habitats. It has greatly decreased, with recent records of small amounts in only three localities on well-illuminated *Salix* and *Sambucus*. Sporophytes common, needed for identification, dehiscing March.

*Ulota crispa* : **BURL**; **CY**; **D**, 2; F1; G1, 3; 4; H; I1; J1, 2, 3, 5, 6; K; N3; Q; **SGW**.

Frequent as an epiphyte on *Corylus*, *Acer*, *Salix*, *Sambucus* and *Fraxinus* in humid woodland and carr; formerly on *Ulmus*. Several records are from logs. Sporophytes common, maturing summer-autumn. Var. *crispa* and var. *norvegica* (*U. bruchii* Hornsch ex Brid.) are both present in the Reserve; because ripe capsules are needed for identification the data are too incomplete to indicate distributions. For microscopical characters see Rosman-Hartog & Touw (1987) and Smith & Proctor (1993).

*Ulota phyllantha* : **BURL**; C; **CY**; **D**, 2; E1, 4, 6; **F2**; G1, 2, 3, 4; **H**; I1, 2, 3; J1, 2, 5; K; L; N3; **SGW**.

Abundant on *Salix*, frequent on *Fraxinus*, *Acer* and *Sambucus* and occasional on other broadleaves in open or lightly-shaded habitats. Often the commonest epiphytic bryophyte in scrub and carr exposed to salt-bearing winds, e.g. Backslope and Stokeley Marsh, but also luxuriant in sheltered carr near Deer Bridge. Absent from closed woodland, except in the uppermost branches of trees, and not recorded from stone.

**Isobryales**

\**Fontinalis antipyretica* : **BURL**.

Local, on stones in the River Gara.

*Cryphaea heteromalla* : **BURL**; C; **CY**; D2; E1, 2, 6; F1; G1, 2, 4; **H**; I1, 2, 3; **J1**, 2, 4, 5, 6; **K**; L; M; N1, 3; SGW.

A common epiphyte, especially frequent on *Sambucus* but also on boles and branches of *Salix*, *Acer*, and *Fraxinus*, once on *Corylus*; earlier, recorded on *Populus*, *Alnus* and *Ulmus*. Often luxuriant in sheltered, humid sites, e.g. on a bush inside the ruins of Ireland Cottage, and absent in exposed carr, e.g. centre of Stokeley Marsh. Sporophytes common, dehiscing October.

†*Pterogonium gracile* : **CY**.

On boles of *Populus* on Causeway, February 1967; not found again 1972 or later.

*Leptodon smithii* : E6; G1, 2, 4; H; I1, 3; J5; **K**; N3.

Now local on mature and usually well-lit tree boles. Recent records are from *Acer*, *Fraxinus* and *Quercus* but earlier ones were on *Ulmus* and *Sambucus*. Also on shaded *Salix* base near water level in Stokeley Marsh.

*Neckera pumila* : **BURL**; **CY**; D, 1; E1, 6; **F1**; G1, 2, 4; **J1**, 2, 3, 4, 5, 6; **K**; Q. Common and locally abundant epiphyte on *Fraxinus*, *Corylus* and *Acer*, rarer on other broadleaves, in sheltered woodland and carr. Sporophytes very rare: a single capsule seen in J5.

*Neckera complanata* : **BURL**; **CY**; D; E6; **F1**; G3, 4; **J1**, 2, 4, 5, 6; **K**; O; Q; SGW.

Frequent in humid woodland on trunks of mature trees, particularly *Fraxinus*, *Acer* and *Sambucus*, and persisting on fallen trunks and logs. Occasional on shaded walls and cliff faces.

*Homalia trichomanoides* : **BURL**; J2; **Q**.

Very rare in the Reserve and not seen in the earlier survey although once recorded in an unspecified compartment of Slapton Wood: "M.S.F.", 1959; H.L.K. Whitehouse, 1960. Recently, seen in Reserve only on a deeply-shaded rock face near Slapton Wood Stream; also infrequent on logs, boulders and tree bases by the River Gara in Burlestone Wood and Leader Wood.

*Thamnobryum alopecurum* : **BURL**; CH;

D2; E6; F1, 2; G4; H; J1, 2, 4, 5; **K**; **Q**.

Luxuriant on shaded and irrigated rock faces, logs and tree roots by streams in sheltered valley woodland. Scarce and often stunted elsewhere on shaded tree bases, cliffs and old walls, usually near water. Sporophytes in Leader Wood and Goldswell Quarry, autumn.

**Hookeriales**

*Hookeria lucens* : **BURL**; **F1**; J1, 2, 4, 5, 6; **K**; **Q**.

Restricted to shaded and humid sites on banks, boulders, streambanks and irrigated cliffs in the main woodland areas, sometimes locally abundant. Sporophytes frequent.

**Thuidiales**

*Leskea polycarpa* : **CY**; D, 1, 2; E2, 6; F2; G2; I1.

Occasional on silt-covered tree bases, mostly *Salix*, and logs on the Ley-side fringes where it is liable to immersion. Sporophytes common, ripening spring-summer.

*Heterocladium heteropterum* : **BURL**; **J1**, **2**, **6**; **Q**.

Most of the records refer to var. *flaccidum*, but the larger var. *heteropterum* has also been reported in J1 and BURL. The species is local on deeply shaded stones and rock faces in humid woodland, often associated with *Lejeunea lamacerina*.

<sup>†</sup>*Anomodon viticulosus* : **G4**; **J1**.

Formerly, rare in the Reserve on *Ulmus* boles; recently, only seen outside the Reserve on a mortared roadside wall at Gara Mill.

*Thuidium tamariscinum* : **BURL**; **J1**, **2**, **3**, **4**, **6**; **Q**.

Restricted to humid woodland where locally abundant on earth banks and luxuriant on irrigated dolerite cliffs; avoids deep shade.

## Hypnobryales

*Cratoneuron filicinum* : **BURL**; **G3**; **I1**, **2**; **J2**; **O**.

Rare, on stones in streams and by Lower Ley and on a moist trackside.

*Amblystegium serpens* : **BURL**; **C**; **CH**; **CY**; **D2**; **E1**, **4**, **5**, **6**; **F2**; **G1**, **2**, **4**; **H**; **I1**, **2**, **3**; **J1**, **5**; **K**; **L**; **M**; **N1**, **3**; **O**; **Q**; **SV**.

Common, its principal habitats are shaded niches in mortared stonework, branches of *Sambucus* and branches and bases of *Salix* in marshes, but it also occurs on other shaded, base-rich substrata. Sporophytes occasional or overlooked, ripening spring-summer.

*Amblystegium tenax* : **BURL**; **I1**; **J1**, **2**, **4**, **5**; **K**; **SV**.

Recorded only once in the earlier survey; but now locally common on stones, concrete and gritty detritus in streams in woodland and in a spring in the village. On boulders in the River Gara it forms a zone below *Thamnobryum alopecurum* and above *Fissidens rivularis*. Sporophytes occasional, ripening spring-summer.

*Amblystegium varium* : **CY**; **D1**, **2**; **E2**, **4**; **F2**; **G1**, **2**, **4**; **I2**, **3**.

Occasional on bases of *Salix* and associated mud, and on mossy stones, in the marshes and Ley-side fringes; formerly on *Ulmus*. Easily confused with *A. serpens* in the field but known by its slightly larger size and stronger, wavy nerve which reaches the leaf apex. Probably overlooked in the recent survey. Sporophytes occasional, ripe spring-summer.

<sup>†</sup>*Amblystegium humile* : **F2**.

Formerly, on mud under *Carex paniculata* hummocks; not found again.

*Amblystegium riparium* : **BURL**; **CY**; **D**, **1**, **2**; **E2**, **4**, **6**; **F1**, **2**; **G1**, **2**, **3**, **4**; **I1**, **2**; **L**; **O**.

Common on rotten wood, stones, tree bases, plant litter and mud in Ley-side fringes, marshes and streams. Sporophytes abundant, ripening in spring.

*Drepanocladus aduncus* : **F2**.

Very rare, on silted wooden sleepers supporting marsh boardwalk.

*Calliergon cordifolium* : **CY**; **F1**; **G1**.

Rare, only seen recently on mud in tall reedswamp.

*Calliergon cuspidatum* : C; CH; **CY**; D, 1; G1; L; O.

Scarce, in moist grassland, marshes and shaded stone gutter in churchyard.

*Isothecium myurum* : BURL; E6; F1; G4; **f1**, 2, 4, 5, 6; **K**; L; **Q**; SGW. Occasional on bases of trees, particularly *Fraxinus*, in sheltered woodland. Also on cliffs and on logs, soil and rocks by streams. Sporophytes infrequent, ripening autumn-winter.

*Isothecium myosuroides* : **BURL**; **CY**; **D**, 2; E6; **F1**, 2; G1, 2, 4; **H**; I2, 3; **J1**, 2, 3, 4, 5, 6; **K**; L; **Q**; SGW. Abundant on slate outcrops, logs and tree boles in woodland, carr and Ley-side fringes. Recorded on a range of broadleaves and *Pinus* but commonest on *Fraxinus* and absent from *Sambucus*. Ascends many metres on sheltered boles in Slapton Wood. Liable to inundation in some Ley-side habitats. Rare on soil. Sporophytes frequent.

*Scorpiurium circinatum* : SV. Rare on mortared stonework, roadside wall on south-east side of Field Centre.

*Homalothecium sericeum* : **BURL**; CH; **CY**; **E6**; **F1**; G1, 2, 4; **H**; I1, 3, **J1**, 2, 5, 6; **K**; **Q**; SV. Formerly, commonest as an epiphyte on *Ulmus* but now most frequent on *Sambucus* and *Fraxinus*; also on *Quercus*, *Salix*, *Acer* and *Corylus*. Frequent on mortared walls and logs; once on well-lit quarry cliff. Sporophytes rare, only in sheltered localities, in spring.

*Brachythecium albicans* : **B**; **C**. Frequent on sparsely vegetated

shingle on the Crest, where it is one of the most conspicuous species in winter, rarer on Backslope.

<sup>†</sup>*Brachythecium salebrosum* : **CY**.

In small quantity on shaded branch of *Salix* growing in reedswamp, with sporophytes, February 1967; not found again.

*Brachythecium rutabulum* : **B**; **BURL**; **C**; CH; **CY**; **D**; E1, 4, 6; F1, 2; G1, 2, 3, 4; **H**; I1, 2, 3; **J1**, 2, 4, 5, 6; **K**; L; M; N1, 2, 3, 4; **O**; **Q**; SB; SGW.

Abundant on rotten logs, soil, plant litter, in grassland and on mortared stonework in shade. Also very common as an epiphyte on branches and bases of *Sambucus*, *Fraxinus*, *Acer* and, formerly, *Ulmus*. Sporophytes infrequent or overlooked, in moist localities only, ripe in early autumn.

*Brachythecium rivulare* : **BURL**; **CY**; **D**, 1; **F1**, 2; **G1**, 2, 4; **J1**, 2, 4, 5; N1; SV.

Plentiful on mud and plant litter in marshes and carr, also on stones, gritty detritus and once on rusty ironwork, in and by streams.

*Brachythecium velutinum* : **BURL**; J5. Very rare in Reserve, on fallen *Acer* trunk.

<sup>†</sup>*Brachythecium populeum* : **BURL**; **CY**; I2; L; **f1**; M; **Q**.

Formerly, uncommon in Reserve on shaded slate outcrops and walls, also rare on *Salix* in marshes and *Sambucus* in woodland. Recently, only seen outside Reserve, on well-illuminated stones in woodland and a quarry cliff, with sporophytes, ripe in spring.



*Brachythecium plumosum* : J1.

Very rare, flushed rocks on sloping woodland track, with sporophytes.

*Pseudoscleropodium purum* : B; C; CH; J6.

Restricted to moist or lightly shaded grassland, very locally abundant.

*Scleropodium cespitosum* : B; CY; E2, 6; F2; G4; I1.

Only recorded twice in the earlier survey and has perhaps increased since. Now, occurs sparingly on logs, rocks and tree bases by the Lower Ley; also on sandy curbstone of A379 and on mortared stonework.

*Scleropodium tourettii* : B; C.

Rare, in short or trampled turf on the Backslope and Crest.

*Cirriphyllum piliferum* : BURL; D; F1; G2; J1, 2, 5; N1.

Frequent in early survey on soil, plant litter, logs, mud, stones and among grass in woodland and marshes. Recently, only a single record from the Reserve, on moist woodland soil.

*Cirriphyllum crassinervium* : BURL; CH; M; Q.

Formerly, in Reserve on large stone in boundary wall of M; recently, only in stone gutter around church. Outside Reserve on cliff in Q.

*Rhynchostegium riparioides* : BURL; I3; J1, 2, 4, 5; K; N1; Q.

Occasional on stones in woodland streams and on a flushed quarry cliff; formerly, on old slate wall of fishing hut. Sporophytes common, developing autumn-spring.

†*Rhynchostegium murale* : G4; H; K.

Formerly, on breccia stones on cliff, ruins, walls and *Ulmus* roots, with

sporophytes in February. Not found again.

*Rhynchostegium confertum* : BURL; C; CH; CY; D; E1, 4, 5, 6; F1, 2; G1, 2, 4; H; I1, 2, 3; J1, 2, 5; L; M; N1; O; Q.

Abundant on *Sambucus* bark in many situations and slightly less so on mortared stone walls in shade; also on logs, stone, soil and bases and branches of other broadleaves. Sporophytes very common, ripening in autumn.

*Rhynchostegium megapolitanum* : C.

Very rare, recently seen only on steep shingle against A379 road south of Slapton Bridge.

*Eurhynchium striatum* : BURL; D; F1; J1, 2, 3, 4, 5, 6; K; Q; SGW.

Locally abundant on soil and logs in sheltered woodland, especially near streams.

*Eurhynchium pumilum* : BURL; E5; G2, 3, 4; H; I1, 2, 3; J1, 5; K; M; N1, 3; O; Q; SGW.

Common on moist earth banks, shaded stones, slate outcrops, old walls and irrigated cliffs in woodland, on Ley-side cliffs and by tracks and streams.

*Eurhynchium praelongum* var.

*praelongum* : B; BURL; C; CH; CY; D, 1, 2; E1, 4, 5, 6; F1, 2; G1, 2, 3, 4; H; I1, 2, 3; J1, 2, 3, 4, 5, 6; K; L; M; N1, 2, 3, 4; O; Q; SGW.

The commonest bryophyte in the area, abundant in woodland, scrub, hedgerows, marshes and Ley-side cliffs. Grows on soil, logs, plant litter, rocks, walls and among grass and is a common epiphyte on bases and branches of many broadleaf trees. One of the few mosses

tolerating the dry and saline conditions of the shingle ridge Crest. Sporophytes rare, ripening autumn-winter.

*Eurhynchium praelongum* var. *stokesii* :

**BURL**; J1, 2, 6; Q.

Rare but locally luxuriant on rotten logs and banks in humid valley woodland, with sporophytes, occasional.

*Eurhynchium swartzii* : **BURL**; **E6**; **F1**; G2, 4; **J1**, 2, 4, 5; **K**; L; N1, 2, 3, 4; O; Q.

Occasional on moist, shaded soil, stones and plant litter by streams and paths.

*Eurhynchium schleicheri* : G4.

Very rare, sparingly on shaded track bank among tree roots, Marsh Lane.

*Eurhynchium speciosum* : CY; D, 2; F1, 2; G1, 3, 4.

Has evidently increased or was overlooked in earlier survey.

Occasional on mud and plant litter in reedswamp, carr and on an island in the Higher Ley.

*Rhynchostegiella tenella* : **BURL**; **CY**; **E5**; **G4**; H; I1, 3; **J1**, 2; **K**; L; O; **Q**; SV.

Common in shaded niches on calcareous mortar of old stone walls and parapets. Also on concrete, a quartzite boulder on shore of the Lower Ley and on a cliff and fire-blackened log in Q. Sporophytes frequent, ripening autumn-winter.

*Plagiothecium latebricola* : L.

Once only: sparingly on a well rotted log with *Orthodontium lineare*, with gemmae.

*Plagiothecium denticulatum* : **BURL**; J1.

Rare, on shaded cliffs in woodland, with sporophytes.

*Plagiothecium ruthei* : **D**.

Well-marked plants with strongly asymmetrical, undulate leaves: locally frequent on peaty stumps on an island in the Higher Ley, with sporophytes.

*Plagiothecium succulentum* : H; J1; K; Q.

Rare, on strongly shaded cliffs, earth banks and *Quercus* base.

*Plagiothecium nemorale* : **BURL**; F1, 2; **G2**, 4; H; I1, 2, **J1**, 2, 4, 5, 6; **K**; L; Q; SGW.

Common on earth banks, logs, stumps and rock outcrops in woodland and shaded Ley-side cliffs; rare on tree bases; absent from waterlogged soils.

*Plagiothecium undulatum* : **BURL**; J1, 6.

Very rare in the Reserve: two large patches on logs in J1; formerly, on steep slate outcrop in J6, not found again.

*Isopterygium elegans* : **BURL**; **G4**; **H**; I2; **J1**, 2, 3, 4, 5, 6; **K**; L; Q.

Common on steeply-inclined earth surfaces and in soil-filled niches in slate outcrops and cliffs in woodland and the Ley-side fringes. Not uncommon on rotten stumps and logs in woodland.

*Hypnum cupressiforme* var. *cupressiforme* :

**B**; **BURL**; **C**; CH; CY; **D**, 2; **E6**; **F1**, 2; G1, 2, 4; **H**; I1, 2, 3; **J1**, 2, 3, 4, 5, 6; **K**; L; **M**; N1; Q; SGW.

Common and widespread, especially on logs in woodland and Ley-side fringes but also on boles and branches of most common trees and *Ulex*. Rarer on walls, boulders and soil but frequent in turf on shingle ridge. Sporophytes infrequent or overlooked, maturing in winter.

*Hypnum cupressiforme* var. *resupinatum* :  
**BURL; C; CH; CY; D, 1, 2; E4, 6;  
F1, 2; G1, 2, 3, 4; H; I1, 2, 3; J1, 2,  
3, 4, 5, 6; K; L; M; N1, 3; O; Q;**  
SGW; SV.

An abundant epiphyte on all  
common broadleaved trees.  
Frequent on stone walls and slate  
outcrops, less common on logs and  
stumps. Sporophytes infrequent,  
maturing in winter.

*Hypnum cupressiforme* var. *lacunosum* : **C.**  
Local on bare shingle and in short  
turf.

*Hypnum mammillatum* : BURL; F2;  
G1, 4; J1, **J2, 3, 5, 6; K; SGW.**  
Frequent as an epiphyte of *Acer*,  
*Castanea*, *Fraxinus*, *Ilex*, *Crataegus*  
and *Salix* in woodland; once on a  
stone. Under-recorded in the earlier  
survey. Sporophytes infrequent.

*Hypnum jutlandicum* : BURL; **C; J3, 5, 6.**  
Rare, in short turf on leached ridges  
on Backslope, also on soil heap and  
log in south-facing woodland.

\**Ctenidium molluscum* : BURL; **Q.**  
Recently, seen only on a single  
boulder close to the River Gara in  
Burlestone Wood.

*Rhytidiadelphus squarrosus* : **C; CH; CY.**  
Rare in moist grassland; on a few  
grassy tomb mounds in CH.

†*Rhytidiadelphus loreus* : BURL; **J?**.  
Formerly, in Reserve in an  
unspecified compartment of Slapton  
Wood, H.L.K. Whitehouse, 1960,  
but not found again in either survey.  
Recently, only seen sparingly on wet  
cliff and log in Leader Wood.

## DISCUSSION

The bryophyte flora of the Slapton Ley Nature Reserve (including Slapton village and church) comprises 34 liverwort taxa and 163 mosses. A further 12 liverwort species, 1 hornwort and 17 mosses have been recorded in habitats examined outside the Reserve.

Although the flora is not rich compared to that for the whole of Devon (146 liverworts, 456 mosses, Corley & Hill, 1981), and it contains few county rarities, it is strikingly species-rich compared to other similar coastal locations for which a comprehensive list of bryophytes is available (Table 1).

For instance, it comfortably exceeds the totals recorded for the parish of Dale (Dalby, 1966), an area almost four times as large. Many more species are recorded from Guernsey and Jersey but these have considerably greater areas, and a wider habitat diversity which includes heaths, bogs, numerous rock exposures and mature woodland. The Slapton flora is numerically comparable with that of Belle-Ile (Bates, 1991), an island off the coast of Morbihan, southern Brittany, which is nearly fifty times larger.

The bryophyte floras of several of these coastal localities are severely constrained by lack of shelter, the absence of mature woodland and shortage of moisture. Bryophytes are numerous at Slapton because there is a wide diversity of habitats including wetlands and moist woodlands. While there are few rarities, compared to the lichen and fungal floras (Hawksworth, 1972, 1976, 1986), the Slapton bryophyte flora is notable for its strong representation of species with Mediterranean affinities, some of which are uncommon in Britain, and for a luxuriant epiphytic flora.

TABLE 1. *Numbers of bryophyte species and, in parentheses, infraspecific taxa recorded in the Slapton Ley National Nature Reserve and its environs compared with numbers recorded at other coastal sites*

Locality	Area (ha)	Liverworts	Mosses	Source
Slapton Ley NNR	188	33 (1)	153 (10)	This paper
Slapton Ley NNR plus environs		45 (1)	170 (10)	This paper
Alderney Channel Islands	800	30	138 (7)	Bates (1989b)
Belle Ile, Brittany	8,750	46	165 (13)	Bates (1991)
Cape Clear Island, Co. Cork	639	27	73	Bates (1973) & unpublished data
Parish of Dale, Pembrokeshire SW Wales	739	25	98	Dalby (1966)
Guernsey Channel Islands	7,800	59 (3)		Paton (1969)
Handa Island NW Scotland	318	39	113	Brookes (1970)
Jersey Channel Islands	11,700	78 (4)	224 (16)	Du Feu (1966) and <i>pers. comm.</i> Du Feu & Paton (1972)
Isle of May E. Scotland	58	12 (1)	49 (1)	Watson (1953)
Skokholm Pembrokeshire SW Wales	97	30	62	Gillham (1954)

### *Habitat Diversity*

The main elements of the Slapton bryophyte flora are the species occurring on shaded soil, marshland species and epiphytes. An important limitation is the absence of true heathland, a habitat which is widespread in many of the sites listed in Table 1.

The nearest approach to heath in the Reserve is provided by a ridge on the Backslope a few hundred metres south of Slapton Bridge. Leaching is postulated (e.g. by Mercer, 1966) to explain the occurrence in low trampled turf of several calcifuge bryophytes, e.g. *Hypnum jutlandicum*, *Polytrichum juniperinum* and *Cephaloziella divaricata*, and *Cladonia* lichens. Other heathland bryophytes such as *Campylopus pyriformis* and *Pohlia nutans* and ericaceous shrubs, however, are lacking, perhaps owing to the relatively low organic status and poor moisture retentiveness of the shingle soil. Several of the more interesting bryophytes found in other southern coastal localities (Table 1), but lacking at Slapton, e.g. *Archidium alternifolium*, *Fossombronia* spp., *Gongylanthus ericetorum*, *Scapania compacta* and *Riccia* spp., are species of heathland or heathy banks.

Stable substrata rich in calcium are extremely rare in the Reserve. The shingle forming the Crest and parts of the Backslope is rich in calcareous shell fragments but

surprisingly few of the bryophytes present appear to be strict calcicoles. *Barbula hornschuchiana* and *Rhynchostegium megapolitanum* are probably the only examples of calcicoles in this habitat. The shingle is not blown inland, unlike the calcareous shell-sand which is responsible for the occurrence of numerous calcicoles on Alderney and Belle-Ile (Bates, 1989b, 1991). An important assemblage of calcicole bryophytes grows on mortared slate walls and concrete. Most of these species, including *Orthotrichum anomalum*, *Rhynchostegiella tenella*, *Schistidium apocarpum*, *Tortella nitida* and *Trichostomum crispulum*, are unknown on natural substrata at Slapton, but *Grimmia pulvinata*, *Homalothecium sericeum*, *Tortula muralis* and *Zygodon viridissimus* also occur on slate outcrops or tree bark.

The dolerite exposures in the Burlestone Wood complex are more basic than the slate exposures in the Reserve and several of the more interesting species in BURL can be considered calcicolous or basiphilous, e.g. *Marchesinia mackaii*, *Plagiochila killarniensis* and *Porella arboris-vitae*.

The River Gara and the other major streams in the Reserve also appear to be moderately calcareous, judging by the occurrence of the aquatics *Amblystegium tenax*, *Fissidens crassipes* and *Rhynchostegium riparioides* and the abundance of *Thamnobryum alopecurum* on emergent boulders. In their more acidic headwaters, Devon streams often support a calcifuge flora in which the latter two species are replaced by the similar *R. lusitanicum* and *Isothecium holtii*, and *Nardia compressa*, *Scapania undulata* and *Racomitrium aciculare* become common.

The luxuriant but mildly basiphilous flora in BURL differs appreciably from that seen in the upland oakwoods on and around Dartmoor. The latter are characterised by an abundance of robust calcifuge mosses such as *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi* and *Rhytidiadelphus loreus* and the liverworts *Plagiochila spinulosa*, *P. punctata*, *Diplophyllum albicans* and *Scapania gracilis* (Proctor, 1964). Physiological causes of calcicole and calcifuge behaviour in bryophytes are discussed by Bates (1992a).

Apart from the stone walls, extensive well-illuminated exposures of rock are almost completely lacking in the Reserve, however, fewer bryophytes exploit this habitat than is the case for lichens (Hawksworth, 1972). *Grimmia trichophylla* var. *subsquarrosa* is the only moss restricted to this habitat in the Reserve. Shaded rock exposures occur in many of the woodlands and Leyside fringes and support a wide range of bryophytes but, within the Reserve, only *Heterocladium heteropterum* and *Plagiothecium denticulatum* appear to be limited to this habitat. In contrast, the majority of the species restricted to Burlestone Wood and Goldswell Quarry are specialists of shaded rock faces.

No coastal cliffs occur in the Reserve but small populations of the salt-tolerant mosses *Schistidium maritimum*, *Tortella flavovirens* and *Pottia crinita* occur in rock crevices within the spray zone at Torcross Point, just south of the Reserve boundary. Experimental studies (Bates & Brown, 1974) have shown that *S. maritimum* and *T. flavovirens* differ from most mosses in resisting increases in cell permeability when wetted with seawater. They regain photosynthetic activity when the shoots are washed with freshwater, e.g. rain, whilst the inland types are irreversibly damaged by salt water (Bates & Brown, 1975).

### *Bryophyte Life-forms and Life-strategies*

Although smaller in scale, bryophytes rival the vascular plants in their diversity of form and ecological adaptation. Of three useful related concepts, **growth-form** is essentially the morphological, and **life-form** the ecological expression of the structure

and manner of growth of the plant (Gimingham & Robertson, 1950; Gimingham & Birse, 1957; Mägdefrau, 1982), while **life-strategy** emphasises temporal, life-cycle and functional dimensions of its ecological adaptation (During, 1979, 1992; Grime *et al.*, 1990). In the last section, habitats were considered on a traditionally human scale. But at the scale of the individual bryophyte, habitats are intricate and the substrates on which the plants actually grow vary greatly in nature and permanence. Bryophytes are correspondingly diverse in their ecological adaptations and pattern of allocation of resources between vegetative growth, and reproduction and dispersal—either through production of spores or vegetative propagules.

During (1979) proposed a classification of bryophyte life-strategies comprising six main types.

**Fugitive** species occupy unpredictable habitats of short duration. They are ephemerals quick to grow and fruit, producing abundant freely dispersed spores; *Funaria hygrometrica* is the classic example.

**Colonists** occupy the early stages of succession in open habitats. They also, characteristically, show high reproductive effort but are, typically, longer-lived with vigorous growth (and sometimes show abundant production of asexual propagules) in their early stages, and sexual reproduction only after a year or more. They include many small weedy species such as *Ceratodon purpureus* and *Bryum bicolor* as well as pioneers on harder substrata including *Grimmia pulvinata*.

**Annual shuttle** species grow in habitats which are seasonal but reappear, predictably, in the same place each year. They are, typically, small ephemeral plants with little or no asexual reproduction but which regularly produce sporophytes—often small and simple and often with rather large spores. They include winter annuals, e.g. *Phascum cuspidatum*, *Pottia* spp., and *Riccia sorocarpa* in situations that are sun-baked in summer, and summer annuals (e.g. *Physcomitrium pyriforme*) on mud inundated in winter.

**Short-lived shuttle** species occupy temporary habitats of longer duration, not so tied to the seasons, and show a similar emphasis to the last group on sexual reproduction; examples are *Pottia heimii* on bare patches in upper saltmarshes, and the Splachnaceae which grow on animal dung (*Splachnum ampullaceum* is not infrequent on Dartmoor).

**Perennial shuttle** species include all the typical epiphytic bryophytes, long-lived, with moderate reproductive effort variously divided between production of spores (*Ulota crispa*, *Orthotrichum tenellum*, *Hypnum cupressiforme* and *Frullania dilatata*) and asexual propagules (*Ulota phyllantha*, *Orthotrichum lyellii*, *Neckera complanata* and *Metzgeria fruticulosa*).

**Perennial stayers** occupy essentially—permanent habitats, for instance on the woodland floor or in bogs and fens, and are represented by the tall turfs or large cushions of *Dicranum majus* and the big *Polytrichum* species, *Leucobryum*, *Sphagnum*, and the many mat-forming pleurocarpous mosses of woodland.

Grime's concept that the ecological adaptation of a species represents a balance between three basic adaptive traits—ruderal, competitive, stress-tolerant—provides another way of looking at bryophyte life-strategies, which partly overlaps and partly complements During's scheme (Grime *et al.*, 1990; During, 1992).

Life-form and life-strategy categories are, of course, not sharply bounded but they can provide a useful framework for considering features of the ecology and population biology of bryophytes as well as the structure and dynamics of bryophyte communities.

*Epiphytes and Air Quality*

Visitors to Slapton may be surprised at the abundance and luxuriant growth of epiphytic species such as *Cololejeunea minutissima*, *Cryphaea heteromalla*, *Neckera pumila*, *Orthotrichum tenellum* and *Ulota phyllantha*. A major factor is the low level of sulphur dioxide (SO<sub>2</sub>) atmospheric pollution which has eliminated epiphytes in urban areas and over much of the Midlands and eastern England. The annual mean and recorded daily maximum SO<sub>2</sub> concentrations in the Slapton area are about half of the corresponding figures for the Weald or the country around Oxford, a third of those in the Birmingham area, and a quarter of the concentrations around Doncaster and Sheffield (Table 2).

TABLE 2. *Atmospheric pollutants and rainfall acidity in the Slapton area during 1986–1988 compared with two industrial areas in the Midlands and two rural areas in Southern England (interpolated data of UKRGAR, 1990)*

Region	Rainfall pH	Ca <sup>++</sup>	SO <sub>4</sub> <sup>-</sup>	NO <sub>3</sub>	NH <sub>4</sub> <sup>+</sup>	SO <sub>2</sub>	NO <sub>x</sub>
Slapton area	4.75	13.3	29	20	22	3.7 (49)	0.55
Ashdown Forest, East Sussex	4.62	23.9	53	32	40	8.4 (80)	0.88
Oxford area	4.53	30.3	78	39	50	5.8 (101)	0.78
Birmingham area	4.33	28.0	66	33	41	9.1 (139)	0.73
Sheffield area	4.33	40.9	89	35	42	12.6 (228)	1.08

**Notes:**

1. Rainfall pH refers to volume-weighted mean rainwater pH, 1986–1988.
2. The next four columns refer to volume-weighted mean concentrations of calcium, non-marine sulphate, nitrate and ammonium ions in rainwater measured in microequivalents per litre. The levels of these ions, to a large extent, determine the acidity of the rainwater.
3. SO<sub>2</sub> refers to the 1988 annual mean daily and (maximum concentrations) of gaseous sulphur dioxide measured as micrograms of SO<sub>2</sub> · m<sup>-3</sup> of air.
4. NO<sub>x</sub> denotes wet, dry and cloudwater deposition of nitrate and nitrogen oxides, 1986–1988 (grams nitrogen m<sup>-2</sup> · yr<sup>-1</sup>, and is based on the sum of direct measurements of wet-deposited nitrate with estimates of cloud water deposition and seeder-feeder enhancement, and computed estimates of dry deposition of nitrogen dioxide and nitric acid.

The moss *Dicranoweisia cirrata*, which in Devon is mainly a species of acid granite rocks, is an abundant epiphyte in moderately polluted parts of Britain and, like the SO<sub>2</sub>-tolerant lichen *Lecanora conizaeoides*, is believed to have increased in abundance during the past century (Jones, 1991). The rarity of both species at Slapton is indicative of high air quality.

Differences between the epiphytic floras of the Reserve units arise from the patchy distributions of host trees and the effects of exposure and shading. Epiphytic bryophytes are generally not restricted to specific host trees but respond to the intensities of physical and chemical factors acting at the bark surface (Bates & Brown, 1981; Palmer, 1986). Bark acidity is believed to be one of the major factors influencing bryophyte distribution (Barkman, 1958; Bates & Brown, 1981; Bates 1992b). Fig. 3 reports bark

pH values for ten common tree species at Slapton. The procedure employed for these determinations, which uses a flat-tipped electrode applied to the bark surface, yields values which are slightly lower than those obtained using aqueous extracts of ground bark (Farmer *et al.*, 1990). Nevertheless, the data accord well with information obtained at other sites (Barkman, 1958; Rose, 1974; Bates & Brown, 1981). The results emphasise the acid nature of *Castanea* bark, one of the poorest substrata for epiphytic bryophytes at Slapton, and the near neutral conditions occurring on that of *Sambucus* and *Fraxinus* which are productive species for epiphytes. *Corylus* also has bark of relatively high pH but it is thin and hard and has a much lower water-holding capacity than *Sambucus* and generally bears a poorer epiphytic flora. The pH values for *Acer pseudoplatanus* and *Quercus robur* lie towards the lower end of the reported ranges for these two species.

Slapton escaped the severe "acid rain" from the traditional major industrial areas which, in the English Lake District for example, has caused a lowering of bark pH and loss of buffering capacity in *Quercus* (Farmer *et al.*, 1991, 1992). In recent decades, urban SO<sub>2</sub> pollution, in the vicinity of the big cities and industrial conurbations, has declined and the current, more diffuse, pattern is heavily influenced by emissions from power stations, concentrated particularly in the north-east Midlands and South Yorkshire. It is there that the highest average concentrations of atmospheric pollutants now occur. South-west England remains one of the least polluted parts of the country (Table 2; UKRGAR, 1990).

The pH of rainwater reflects a balance between acid emissions and basic substances such as airborne calcareous dust, so the highest pH values in rainwater in southern Britain are in the limestone and chalk country of Somerset and neighbouring parts of Wiltshire and Dorset, rather than in South-west England or West Wales where the acid input is least. The relatively low bark pH values for *Acer* and *Quercus* at Slapton are likely to be a consequence of the relatively non-calcareous soils, because soil base status can influence the pH of the bark of *Quercus* (Bates, 1992b). Some epiphytes are strongly affected by exposure to salt-laden winds. *Ulota phyllantha* and *Cololejeunea minutissima* are particularly abundant in exposed situations at Slapton whilst many others, e.g. *Cryphaea heteromalla*, appear to prefer sheltered localities. *U. phyllantha* is known to be salt-tolerant (Bates & Brown, 1975) and it may require bark which has an appreciable magnesium content (Bates, 1992b).

### Phytogeography

Several attempts have been made to classify bryophytes into distribution types based on their ranges in Europe. Many of the bryophytes found at Slapton are widespread on the continent and a few can be termed "cosmopolitan", e.g. *Bryum argenteum*, *Ceratodon purpureus*, *Schistidium apocarpum*, with respect to latitude (Schofield, 1992). Numerous British bryophytes belong to the "Atlantic" category and are restricted to the areas of higher rainfall which fringe the Atlantic coast of Europe. "Mediterranean" bryophytes have their main areas of dispersion in the warm zone of olive (*Olea europaea*) cultivation which surrounds the Mediterranean Sea (Polunin & Walters, 1985) and is characterised by arid summers and mild, wet winters. Atlantic and Mediterranean taxa represent 9.6% and 17.3%, respectively, of the Reserve bryophyte flora, or 12.4% and 15.9% when the environs are included (Table 3). Ratcliffe (1968) demonstrated that the distribution ranges of Atlantic bryophytes correlate strongly with rainfall patterns, notably with average numbers of "wet days" (days with  $\geq 1$  mm precipitation). Species



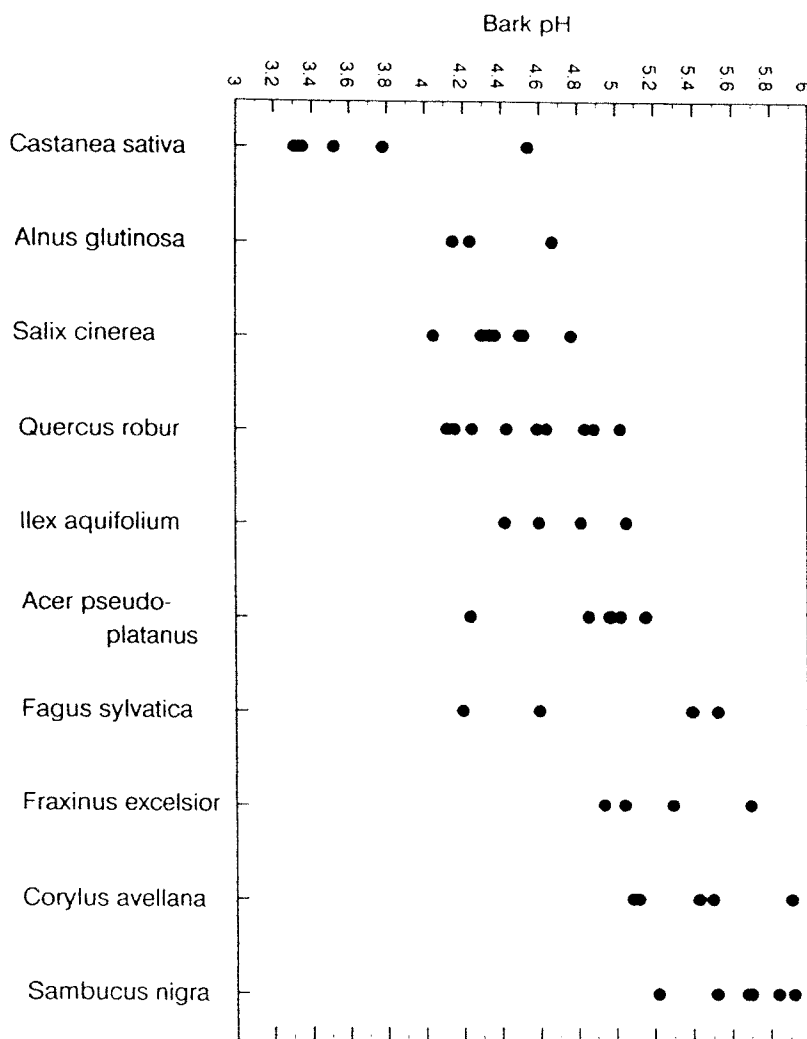


FIG. 3.

Example pH values of the bark of ten common trees sampled at random in the Slapton Ley NNR. Pieces of bark were removed with a knife and dried in envelopes over anhydrous calcium chloride in a desiccator. The bark was wetted with 25 mM potassium chloride solution and pH measured with a BDH Gelplas Flat Tip Combination Electrode as described by Farmer *et al.* (1990). Each point represents the mean of two determinations from bark collected at breast height on the trunk or a major axis of a single tree.

strictly confined to the Atlantic Zone in Europe are sub-divided by Ratcliffe into Northern, Southern and Widespread elements (Table 3). The two examples occurring in the Reserve, *Cololejeunea minutissima* and *Lejeunea lamacerina*, are among the least moisture-demanding of the strictly Atlantic species. *Porella pinnata*, found on a boulder in the River Gara at Burlestone Wood, is normally limited to areas with 140–160 wet days (Ratcliffe, 1968).

In ravines, the requirement of Atlantic bryophytes for frequent rainfall can be partly offset by the continuous high humidities arising from the sheltering and shading effect of the topography (see Proctor, 1980, for examples). Although *C. minutissima* is a common epiphyte at Slapton, it is strongly restricted to the southern and south-western fringe of the British Isles (Fig. 4A).

TABLE 3. *Atlantic and Mediterranean bryophytes recorded in Slapton Ley NNR and its environs (after Ratcliffe, 1968, and Gaume, 1953, 1954)*

Group	Species	Species
<b>Southern Atlantic</b>	<i>Cololejeunea minutissima</i> <i>Marchesinia mackaii</i> †	<i>Plagiochila killarniensis</i> *† <i>Porella pinnata</i> †
<b>Widespread Atlantic</b>	<i>Lejeunea lamacerina</i> <i>Lophocolea fragrans</i> †	<i>Saccogyna viticulosa</i> †
<b>Sub-Atlantic</b>	<i>Calypogeia arguta</i> <i>Lejeunea ulicina</i> <i>Metzgeria fruticulosa</i> <i>Porella arboris-vitae</i> † <i>Heterocladium heteropterum</i> <i>Hookeria lucens</i> <i>Hypnum cupressiforme</i> var. <i>resupinatum</i>	<i>Orthotrichum pulchellum</i> <i>Pterogonium gracile</i> <i>Ptychomitrium polyphyllum</i> <i>Schistidium maritimum</i> <i>Scleropodium cespitans</i> <i>Scleropodium tourettii</i> <i>Ulota phyllantha</i> <i>Zygodon conoideus</i>
<b>Western British</b>	<i>Metzgeria conjugata</i> † <i>Nowellia curvifolia</i> <i>Riccardia chamedryfolia</i> <i>Riccardia palmata</i>	<i>Grimmia hartmannii</i> † <i>Oxystegus tenuirostris</i> †
<b>Mediterranean-Atlantic</b>	<i>Epipterygium tozeri</i> <i>Fissidens rivularis</i> † <i>Leptodon smithii</i> <i>Pottia crinita</i>	<i>Scorpiurium circinatum</i> <i>Tortella flavovirens</i> † <i>Tortella nitida</i> <i>Trichostomum brachydontium</i>
<b>Mediterranean</b>	<i>Barbula cylindrica</i> <i>Barbula hornschuchiana</i> <i>Barbula revoluta</i> <i>Barbula tophacea</i> <i>Barbula trifaria</i> <i>Barbula vinealis</i> <i>Bryum bicolor</i> <i>Bryum radiculosum</i> <i>Cirriphyllum crassinervium</i> <i>Cryphaea heteromalla</i> <i>Desmatodon convolutus</i> <i>Eurhynchium pumilum</i> <i>Eurhynchium speciosum</i> <i>Fissidens crassipes</i>	<i>Fissidens incurvus</i> <i>Funaria fascicularis</i> <i>Orthotrichum diaphanum</i> <i>Orthotrichum tenellum</i> <i>Physcomitrium pyriforme</i> <i>Pohlia carnea</i> <i>Pottia recta</i> † <i>Rhynchostegiella tenella</i> <i>Rhynchostegium confertum</i> <i>Rhynchostegium megapolitanum</i> <i>Rhynchostegium murale</i> <i>Tortula laevispila</i> <i>Weissia microstoma</i> <i>Zygodon viridissimus</i>

#### Notes

\* Placed in this group by Paton (1977b). † Only seen outside the Reserve.

Southern Atlantic species appear to require both moist and warm conditions whereas the Widespread Atlantic group, to which *L. lamacerina* belongs, is dependent upon regular moisture (Fig. 4B) but appears relatively indifferent to temperature (Ratcliffe, 1968). Northern Atlantic species are absent from the Slapton area and only one or two occur in the cooler uplands of Dartmoor. Many Atlantic bryophytes at Slapton belong to the Sub-Atlantic group. These increase in abundance in the higher-rainfall areas of Europe but are less strongly confined to them. Several Sub-Atlantic bryophytes are common in the Slapton flora. The Western-British contingent comprises bryophytes which have an oceanic range in Britain but which are not restricted to the Atlantic fringe in the rest of Europe. None of these is common at Slapton. Mediterranean-Atlantic species are plentiful in coastal Mediterranean areas and also extend north-westwards along the Atlantic coast to Britain where they are often in habitats which are severely desiccated in summer. A good example is *Tortella nitida* which is abundant on sunny walls in Slapton village (Fig. 4C). This pattern is also well shown by *Epipterygium tozeri*, a delicate moss common on shaded acidic banks in the Reserve (Fig. 5).

In the Mediterranean region, *E. tozeri* disappears during the intensely dry summer but it regenerates in autumn from spores and from multicellular tubers produced on the rhizoids (Arts & Nordhorn-Richter, 1986). It also forms stems with bulbous bases and detachable axillary bulbils which have enhanced desiccation resistance and allow survival of summer drought. In Britain, the plant normally persists during the summer and it has been observed at Slapton in August and September.

The epiphyte *Leptodon smithii* is a much rarer Mediterranean-Atlantic moss in Britain but not infrequent at Slapton. As Mediterranean species would normally grow only during the moist winter period it can be expected that the occurrence of suitable temperatures during winter may be critical for their survival. In the British Isles, *Leptodon smithii* is only present in areas where the annual average air temperature exceeds 10°C (Fig. 4D). The correlation with isotherms of winter temperature is poorer than might be expected. This is possibly because *L. smithii* not only requires a reasonable winter temperature to make growth but also needs hot summer conditions to exclude potential competitors.

The remaining Mediterranean species in Table 3 have their ranges centred on that sea but also extend northwards to varying degrees. Liverworts, which are often more desiccation-sensitive than mosses, are noticeably absent from this and the Mediterranean-Atlantic group at Slapton. Drought-tolerant mosses of the order Pottiales, which have many xeromorphic features, are extremely well represented. Several of the Mediterranean species are plentiful at Slapton, e.g. *Orthotrichum tenellum* is more frequent than *O. affine* which is normally the commoner epiphyte in Britain.

The richness of the Mediterranean element at Slapton is due to the combined effects of its warm, sunny lowland situation, and the mild winter temperatures resulting from its south-western and coastal location. Similarly, the occurrence of several Atlantic species is a consequence of moderately high rainfall and the presence of sheltered wooded valleys. However, many of the moisture-demanding species, found in the upland valleys around Dartmoor (Proctor, 1964), are absent. The cellular adaptations which enhance survival of desiccation in many bryophytes are beginning to be understood (Proctor, 1990), but the exact physiological mechanisms which determine the "Atlantic" type of ecological behaviour are still a matter of conjecture. Many such species occur in sheltered and moist, but freely draining, habitats and most are probably moderately, but not extremely, desiccation tolerant.

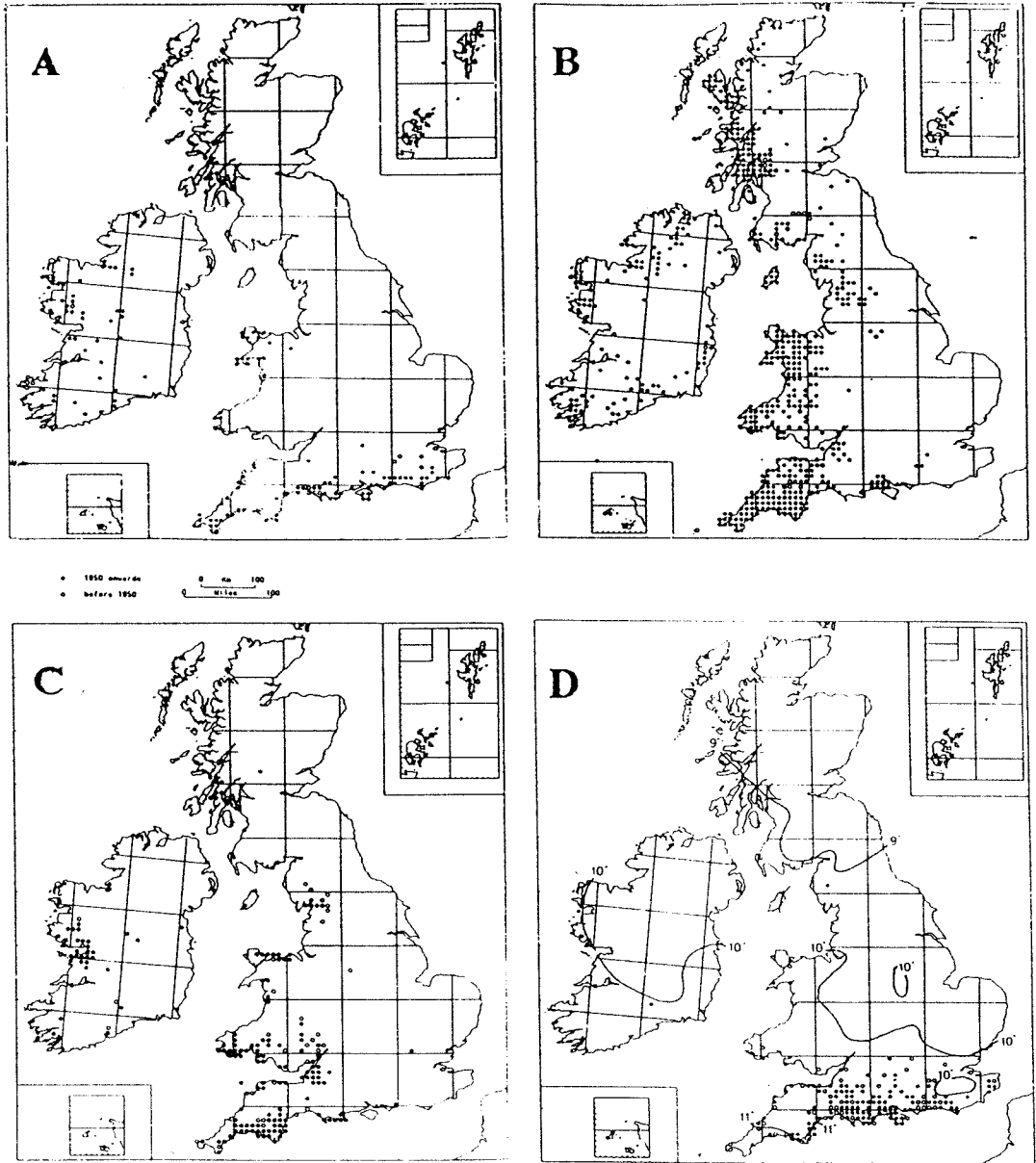


FIG. 4.

A: Distribution of the Southern Atlantic liverwort *Cololejeunea minutissima* and; B: Distribution of the Widespread Atlantic liverwort *Lejeunea lamacerina* in the British Isles; C: Distribution of the Mediterranean - Atlantic moss *Tortella nitida*; D: A provisional distribution map of the Mediterranean-Atlantic moss *Leptodon smithii* in the British Isles showing its restriction to areas of high average temperature. Plotted by the Biological Records Centre from data collected for the British Bryological Society Mapping Scheme. The isotherms (in D) represent annual means of mean monthly temperature for the period 1941-1970, after Tout (1976).

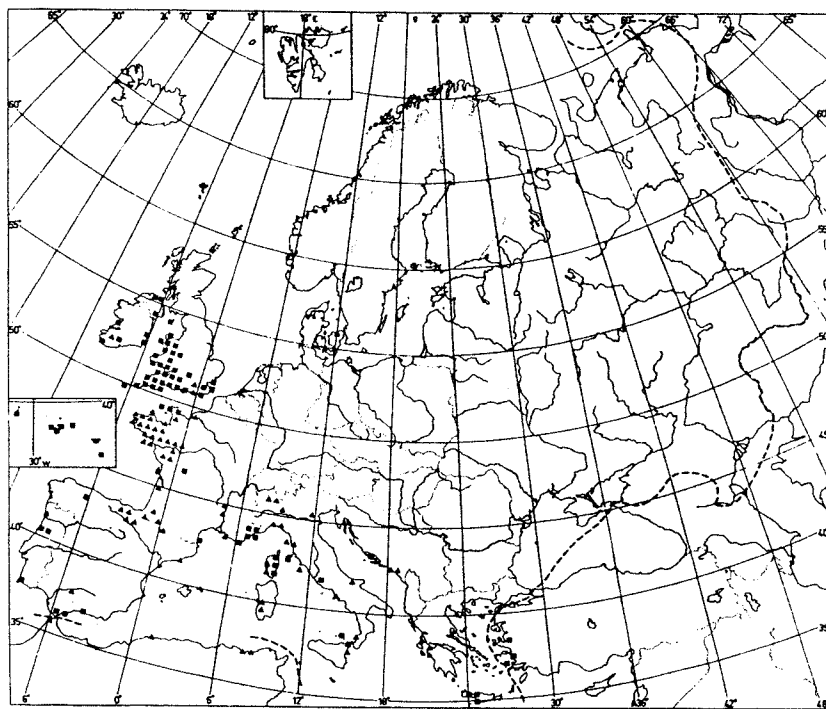


FIG. 5.

European distribution of the Mediterranean – Atlantic moss *Epipterygium tozeri* mapped in 50-km squares of the UTN grid, after Arts & Nordhorn-Richter (1986). Triangles denote records before 1950 and squares represent later records. Reproduced from the Journal of Bryology with permission of Blackwell Scientific Publications.

Numerous widely distributed bryophytes are intolerant of drying, e.g. *Pellia epiphylla* and *Rhizomnium punctatum*, but permanently-wet habitats occur even in dry regions, so these plants do not exhibit “Atlantic” distribution patterns.

Many Atlantic species appear to do best in places which provide a combination of moderate illumination, a reasonably regular but not excessive supply of moisture, and a low saturation deficit. But the requirements of different species are quite varied, so the problem is a complex and intriguing one which invites further investigation.

#### *Ancient Woodland Indicators*

Several groups of organisms have been employed as biological indicators of ancient woodland. This approach, utilising lichens, has already been applied in Slapton Ley NNR (Hawksworth, 1986). The underlying principle is that some species (the “indicators”) are unable to spread readily to isolated woodlands (or plantations) in the relatively dry, man-altered landscapes of today. Lichen and bryophyte species often disperse more freely, and become less useful as indicators, in the wetter oceanic areas of western Britain. Rose (1992) provided a tentative list of 16 liverworts and 37 mosses which appear to indicate ancient woodland in lowland Britain. Table 4 summarises the occurrence of these species in the units of woodland at Slapton. The results largely support the conclusions of Hawksworth (1986) employing lichens and they agree with the suspected recent origin of most of the woods (Mercer, 1966; Burton & Mercer, 1978).

TABLE 4. *Ancient woodland indicator bryophytes (sensu Rose, 1992) in selected compartments of Slapton Ley National Nature Reserve and environs*

Unit	Indicators	N
F 1	<i>Chiloscyphus polyanthos</i> , <i>Plagiochila asplenoides</i> , <i>Cirriphyllum piliferum</i> , <i>Eurhynchium striatum</i> , <i>Homalothecium sericeum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Rhizomnium punctatum</i> , <i>Thamnobryum alopecurum</i> .	12
F 2	<i>Chiloscyphus polyanthos</i> , <i>Isothecium myosuroides</i> , <i>Rhizomnium punctatum</i> , <i>Thamnobryum alopecurum</i> .	4
G1	<i>Radula complanata</i> , <i>Homalothecium sericeum</i> , <i>Isothecium myosuroides</i> , <i>Leptodon smithii</i> , <i>Neckera pumila</i> .	5
G2	<i>Cirriphyllum piliferum</i> , <i>Eurhynchium pumilum</i> , <i>Homalothecium sericeum</i> , <i>Isothecium myosuroides</i> , <i>Leptodon smithii</i> , <i>Neckera pumila</i> , <i>Orthotrichum lyellii</i> , <i>Rhizomnium punctatum</i> .	8
G4	<i>Radula complanata</i> , <i>Anomodon viticulosus</i> , <i>Eurhynchium pumilum</i> , <i>Homalothecium sericeum</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Leptodon smithii</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Orthotrichum lyellii</i> , <i>Rhizomnium punctatum</i> , <i>Thamnobryum alopecurum</i> .	12
H	<i>Radula complanata</i> , <i>Eurhynchium pumilum</i> , <i>Homalothecium sericeum</i> , <i>Isothecium myosuroides</i> , <i>Leptodon smithii</i> , <i>Neckera pumila</i> , <i>Thamnobryum alopecurum</i> .	7
I1	<i>Eurhynchium pumilum</i> , <i>Homalothecium sericeum</i> , <i>Leptodon smithii</i> .	3
I2	<i>Eurhynchium pumilum</i> , <i>Isothecium myosuroides</i> .	2
I3	<i>Eurhynchium pumilum</i> , <i>Homalothecium sericeum</i> , <i>Isothecium myosuroides</i> , <i>Leptodon smithii</i> .	4
J 1	<i>Plagiochila asplenoides</i> , <i>Radula complanata</i> , <i>Brachythecium populeum</i> , <i>Brachythecium plumosum</i> , <i>Cirriphyllum piliferum</i> , <i>Eurhynchium pumilum</i> , <i>Eurhynchium striatum</i> , <i>Homalothecium sericeum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Plagiothecium undulatum</i> , <i>Rhizomnium punctatum</i> , <i>Rhytidiadelphus loreus</i> , <i>Thamnobryum alopecurum</i> .	17
J 2	<i>Chiloscyphus polyanthos</i> , <i>Plagiochila asplenoides</i> , <i>Radula complanata</i> , <i>Cirriphyllum piliferum</i> , <i>Dicranum majus</i> , <i>Eurhynchium striatum</i> , <i>Homalia trichomanoides</i> , <i>Homalothecium sericeum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Rhizomnium punctatum</i> , <i>Thamnobryum alopecurum</i> .	15
J 3	<i>Eurhynchium striatum</i> , <i>Isothecium myosuroides</i> , <i>Leucobryum juniperoideum</i> , <i>Neckera pumila</i>	4
J 4	<i>Chiloscyphus polyanthos</i> , <i>Radula complanata</i> , <i>Eurhynchium striatum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Thamnobryum alopecurum</i> .	9

continued

Unit	Indicators	N
K	<i>Plagiochila asplenioides</i> , <i>Radula complanata</i> , <i>Cirriphyllum piliferum</i> , <i>Eurhynchium pumilum</i> , <i>Eurhynchium striatum</i> , <i>Homalothecium sericeum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Leptodon smithii</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Thamnobryum alopecurum</i> .	13
L	<i>Brachythecium populeum</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Orthotrichum lyellii</i> , <i>Plagiothecium latebricola</i> .	5
N 3	<i>Radula complanata</i> , <i>Eurhynchium pumilum</i> , <i>Leptodon smithii</i> .	3
Q	<i>Plagiochila asplenioides</i> , <i>Brachythecium populeum</i> , <i>Eurhynchium pumilum</i> , <i>Eurhynchium striatum</i> , <i>Homalia trichomanoides</i> , <i>Homalothecium sericeum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Thamnobryum alopecurum</i> .	12
SGW	<i>Radula complanata</i> , <i>Eurhynchium pumilum</i> , <i>Eurhynchium striatum</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>Orthotrichum lyellii</i> .	7
BURL	<i>Chiloscyphus polyanthos</i> , <i>Frullania tamarisci</i> , <i>Lejeunea cavifolia</i> , <i>Plagiochila asplenioides</i> , <i>Plagiochila porelloides</i> , <i>Porella arboris-vitae</i> , <i>Radula complanata</i> , <i>Saccogyna viticulosa</i> , <i>Trichocolea tomentella</i> , <i>Brachythecium populeum</i> , <i>Cirriphyllum piliferum</i> , <i>Dicranum majus</i> , <i>Eurhynchium pumilum</i> , <i>Eurhynchium striatum</i> , <i>Fissidens exilis</i> , <i>Homalia trichomanoides</i> , <i>Homalothecium sericeum</i> , <i>Hookeria lucens</i> , <i>Isothecium myosuroides</i> , <i>I. myurum</i> , <i>Neckera complanata</i> , <i>N. pumila</i> , <i>Plagiothecium undulatum</i> , <i>Rhizomnium punctatum</i> , <i>Rhytidiadelphus loreus</i> , <i>Thamnobryum alopecurum</i> .	26

Thus the highest indicator scores in the Reserve, for J1, J5 (in Slapton Wood) and K (in France Wood), are near the boundary between “poor” (N <15) and “moderate” (N=15–20) in Rose’s scale of ancient woodland status. Scores are particularly low for the young wood developing on America Fields (N3) for Hartshorn Plantation (L) and the shaded cliff units (I1-3). The older carr units (F1, G4) have the highest indicator scores of the marshes. The Burlestone Wood complex (BURL), by contrast, just falls into the “exceptional conservation value” category.

It should be noted that Table 4 includes species which have not been seen recently. Indicator scores based only on species seen in 1990–93 would be lower, in many cases. Also, from a biological point of view, Slapton lies in the “highland zone” of Britain (Pearsall, 1968). Its oceanic climate and hard rock topography will tend to make the occurrence of moisture-requiring “indicators” more likely than in the lowlands and thus provide an over-optimistic picture of woodland antiquity.

### Changes

In this section we attempt to summarise the main changes which have occurred in the bryophyte flora between the late 1960s-early 1970s and 1990–1993. Twenty seven taxa, recorded in the Reserve during the earlier survey, were not found again in the later one, but many new records were made.

Two approaches have been used to identify the more significant trends. First, net decreases or increases in the numbers of Reserve units occupied by individual species have been examined (Table 5). Only gains of 4 or more units are considered because of the larger number of compartments thoroughly examined in the later survey whereas net losses of 3 or more units are considered of interest.

Second, the similarity of the lists of bryophytes recorded in the individual compartments has been compared for the two surveys by calculating percentage similarity as follows:

$$S = \frac{(B \times 100)}{T}$$

where, S = percentage similarity, B = the number of taxa common to both surveys, T = the total number of taxa recorded in the unit. These results are summarised in Table 6.

In comparing the results of surveys carried out at different times, it is important to consider some pitfalls which can lead to erroneous conclusions. The most important ones are

- 1. changes in taxonomy
- 2. differences in sampling intensity
- 3. differences in competence of the bryologists (Söderström, 1992).

Among the species showing apparent gains in Table 5, *Metzgeria temperata* had not been recognised as British at the time of the earlier survey and would have been recorded as *M. fruticulosa*. Similarly, the "decrease" of *Dicranella varia* may be because some of the early records actually represented *D. staphylinia* which was not described until 1969. Due to increasing understanding of some taxa their "search image" has improved considerably amongst bryologists in recent years. The appearance of *Plagiothecium succulentum* and *Barbula trifaria* may be explicable in this way.

Some of the species changes may result from the larger number of units sampled in the later survey. Also, it is evident that there were different interpretations of the boundaries of some units. Thus ARP included many epiphytes in the Ley shore units (D, E) whereas JWB recorded them for the Leyside fringes only (H, I).

The Reserve streams appear to have received more intensive study in the later survey which may account for the increase in *Conocephalum conicum* and *Amblystegium tenax*. Among the species showing gains in Table 5 there is a large contingent of woodland bryophytes, e.g. *Lejeunea lamacerina*, *Atrichum undulatum*, *Mnium hornum*, *Fissidens bryoides*, *Hypnum mammillatum*, *Isoetecium myurum* and *Thamnobryum alopecurum*, or bryophytes of sheltered conditions, e.g. *Cryphaea heteromalla* and *Ulotia crispa*. This strongly suggests that an extension of woodland conditions has occurred, probably by maturation of scrub on the Leyside fringes and the colonisation of reedswamp by carr. The latter is believed to have accelerated following the cessation of reed-cutting in some areas (Anon, 1988).

The most remarkable loss is of *Orthotrichum pulchellum* a tiny but distinctive epiphyte of elders in well-illuminated and sheltered situations. This indicates that former areas of elder scrub have now changed into more mature types of woodland with over-topping and shading-out of the scrub species and their epiphytes. This appears to have happened mainly in the younger woodland units and in the Leyside fringes. A contributory factor to the loss of *O. pulchellum* and to decreases of *Leptodon smithii*, *Neckera pumila*, *Rhynchostegium murale* and *Tortula* spp. has undoubtedly been the decline of mature *Ulmus* due to Dutch Elm Disease (see Hawksworth, 1986). However,



TABLE 5. A list of bryophytes which have shown net gains or losses in the number of Reserve units occupied at Slapton Ley since the earlier survey

Species	Net change	Species	Net change
<b>Taxa showing a net gain of 4 or more units</b>			
<i>Cololejeunea minutissima</i>	7	<i>Dicranum scoparium</i>	4
<i>Conocephalum conicum</i>	5	<i>Eurhynchium praelongum</i> var. <i>praelongum</i>	5
<i>Lejeunea lamacerina</i>	4	<i>Eurhynchium speciosum</i>	6
<i>Metzgeria furcata</i>	5	<i>Fissidens bryoides</i>	8
<i>Metzgeria temperata</i>	6	<i>Homalothecium sericeum</i>	4
<i>Amblystegium riparium</i>	7	<i>Hypnum cupressiforme</i> var. <i>resupinatum</i>	6
<i>Amblystegium tenax</i>	7	<i>Hypnum mammillatum</i>	8
<i>Atrichum undulatum</i>	4	<i>Isoetecium myurum</i>	5
<i>Barbula cylindrica</i>	5	<i>Mnium hornum</i>	4
<i>Barbula tophacea</i>	5	<i>Orthodontium lineare</i>	4
<i>Barbula trifaria</i>	4	<i>Orthotrichum affine</i>	8
<i>Barbula vinealis</i>	4	<i>Plagiothecium succulentum</i>	4
<i>Brachythecium rutabulum</i>	6	<i>Rhynchostegiella tenella</i>	4
<i>Bryum capillare</i>	4	<i>Scleropodium cespitosum</i>	4
<i>Bryum rubens</i>	6	<i>Thamnobryum alopecurum</i>	7
<i>Bryum ruderales</i>	4	<i>Ulota crispa</i> (both varieties)	6
<i>Cryphaea heteromalla</i>	5	<i>Ulota phyllantha</i>	4
<b>Taxa showing a net loss of 3 or more units</b>			
<i>Barbula fallax</i>	5	<i>Leptodon smithii</i>	3
<i>Brachythecium populeum</i>	3	<i>Neckera pumila</i>	3
<i>Bryum microerythrocarpum</i>	5	<i>Orthotrichum pulchellum</i>	8
<i>Cirriphyllum piliferum</i>	3	<i>Physcomitrium pyriforme</i>	3
<i>Dicranella rufescens</i>	4	<i>Rhynchostegium murale</i>	3
<i>Dicranella varia</i>	7	<i>Tortula laevipila</i> var. <i>laevipiliformis</i>	3
<i>Ditrichum cylindricum</i>	4	<i>Tortula papillosa</i>	3
<i>Fissidens incurvus</i>	4		

some epiphytes which grow commonly on sallow and sycamore are now more frequent, e.g. *Cololejeunea minutissima*, *Metzgeria furcata*, *Hypnum cupressiforme* var. *resupinatum*, *Orthotrichum affine* and *Ulota phyllantha*, indicating increases in the extent of carr and/or the numbers of mature sycamores. *Brachythecium populeum* has also been lost from the Reserve probably, either because of direct shading, or due to overgrowth of the stones on which it grew by ivy (*Hedera helix*) and rampant mosses, themselves benefiting by increased shading.

Bryophytes of bare soil appear to have declined in the Reserve. *Barbula fallax*, *Bryum microerythrocarpum*, *Dicranella rufescens*, *D. varia* (or *D. staphylina*) and *Ditrichum cylindricum* have mostly vanished with the demise of arable land. Early autumn ploughing of fields and the use of fertilisers has caused the virtual disappearance from arable land in Britain of a number of formerly common species. Several of the above plus *Weissia microstoma* and *W. multicapsularis* now appear to be rare species in the Slapton area. Some of these species and *Pseudephemerum nitidum* also occurred in France Wood but now appear to have been lost with the lapse of the original rotational felling and replanting scheme which helped keep tracks open and created bare soil niches.

TABLE 6. *Changes in the floras of selected units of Slapton Ley NNR and environs since the earlier survey. S = percentage similarity between the two surveys. Some infraspecific taxa of minor significance have been omitted*

Unit	Lost	Numbers of taxa		Total	S (%)
		Gained	Common		
B	5	7	13	25	52
C	11	9	37	57	65
CY	18	11	24	53	45
D	7	17	13	37	35
F1	7	12	29	48	60
F2	13	9	14	36	39
G2	32	2	20	54	37
G4	9	23	38	70	54
H	9	15	33	57	58
I1	13	18	24	55	44
I2	10	16	12	38	32
I3	18	14	19	51	37
J1	5	20	50	75	67
J2	6	14	48	68	71
J3	5	10	14	29	48
J4	3	25	12	40	30
J5	10	19	39	68	57
J6	4	32	11	47	23
J1-6	8	19	76	103	74
K	16	20	39	75	52
L	8	11	20	39	51
M	17	5	6	28	21
N2	9	3	2	14	14
N3	13	18	12	43	28
N4	4	8	4	16	25
BURL	16	24	70	110	64
Q	11	23	15	49	31

Changes to the bryophyte flora of the Crest have accompanied the removal of the rubble of the old hotel. *Trichostomum brachydontium*, *Barbula rigidula* and *Pottia crinita* formerly occurred here. *P. truncata* has probably increased and *Funaria hygrometrica* has colonised the red loam introduced for landscaping of the new central car park. Among the marshland bryophytes *Eurhynchium speciosum* and *Amblystegium riparium* appear to have increased (Table 5). Both species exhibit a preference for solute-rich waters and it is conceivable that they are more frequent today because of the increasingly eutrophic conditions in Slapton Ley and its feeder streams (Burt *et al.*, 1983; Trudgill & Heathwaite, 1991). Alternatively, the increase of sallow-carr may be responsible for these changes.

Conspicuous invasions by three species have occurred in the Reserve since the earlier survey but only one, *Orthodontium lineare*, occurs in more than one unit. This is a species introduced to western Europe from the Southern Hemisphere where it is widespread in temperate areas (Söderström, 1992). *O. lineare* was first recorded at Slapton in 1960 but remained rare and was not seen in the survey of ARP. It is not a strong competitor but spreads by producing numerous spores (up to 12 million m<sup>-2</sup> of colony). Success in a particular area seems to depend largely on the presence of suitable habitats, usually decaying wood in well-illuminated sites (Hedenäs *et al.*, 1989a, b). It is

possible that its former scarcity at Slapton reflected a lack of habitats and that, recently, it has gained advantage from the crop of logs left by severe storms in 1987 and 1990. *Dicranum scoparium* may also have increased for this reason (Table 5). It would be instructive to monitor the fate of *O. lineare* in the Reserve woods in future years.

The shingle ridge now supports two species which were absent at the time of the earlier survey. *Campylopus introflexus*, found on leached shingle and a log on the Backslope, is another introduction from the Southern Hemisphere and is now abundant in western Europe. It disperses freely by means of spores and invades gaps, often man-made, in natural vegetation on dry acidic soils. Once established the local population is increased by production of deciduous shoot tips (Söderström, 1992). Sporophytes and vegetative propagules have both been observed in *C.* It will be interesting to see whether *C. introflexus* eventually extends to stumps and soil in woodland clearings at Slapton as it has in many other areas of Britain. The third colonist is the sand dune moss *Tortula ruralis* ssp. *ruraliformis* which is now present in scattered localities along the Crest. This conspicuous moss is unlikely to have been overlooked in the earlier survey and it is just possible that its appearance is due to increased stability of the shingle ridge as described by Hawksworth (1986).

Changes in the overall floras of selected Reserve units are summarised in Table 6. An important point is that, for most compartments, more taxa have been gained than lost. This is perhaps an indication that the sampling intensity was higher during the 1990–1993 survey. However, a general accumulation of moisture-requiring taxa might also be expected in many units as they recover from the severe disturbances experienced during the wartime exercises or undergo other types of succession. Unit G2 is an obvious exception and it appears that an area of woodland bordering this marsh was examined in the earlier survey but not in the later one. It should be appreciated that the percentage similarity between the earlier and later survey lists is partly influenced by the total number of species found. In general the smallest changes appear to have occurred in the established woodland areas which show survey similarities above 50%.

The shingle ridge units have also remained comparatively unchanged considering the small species totals found. At the other extreme several units appear to have suffered considerable floristic change such as the arable land converted to pasture at Hartshorn Fields (N2). Large changes are also indicated in two units of Slapton Wood, J4 and J6. The former was originally described as impenetrable scrub (Mercer, 1966) but is now a more mature type of woodland. The latter has also gained a number of species indicative of more shaded and sheltered conditions, e.g. *Lejeunea lamacerina* and *Heterocladium heteropterum* var. *flaccidum*. A comparable change is also signalled for Goldswell Quarry where several light-demanding species, e.g. *Polytrichum juniperinum* and *Ptychomitrium polyphyllum*, appear to have been lost. A similar loss of bryophytes of open habitats and gain of shade tolerant species occurred at Chawley Brick Pit near Oxford between 1948 and 1985 (Jones, 1986).

Data for the Leyside habitats, e.g. I2, I3, also support the suggestion of an increased development of the tree canopy over the period of this study.

### Conservation

There is little immediate threat to the bryophytes at Slapton but some losses have taken place due to natural successional changes and the destruction of elms by Dutch Elm Disease. Any increase in air pollutants or rain acidity could be catastrophic for the rich epiphytic flora. No serious losses appear to have accompanied the improvements to

sea defences on the shingle ridge (see Hawksworth, 1986). The invasion of the Backslope by *Campylopus introflexus* does not appear to threaten any rare bryophytes as has happened in some dune and heathland sites elsewhere. The continued occurrence of bare shingle patches on the Backslope is important for the maintenance of the more interesting species such as *Rhynchostegium megapolitanum* and *Scleropodium tourettii* and periodic scrub removal may be necessary. Well-illuminated elders provide one of the best hosts for epiphytes and they should be conserved and, if possible, encouraged in different areas (sheltered and exposed) of the Reserve. Many of the elders are now decrepit or overshadowed by trees and some recruitment in clearings is necessary. The neglect of management in France Wood has led to loss of several species of disturbed soil. More use of this unit for teaching might help as would a more active forest management regime. However, the damaged eastern part of France Wood is probably best left to regenerate naturally with wind-firm sycamores rather than risk planting other species.

*Brachythecium populeum* appears to have been lost from the Reserve due mainly to shading and overgrowth of cliffs and stones. It would be worthwhile making an experimental clearance at one former site, e.g. the small quarry in Hartshorn Plantation, to examine the potential for natural re-invasion by this species. Scrub development in the more interesting areas of hard rock exposure (e.g. Broadstone Point) should be controlled.

Arable land has now mostly vanished from the Reserve along with its characteristic bryophytes; however, a luxuriant winter stubble flora has recently been observed in fields abutting onto the Reserve at Middlegrounds. Low inorganic fertiliser inputs and spring rather than autumn ploughing are the optimum requirements for these species and low fertiliser applications should also be encouraged in the remaining pastures at N2.

In studies of small organisms such as bryophytes there will always be a need to collect some specimens for identification in the laboratories using a microscope. Nevertheless, visitors to Slapton are reminded that the populations of many of the more striking and localised species such as *Leptodon smithii*, *Schistostega pennata* and *Scorpiurium circinatum* are tiny. Over-collecting poses a real threat to their continuation. Collecting in the Reserve should only be undertaken with a permit and then only if its effects on the local population would be insignificant.

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