10 | *Lichen Communities in the British Isles: A Preliminary Conspectus*

PETER W. JAMES, DAVID L. HAWKSWORTH
and FRANCIS ROSE

I. Introduction

Compared with investigations into the systematics and geographical distribution of lichens within the British Isles, the study of the structure and composition of the communities they comprise has been sadly neglected. The first author to attempt a detailed survey of the lichens occurring in different habitats in the British Isles was W. Watson. He examined the lichens and bryophytes to be found on sand dunes (Watson, 1918a), calcareous soil (Watson, 1918b), in freshwater (Watson, 1919), arctic-alpine vegetation (Watson, 1925), moorlands (Watson, 1932) and woodlands (Watson, 1936a, 1936b). In this period a few other detailed examinations of particular sites were also carried out, of which the most noteworthy are perhaps those concerned with the marine and maritime species at Howth (Knowles, 1913), sand dune species at Blakeney Point (McLean, 1915), heaths in Breckland (e.g. Farrow, 1916) and upland communities on Cader Idris (Evans, 1932). Data from these and other ecologically orientated lichenological studies were incorporated into Tansley's (1939) classic monograph of the vegetation of the British Isles.

In continental Europe in the early and mid-1920s, the recording of lichen communities began to enter a more quantitative phase, data from

particular quadrats being compiled into tables; communities also started to be provided with latinized names (see Barkman, 1958). This, the phytosociological approach of the Zurich-Montpellier and Uppsala schools, is open to a number of criticisms (see pp. 297–298), and was not readily adopted in the British Isles; indeed, the first author to endeavour to apply continental phytosociological systems to lichen communities in this country appears to have been Laundon (1956, 1958).

Within the last two decades, ecological studies in Britain have been carried out by descriptive (e.g. Alvin, 1960; Brown and Brown, 1969; Dickinson and Thorp, 1968; Sheard, 1968; Sheard and Ferry, 1967), numerical (e.g. Fletcher, 1973a,b; Yarranton, 1967) and phytosociological (e.g. Coker, 1968; Graham, 1971; Hawksworth, 1969, 1972a, 1973a; Laundon, 1956, 1958, 1967, 1970; McVean and Ratcliffe, 1962; Rose and James, 1974) methods. Most of these investigations have, however, been restricted to particular localities or habitats and no attempt either to draw the published information together or to provide a synopsis of the major lichen communities present in the British Isles as a whole has previously been made.

Studies by the present authors, both in the British Isles and elsewhere, have led them to the view that within a single climatically uniform region, each particular substrate *tends* to assume, eventually, a characteristic and often remarkably uniform lichen vegetation under the influence of similar environmental factors. A preliminary survey of these noda in the British Isles is presented here. The volume of data currently available precludes the possibility of a definitive treatment at this time, but an attempt is made here to recognize the *major* alliances present and a few of the more distinctive associations within them.

We hope that this preliminary conspectus will both serve as a stimulus to phytosociological investigations in the British Isles and provide a framework for the future discussion of lichen communities in these islands.

II. The Phytosociological Approach

There are a number of recent reviews concerned with the theory and practice of phytosociological approaches to the study of plant communities (Barkman, 1973; Guinochet, 1973; Hawksworth, 1974; Shimwell, 1971) and these should be consulted for further information on these aspects. The fundamental criticism levelled against phytosociological methods is to question whether plant communities really exist as distinct entities. Investigation by both phytosociological and numerical methods make it clear that groupings can be recognized, but equally clear that all stands

cannot be accommodated within particular units (although the majority generally can be), and may be intermediate between one or more (whether they are defined numerically or by phytosociological methods). Phytosociology, in our opinion, should aim to determine those major noda in the continuum of plant communities which are related to clearly recognizable ecological and environmental parameters, rather than to fit all stands encountered into a rigid system of too strictly defined associations. In most investigations, phytosociologically defined noda are derived essentially by floristic and intuitive methods, but noda can also be recognized as a result of numerical analyses of data obtained from randomized sampling techniques. The relative merits of these approaches have already been the subject of considerable debate, but only recently has a comparison been made between intuitive phytosociological and a number of numerical approaches (Frenkel and Harrison, 1974). These authors found that the intuitive phytosociological method was extremely valuable for the rapid reconnaissance and establishment of basic groupings, particularly in terms of the man-hours expended, although a combination of both methods was likely to prove more useful than either on its own in the production of an entirely comprehensive system.

In the case of lichen communities, the design of a randomized sampling technique or programme which will lead to the detection of the major noda presents special problems, mainly unsolved as yet, on account of the large number of variables involved affecting the communities. For this reason, intuitive methods of sampling are currently the most satisfactory means of detecting the diversity of the lichen communities in an area.

*A. Nomenclature**

Accepting that the subjective, or intuitive, method is a valid one for the recognition of major noda, the question then arises as to whether such noda should be provided with latinized names and ordered in a hierarchical system. The provision of a latinized name enables (or should enable) the concept of a particular community to be readily communicated and

* While this work was in press, a Code of Phytosociological Nomenclature prepared by the Nomenclature Commission of the International Society for Vegetation Science appeared (Barkman *et al.*, 1976). Many of the procedures followed in this chapter are in line with proposals in this Code, with two particularly important exceptions: (1) changing the generic stems to conform to current idiotaxonomic usage is rejected, and (2) a starting point date of 1910 is proposed whereas we followed Barkman (1958) who proposed 1922 for epiphytic communities. If this Code becomes accepted by the botanical community at large (i.e. at an International Botanical Congress) it will thus be necessary to change some of the syntaxonomic names employed in this chapter.

discussed in the literature; for reasons of precision such names require author citations and rules to control their validity and application. Although somewhat complex systems of rules have been proposed (e.g. Meijer-Drees, 1953; see Hawksworth, 1974), no internationally accepted code comparable to the International Code of Botanical Nomenclature is currently available. Thus, even within Europe, variations in the procedures followed in naming plant communities exist. One of the most important of these from the point of view of the stabilization of names is the practice of changing the names of phytosociological units as the names of the species utilized in those units are changed; Laundon (1967) did not do this, for example, while some authors have, and yet they have left author citations for the syntaxon unchanged (e.g. Kalb, 1970; Wirth, 1972). Other problems arise when authors adopt latinized names based on relevé data in earlier works where the original authors not only did not coin latinized names, but also gave no indication that they considered their communities of syntaxonomic value, as in Klement's (1955) treatment of Almborn's (1948) "communities".

In our view, a closer correspondence between the procedures of syntaxonomy and the rules of idiotaxonomy (namely the International Code of Botanical Nomenclature, Stafleu *et al.*, 1972) is required and to this end we have endeavoured to apply the following criteria in this chapter. In a few cases (see p. 353) the nomenclatural situations are so complex that we have preferred to follow continental usage even where this is almost certainly contrary to the views expressed below; it may be that a case could be made for the conservation of some extremely well established names of syntaxa.

1. Names in all languages are accepted and latinized *provided that their authors accorded them a phytosociological rank.* Thus, tables of records to show taxa associated with a species in autecological studies are rejected and syntaxa referred to by their authors as "communities", "noda" etc., are omitted unless the original author latinized them (i.e. implied they had phytosociological rank). Under this rule the "communities" of Almborn (1948) and the "noda" of Rose and James (1974) are thus considered invalid.

2. In cases where community names *not* fulfilling criterion (1) above have been taken up later and attributed to the earlier author either alone or as a "combination", such names are treated as new and attributed to the later author alone.

3. Where the name of a syntaxon fulfilling criterion (1) and based on two or more specific names is contracted by a later author, it is treated as a new name and attributed to the later author alone. This procedure seems desirable as such names are frequently open to contraction in a number of

different ways. Names of syntaxa based on either (i) a single specific epithet (e.g. *Amaretum* Almb., *Conizaeoidion* Laund.), (ii) two species of different genera, or (iii) more than two species, are treated as unacceptable here; for simplicity it might, however, be preferable to take this further and accept only names based on a single generic and a single specific name.

4. The principle of homonymy is difficult to apply in the earlier lichen phytosociological literature as author citations to syntaxa were rarely provided and the names were not latinized (e.g. Hilitzer, 1925). Some syntaxonomists have treated all such names as distinct and homonyms of the first name published. We have accepted the first publication as the acceptable one where other criteria of acceptability are complied with. Definite homonyms (i.e. cases where an author clearly intended to describe a new syntaxon, being unaware of the existence of an earlier homonym) must clearly be rejected. "Misapplied" names of syntaxa are not considered in synonymies presented here as they can have no nomenclatural significance.

5. With respect to the descriptive data accompanying names of associations, subassociations or variants acceptable under criterion (1), where such names are "nomina nuda" (i.e. lack any information as to the species present and their frequencies), they are considered invalid. Such data provided either in text or tabular form is acceptable in our view. Ideally, tables with several records, one of which is designated as the "type record", should be presented by authors describing new syntaxa today. Names of alliances and suballiances are treated as validly published if one or more validly published subordinate taxon is indicated; where no type is clearly designated, the association name based on the same species name as the higher syntaxon is treated as its holotype.

6. The correct name for an association is taken to be a combination of the earliest available acceptably published syntaxal epithet, combined or recombined where necessary, with a name derived from the modern idiotaxonomic genus in which that species epithet is currently placed; changes in *species* names are not followed in syntaxal names here. Where names are recombined, the author of the recombination is indicated and that of the basionym placed in brackets before the later author's name; the same method of citation is followed when there is a change of syntaxonomic rank even if the actual name is unaltered (as in the case of a transfer from suballiance to alliance).

Although contrary to procedures in the International Code of Botanical Nomenclature, it will be noted from the above (criterion 1) that the syntaxonomist's usual practice of accepting names in languages in addition to Latin is followed here. Whether it is advisable to continue this may be

debatable, as while devalidation would very considerably reduce the number of syntaxal names to be considered by modern syntaxonomists, at the same time it would lead to changes in some of the better known and widely accepted community names.

In our opinion, the adoption of an internationally agreed set of rules of phytosociological nomenclature is urgently required, as only through this will stability and consistency in the application of names be achieved. Ideally, this matter should be considered by the XIIIth International Botanical Congress to be held in Sydney in 1981.

B. Taxonomy

The phytosociological approach, in addition to the technical nomenclatural problems outlined above, is beset by a number of taxonomic difficulties when one considers the application of existing lichen community names:

1. There is an extremely large number of names of lichen communities already published to consider. Delzenne-van Haluwyn (1976) compiled about 1700 but her listing is very far from complete and the actual number is probably considerably in excess of 2500 to judge from an unpublished catalogue of lichen syntaxal names drawn up by D. L. Hawksworth in connection with the preparation of the present contribution. Furthermore, copies of many of the earlier papers in this field which appeared in the 1920s are extremely difficult to locate; this also applies to some articles published in central and eastern Europe in the 1940s. In the case of the names of syntaxa cited here with full details of their place of publication, all have been checked by us in their original sources. It proved necessary to spend an inordinate amount of time during this study in bibliographical work.

2. In relevés a considerable number of the species recorded may present idiotaxonomic difficulties in themselves or have been incorrectly named; in some instances the names of associations have been based on misdetermined material or have had their characteristic and faithful species wrongly identified. As phytosociologists (perhaps fortunately from the standpoint of conservation) rarely collect samples of all taxa in their relevés and preserve them in herbaria, in many cases the true identity of species included cannot always be definitely ascertained by later workers.

3. A considerable number of the described associations may not have been based on representative stands, i.e. they may have been recognized on the basis of an insufficient preliminary subjective assessment of the major noda of a large geographical area. In practice, associations have generally been described from rather small geographical regions and relatively few studies have considered even whole countries, let alone major climatic zones (e.g. the Atlantic coasts of Europe). For this reason, species stated

to be characteristic of or faithful to particular associations may not really be so over the full range of the association if they are limited by factors other than those limiting the association as a whole.

4. Lichen communities of similar floristic content on different substrates have frequently been provided with different names because of this rather than their species composition; some communities with identical species compositions do, however, occur on both trees and siliceous rocks. Lastly, it has been argued that epiphytic communities in particular should not be recognized (and so not accorded names) independently from the vascular plant (tree) phytosociological taxa in which they occur; in our view, epiphytic communities merit independent recognition as they may occur (i) on the bark of different trees, (ii) in quite different higher plant syntaxa (i.e. woodland types), and (iii) are influenced by environmental factors other than those determining the presence or absence of their phorophytes. It should perhaps be noted that this is contrary to the situation with macromycetes which are often host-dependent owing to mycorrhizal or other nutritive associations and so have generally been studied within their host communities and not given latinized names (see Hawksworth, 1974, for selected references to examples of this approach); the only major departure from this approach is Darimont's (1975) important study in which numerous fungal syntaxa are proposed.

Some additional problems arise from the effects of man on lichen communities. In general, man's influence on lichen communities leads to a simplification in them; thus, in areas subjected to, for example, air pollution, agricultural sprays or trampling, species normally dominant, characteristic or faithful of an association may be rare in, or absent from it. In the case of phytosociological surveys in areas extensively influenced by man, there is consequently a tendency to recognize as distinct phytosociological taxa communities which are essentially simplified facies of those occurring in unaffected areas. If, however, a sufficiently large number of relevés were made over the whole range from the affected to unaffected areas, a gradual continuum could be found; we feel that such simplified communities should not be recognized formally. A few communities now predominating in areas affected by man, however, do merit recognition in that they can form identical communities in unaffected areas (e.g. the *Lecanoretum pityreae*, the *Xanthorion* associations of dust-enriched barks in natural forests in dry areas of Mediterranean Europe; see pp. 321 and 342, respectively).

One final factor to be borne in mind is that of the relationship between communities themselves; such relationships may be either spatial or temporal (e.g. successional). In some instances seral communities may

merit phytosociological recognition where they persist for considerable periods of time, represent distinctive noda and differ markedly in species content from those to which they lead (e.g. some communities on smooth young branches and twigs). In contrast, where succession follows the pattern of a gradual migration of species into a community with little or no elimination of pioneer species, formal recognition of the essentially species-poor pioneer facies of the "community" appears superfluous.

Hierarchical classifications of varying complexity above the rank of alliance were adopted by Mattick (1951), Klement (1955) and Barkman (1958) whose systems have been followed, sometimes with modifications, by most recent lichen phytosociologists. We have not recognized any taxa above the rank of alliance here as the described higher syntaxa have been largely based on substrate and abstract species content concepts, with little reference to the climatic and environmental factors controlling their development. As it would clearly be unsatisfactory to propose a scheme of higher syntaxa on the basis of the British data alone, this aspect is not considered further here.

In the treatment for the British Isles presented in this contribution, we have tended to adopt wider concepts of some communities than previous authors, e.g. Barkman (1958); only by doing this does it seem possible to relate many of the associations to environmental factors (albeit in a qualitative way at present) and view the communities as an interlocking mosaic in which the noda occur in different habitats. Narrow concepts of associations, like very narrow species concepts in idiotaxonomy, tend to confuse rather than to clarify; we feel that it is important to endeavour to recognize the major peaks (noda) in the continuum of lichen communities but of very doubtful value to attempt to distinguish minor undulations in the topography of the cline. Our approach might thus be regarded as "synusial" in the sense of Barkman (1973), but we feel it is unnecessary to develop a system of synusial names independent of those proposed for syntaxa.

The procedure adopted in the selection of the communities to be recognized in this preliminary conspectus was consequently (1) an initial selection based on the species present (i.e. floristic), and (2) an attempt to correlate these with environmental factors in so far as these can be judged from field observations alone. The communities distinguished by this approach appear to be the most worthy of syntaxonomic recognition. Most of such communities contain both a number of lichens more or less faithful (confined) to them, and also groupings of characteristic but not strictly faithful species (i.e. those also regularly occurring in one or more other noda).

In the course of field work in the British Isles we have found that on the

discovery of one or two species either characteristic of or faithful to a particular community (e.g. the *Lobarion*) it is well worth spending further time searching for additional members of that community. A knowledge of the composition of the various communities described here is consequently an aid to the making of comprehensive surveys of the species present in a particular site.

III. Epiphytic Communities

The very large number of factors determining the development of particular corticolous and lignicolous assemblages of lichens have been the subject of detailed reviews by Barkman (1958) and Brodo (1974) whose works should be consulted for further information on these aspects. Amongst the more important of these in the British Isles are: (1) degree of illumination; (2) humidity of the environment; (3) age of the bark surface; (4) degree of corrugation of the bark; (5) degree and rate of sloughing of bark; (6) continuity and age of woodland cover in a particular site; (7) inclination of surfaces; (8) aspect; (9) degree of bark leaching by rain; (10) degree of impregnation of bark with organic nutrients; (11) air pollution; (12) pollution by agricultural chemicals; (13) pH of the bark surface; (14) basic nutrient status of bark; (15) presence of tannins, betulin or resins etc., and (16) moisture-retaining and absorbing properties of the bark.

As corticolous communities occur on a living substrate they are particularly fluid and this dimension has to be borne in mind in their delimitation as transitions between noda will inevitably be of frequent recurrence.

The epiphytic lichen communities of the British Isles are arranged here in eleven alliances. These are treated alphabetically, as are the associations within them, for ease of reference. The main relationships of the alliances to each other are summarized in Fig. 1 and the following key illustrates the main floristic differences between them.

1. Old forest indicator species (see Table II; e.g. *Lobaria* spp., *Nephroma* spp., *Pachyphiale cornea*, *Pannaria* spp., *Parmeliella* spp., *Sticta* spp. and *Thelotrema lepadinum*) frequent to abundant ..... *Lobarion pulmonariae* (p. 322).
   Old forest indicator species absent or rare 2

2. Crustose lichens dominant 3
   Foliose and/or fruticose lichens dominant 6

3. Arthoniales, stalked Caliciales, Hysteriales (including Lecanactidaceae), *Lepraria* spp., or pyrenocarpous lichens dominant 4
   Lecanorales or *Cyphelium* dominant 5

4. Arthonioid, lirelliform or pyrenocarpous lichens dominant; communities of young twigs or smooth bark often in somewhat shaded situations ..... *Graphidion scriptae* (p. 314).
   Caliciales, Lecanactidaceae, *Arthonia impolita* or *Lepraria* spp. dominant; communities of dry bark, bark recesses, or quickly drying lignum ..... *Calicion hyperelli* (p. 306).

5. *Lecanora chlarotera*, *L. confusa*, *L. pallida*, *Lecidea symmicta* or *Lecidella elaeochroma* abundant; pioneer communities of twigs forming mosaics of small juxtaposed thalli ..... *Lecanorion subfuscae* (p. 318).
   Bacidia chlorococca, *Cyphelium inquinans*, *Lecanora conizaeoides*, *L. varia* or *Lecidea scalaris* abundant to dominant; communities not confined to twigs, often in moderately polluted areas, often forming extensive pure stands and rarely mosaic-like ..... *Lecanorion variae* (p. 319).

6. *Acrocordia*, *Anaptychia*, *Buellia*, *Caloplaca*, *Gyalectina*, *Physcia*, *Physciopsis*, *Physconia*, *Teloschistes* or *Xanthoria* species, or *Parmelia acetabulum*, *P. elegantula*, *P. laciniatula* or *P. quercina* frequent to dominant; communities of nutrient-rich or nutrient-enriched barks in well lit situations .. *Xanthorion parietinae* (p. 342).
   Above genera and species rare or absent; communities of mainly nutrient-poor barks 7

7. *Cladonia* species dominant; on bark in humid situations, rotting wood, stumps and tree bases .... *Cladonion coniocraeae* (p. 313).
   Cladonia species not dominant; communities mainly of well lit sites 8

8. *Ramalina* and/or *Usnea* species dominant .. *Usneion barbatae* (p. 338).
   Alectoria, *Bryoria*, *Cetraria*, *Hypogymnia*, *Parmelia*, *Parmeliopsis*, *Platismatia* or *Pseudevernia* species dominant 9

9. *Parmelia caperata*, *P. perlata*, *P. reticulata*, *P. revoluta* or *P. soredians* present to dominant or co-dominant; communities of well lit moderately acid barks becoming rare in northern Endland and Scotland ..... *Parmelion perlatae* (p. 330).
   Alectoria, *Bryoria*, *Cetraria*, *Parmelia laevigata*, *P. taylorensis*, *Parmeliopsis*, *Platismatia* or *Pseudevernia* species dominant 10

10. *Parmelia laevigata*, and/or *P. taylorensis* present; *Cetrelia*, *Menegazzia*, *Mycoblastus*, *Ochrolechia* or *Sphaerophorus* species often present to abundant; communities of well lit extremely acid leached bark in areas of exceptionally high rainfall .. *Parmelion laevigatae* (p. 327).

Alectoria, *Bryoria*, *Cetraria*, *Hypogymnia*, *Parmelia saxatilis*, *Parmeliopsis*, *Platismatia* or *Pseudevernia* species present to dominant or co-dominant; communities of acid barks commonest in northern and upland areas of England and central and eastern Scotland with lower rainfall . . *Pseudevernion furfuraceae* (p. 334).

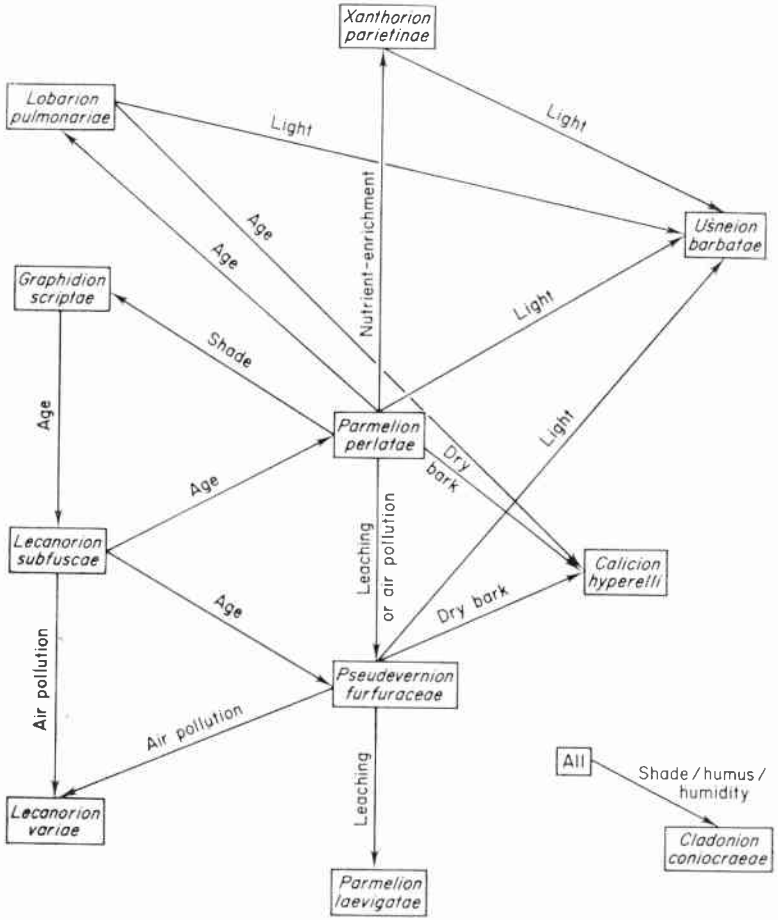

FIG. 1. Principal relationships between the epiphytic alliances present in the British Isles.

All. 1. *Calicion hyperelli*

Calicion hyperelli Čern. & Hadač, *in* Hadač, *Příroda* **36,** 254 (1944) [notes only seen]; type: *Lecanactidetum abietinae* Hil.—*Coniocybion gracilentae* Klem., *Beih. Feddes Repert.* **135,** 146 (1955).—*Leprarion* Almb., *Bot. Notiser, Suppl.* **1** (2), 33 (1948).—*Calicion viridis* Fab., *Monogr. Bot., Warsaw* **26,** 24 (1968) [as "Hadač em. Barkm."].

This large and species-diverse alliance is united by a common habitat rather than its species composition, which varies very greatly from one association to another. The alliance is characteristic of aged dry bark of deciduous trees and decorticate wood in well lit situations. The associations include many species which are strictly faithful to them; a rather unusual situation for epiphytic lichen communities. Many occur in ecological niches where they either never receive direct rain (i.e. are entirely dependent on atmospheric humidity for their moisture) or are in very exposed sites where their substrates dry out very rapidly following rain.

Arthonietum impolitae Almb.

Bot. Notiser, Suppl. **1** (2), 33 (1948).—*Impolitetum* Almb., *K. svenska Vetensk-Akad. Avh. naturvsk.* **11,** 27 (1955).

This markedly xerophilous community was treated by Barkman (1958) in a rather broader sense than is adopted here (see p. 309). We take it up for *Arthonia impolita* dominated communities on dry, well lit, often somewhat basic, barked trees in southern England. The association is rather poor in species but *Schismatomma decolorans* is a particularly common component of it. This association is not infrequent on trees in pastures where *Buellia canescens*, *B. punctata*, *Catillaria griffithii* and *Lecanora expallens* may enter into it.

Calicietum abietini Kalb

Hoppea [*Denkschr. Regen. bot. Ges.*] **26,** 104 (1966).

This association, characterized by stands of *Calicium glaucellum*, or rarely *C. abietinum*, is optimally developed on decorticate pine wood in the Scottish Highlands when additional members of the Caliciales enter into it (e.g. *Chaenotheca brunneola*) but is also encountered occasionally throughout the British Isles in this habitat and also on the exposed wood of a wide range of deciduous trees and, more rarely, fence-posts. *Chaenotheca trichialis* is also a locally important component of this association, but can also occur in a facies of the *Calicietum hyperelli* (see below). Many distinct noda may perhaps be recognized within the *Calicietum abietini* in the Scottish Highlands but these are too poorly understood at the present time to describe here.

Calicietum hyperelli Hil.

Spisy Přírod. Fac. Karl. Univ. **41,** 98 (1925) [as "Association à *Calicium hyperelum*" (*sic*)].—*Chaenothecetum melanophaeae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 356 (1958).

This association was described by Hilitzer (1925) for communities dominated by *Calicium viride* and in which *Lecanactis abietina* was often a major component. In the British Isles this generally species-poor association occurs on dry, rough or moderately smooth (e.g. *Acer*) bark of deciduous trees in lowland areas (most frequently in those subjected to moderate air pollution) and also on coniferous trees in central and eastern Scotland. Communities dominated by *Lecanactis abietina* appear distinct from the *Calicietum hyperelli* in the British Isles and that species is rarely a major component of this association here. *Lecanora expallens*, *Lecidea scalaris*, *Lepraria incana*, sometimes *Buellia schaereri* (central and eastern Scotland), *Catillaria griffithii* and *Schismatomma decolorans*, enter this association but it most commonly consists of almost pure stands of *Calicium salicinum*, *C. viride*, *Chaenotheca ferruginea* and *Lepraria candelaris*. *Chaenotheca ferruginea* predominates in polluted areas whilst *Schismatomma virgineum* occurs in the driest facies of this association.

In lowland Britain the *Calicietum hyperelli* is most commonly found on the dry (usually north-east) sides of well lit deciduous trees which carry either the *Parmelion perlatae* or *Xanthorion parietinae* on their better lit and wetter sides. Allied to this association is a further easily overlooked community which may be distinct, which occurs in dry sheltered bark crevices of rather basic-barked trees (e.g. *Fraxinus*, *Salix*, *Ulmus*) particularly in south-east England and central Scotland. This community is dominated by *Chaenotheca trichialis* together with *C. hispidula*, *C. carthusiae*, *C. laevigata* and *Coniocybe sulphurea*.

Coniocybetum furfuraceae Kalb

Ber. bayer. bot. Ges. **41,** 70 (1969).

The *Coniocybetum furfuraceae*, characterized by abundant *Coniocybe furfuracea*, occurs in more shaded sites than the *Calicietum hyperelli* and when on trees is restricted to basal crevices, exposed roots etc. This association is not exclusively corticolous and also occurs on soft humus and in rock crevices where it is protected from direct rain. The *Coniocybetum furfuraceae* is mainly restricted to western and northern parts of the British Isles. When on rock this association may include elements of the *Micareetum sylvicolae* (p. 366) and its relationships to that community merit further study.

Lecanactidetum abietinae Hil.

Spisy Přírod. Fac. Karl. Univ. **41,** 94 (1925) [as "Association à *Lecanactis abietina*"].

Communities dominated by *Lecanactis abietina* occur in generally similar habitats to the *Calicietum hyperelli* but favour somewhat more shaded and humid situations, for example dry, very acid bark of *Pinus* or *Quercus* within a wood rather than isolated trees in pastures. The association can perhaps be viewed as a dry bark counterpart of the *Parmelietum laevigatae*. Where this association is optimally developed, the *L. abietina* with apothecia, *Calicium viride* is often completely absent, and while *Chaenotheca ferruginea* is often to be found in the vicinity, it tends to be on slightly less sheltered parts of the trunks and to represent a fragment of the *Calicietum hyperelli* rather than forming a part of the present association. The *Lecanactidetum abietinae* is rather poor in species in the British Isles although *Lepraria incana* and *Schismatomma decolorans* may occur in it from time to time. *Arthonia leucopellaea*, *Lecanactis amylacea* and sometimes *L. corticola* or *L. dryophila*, are rare members of this association occurring in, for example, south-western and north-eastern Scotland and the New Forest. In old woodland areas *Schismatomma niveum* is also a frequent member of this association.

Lecanactidetum premneae ass. nov. (Table I, Fig. 2)

This very distinctive association, the "*Schismatomma decolorans–Lecanactis premnea–Opegrapha lyncea* community" of Rose and James (1974), appears to ultimately become the post-climax community of very ancient (over 300 years) *Quercus* trees and can cover their entire surfaces both in open parklands and in forested areas (e.g. the New Forest) in southern Britain. It colonizes bark surfaces which have become dry and brittle with age and lost their water-holding capacity but retained a relatively high pH. Though an association clearly relict from ancient forests, it does not need a forest microclimate to survive and can occur on ancient, now isolated, trees. The association is unknown in Scotland and appears very rarely in Ireland.

The characteristic species of the *Lecanactidetum premneae* are *Lecanactis premnea*, *Opegrapha lyncea*, *O. prosodea* (extreme south of England only), *Schismatomma decolorans*, and sometimes *S. virgineum*. *Arthonia impolita* and *Buellia canescens* are sometimes present in pasture sites. Although almost entirely restricted to aged *Quercus* (though also known on aged *Fagus*), a facies of this association (lacking *O. lyncea*) occurs on extremely ancient *Taxus* trees (usually in churchyards).

This community has been little understood in the past, doubtless due to the scarcity of ancient *Quercus* trees outside the British Isles, but elements of it were included by Barkman (1958) in his rather broad concept of the

TABLE I.*

Lecanactidetum premneae ass. nov.

Species	Stands							
	1	2	3	4	5	6	7	8
Arthonia impolita	3.3	–	–	–	–	1.3	1.3	–
Buellia canescens	–	–	–	–	–	+.2	3.2	–
Catillaria griffithii	+.2	–	+.2	–	–	–	–	–
Chaenotheca brunneola	–	–	–	–	–	+.0	–	–
Cladonia coniocraea	–	–	–	–	+.0	+.2	–	–
C. parasitica	–	–	–	–	+.0	–	–	–
Enterographa crassa	–	–	2.2	2.3	2.3	2.3	–	–
Haematomma ochroleucum var. *porphyrium*	–	1.2	–	–	–	–	–	–
Lecanactis abietina	–	–	+.2	–	–	–	–	–
L. premnea	1.2	3.3	4.5	3.3	2.3	–	1.2	3.3
Lecanora expallens	+.2	–	–	–	–	–	–	2.3
Lecidea granulosa	–	–	–	+.2	–	–	–	–
L. quernea	+.2	–	+.0	–	–	+.0	1.2	–
L. uliginosa	–	–	–	–	+.2	–	–	–
Lepraria candelaris	–	–	2.3	–	+.2	–	–	1.2
L. incana	+.2	–	2.1	2.2	1.2	1.2	–	–
Normandina pulchella	–	–	–	+.2	–	–	–	–
Opegrapha lyncea	–	2.3	–	1.2	2.3	1.3	+.2	2.3
O. prosodea	–	–	–	–	–	–	1.2	–
Parmelia caperata	–	–	–	–	–	+.0	–	–
P. glabratula	–	–	–	+.2	–	–	+.0	–
P. sulcata	–	–	–	1.2	–	–	–	–
Pertusaria hemisphaerica	–	–	–	–	–	–	–	1.3
P. hymenea	–	–	+.1	–	–	–	–	–
Phlyctis argena	–	–	–	–	–	–	–	+.3
Ramalina farinacea	–	–	–	+.0	–	–	–	–
Rinodina roboris	–	–	–	+.0	–	–	1.2	–
Schismatomma decolorans	4.3	3.3	+.1	3.3	2.2	3.3	4.4	1.3
Hysterium angustatum	–	–	1.1	–	–	–	–	–
Bryum capillare	–	–	–	+.0	–	–	–	–
Hypnum cupressiforme	–	–	–	+.2	+.0	+.0	–	–
Isothecium myosuroides	–	–	–	+.2	–	–	–	–
Lophocolea heterophylla	–	–	–	+.2	+.0	–	–	–
Metzgeria furcata	–	–	–	+.2	–	–	–	–
Mnium hornum	–	–	–	+.0	–	–	–	–
Orthodontium lineare	–	–	–	–	+.0	–	–	–

*See p. 408 for notes on relevé tables.

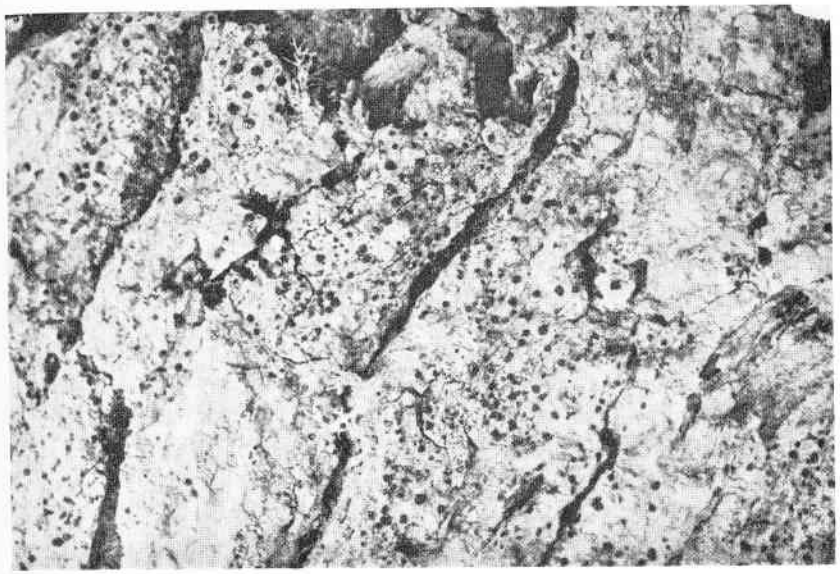

FIG. 2. *Lecanactidetum premneae* on dry bark on an ancient oak. Species present include: *Calicium viride*, *Lecanactis premnea* (predominating), *Lepraria incana*, *Ramalina farinacea* and *Schismatomma decolorans* (Hampshire: New Forest, Vinney Ridge, 1969, P. W. James).

1. Cumbria, Naworth Park (35/– – 6 – –): old *Quercus* in pasture, 1·0 m diam, incl. 90°, aspect SW, 0·5 × 0·5 m, cover 60%, 31 August 1973, F.R.
2. Hampshire, New Forest, Moyles Court (41/1––0––): ancient *Quercus* by road, 2·5 m diam, incl. 90°, aspect N, 1·0 × 0·5 m, cover 70%, 20 September 1967, F.R.
3. Hampshire, New Forest, Eyeworth Wood (41/2 – – 1 – –): *Quercus robur*, 0·6 m diam, incl. 90°, aspect E, 1·0 × 0·5 m, cover 90%, 25 June 1968, F.R. and J. J. Barkman.
4. Kent, Lullingstone Park (51/5 – – 6 – –): ancient *Quercus* in relict valley forest, 1·6 m diam, incl. 90°, aspect S, 1·0 × 1·0 m, cover 60%, 10 January 1969, F.R.
5. Norfolk, Merton Park, Merton Oaks Wood (52/9 – – 9 – –): ancient *Quercus* in wood, 3·0 m diam, incl. 90°, aspect S, 1·0 × 1·0 m, cover 70%, 5 June 1970, F.R.; *type record*.
6. Norfolk, Kimberley Park (63/0 – – 0 – –): ancient *Quercus* by drive in parkland, 2·0 m diam, incl. 90°, aspect S, 1·0 × 1·0 m, cover not determined, 8 March 1969, F.R.
7. Sussex, Parham Park (51/0 – – 1 – –): very old *Quercus* in park, 1·5 m diam, incl. 90°, aspect N, 1·0 × 0·5 m, cover 90%, 5 November 1968, F.R.
8. Wiltshire, Longleat Park (31/8 – – 4 – –): ancient *Quercus* in open parkland, 3·0 m diam, incl. 90°, aspect S, 1·0 × 1·0 m, cover 70%, 5 June 1970, F.R.

Arthonietum impolitae treated above. It certainly occurs in France in the Fôret de Fontainebleau and Brittany.

Leprarietum candelaris (Matt.) Barkm.

Phytos. Ecol. Crypt. Ep., 355 (1958).—*Lepraria candelaris* Gesellschaft Matt., *Ber. West-preuss. bot.-zool. Ver.* **59,** 16 (1937).

The *Leprarietum candelaris* is dominant on the dry north and east sides of hardwood trees in forests in relatively unpolluted parts of the British Isles where the rainfall is rather low (particularly in north-east Scotland near the Moray Firth). Elsewhere in southern and eastern England it is largely confined to dry bark crevices, where it is often associated with *Schismatomma decolorans*, although it does occasionally spread from crevices to fully exposed, raised flattened bark surfaces in a few low-rainfall southern areas (e.g. extreme south Devonshire).

The *Leprarietum candelaris* is closely related to the *Calicietum hyperelli* and appears to be a more lowland counterpart of it in the British Isles.

Leprarietum incanae ass. nov. prov.

This association has a similar ecological amplitude to the *Coniocybetum furfuraceae* occurring not only on the shaded parts of trees but also on humus, on dry powdery soil in rock crevices and on rock. *Lepraria incana* often occurs in almost pure stands but *Cladonia coniocraea*, *Lecidea granulosa* and *L. uliginosa* frequently enter into the association on trees. The *Leprarietum incanae* is the most shade and air-pollution tolerant of the associations of the *Calicion hyperelli* treated here extending far into urban areas in cracks of the bark on the basal parts of deciduous trees.

Opegraphetum fuscellae Almb.

Bot. Notiser, Suppl. **1** (2), 140 (1948).—*Fuscelletum* Almb., *K. svenska Vetensk-Akad. Avh. natursk.* **11,** 37 (1955).

A rather species-poor community dominated by *Opegrapha vermicellifera* occurring mainly in woodlands on dry bark of deciduous trees but sometimes spreading on to adjacent *Hedera* stems or siliceous rocks. Additional important components include *O. ochrocheila*, *O. vulgata* and *Pyrenula nitida*. This association occurs on a wide range of deciduous trees, although also known from conifers, but in Britain prefers somewhat base-rich barks. Interestingly, like the *Parmelietum revolutae* (see p. 331) it is found on conifers only in areas where there is little or no air pollution.

Two facies of this community can be recognized in the British Isles: (1) the typical nodum on shaded basic barks (e.g. *Ulmus*) with *Opegrapha vermicellifera*, *O. ochrocheila* and *O. lichenoides*, and (2) one on shaded more acid barks (e.g. *Fagus*) where *O. niveoatra* predominates and *Pertusaria leioplaca* and *Graphis* species are characteristically present. The *Opegraphetum fuscellae*, as conceived here, has a rather southern and western distribution in the British Isles.

All. 2. *Cladonion coniocraeae*

Cladonion coniocraeae Duvign., *Bull. Soc. r. bot. Belg.* **74,** 49 (1942); type: *Cladonietum coniocraeae* Duvign.

This alliance was first described from Belgium for communities dominated by *Cladonia coniocraea* and applied to British communities by Laundon (1956, 1958, 1967) and later authors. Two associations are recognized in Britain both of which can occur on tree bases and peaty soils.

Cladonietum cenoteae Frey

Veröff. Geobot. Inst. Rubel **4,** 249 (1927).

This association, first described from Scandinavia, is used here in its original somewhat restricted sense (see below) for the *Cladonia*-rich communities which are found on very dry and acidic tree bases, dead stumps and on peaty soil under mature native pine woods in the Scottish Highlands. It is particularly well developed in the Glen More and Rothiemurchus Forests where it includes as its characteristic species the rare or local *C. botrytes*, *C. carneola*, *C. cenotea*, *C. deformis* and *C. nemoxyna* as well as the more widespread *C. furcata*, *C. gonecha*, *C. gracilis*, *C. scabriuscula* and other moorland *Cladoniae*.

Cladonietum coniocraeae Duvign.

Bull. Soc. r. bot. Belg. **74,** 49 (1942).

The *Cladonietum coniocraeae* is a well marked community which is both pollution tolerant in the British Isles and has a wide ecological amplitude, occurring on the bases of shaded trees (sometimes extending far up the trunks in ravine-like sites), rotting wood, clayey and peaty soils, and siliceous rocks in damp situations. The community, when optimally developed, is rich in species of *Cladonia*, although *C. coniocraea* is the most important; others commonly encountered include *C. chlorophaea*, *C. digitata*, *C. fimbriata*, *C. macilenta*, *C. pyxidata* s. str. and *C. squamosa*. On

TABLE IV.

Parmelietum revolutae Klem.

Species	Stands 1	2	3	4	5	6	7	8
Candelariella vitellina	–	–	–	2.3	–	–	–	–
Catillaria griffithii	–	–	–	–	+.2	–	–	–
Evernia prunastri	–	–	2.3	–	1.2	1.2	1.2	2.2
Hypogymnia physodes	–	–	+.0	–	+.1	–	2.2	1.2
Lecanora chlarotera	–	–	–	–	+.2	+.2	1.2	–
L. conizaeoides	–	2.2	–	–	–	–	–	–
L. expallens	–	1.2	–	3.2	–	+.2	3.2	–
Lecidea quernea	–	–	+.0	–	4.3	3.3	–	–
Lecidella elaeochroma	–	–	–	–	–	+.0	–	1.2
Lepraria candelaris	–	–	–	–	1.2	–	–	–
L. incana	+.2	–	–	–	–	+.0	–	–
Ochrolechia yasudae	–	–	–	–	2.2	–	2.4	–
Parmelia caperata	2.3	1.2	1.3	3.3	1.2	2.3	1.4	1.2
P. glabratula	+.2	1.2	2.3	1.3	–	+.2	2.2	–
P. perlata	3.4	–	–	–	–	–	–	2.3
P. reticulata	–	+.2	–	–	1.2	–	–	–
P. revoluta	–	1.2	1.3	–	–	–	–	–
P. saxatilis	3.3	–	1.3	–	–	–	–	–
P. soredians	–	2.3	–	–	–	–	–	–
P. subrudecta	–	1.2	–	–	–	2.2	1.3	+.0
P. sulcata	–	3.2	2.3	1.3	–	4.3	1.2	+.0
Pertusaria albescens	–	–	–	+.1	–	–	–	–
var. *corallina*	–	–	–	3.2	–	–	–	–
P. amara	1.3	–	–	–	3.2	1.3	+.2	–
P. pertusa	1.2	1.3	–	–	1.2	2.3	–	–
Phlyctis argena	–	1.2	–	–	–	1.3	–	–
Ramalina farinacea	+.0	2.2	+.0	–	1.1	+.0	+.2	+.0
R. fastigiata	–	–	–	–	–	+.0	–	–
Hysterium angustatum	–	–	–	–	–	+.0	–	–
Cololejeunea minutissimus	–	–	–	–	–	–	–	1.2
Frullania dilatata	–	–	–	–	–	+.2	–	3.3
Hypnum cupressiforme	1.2	–	–	+.2	1.3	1.3	–	4.3
Metzgeria furcata	–	–	–	–	–	–	–	1.2
M. fruticulosa	–	–	–	–	–	–	–	+.0
Ulota phyllantha	–	–	–	–	–	–	–	2.2
Zygodon viridissimus	–	–	–	–	–	–	–	+.2

western Scotland north to Skye and Applecross, and parts of Angus, Fife and Perthshire. Its replacement in the north and east of the British Isles (and also in the central Welsh uplands) by the *Pseudevernietum furfuraceae* as the main community on well lit hardwood trees appears to be due to climatic factors, though whether low winter temperatures or lack of summer sunshine and warmth are the limiting factors is unclear. In high-rainfall upland areas the *Parmelietum revolutae* gives way to the *Parmelietum laevigatae*.

The association similarly gives way to the *Pseudevernietum furfuraceae* in northern continental areas (e.g. Denmark, north Germany), but is very general in France north of the Mediterranean area.

The species most commonly encountered in this association are *Catillaria griffithii*, *Evernia prunastri*, *Hypogymnia physodes*, *Lecanora chlarotera*, *L. expallens*, *Lecidea quernea*, *Ochrolechia yasudae*, *Parmelia caperata*, *P. glabratula* ssp. *glabratula*, *P. perlata*, *P. saxatilis*, *P. subaurifera*, *P. subrudecta*, *P. sulcata*, *Pertusaria albescens*, *P. amara*, *P. hemisphaerica*, *P. pertusa*, *Phlyctis argena* and *Ramalina farinacea*. Additional important components in the south and/or east include *Parmelia borreri*, *P. reticulata*, *P. soredians*, *Pertusaria coccodes*, *P. flavida* and *Rinodina roboris*. *Parmelia perlata* is abundant only where air pollution levels are extremely low (e.g. relevés from Slapton, S. Devon, in Hawksworth, 1972a). Bryophytes are generally poorly represented in this association, the most frequently

1. Cumbria, Borrowdale, Manesty Park (35/2 – – 1 – –): *Quercus* at edge of wood, 0·8 m diam, incl. 90°, aspect SW, 0·5 × 0·5 m, cover 75%, 4 June 1969, F.R., D.L.H. and B.J.C.
2. E. Kent, Hothfield Park (51/9 – – 4 – –): old *Quercus*, 1·0 m diam, incl. 90°, asp. S, 1·0 × 1·0 m, cover 60%, 7 April 1969, F.R.
3. E. Kent, near Ashford, Willesborough Lees (61/0 – – 4 – –): *Quercus* in open pasture, 1·0 m diam, incl. 90°, aspect SW, 1·0 × 1·0 m, cover 70%, 24 September, 1968, F.R.
4. E. Kent, Maidstone, Mote Park (51/7 – – 5 – –): *Fraxinus*, 0·8 m diam, incl. 90°, aspect not indicated, 0·5 × 0·5 m, cover 80%, 10 September 1968, F.R.
5. E. Kent, Otham, Gore Court (51/7 – – 5 – –): *Fraxinus* in parkland, 1·0 m diam, incl. 90°, aspect SE, 2·0 × 0·5 m, cover 90%, 6 September 1968, F.R.
6. W. Kent, Plaxtol (51/6 – – 5 – –): *Fraxinus* in valley, 0·6 m diam, incl. 90°, aspect S, 1·0 × 2·0 m, cover 90%, September 1967, F.R.
7. Surrey, Burstow, Westlands Farm (51/3 – – 4 – –): *Quercus robur*, 0·7 m diam, incl. 90°, aspect S, 1·0 × 0·5 m, cover 80%, July 1968, F.R.
8. E. Sussex, Fairlight undercliff (51/8 – – 1 – –): *Quercus*, 0·3 m diam, incl. not indicated, aspect S, 1·0 × 0·2 m, cover 90%, 1 March 1969, F.R. and P.W.J.

dry decorticate wood *C. coniocraea* may be almost entirely replaced by *C. parasitica*, and in damp woods in the south and south-west, the rather rare *C. caespiticia* also enters into the association. The most pollution-tolerant facies of this community, however, merely comprises swards of *C. coniocraea* and/or *C. macilenta*. The association intergrades with other noda containing species such as *Lecidea granulosa*, *L. uliginosa*, *Micarea prasina*, *Peltigera canina*, *P. polydactyla*, *P. praetextata* and *Sphaerophorus globosus*. Bryophytes are important components in this community, the introduced *Orthodontium lineare* (see Rose and Wallace, 1974) being particularly characteristic in the south-eastern and Midland counties. In relatively unpolluted areas *Usnea*-rich facies occur in better lit sites but these, following Barkman (1958), are placed in the *Cladonieto–Usneetum tuberculatae* here (see p. 338).

The *Cladonietum coniocraeae* has been treated as a synonym of the *Cladonietum cenoteae* by a number of lichen phytosociologists (e.g. Wilmanns, 1966) following Klement (1955), but this view was rejected for the British Isles by Hawksworth (1972a); from the information provided above it will be evident that these two associations differ fundamentally in species composition, habitat and distribution and thus clearly merit treatment as distinct associations.

Various infrassociational taxa have been described within this association (e.g. var. *macrocladonietum digitatae* Duvign., var. *microcladonietum coniocraeae* Duvign., var. *sphaerophoretum globosae* Duvign., subass. *cladonietum digitatae* Klem.) and while most can be recognized within the British Isles they appear to be of minor synsystematic value.

All. 3. *Graphidion scriptae*

Graphidion scriptae Ochsn., *Jahrb. St. Gall. naturw. Ges.* **63,** 49 (1928); type: *Pyrenuletum nitidae* Hil.—*Graphidion* Almb., *K. svenska VetenskAkad. Avh. natursk.* **11,** 21 (1955); type: *Nitidetum* Almb.

This particularly well marked alliance is characteristic of smooth bark, usually on young trees, branches or twigs, and comprises two distinct elements, (1) the pioneer community of trees, and (2) some communities persisting on mature trees with smooth bark or restricted to deep shade. The *Graphidion scriptae* is characterized by a wide range of crustose species and where macrolichens are encountered within its associations they can be viewed as pioneers of subsequent successional stages. Most of the crustose species involved are esorediate with either lirellate or pyrenocarpous ascocarps.

The alliance is entirely restricted to the bark of deciduous trees in the British Isles. While it evidently merits subdivision into several associations,

few studies have been made on this alliance in Britain so far and the following treatment is consequently to be regarded as provisional.

In more humid situations, especially on inclined boughs of *Corylus* and *Salix* in sheltered sites in western Britain and western France, the alliance becomes rapidly enriched by other taxa, both of bryophytes and foliose lichens, characteristic of the *Lobarion pulmonariae* or *Parmelion laevigatae*. The commonly occurring bryophytes include species of *Ulota* (particularly *U. bruchii* and *U. crispa*, with *U. phyllantha* in maritime situations and *U. drummondii* and *U. hutchinsiae* in hyper-oceanic sites) and *Orthotrichum* (particularly *O. affine*, *O. pulchellum*, *O. striatum* and *O. tenellum*) and hepatics such as *Frullania dilatata*, *Lejeunea ulicina*, *Metzgeria furcata* and *Radula complanata*.

Communities in this alliance are generally air-pollution intolerant. In drier unpolluted areas its species may persist on the trunks of mature *Quercus* on the level surfaces between the furrows in the bark, but in high rainfall areas they will only persist on phorophytes which have smooth bark throughout their lives (e.g. *Corylus*, *Fagus*, *Ilex*, *Salix* and *Sorbus*). The alliance may also occur as species-poor variants on medium aged *Betula* in moister parts of the British Isles but it is not typically developed on that tree.

Some hyper-oceanic lichens occur within communities of this alliance (e.g. *Anthracothecium pyrenuloides*, *Arthothelium* species (excluding *A. ruanum*), *Dermatina swinscowii*, *Graphina ruiziana*, *Lecanactis homalotropum*, *Thelotrema subtile*, *Leptogium hibernicum*, *Pyrenula dermatodes*, *P. laevigata*, *Thelotrema monosporum* and *Tomasellia ischnobela*) but the synsytematics of these have not been investigated and so these are not considered in the associations recognized below. They tend to occur where *Lobarion* on trunks is rich in members of the Pannariaceae, but rather poor in *Lobaria*, *Pseudocyphellaria* and *Sticta* species, as in the Glasdrum National Nature Reserve, Argyllshire.

Arthopyrenietum punctiformis ass. nov. prov.

This name is adopted provisionally here for the pioneer community of twigs and saplings dominated by pyrenocarpous lichens with endophloeodal thalli, and includes *Arthonia aspersella*, *A. punctiformis*, *A. radiata*, *A. tumidula*, *Arthopyrenia fallax*, *A. punctiformis*, *Dermatina quercus* (second or third year oak twigs), *Opegrapha atra*, *Stenocybe pullatula* (confined to *Alnus* twigs) and *Tomasellia gelatinosa* (mainly on *Corylus*). The age of the twigs and the degrees of preliminary scarring influence the intrusion of additional hypophloeodal species which first appear around leaf and girdle scars. *Lecanora carpinea*, *L. chlarotera*, *L. confusa*, *Lecidea symmicta*, *Lecidella elaeochroma* and *Rinodina sophodes* indicate transitions

to the *Lecanoretum subfuscae*, whilst in more polluted areas *Bacidia chlorococca* and *Lecanora conizaeoides* indicate transitions to the *Bacideetum chlorococcae* and *Lecanoretum pityreae*, respectively. On saplings a facies dominated by *Porina chlorotica* var. *carpinea* with much *Opegrapha atra* and *O. vulgata* and little or no *Arthonia punctiformis* is particularly distinctive; this frequently includes species of the *Lecanoretum subfuscae* (well lit sites) or *Pyrenuletum nitidae* (shaded sites) representing transitions to those associations.

Graphidetum scriptae Hil.

Spisy Přírod. Fac. Karl. Univ. **41,** 90 (1925) [as "Association à *Graphis scripta*"]. —*Graphinetum platycarpae* var. *graphinetum anguinae* D. Hawksw., *Fld Stud.* **3,** 548 (1972).

This name is taken up here for communities of moderately shaded smooth bark dominated by some of the larger lirelliform crustose lichens (e.g. *Graphina anguina, Graphis elegans, G. scripta, Phaeographis dendritica* and *P. lyellii*). It characteristically occupies less densely shaded sites than the *Pyrenuletum nitidae*, transitions to which are not infrequent. *Arthonia lurida* is also commonly found in this association. In its well developed form this association is essentially oceanic; only *G. scripta* of the species listed above occurs in any quantity in continental areas of Europe.

On *Ilex*, particularly in the New Forest and south-west Ireland, a species-rich variant of this association occurs which includes *Arthonia stellaris, Arthothelium ilicinum, Mycoporellum sparsellum* and *Stenocybe septata*, together with much *Thelotrema lepadinum*.

Although Barkman (1958) subsumed Hilitzer's association within the *Pyrenuletum nitidae*, Hilitzer appears to have recognized the distinctness of these noda and thus his name is adopted here.

Pertusarietum amarae Hil.

Spisy Přírod. Fac. Karl. Univ. **41,** 87 (1925) [as "Association à *Pertusaria amara*"]. —*Pertusarietum hemisphaericae* Klem., *Beih. Feddes Repert.* **135,** 140 (1955) [as "Almborn 1948"].—*Pertusarietum wulfenii* Klem., *Beih. Feddes Repert.* **135,** 134 (1955) [as "Almborn 1948"].—*Amaretum* Almb., *K. svenska VetenskAkad. Avh. natursk.* **11,** 15 (1955).

This association was used by Barkman (1958) in a rather restricted sense but has been subsequently adopted by, for example, Fabisewski (1968) who recognized three variants. The *Pertusarietum amarae* is interpreted here as comprising somewhat shade-tolerant communities, often on rather less smooth bark, in which species of *Pertusaria* predominate. The community

is particularly well developed on *Fagus* in the New Forest and *Carpinus* in south-east England. *Pertusaria hymenea* and *P. pertusa* are the most important components although other species of the genus provide high cover values locally (e.g. *P. hemisphaerica, P. leioplaca*). In old forests *Haematomma elatinum, Lecidea cinnabarina* and *Thelotrema lepadinum* also enter into it and the lirelliform species generally present (other than *Graphis elegans*) become replaced by verrucose-fertile and verrucose-sorediate taxa (characterized by *Pertusaria*).

The *Pertusarietum amarae* shows some tendency to intergrade with the *Pyrenuletum nitidae* and could be viewed alternatively as an extreme facies of that association.

Pyrenuletum nitidae Hil.

Spisy Přírod. Fac. Karl. Univ. **41,** 91 (1925) [as "Association à *Pyrenula nitida*"]. —*Lecanoretum glabratae* Klem., *Beih. Feddes Repert.* **135,** 132 (1955) [as "Almborn 1948"].—*Nitidetum* Almb., *K. svenska VetenskAkad. Avh. natursk.* **11,** 21 (1955).—*Porinetum carpineae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 382 (1958) [as "*nov. ass. prov.*"].

The *Pyrenuletum nitidae*, principally characterized by extensive mosaics of *Enterographa crassa* and/or *Pyrenula nitida* and *P. nitidella*, occurs on a wide range of smooth-barked deciduous trees when growing in deep shade. Many species may accompany it, of which *Arthonia lurida, A. radiata, A. spadicea, A. tumidula, Graphis scripta, Opegrapha atra, O. viridis, O. vulgata, Pertusaria leioplaca* and *Phaeographis dendritica* merit particular note; some of these species may be very important components of this association locally. Further east in Europe (e.g. eastern Denmark) this association is important on *Fagus* in old dry forests; *Opegrapha viridis* usually occurs in such sites but *Enterographa crassa* is normally absent.

According to Barkman (1958) the *Opegraphetum herpeticae* Almb. (syn. *Rufescentetum* Almb.) is closely allied to the *Pyrenuletum nitidae*. While the components of this association occur in the British Isles they do not appear to constitute a well defined association here; *Opegrapha rufescens*, for example, is essentially a species of aged dry bark underhangs of *Fraxinus*, more rarely *Quercus*, and is perhaps better placed with other associations characteristic of this habitat (see pp. 308–309). The *Arthonietum luridae* Kalb, described from Germany, seems only doubtfully distinct from our concept of the *Pyrenuletum nitidae*. The *Porinetum carpineae* of Barkman (1958) appears to be merely an early stage of the *Pyrenuletum nitidae* and so is not recognized separately here; this facies, not usually found on young twigs, includes *Microthelia micula, Porina chlorotica* var. *carpinea* and *P. leptalea*.

All. 4. *Lecanorion subfuscae*

Lecanorion subfuscae Ochsn., *Jahrb. St. Gall. naturw. Ges.* **63,** 50 (1928); type: *Lecanoretum subfuscae* Hil.—*Lecanorion carpineae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 390 (1958); type: *Lecanoretum carpineae montanum* Barkm.—*Olivaceion* Laund., *Lond. Nat.* **37,** 72 (1958) [as *nom. nov.* for "*Lecanoretum subfuscae* Ochsn. p.p."].

The nomenclature of this alliance is extremely complex. Barkman (1958) rejected Ochsner's name as highly ambiguous because of the confusion which surrounds the name *Lecanora subfusca* but, as is the case with the *Usneion barbatae* discussed below (p. 338), since there can be little doubt that the composition of the alliance corresponds to Barkman's *Lecanorion carpineae*, Barkman's terminology is rejected here as it has been by, for example, Kalb (1970) and Hawksworth (1972). For further information on the nomenclature of this alliance, Kalb's (1970) detailed discussion should be consulted.

The *Lecanorion subfuscae* is essentially a pioneer community of *well lit* twigs and young trees characterized by species of *Lecanora* (particularly the *L. subfusca* species complex) and other hyperphloeodal crustose species forming intricate mosaics. A single association is recognized within it in the British Isles.

Lecanoretum subfuscae Hil.

Spisy Přírod. Fac. Karl. Univ. **41,** 84 (1925) [as "Association à *Lecanora subfusca*"].—*Lecideeto parasemo-Phlyctideetum* Hil., *Spisy Přírod. Fac. Karl. Univ.* **41,** 89 (1925) [as "Association à *Lecidea parasema* et *Phlyctis*"].—*Lecanoretum allophanae* Duvign., *Bull. Soc. r. bot. Belg.* **74,** 39 (1942) [as "*nom. nov.*"].—*Lecanoretum carpineae atlanticum* Barkm., *Phytos. Ecol. Crypt. Ep.*, 392 (1958).

This association, which is widespread through the British Isles, is particularly rich in species, the most important components being *Lecanora chlarotera*, *L. chlarona*, *L. pallida* and *Lecidella elaeochroma*. Other species frequently present include *Arthonia radiata*, *Buellia griseovirens*, *Graphis scripta*, *Lecanora carpinea*, *L. confusa*, *L. expallens*, *L. intumescens*, *Lecidea symmicta*, *Opegrapha atra*, *Parmelia exasperata*, *P. subaurifera*, *Pertusaria leioplaca*, *Phlyctis argena*, and *Rinodina sophodes*, together with the mosses *Ulota bruchii* (near the coast) and *U. phyllantha*. In slightly more shaded situations *Catillaria lightfootii*, *Haematomma elatinum*, *Lecanora jamesii*, *Lecidea tenebricosa* and *Phlyctis agelaea* enter into the association in the south and west. In southern Britain the association eventually gives way to the *Parmelietum revolutae* on deciduous trees as the macrolichens in

that association tend to grow over the mosaics of crustose species characteristic of the *Lecanoretum subfuscae*. With increasing shade, in contrast, the *Lecanoretum subfuscae* merges into the *Graphidetum scriptae* to such an extent that stands which are difficult to assign conclusively to one or the other association are not uncommon. On *Prunus spinosa* and *Salix repens* in some coastal situations (e.g. Dungeness, Kent and Berry Head, South Devonshire), however, the association includes *Lecanora chlarotera*, *L. confusa*, *Lecidea symmicta* and *Lecidella elaeochroma* but is atypical in an abundance of *Caloplaca cerina;* this distinctive facies also occasionally includes *Ramalina baltica* indicating an affinity with the *Ramalinetum fastigiatae*.

Several allied associations may well occur in other parts of Europe but are in need of further investigation as Barkman's (1958) treatment of them is evidently unsatisfactory. The *Lecanoretum laevis* Barkm., in which *Lecanora chlarotera* is replaced by *L. laevis* and *Lecidella elaeochroma* replaced by *Lecidea euphorea*, is certainly distinct being characteristic of warmer areas and starting to appear in southern France; the *Lecanoretum laevis* is also a pioneer twig community and has a wide geographical range extending into, for example, the forests of the Azores and West Pakistan. Particularly in the more southerly parts of Europe (e.g. southern and western France), *Teloschistes chrysophthalmus*, *T. flavicans* and *Usnea flammea* appear to enter into communities which might be considered a regional variant of the *Lecanoretum subfuscae*.

All. 5. *Lecanorion variae*

Lecanorion variae Barkm., *Phytos. Ecol. Crypt. Ep.*, 362 (1958); type: *Psoretum ostreatae* Hil.—*Conizaeoidion* Laund., *in* Kettering and District Field Club, *First Fifty Years*, 92 (1956) [*nom. illegit.*]

This alliance is employed here for four associations, three of which are particularly tolerant of sulphur dioxide air pollution. These do not appear to be merely species-poor facies of other more pollution-sensitive assemblages of species as they occur from time to time in relatively unpolluted parts of the British Isles, particularly on lignum and the acid bark of coniferous trees.

The name of this alliance is misleading as it was based on the assumption that *Lecanora conizaeoides* (syn. *L. pityrea*) was simply a form of *L. varia*. Despite some recent Czechoslovakian studies implying the contrary (for details see Hawksworth, 1973b), this conclusion is taxonomically unacceptable as these taxa differ chemically, morphologically and in their respective distributions.

The *Caloplacetum phloginae*, placed in this alliance with some hesitation by Barkman (1958), is subsumed under the *Physcietum ascendentis* of the *Xanthorion* here (see p. 344).

Bacidietum chlorococcae LeBlanc

Can. J. Bot. **41,** 615 (1963) [as "Union à *Bacidia chlorococca*"].—Kalb, *Hoppea* [*Denkschr. Regensb. bot. Ges.*] **26,** 110 (1966) [as "*ass. nov.*"].

Although frequently overlooked, *Bacidia chlorococca* is widespread and very tolerant of air pollution (see Ahti and Vitikainen, 1974) entering far into urban areas in *Desmococcus* (*Pleurococcus* auct.)-dominated swards on deciduous trees whose barks have been impregnated with soot. This species-poor association often includes only *Bacidia chlorococca* and *Desmococcus* and appears even more pollution tolerant than the *Lecanoretum pityreae*. The *Bacidietum chlorococcae* tends to prefer somewhat more sheltered sites than the *Lecanoretum pityreae*, occurring, for example, on twigs and young branches of trees, and *Calluna* and *Ulex* stems; intermediates between the two associations are not uncommon, particularly on *Calluna*, where *Buellia pulverea* and *Micarea nitschkeana* may also occur.

Cyphelietum inquinantis Kalb

Diss. Bot., Lehre **9,** 34 (1970) [as "*Cyphelium*"].

This recently described association is characterized mainly by the abundance of *Cyphelium inquinans*, *Lecanora varia* and *Parmeliopsis ambigua*. It is possible that the *L. varia* reported by Kalb (1970) included *L. conizaeoides;* both these species occur in this association in the British Isles although not throughout its whole range. The *Cyphelietum inquinantis* is essentially a somewhat continental association which consequently has an eastern distribution in the British Isles. In lowland England it occurs mainly on decorticate horizontal rails, or on fence-posts, while in the Scottish Highlands (probably its original habitat), it is found occasionally on bark and decorticate pine wood in old pine forests where *Xylographa abietina* may be present in it as it is in the Alps. In south-east England *Parmeliopsis aleurites* is an additional component and elements of the *Pseudevernietum furfuraceae* may also enter into the association.

The *Cyphelietum inquinantis* has strong affinities with the *Calicion hyperelli* and is placed here, following Kalb (1970), because of the presence of *Lecanora conizaeoides* and (or) *L. varia*. The relationships of this association with the *Lecanoretum variae* Frey require investigation.

It is possible that the very rare eastern *Cyphelium notarisii* communities in Britain are a facies of this association (or perhaps the little understood *Cyphelietum tigillaris* Klem.) but too few data are available to make any reliable assessment as to their syntaxonomic status in Britain at the present time. As an example of the composition of this facies the following relevé may be cited: *Cyphelium notarisii* (2.3), *C. inquinans* (2.3), *Lecanora conizaeoides* (2.3), *L. varia* (1.3), *Ramalina fastigiata* (1.2) and *Xanthoria polycarpa* (2.2) [E. Sussex, Winchelsea Beach, Rye Harbour (51/9– – 1 – –): wooden post 250 m from the sea, incl. 90°, aspect 225°, 0·2 × 0·2 m, 17 April 1976, F.R.].

Lecanoretum pityreae Barkm.

Phytos. Ecol. Crypt. Ep., 363 (1958).

This is an extremely uniform association which characteristically includes only a single species, *Lecanora conizaeoides*, forming extensive pure continuous swards on well lit deciduous trees which can cover them from base to uppermost twigs. It is, however, optimally developed only where mean winter sulphur dioxide levels are in the range 55–150 $\mu g\ m^{-3}$, and in this range commonly also occurs on sandstones (particularly in the southern Pennines) and peaty moorland soils. Where air pollution levels are in the lower part of this range the association is also occasionally found on coniferous trees. The *Lecanoretum pityreae* appears to be pollution tolerant or a pollution exploiter rather than one needing pollution to survive as it does occur in parts of Britain almost entirely free of any air pollution; interestingly, in such areas it is almost entirely restricted to decorticate wood (especially fence-posts) and either twigs or acid-barked trees (e.g. birch and coniferous trees) and usually found in sites frequented by visitors from parts of the country where it is common. The association appears to have poor competitive ability where there is little air pollution and fails to encroach on communities already established.

The *Lecanoretum pityreae* is the commonest or only association on trees over large tracts of the British Isles extending northwards from the Thames valley, through the Midlands, and into northern Lancashire in the west and Northumberland in the east. More detailed information as to the behaviour of *Lecanora conizaeoides* in Britain is included in Hawksworth *et al.* (1973, 1974). In damper sites, the association frequently intergrades with the *Bacidietum chlorococcae* on twigs, *Calluna* stems etc.

Few other species ever form important components of this association. The most frequently encountered is perhaps *Lepraria incana*, especially in bark crevices or near the bases of trees, although plants of *Hypogymnia*

physodes, *Parmelia saxatilis* and *Parmeliopsis ambigua*, for example, start to occur with increasing frequency towards the lower end of its sulphur dioxide optimal concentration range; these latter plants represent intergrades with the species-poor pollution variant of the *Pseudevernietum furfuraceae* mentioned below (p. 337). Where bark is nutrient enriched, particularly by soot, *Desmococcus vulgaris* also enters into this association. The *Lecanoretum pityreae* is often attacked by *Athelia arachnoidea* (Berk.) Jül. which can form large pale lesions in it.

Lecideetum ostreatae (Hil.) comb. nov.

Psoretum ostreatae Hil., *Spisy Přírod. Fac. Karl. Univ.* **41,** 99 (1925) [as "Association à *Psora ostreata*"].—*Lecideetum ostreatae* Schulz [Schulz-Korth], *Beih. Feddes Repert.* **67,** 48 (1931) [as "*Lecidea ostreata*-Ass."].—*Lecideion ostreatae* Laund., *in* Kettering and District Field Club, *First Fifty Years*, 94 (1956) [as "*Lecidion*"].—*Lecideetum scalaris* Kalb, *Diss. Bot., Lehre* **9,** 37 (1970) [as "Hilitzer 1925"].

This air pollution-tolerant association is mainly confined (in moderately polluted areas) to the bark of deciduous trees in sheltered, well lit sites, but, like the *Lecanoretum pityreae*, will also occur on coniferous trees at lower sulphur dioxide levels. Although an essentially corticolous community it is also occasionally encountered on decorticate wood (particularly fence-posts and tree stumps), sandstones and brick in moderately polluted parts of the British Isles. *Lecidea scalaris* predominates in the association and is sometimes the only species present. *Cladonia coniocraea*, *C. fimbriata*, *Lecanora conizaeoides* and *Lecidea granulosa* may also occur but generally have low cover values. The *Lecideetum ostreatae* also occurs on charred trunks; *Lecidea scalaris* often fruits in this habitat and *Lecidea friesii* and *Toninia carodocensis* may also be components of this specialized facies.

All. 6. *Lobarion pulmonariae*

Lobarion pulmonariae Ochsn., *Jahrb. St. Gall. naturw. Ges.* **63,** 64 (1928); type: *Lobarietum pulmonariae* Hil. [syn. *Nephrometum laevigatae* Barkm.].

The *Lobarion pulmonariae* (Fig. 3) is composed mainly of large foliose lichens and robust bryophytes and appears to be the natural forest climax community on mature hardwood trees with barks of pH 5·0–6·0 in western Europe outside areas with Mediterranean climates. It is now very much fragmented in distribution due to the felling and management of primeval forests, drainage and various forms of pollution. In drier areas it tends to be confined either to sheltered glades in more open forests where there is more light, or to the upper boughs of trees. Outside western

FIG. 3. *Lobarion pulmonariae* on oak. Predominant species: *Lobaria amplissima* (with cephalodia) and *L. pulmonaria* (Argyllshire: Ardnamurchan Peninsula, Camasine, 1967, F. Rose).

Scotland and Brittany it is largely restricted to mature or older tree trunks but in these two regions it will occur on relatively young trees and even old *Corylus* bushes. In parts of Scotland with high humidities it is even able to colonize planted trees or avenues while elsewhere it has acquired an essentially relict status; i.e. become confined to primary woodland relics with old trees. The *Lobarion* is rarely well developed in coppice woodlands unless numerous old standard trees are present but persists in many sites in England on sheltered ancient parkland *Fraxinus*, *Quercus* and *Ulmus* trees. In drier areas (e.g. Sussex, north-east England, eastern Scotland) it is usually best developed in forest relics in sheltered humid valley floor sites or on trees close to rivers in gorges.

Today the alliance is unable to spread in drier districts into woodlands less than 200 years old unless these adjoin, or have adjoined, ancient woodlands from which dispersal could take place when the trees reached sufficient maturity. The ability to colonize younger trees and exist in more shaded sites in wetter climatic zones may be due to (1) a higher annual growth rate (longer growing season) of the macrolichens concerned in the constantly humid environments, and (2) photosynthesis being able to occur for longer periods in moist conditions and thus compensating for lower light intensities.

There is little doubt, to judge from literature sources and field evidence from relict sites, that this alliance was formerly quite general as the epiphytic community of the mature trees of lowland and lower montane forests of western Europe outside areas of intense Mediterranean summer drought (even in these areas it does, however, seem to have existed in sheltered, locally more humid, sites). In Mediterranean forest areas it is normally replaced by communities of the *Xanthorion* alliance. It may always, as is the case at the present time, have been only well developed (outside more oceanic areas) on better lit trees at the edges of glades. In the central European mountains and the Pyrenees, the *Lobarion* is also developed locally in open forest stands of coniferous trees (particularly *Abies pectinata* which has a less acid and more water- and nutrient-retentive bark than most other conifers). Evidence for the former paramount importance of the *Lobarion* in the European hardwood forests is provided by (1) the large number of species present in it, most of which today show highly disjunct and presumably fragmented distributions, (2) the relatively high constancy of many of these species over the whole geographical range of the alliance (which is by no means purely oceanic), (3) the number of faithful species it contains (i.e. species only present in communities of this alliance), and (4) its occurrence in forest situations on a very wide range of deciduous trees (only on *Alnus* which has a very acid bark, pH 4·5, is it really rare).

The synsystematics of this alliance are extremely complex. Several distinct associations occur within it but the delimitation and nomenclature of these are currently unclear. As we propose to deal with the *Lobarion* in some detail in a future publication only a brief discussion of the principal noda of the alliance seen in Britain is included here. Attention is, however, drawn to the detailed discussions of it in the southern Black Forest and Canary Islands by Wirth (1968) and Klement (1965), respectively.

The "typical" western European nodum of this alliance, termed the *Nephrometum lusitanicae* by Barkman (1958), comprises a large number of species, the most constantly occurring of which are listed in Table II. A particular feature of the nodum is the abundance of bryophytes which form a substrate on which the macrolichens grow. Even within the western European range of this nodum, many stands attributable to it lack many, or even all, of the macrolichens characteristic of it as a result of the effects of man. Such species-poor communities probably always occurred on more shaded trees, and as a pre-climax sere to the full species-rich nodum; these may be considered a "pre-*Lobarion*" community and usually comprise the species indicated by [c] in Table II. In many parts of southern England, and also in Normandy and Picardy in northern France, the *Lobarion* is in large measure found only as this pre-*Lobarion* nodum. Even

TABLE II.

Some components of the Lobarion pulmonariae *in the typical western European facies of the alliance* (= Nephrometum lusitanicae *Barkm.*).

Arthonia didyma[a c]	*Parmeliella atlantica*
Acrocordia gemmata[a c]	*P. corallinoides* aggr.[a]
Bacidia affinis[a]	*P. plumbea*[a]
B. biatorina[a]	*Peltigera collina*[a]
Biatorella ochrophora[a]	*P. horizontalis*[a]
Catillaria atropurpurea[a c]	*P. praetextata*[b]
C. sphaeroides[a]	*Pertusaria hemisphaerica*[c]
Dimerella lutea[a c]	*P. hymenea*[c]
Evernia prunastri[b]	*P. pertusa*
Haematomma elatinum	*P. velata*[a c]
Lecanora quercicola[a]	*Porina coralloidea*[a]
Lecidea cinnabarina	*P. hibernica*[a]
Leptogium lichenoides[b]	*P. leptalea*
L. teretiusculum	*Ramalina farinacea*[b]
Lithographa dendrographa[c]	*Rinodina roboris*[b]
Lobaria amplissima[a]	*Sticta limbata*[a]
L. laetevirens[a]	*S. sylvatica*[a]
L. pulmonaria[a]	*Thelopsis rubella*[a c]
L. scrobiculata[a]	*Thelotrema lepadinum*[c]
Nephroma laevigatum[a]	
Normandina pulchella[b c]	Bryophytes
Opegrapha sorediifera[a c]	*Antitrichia curtipendula*[a]
Pachyphiale cornea[a c]	*Camptothecium sericeum*[b c]
Pannaria mediterranea[a]	*Frullania fragillifolia*[a]
P. pityrea[a]	*F. tamarisci*[b c]
P. rubiginosa[a]	*Isothecium myosuroides*[a c]
Parmelia crinita[a c]	*Neckera complanata*[b c]
P. glabratula[b]	*N. pumila*[b c]
P. reddenda[a c]	*Orthotrichum lyellii*[b c]
P. revoluta[b c]	*Pterogonium gracile*[a]
P. saxatilis[b]	*Zygodon baumgartneri*[a c]

[a] = species more or less faithful to this nodum.
[b] = companion species occurring with a high constancy.
[c] = species also of the "pre-*Lobarion*" pioneer community (see p. 324).

in the New Forest (see Rose and James, 1974) and parts of south-west England the pre-*Lobarion* is much more frequent than noda closely comparable to the *Nephrometum lusitanicae*.

In central, eastern and southern Scotland and parts of northern England,

away from the more humid western and southern counties, the *Lobarion* tends to be relatively species poor. Often only *Lobaria pulmonaria* (and sometimes *L. scrobiculata*) represent that genus, *Sticta* species are usually absent, and the cyanophilous species may be represented only by *Parmeliella plumbea* (or *Pannaria rubiginosa* in north-east Scotland, e.g. Darnaway Forest). The same pattern of impoverishment appears to occur in this alliance in the forests of north, central and eastern Europe (e.g. Denmark, Poland).

Conversely, in south-west England, North Wales and, more particularly, western Scotland, Brittany and the French Pyrenees, additional species absent further east become locally common (e.g. *Lopadium pezizoides*, *Parmeliella atlantica*, *Pseudocyphellaria crocata*, *P. intricata*, *Sticta canariensis* (*S. dufourii* morphotype), *S. fuliginosa*; in a few areas of western and southern England and Wales, also *Rinodina isidioides*). An especially species-rich facies of this alliance occurs in moist valley-bottom woods in sheltered lowland situations in western Scotland, particularly on inclined boughs of old *Corylus* or *Salix atrocinerea* in wet carr woodland; this includes fewer crustose lichens but all four British *Lobaria* species (all fertile in western Scotland; all but *L. laetevirens* rarely so elsewhere), *Pannaria*, *Parmeliella* and *Pseudocyphellaria* species and, occasionally, also *Heterodermia obscurata*. In such constantly wet conditions *Cetrelia olivetorum* s.l., *Menegazzia terebrata*, *Parmelia endochlora*, *P. laevigata* and *P. taylorensis* (all species usually found only in the *Parmelion laevigatae*, see p. 327) may also occur, together with *Leptogium* species (particularly *L. burgessii*), *Parmelia sinuosa* (on twigs) and *Ulota* species. This nodum, which is very distinctive when well developed, shows affinities with both the *Parmelion laevigatae* (although on far less acid bark) and, through *Lecanora jamesii* communities, to the *Graphidion scriptae* (generally of smooth-barked twigs and small branches). In such sites in western Scotland and south-west Ireland, small twigs and branches often support *Graphidion* with *Lecanactis homalotropum* and *Thelotrema subtile* (see p. 315).

A euoceanic moss-dominated facies of the *Lobarion* in south-west Ireland characteristically includes *Leptogium brebissonii*, *L. burgessii*, *Lobaria pulmonaria*, *Porina hibernica*, *Pseudocyphellaria lacerata* and *Sticta canariensis* (the *S. dufourii* morphotype occurring in deep shade).

In western Ireland (particularly in the Burren, Co. Clare; e.g. Poulavallan, Den of Clab) a facies of the *Lobarion* occurs on *Corylus* in relict *Corylus* woodlands of the limestone pavements. In this community *Lobaria* species are now lacking (currently restricted to mixed *Quercus* forest areas in Ireland) but *Pannaria*, *Parmeliella* and *Sticta* species are abundant and *Leptogium burgessii*, *Normandina pulchella* and *Usnea* species occur on larger stems. *Thelotrema subtile* is present in these communities in Connemara and south-west Ireland.

Fraxinus–Ulmus forest, especially when on basic soils over limestone, basic volcanic rocks, or on rich alluvial soils, supports a further distinctive community of the *Lobarion* in which, in addition to the taxa marked [a] in Table II, there is a particularly rich development of species of *Pannaria* (including *P. sampaiana*), *Parmeliella*, *Collema* (*C. fasciculare*, *C. furfuraceum*, *C. nigricans* and *C. subflaccidum*) and *Leptogium* (*L. azureum*, *L. burgessii*, *L. cyanescens*, *L. hibernicum* and *L. saturninum*); *Lithographa dendrographa* may also belong here. This community is now well developed only in a few areas of western Scotland where it occurs both in open forest and on isolated well lit old trees (e.g. Loch Melfort; Ellary Woods, Loch Caolisport; Rassal Wood, Kishorn; Mull; Sunart; Loch Arkaig); fragments do, however, persist in southern (e.g. New Forest, Cranborne Chase) and western England, Wales, the Lake District (e.g. Gowbarrow) and parts of western Ireland. Also, as members of this community there may be the very rare British species *Arctomia delicatula* (euoceanic), *Collema occultatum* and *Pannaria ignobilis* (a valley species of the central Highlands, often found on trees which have *Bryoria capillaris* on their twigs).

All. 7. *Parmelion laevigatae*

Parmelion laevigatae all. nov.; type: *Parmelietum laevigatae* P. James *et al.* (monotype).

This new alliance contains a single association:

Parmelietum laevigatae ass. nov. (Table III, Fig. 4)

This is a well marked community characteristic and general on the western side of the British Isles, including parts of south-west Ireland, and is also present in western Brittany. It is largely restricted to *Betula* and *Quercus* (although it can be encountered on *Alnus* and mossy rocks) and confined to exposed, often upland, woodland sites with high rainfall (127–229 cm year^{-1}) and with at least 180 wet days year^{-1}. The only sites for this community outside the 180 wet-day isoline (see Ratcliffe, 1968; Coppins, 1976) are in north Pembrokeshire but, were more meteorological data available, we suspect they also would be within this isoline. The *Parmelietum laevigatae* is essentially an association of well lit hardwood forests, and appears to be correlated with exposure to heavy rain which leaches the upper horizons of the bark. The pH of bark supporting this community is

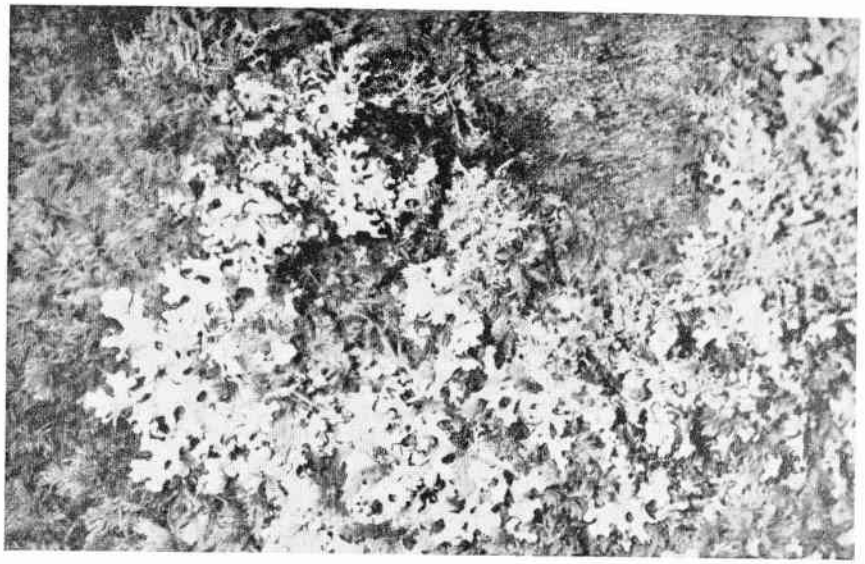

FIG. 4. *Parmelietum laevigatae* on mossy boulder. Predominant species: *Parmelia laevigata* and *Sphaerophorus globosus* (Argyllshire: Salen, 1967, P. W. James).

1. Argyllshire, Loch Sunart, Camasine (17/7 – – 6 – –): *Quercus* bough, 0·2 m diam, ± horizontal, 1 × 0·2 m, cover 90%, September 1970, F.R.
2. Gwynedd (Merioneth), Coed Ganllwyd, below Rhaedr-ddu (23/7 – – 2 – –): 3 adjacent *Betula pubescens* trunks in wood, *c.* 15 cm diam, incl. 70°, aspect WSW, 1 × 0·4 m, cover 75%, 1 April 1975, F.R.
3. Gwynedd (Merioneth), Coed Maen Ymenyn (23/848355): siliceous rock boulder, incl. 80°, aspect SE, 1 × 1 m, cover 70%, 27 March 1975, F.R.
4. Cumbria, Borrowdale, Castle Crag Woods (35/2 – – 1 – –): *Quercus petraea*, 1 m diam, incl. 85°, aspect SE, 1 × 0·5 m, cover 100%, 27 July 1971, F.R.; *type record*.
5. Cumbria, Eskdale, Dalegarth Woods (34/2 – – 9 – –): *Quercus* in wooded ghyll below Stanley Force, 0·8 m diam, incl. 90°, aspect N, 1 × 1 m, cover 90%, 25 July 1970, F.R.
6. Cumbria, Borrowdale, Thorneythwaite Wood, (35/2 – – 1 – –): *Quercus petraea* in woodland, 0·6 m diam, incl. 90°, 1 × 0·5 m, cover 70%, 25 July 1971, F.R.
7. Cumbria, Borrowdale, Seatoller, Low Stile Wood (35/2 – – 1 – –): *Quercus* (?) in woodland, 0·5 m diam, incl. 90°, aspect SW, 1 × 0·5 m, cover 90%, 26 July 1971, F.R.
8. Cumbria, Borrowdale, Seatoller, Low Stile Wood (35/2 – – 1 – –): *Quercus petraea* in open woodland, 0·5 m diam, incl. 90°, aspect SE, 0·5 × 0·5 m, cover n.a., 27 July 1971, F.R.

TABLE III.

Parmelietum laevigatae ass. nov.

Species	Stands							
	1	2	3	4	5	6	7	8
Cetrelia olivetorum s.l.	–	–	–	–	1.2	–	+.2	–
Cladonia chlorophaea	1.2	+.2	–	+.2	–	–	–	–
C. coniocraea	–	–	–	2.2	+.2	–	2.2	–
C. ochrochlora	1.2	–	–	–	–	–	–	–
Cornicularia aculeata	–	–	+.2	–	–	–	–	–
Evernia prunastri	–	–	–	–	–	–	+.0	–
Hypogymnia physodes	–	+.2	–	1.2	+.0	–	1.2	1.2
H. tubulosa	1.2	+.0	–	–	–	–	–	–
Menegazzia terebrata	2.3	1.2	–	–	1.3	–	–	–
Micarea sp.	–	–	–	–	–	–	–	3.4
Mycoblastus sanguinarius	–	–	–	1.3	–	–	–	1.3
Ochrolechia androgyna	–	+.2	–	3.2	3.3	–	4.4	2.3
O. tartarea	–	–	–	2.4	–	–	–	–
Parmelia crinita	2.2	–	–	–	–	–	–	–
P. glabratula	–	–	–	–	–	–	+.0	+.2
P. laevigata	2.2	4.3	–	3.2	+.2	3.3	–	1.3
P. saxatilis	–	1.3	+.2	–	–	–	1.2	2.2
P. taylorensis	2.2	–	2.2	–	–	2.3	+.2	2.3
Pertusaria amara	–	–	–	–	–	–	–	+.2
Platismatia glauca	2.3	1.3	+.2	1.2	1.2	–	–	–
Sphaerophorus globosus	–	+.2	+.2	+.0	–	–	–	–
Usnea inflata	–	1.2	–	–	–	–	–	–
U. subfloridana	2.2	–	–	–	+.2	–	–	–
Barbilophozia attenuata	–	–	–	–	2.3	–	–	–
B. floerkii	–	–	2.3	–	–	–	–	–
Bazzania trilobata	–	–	–	–	1.3	–	–	–
Dicranum fuscescens	–	–	–	+.2	–	–	–	–
D. scoparium	–	+.2	–	1.2	–	–	1.2	–
Diplophyllum albicans	–	–	3.3	–	–	–	–	–
Frullania tamarisci	–	–	–	–	–	–	1.2	–
Hypnum cupressiforme	3.3	–	–	–	–	–	2.2	+.2
Isothecium myosuroides	–	–	1.2	–	–	–	2.3	–
Lepidozia reptans	–	–	–	–	1.2	–	–	–
Lophozia ventricosa	–	–	–	+.2	–	–	–	–
Plagiochila punctata	–	–	–	–	2.3	–	–	–
Polytrichum formosum	–	–	+.0	–	–	–	–	–
Rhacomitrium heterostichum	–	–	1.2	–	–	–	–	–
Scapania gracilis	–	–	1.2	+.2	2.3	–	–	–
Algal crust	–	–	–	3.3	–	–	–	–

in the range pH 3·75–4·60, contrasting with the *Parmelion perlatae* and *Lobarion pulmonariae* with bark pH values almost always over pH 5·0 and, in the case of the latter, sometimes over pH 6·0.

The *Parmelietum laevigatae* is particularly characteristic of the following areas in Britain:

1. High-level oak woods round the edges of Bodmin Moor, Cornwall, at 650–750 ft (*c.* 220–230 m),
2. Exposed upland oak woods of Dartmoor, Devonshire (e.g. Black Tor Copse, Wistmans Wood), at 1200–1450 ft (*c.* 360–440 m),
3. Upper parts of valley oak woods on Exmoor and the Quantock Hills, Somerset,
4. Oak-birch woodland in high rainfall areas of the Lake District,
5. Upland oak woods in western Wales, at 600–1500 ft (*c.* 200–450 m), and
6. Generally in more exposed oak–birch woodlands in western Scotland, at 150–1200 ft (*c.* 50–360 m), as far north as Wester Ross.

Altitude appears to be less important than exposure to rain-bearing winds in determining its occurrence. Oak woods below the indicated levels, if sufficiently undisturbed, support the *Lobarion pulmonariae*. Transitions between these communities are very abrupt in southern Britain (e.g. on Dartmoor and Exmoor), but much more gradual in western Scotland.

Fragmentary forms of this association occur in valley bottoms throughout western Britain on the naturally more acid bark of *Alnus*. This association is primarily characterized by *Mycoblastus sanguinarius*, *Ochrolechia androgyna*, *O. tartarea*, *Parmelia laevigata* and *P. taylorensis*. Other species largely faithful to it include *Bryoria smithii*, *Cetrelia olivetorum* s.l., *Menegazzia terebrata*, *Parmelia endochlora* and *Pertusaria ophthalmiza* (in Scotland). *Sphaerophorus* species are frequently important components, *Cladonia* species are often present, and the community is rich in calcifuge bryophytes, particularly *Dicranum scoparium*, *Hypnum cupressiforme* var. *filiforme*, *Isothecium myosuroides*, *Plagiochila punctata*, *P. spinulosa* and *Scapania gracilis*.

Where this association occurs on mossy rocks and boulders it is usually in those upland woods where it is also present on the trees.

All. 8. *Parmelion perlatae*

Parmelion perlatae nom. nov.—*Trichoterion* Laund., *Lond. Nat.* **37,** 73 (1958) [*nom. illegit.*].—*Parmelion caperatae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 450 (1959) [as "suballiance"]; type: *Parmelietum revolutae* Klem.—Non *Parmelion caperatae* Felf., *Acta geobot. Hung.* **4,** 55 (1941); type: *Parmelietum caperatae* Felf.—

? Non *Parmelion perlatae* Follm., *Ber. dtsch. bot. Ges.* **80,** 201 (1967) [*nom. nud.*]; type not stated.

This alliance, in its various facies, is the characteristic community of well lit mature deciduous trees in areas of little or no air pollution in lowland Britain. In north-eastern England, central Wales and central and eastern Scotland the alliance is replaced by the *Pseudevernion furfuraceae* as the dominant epiphytic community of well lit trees.

The *Parmelion perlatae* is characterized by the abundance of *Parmelia caperata* and *P. perlata*. A single very variable association within it is recognized here as present in the British Isles.

Parmelietum revolutae Klem. (Table IV)

Beih. Feddes Repert. **135,** 163 (1955) [as "Almborn 1948"].—*Parmelietum revolutae* var. *parmeliosum laetevirentis* Barkm., *Phytos. Ecol. Crypt. Ep.*, 452 (1958) [*nom. superfl.*].—*Parmelietum revolutae* var. *caperatosum* Barkm., *Phytos. Ecol. Crypt. Ep.*, 454 (1958).—*Parmelietum cervicornis* Duvign., *Bull. Soc. r. bot. Belg.* **74,** 47 (1942) [*nom. illegit.*].—*Parmelietum subauriferae* Duvign., *Bull. Soc. r. bot. Belg.* **74,** 47 (1942).—*Parmelietum trichotero-scortea* Barkm., *Phytos. Ecol. Crypt. Ep.*, 450 (1958).—Non *Parmelietum caperatae* Felf., *Acta geobot. Hung.* **4,** 55 (1941).

This association is best developed on the trunks and ascending boughs of *Fraxinus*, *Quercus*, *Larix* (in Ireland) and other rough-barked trees of 0·3–1·0 m diam in parklands, by minor roads, in pastures and more open woodlands; it is restricted to upper well lit parts of trees in dense woodlands where it may occur above a zone of either *Lobarion* or *Graphidion*. The association has a very wide phorophyte range, however, and will also occur on the smooth bark of *Fagus*, *Acer* and *Ulmus* species where the bark has not been unduly enriched by dust or animal matter. Sulphur dioxide pollution and agricultural chemicals impoverish it to varying degrees. With increasing bark acidity it tends to grade into the species-poor facies of the *Pseudevernietum furfuraceae* (see p. 335), whilst with decreasing bark acidity the *Buellietum punctiformis* or algal-dominated communities may be produced. Although not usually encountered on coniferous trees, in the most unpolluted parts of southern and western Britain (particularly near the sea), it is occasionally found on mature well lit trunks of *Picea abies*, *Pinus sylvestris* and *Larix*. Most pH values from bark beneath this association fall within the range pH 5·0–5·5.

The *Parmelietum revolutae* is best developed in southern and western lowland areas, occurring today in the eastern and northern parts of East Anglia, throughout the counties south of the Thames, west Midlands, Welsh lowlands (especially near the coast), Lake District, lowland coastal

encountered being *Dicranoweissia cirrata*, *Hypnum cupressiforme* and *Orthotrichum lyellii*.

The *Parmelietum revolutae* is particularly rich in species and many others, in addition to those mentioned above, occur from time to time in varying amounts. Nevertheless, only two species approach being strictly faithful to it in Britain: *Parmelia soredians* (which also rarely occurs on decorticate wood and stonework) and *P. reticulata* (most frequent in the east and south-east). It is perhaps unfortunate that the name of this association is based on that of *P. revoluta* as that species is not particularly common in it, tending to be most frequent in either slightly shaded sites or on the smoother and less water-retentive bark of *Alnus* and *Fagus* in southern woodlands. In Kent and East Anglia *P. acetabulum*, more characteristically a species of the *Xanthorion*, also occurs in the *Parmelietum revolutae* as it does in parts of Belgium and France; this phenomenon may be correlated with climatic factors approaching those optimal for this particular species (i.e. generally drier and warmer summers).

The original record of the *Parmelietum caperatae* Felf., described from Hungary, is even more transitional between the *P. revolutae* and the *Xanthorion* as it included not only *Parmelia acetabulum* but also *Anaptychia ciliaris*, *Physconia pulverulenta* and *Xanthoria parietina*. Felföldy's name is thus not taken up for the *Parmelietum revolutae* here; his community may be referred to the *Parmelietum acetabulae* var. *parmeliosum caperatae* Ochsn. (Ochsner, 1928: 62).

All. 9. *Pseudevernion furfuraceae*

Pseudevernion furfuraceae (Barkm.) comb. nov.—*Parmelion furfuraceae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 456 (1958) [as "suballiance"], basionym; type: *Parmelietum furfuraceae* Hil.—*Parmelion saxatilis* Barkm., *Phytos. Ecol. Crypt. Ep.*, 450 (1958); type: *Parmelietum furfuraceae* Hil.; nom. illegit. [non *Parmelion saxatilis* Klem., *Ber. bayer. bot. Ges.* **28,** 257 (1950); type: *Parmelietum conspersae* Klem.].—*Physodion* Waldh., *K. svenska VetenskAkad. Avh. natur.* **4,** 90 (1944); type: "*Parmelia physodis*-förbundet DR. 1942".—*Parmeliopsidion ambiguae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 466 (1958) [as "suballiance"]; type: *Parmeliopsidetum ambiguae* "Hil."—*See also* Follmann (1974).

This alliance, most frequently termed the "*Physodion*" by British authors since Laundon (1956), is essentially a northern, more acidic substrate-requiring counterpart of the *Parmelion perlatae* in the British Isles. It is characteristic of trees with moderately acidic barks in well lit situations and is widespread throughout large areas of northern England, central Wales and central and eastern Scotland. Under pollution stress, where bark tends to become somewhat acidified, it occurs further south as

species-poor communities. While in Scotland it is widespread on coniferous and deciduous trees, in areas not subject to pollution stress in southern England it is mainly restricted to coniferous trees, birch and fence-posts. These factors suggest it tends to prefer more acidic substrates than the *Parmelion perlatae*. It largely replaces the *Parmelion perlatae* in lowland Scandinavia east of western Norway.

The *Pseudevernion furfuraceae* is not exclusively corticolous, however, and has similar associations and compositions when growing on siliceous rocks. It is found throughout the British Isles on acidic rocks wherever these occur. The characteristic species of the alliance are *Bryoria fuscescens*, *Cetraria chlorophylla*, *Hypogymnia physodes*, *H. tubulosa*, *Ochrolechia androgyna*, *Parmelia saxatilis*, *P. sulcata*, *Parmeliopsis ambigua*, *Platismatia glauca* and *Pseudevernia furfuracea*. Two associations in this alliance may be recognized in the British Isles at the present time.

Pseudevernietum furfuraceae (Hil.) Kalb (Table V)

Diss. Bot., Lehre **9,** 59 (1970).—*Parmelietum furfuraceae* Hil., *Spisy Přírod. Fac. Karl. Univ.* **41,** 122 (1925) [as "Association à *Parmelia furfuracea*"].—*Parmelietum furfuraceae-physodes* Frey & Ochsn., *Arvernia* **2,** 78 (1926).—*Parmelietum saxatilis* Hil., *op. cit.* **41,** 143 (1925) [as "Association à *Parmelia saxatilis*"].—*Parmelietum sulcatae* Hil., *op. cit.* **41,** 151 (1925) [as "Association à *Parmelia sulcata*"].—*Hypogymnio physodis–Parmelietum saxatilis* Wirth, *Diss. Bot., Lehre* **17,** 211 (1972) [as "(Hil. 1927) nom. nov."].—*Physodeto-sulcatetum* DR., *Svensk bot. Tidskr.* **39,** 148 (1945).—*Physodetum* Almb., *K. svenska VetenskAkad. Avh. natur.* **11,** 39 (1955).—*Parmeliopsidetum ambiguae* subass. *platismatietosum glaucae* Kalb, *Hoppea* [*Denkschr. Regensb. bot. Ges.*] **30,** 84 (1972).—*See also* Follmann (1974).

This association is very variable and some authors have recognized numerous subassociations and variants within it (e.g. Barkman, 1958; Fabizewski, 1968; Kalb, 1970); Hawksworth (1969) noted the presence of several of these in Derbyshire. Essentially it has a composition as for the alliance but can be simplified under air pollution stress to *Hypogymnia physodes–Parmelia saxatilis–Platismatia glauca* communities (sometimes with *Pseudevernia furfuracea*) such as are particularly widespread and luxuriant on trees and siliceous rocks over large areas of central and northern England. *Bryoria fuscescens* is particularly common in the north and in upland areas of the south-west (e.g. Dartmoor). Facies rich in *Parmeliopsis ambigua* are also not uncommon under moderate pollution stress. A valuable résumé of the syntaxonomy of this association and its composition is provided by Follmann (1974).

In the south, *Evernia prunastri*, *Lecanora pallida*, *Pertusaria amara* and

TABLE V.

Pseudevernietum furfuraceae (Hil.) Kalb.

Species	Stand 1	2	3	4	5	6	7	8	9	10
Bryoria fuscescens	4	6	6	4	9	7	4	7	–	–
Calicium viride	–	–	–	+	–	–	–	–	–	–
Cetraria chlorophylla	+	–	–	7	–	4	–	+	–	–
Evernia prunastri	+	–	–	+	–	–	–	–	–	–
Huilia macrocarpa	–	–	–	–	–	–	–	+	–	–
Hypogymnia physodes	4	6	6	2	+	4	3	+	5	2
H. tubulosa	+	–	–	–	–	+	+	–	–	–
Lecanora conizaeoides	–	–	–	–	–	+	+	–	7	–
L. expallens	+	–	–	+	+	–	–	–	–	–
L. intricata var. *soralifera*	–	–	–	–	–	–	+	–	2	–
L. scalaris	–	–	–	+	–	–	–	–	–	–
Lepraria incana	4	–	–	–	–	–	–	–	–	–
Mycoblastus sanguinarius	–	–	–	–	–	–	+	–	–	–
Ochrolechia androgyna	–	–	–	+	–	–	–	–	–	–
O. turneri	6	–	4	+	–	–	–	–	–	–
Parmelia glabratula	–	–	–	+	–	–	–	–	–	–
P. saxatilis	+	–	–	+	4	–	6	7	5	7
P. sulcata	–	–	–	3	+	–	–	–	–	–
Parmeliopsis hyperopta	–	–	+	–	–	–	–	–	–	–
P. ambigua	–	–	4	–	+	–	–	–	–	–
Phlyctis argena	–	–	–	4	–	–	–	–	–	–
Platismatia glauca	–	–	4	4	4	+	4	–	–	6
Pseudevernia furfuracea	–	5	+	+	+	–	+	–	8	7
Usnea hirta	–	4	–	–	–	–	–	–	–	–
U. subfloridana	+	–	+	+	–	+	–	–	–	–

1. E. Inverness, Rothiemurchus Forest, Loch an Eilein (27/895077): *Larix europaea*, incl. 79°, aspect 130°, pH 4·02, 10 × 10 cm, cover 58%, 3 August 1968, D.L.H.
2. E. Inverness, N. of Croftmore, near Boat of Garten (28/945175): palings by roadside, incl. 0°, aspect horizontal, pH 4·38, 10 × 10 cm, cover 80%, 4 August 1968, D.L.H.
3. E. Inverness, Glen More Forest (28/985078): *Pinus sylvestris* ssp. *scotica*, incl. 73°, aspect 270°, pH 4·02, 10 × 10 cm, cover 81%, 4 August 1968, D.L.H.
4. E. Inverness, near Croftmore, near Boat of Garten (28/934154): *Betula* sp., incl. 71°, aspect 225°, pH 4·67, 10 × 10 cm, cover 72%, 4 August 1968, D.L.H.

P. pertusa are often also found in this association in *Quercus* forests on very acid soils where they may give high cover values; this community perhaps constitutes a distinct subassociation but is in need of further investigation. Bark samples under this association indicate that it is optimally developed in the pH range 3·0–4·0. For details of substrate preference see under the alliance above.

Parmeliopsidetum ambiguae Frey

Ver. naturf. Ges. Basel **35,** 319 (1923).—*Parmeliopsidetum* DR., *Svensk bot. Tidskr.* **39,** 148 (1945).

This community is rather poorly represented in the British Isles where it is found mainly on decorticate coniferous wood in central and eastern Scotland. It is also sometimes encountered on conifers and birch trees themselves, however, and is clearly closely allied to the *Pseudevernietum furfuraceae* from which it differs in the abundance of *Parmeliopsis aleurites*, *P. ambigua* and *P. hyperopta*. It should be noted that this community is quite distinct from the *Parmeliopsis ambigua*-rich facies of the *Pseudevernietum furfuraceae* sometimes developed under pollution stress (p. 335).

At first we were inclined not to recognize this syntaxon as distinct in Britain but an examination of the data of Frey (1923) and Barkman's observations (1958) shows that the *Parmeliopsis*-rich communities of the Scottish Highlands are most probably species-poor variants of this association. Additional characteristic species of this essentially subboreal association now rarely found in Britain include *Cetraria juniperina*, *C. pinastri* and *C. sepincola*. In northern Europe this association appears to be

5. Lanarkshire, between Coulter and Biggar (36/0 – – 3 – –): *Fraxinus excelsior*, incl. 90°, aspect 205°, pH 4·77, 10 × 10 cm, cover 90%, 29 July 1968, D.L.H.
6. Peeblesshire, NE of Dolphinton (36/1 – – 4 – –): *Fagus sylvatica*, incl. 82°, aspect 180°, pH 5·25, 10 × 10 cm, cover 60%, 29 July 1968, D.L.H.
7. Derbyshire, Birchover, Rowtor Rocks (43/235622): millstone grit rocks, incl. 60°, aspect 225°, 10 × 10 cm, cover 70%, 28 August 1967, D.L.H.
8. Sutherland, Halladale, near Achiemore (29/8 – – 5 – –): Old Red sandstone outcrop, incl. 82°, aspect 270°, 10 × 10 cm, cover 80%, 12 August 1968, D.L.H.
9. Derbyshire, Chatsworth, near Beeley Lodge (43/265684): millstone grit wall, incl. 0°, aspect horizontal, 10 × 10 cm, cover 80%, 4 April 1967, D.L.H.
10. Derbyshire, Holloway, Dethick Lea Hall Farm (43/335575): millstone grit wall, incl. 0°, aspect horizontal, 10 × 10 cm, cover 100%, 15 March 1967, D.L.H.

particularly frequent on birch twigs, and communities with *Cetraria chlorophylla*, *C. sepincola* and *Parmelia septentrionalis* on birch twigs in the Scottish Highlands are thus placed here.

The synsystematics of the *Parmeliopsidetum ambiguae*, discussed in some detail by Barkman (1954), remain poorly understood. A considerable number of taxa at subassociation and variant ranks have been described in it which require re-evaluation on a European scale.

All. 10. *Usneion barbatae*

Usneion barbatae Ochsn., *Jahrb. St. Gall. naturw. Ges.* **63,** 68 (1928); type: *Usneetum barbatae* Ochsn.—*Usneion dasypogae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 475 (1958); type: *Usneetum dasypogae* Frey [= *Letharietum divaricatae* Frey]. —*Usneion florido-ceratinae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 470 (1958); type not designated.

Communities dominated by species of *Usnea*, characteristic of acidic barks and usually in very well lit situations are placed in this alliance. The synsystematics of this alliance in Europe are, however, in a confused state mainly as a result of the currently unsatisfactory species concepts in many groups of *Usnea* species. Five associations can be distinguished in the British Isles, but the names of four may require some revision when the identity of some *Usnea* species used to characterize alliances in continental Europe becomes firmly established.

All associations of this alliance are very sensitive to air pollution and so have more restricted distributions in the British Isles than they did in the early parts of last century.

Cladonieto-Usneetum tuberculatae Barkm.

Phytos. Ecol. Crypt. Ep., 471 (1958).

This association is treated here in the sense of Hawksworth (1972a) to include communities allied to the *Usneetum subfloridanae* in more shaded habitats where *Cladonia* species (e.g. *C. coccifera*, *C. pyxidata*, *C. squamosa*) and bryophytes form major parts of the stands. Also sometimes encountered on acid mossy rocks, this association may perhaps be viewed as an intermediate between the *U. subfloridanae* and the *Cladonietum coniocraeae*. *Usnea flammea*, *U. fragilescens* and *U. inflata* (syn. *U. intexta*) are to be found in this association in more upland areas in addition to *U. subfloridana*.

Ramalinetum fastigiatae Duvign.

Bull. Soc. r. bot. Belg. **74,** 42 (1942).—See Barkman (1958) for lists of probable synonyms.

The *Ramalinetum fastigiatae* (Fig. 5) is a variable association characterized by the dominance of *Ramalina* species (particularly *R. baltica*, *R. calicaris*, *R. duriaei*, *R. farinacea*, *R. fastigiata*, *R. fraxinea*, and rarely *R. pollinaria*). It is widespread and common, favouring better lit, more exposed trees and is particularly common on inclined branches and twigs. Two subassociations and three variants (one unnamed) were accepted by Barkman (1958), all of which occur in the British Isles, but they do not appear to merit separation as transitions are commonly encountered.

FIG. 5. *Ramalinetum fastigiatae* on nutrient-rich bark. Predominant species: *Evernia prunastri*, *Physcia tenella*, *Ramalina farinacea*, *R. fastigiata*, *R. fraxinea* and *Xanthoria parietina* (W. Inverness: Invergordon, 1976, R. O. Millar).

Although this association has generally been placed in the *Xanthorion* we suspect that it may be more closely allied to the *Usneion* as it parallels the *Usneetum articulato-floridae* but is found in somewhat more nutrient-rich sites. Some tendency to intergrade with the *Usneetum subfloridanae* also supports its positioning here.

Usneetum articulato-floridae var. *ceratinae* D. Hawksw.

Fld Stud. **3,** 543 (1972).

This often spectacular community (Fig. 6), which characteristically occurs in very well lit situations and is optimally developed on the uppermost sloping or horizontal boughs of trees, has a markedly southern and south-western distribution in the British Isles. The most important species of the variant are *Usnea articulata*, *U. ceratina*, *U. florida* and *U. rubiginea*, although *U. inflata* (syn. *U. intexta*) and *U. subfloridana* are often also present.

In the southern counties of England a facies dominated by *U. ceratina* and *U. inflata* occurs not uncommonly on almost vertical well lit trunks of *Fagus* and *Quercus* in glades; *U. articulata* is generally absent in this facies although *U. rubiginea* is often present. This nodum may in future merit separation as a distinct association.

The "typical" variant of this association, as interpreted by Barkman (1958), is still present in Brittany and includes *Heterodermia leucomelos*, *Pseudocyphellaria aurata* and *Teloschistes flavicans*. These species are now very rare in Britain, perhaps prefer more nutrient-rich barks, and seem better placed in a separate association, the *Teloschistetum flavicantis* (p. 348), which is always poor in *Usnea* species. The relationships between this community and both the *Usneetum florido-neglectae* Bibinger and the *Usneetum rubicundae* Barkm., both unrecognized in Britain, merit further study.

Usneetum filipendulae ass. nov. prov.

This poorly understood association, which is not validated here in the absence of detailed records, is characteristic of ancient coniferous forests in Scotland and dominated by *Usnea filipendula* and *U. fibrillosa*. *Alectoria sarmentosa*, *Bryoria capillaris*, and sometimes *U. hirta*, may be further important components of this association. It should be noted that this community may perhaps be in reality a species-poor variant of the central and northern European montane *Usneetum barbatae* Ochsn. (for which the later name *Letharietum divaricatae* Frey was employed, perhaps unnecessarily, by Barkman, 1958).

FIG. 6. *Usneetum articulato-floridae* var. *ceratinae* on *Salix* in marsh. Species present include *Evernia prunastri*, *Hypogymnia physodes*, *Parmelia perlata*, *P. sulcata* and *Usnea ceratina* (S. Devon: Slapton, Duck Marsh, 1975, F. S. Dobson).

Usneetum subfloridanae D. Hawksw.

Fld Stud. **3,** 543 (1972).

This is the most widespread association of the *Usneion* in the British Isles but tends to be optimally developed in the south and west. The *Usneetum subfloridanae* is particularly luxuriant on smaller horizontal branches or twigs in very well lit sites and appears to prefer slightly less acid bark than the *Usneetum articulato-floridae* var. *ceratinae*. *Usnea subfloridana* (and/or *U. florida* in the south) predominates in this association although *Ramalina calicaris* and *U. fulvoreagens* (in south-west England) are locally important. Facies rich in *R. calicaris* sometimes show a tendency to intergrade with the *Ramalinetum fastigiatae*. In particularly wet habitats *U. extensa* is also to be found in this association.

The *Usneetum sufloridanae* is able to overgrow pioneer communities of twigs such as the *Arthopyrenietum punctiformis* and *Lecanoretum subfuscae*. It is not to be confused with the *Pseudevernietum furfuraceae* subass. *usneetosum subfloridanae* Kalb (1972) which includes *Bryoria fuscescens* and prefers more acid bark.

All. 11. *Xanthorion parietinae*

Xanthorion parietinae Ochsn., *Jahrb. St. Gall. naturw. Ges.* **63,** 53 (1928); type: *Physcietum ascendentis* Frey & Ochsn.—*Parmelion caperatae* Felf., *Acta geobot. Hung.* **4,** 48 (1941); type: *Parmelietum caperatae* Felf.—*Buellion canescentis* Barkm., *Phytos. Ecol. Crypt. Ep.*, 400 (1958); type: *Ramalinetum duriae* ("Duvign.") Barkm.—? *Teloschistidion chrysophthalmi* Follm., *Ber. dtsch. bot. Ges.* **80,** 202 (1967); type: *Teloschistetum chrysophthalmi* Follm. [*nom. nud.*; ? non Ochsn., 1934.].

This alliance is used here for both corticolous and saxicolous communities. On trees it is characterized either by species of *Buellia*, *Caloplaca*, *Physcia*, *Physconia*, *Ramalina*, *Teloschistes* or *Xanthoria*, or occasionally *Anaptychia ciliaris*, *Bacidia rubella*, *Parmelia acetabulum*, *P. quercina*, *P. laciniatula* or *Candelaria concolor*. It occurs on nutrient-rich, nutrient-enriched or hypertrophicated barks and rocks, usually in well lit situations, and most frequently in sites frequented by birds, farm animals or alongside dusty roads. This alliance is widespread throughout the British Isles especially in the drier south and eastern lowlands. On trees it becomes increasingly dominant southwards in Europe as the Mediterranean is approached where it is the predominant alliance, even in old lowland relict forests. The non-corticolous associations of this alliance in Britain are discussed under the pertinent substrates on pp. 360–361 and 382.

The *Ramalinetum fastigiatae*, placed in this alliance by most previous authors (e.g. Barkman, 1958), is referred to the *Usneion barbatae* here (see p. 339) and is thus not treated below.

Buellietum punctiformis Barkm.

Phytos. Ecol. Crypt. Ep., 405 (1958).

A frequently species-poor association comprising mosaics of *Buellia punctata*, *B. canescens* (sometimes dominant), *Candelariella reflexa*, *C. vitellina*, *Lecania cyrtella*, *Lecanora chlarotera*, *L. sambuci*, *Lecidella elaeochroma*, *Lecidea quernea* and often also with *Xanthoria* species. This community is characteristic of nutrient-enriched or hypertrophicated barks and particularly common in areas of moderate sulphur dioxide and inorganic fertilizer pollution where other associations are not able to develop. It becomes rarer in the extreme north of England and Scotland.

Gyalectinetum carneoluteae D. Hawksw.

Fld Stud. **3,** 545 (1972).

A shade-loving community of nutrient-rich barked trees of the extreme south and south-west England characterized by an abundance of *Gyalectina carneolutea*. Other important components of this community are *Bacidia phacodes*, *B. rubella*, *Lithographa dendrographa* and, sometimes, *Opegrapha prosodea*. Better lit facies show some intergradation with the *Buellietum punctiformis*, whilst more shaded ones include elements of the *Pyrenuletum nitidae*. The presence of *Lithographa dendrographa* may indicate that this association has some affinity to the *Lobarion pulmonariae* (see p. 327).

Parmelietum carporrhizantis Crespo

An. Inst. bot. A. J. Cavanillo **32,** 191 (1975).

Parmelia quercina (syn. *P. carporrhizans*)-dominated communities occur in Britain on very well lit and slightly nutrient-enriched parts of trees, most frequently the upper branches. This is largely a southern European association, however, and is only found in the British Isles with any frequency in the low-rainfall and high-sunshine coastal parts of south Devonshire and Dorset where *P. borreri* and *P. pastillifera* are also characteristic of it. Crespo (1975) recognized two variants and one subassociation (the *parmelietosum endochlorae*). His first variant, with the differential

species *P. caperata* and *P. soredians*, is the type represented in the British Isles.

The *Parmelietum carporrhizantis* has many features in common with the *Parmelion perlatae*, but as it prefers more nutrient-rich sites, it is referred to the *Xanthorion parietinae*.

Parmelietum elegantulae Klem.

Beih. Feddes Repert. **135,** 154 (1955) [as "Almborn 1948"].—*Parmelietum laciniatulae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 446 (1958) [as "(Almborn) Klement 1955"].

This association, distinguished by the frequency of *Parmelia elegantula*, *P. laciniatula* and often *Ochrolechia yasudae*, shows strong affinities with both the *P. acetabulum* facies of the *Physcietum ascendentis* and the *Parmelietum revolutae*. The *Parmelietum elegantulae* is particularly well developed in sites affected by man and appears to require a somewhat lower bark pH than the *Physcietum ascendentis*. It is because of this difference in requirements that it is not subsumed under the *Physcietum ascendentis* here. *Physcia*, *Physconia* and *Xanthoria* are of relatively minor importance in this association as compared to the *Physcietum ascendentis*.

Physcietum ascendentis Frey & Ochsn. (Table VI)

Arvernia **2,** 82 (1926).—*Parmelietum acetabulae* Ochsn., *Jahrb. St. Gall. naturw. Ges.* **63,** 60 (1928).—*Teloschistetum chrysophthalmae* Ochsn., *Revue bryol. lichén.* **7,** 85 (1934).—*Xanthorietum candelariae* Frey, *Ergebn. wiss. Unters. Schweiz. NatnParks, n.f.* **3,** 476 (1952).—*Arthopyrenietum gemmatae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 400 (1958).—*Caloplacetum phloginae* Barkm., *Phytos. Ecol. Crypt. Ep.*, 369 (1958).—See Barkman (1958) for further probable synonyms of these names.

The *Physcietum ascendentis* is treated in a rather broad sense here to include the majority of *Physcia*, *Physconia* and *Xanthoria* dominated communities of nutrient-rich bark in the British Isles. The numerous associations and subassociations recognized for these by continental authors appear to be of limited syntaxonomic importance here. The association is primarily distinguished by high frequencies of *Physcia* (particularly *P. adscendens*, *P. aipolia*, *P. orbicularis*, *P. tenella* and sometimes *P. tribacia*), *Physconia* (*P. enteroxantha*, *P. farrea*, *P. grisea* and *P. pulverulenta*) and *Xanthoria* (*X. candelaria*, *X. fallax*, *X. parietina* and *X. polycarpa*). The association is often very rich in species with 30 or more not infrequently present on single, mature, well lit, nutrient-enriched trees in areas of little air pollution. The predominant species may vary from tree to tree even when these are in close proximity and so this

appears to be of rather limited syntaxonomic value. Communities falling within the concept of the *Parmelietum acetabulae* (including *Anaptychia ciliaris*, *Parmelia acetabulum*, *P. exasperatula* or *P. tiliacea*) represent an eastern facies (Table VI) of the association in Britain and are particularly well developed on well lit mature tree trunks in open parkland sites; this might be interpreted as a distinct variant or subassociation but, as it could also be viewed as the species-rich or optimal facies of a single association which becomes simplified both northwards and westwards in response to climatic stresses progressively eliminating species, it is not treated separately here. The abundance of *Ramalina* species in the association appears to be related to the degree of exposure, these becoming most frequent in well ventilated sites.

Some communities of this association in central and eastern Europe may have some affinities with the *Parmelietum revolutae* (see p. 331). Although primarily corticolous, species-poor communities referable to this association are occasionally encountered on nutrient-enriched calcareous rocks where they can, when optimally developed, include even *Anaptychia ciliaris*.

A community of nutrient-rich *Ulmus* wood tracks dominated by *Bacidia incompta* but including *Caloplaca luteoalba* is tentatively mentioned here but may merit association rank.

Physcietum caesiae Mot.

See p. 360 for details of nomenclature and composition.

Although primarily saxicolous, this association is sometimes well developed on trees or timber heavily impregnated with alkaline dust, for example near limestone-crushing plants and cement works (see Gilbert, 1976). In such situations the corticolous community includes species normally found in it when it occurs on calcareous substrates (e.g. *Lecanora muralis*, *Physcia caesia*).

Physciopsidetum elaeinae (Barkm.) comb. nov.

Physcietum elaeinae Barkm., *Phytos. Ecol. Crypt. Ep.*, 414 (1958).

This association, closely allied to the *Buellietum punctiformis*, is encountered on highly hypertrophicated bark, particularly of *Sambucus*. The variant *buelliosum canescentis* Barkm. is the facies represented in the British Isles and is distinguished by high cover values of *Physciopsis adglutinata* (and sometimes *Physcia orbicularis* and *P. tribacia*). The *Physciopsidetum elaeinae* tends to prefer slightly more shaded habitats and smoother bark than the *Physcietum ascendentis*. Barkman (1958) considered this to be primarily a

TABLE VI.

Physcietum ascendentis Frey & Ochsn. ("eastern facies").

Species	Stands							
	1	2	3	4	5	6	7	8
Acrocordia gemmata	–	–	+.2	–	–	+.0	–	–
Anaptychia ciliaris	–	3.4	2.3	1.2	–	3.3	2.2	2.3
Arthonia impolita	–	–	+.0	–	–	–	–	–
Buellia canescens	+.2	+.2	+.0	1.2	+.2	+.2	1.2	1.2
B. punctata	1.2	+.1	+.0	+.1	+.2	+.0	+.0	+.0
Calicium viride	–	–	–	–	–	+.0	2.2	–
Candelariella vitellina	–	–	–	+.1	+.0	–	–	–
Catillaria griffithii	+.2	–	+.2	+.1	–	–	–	–
Evernia prunastri	–	–	+.0	+.2	–	–	–	–
Gyalecta flotowii	–	+.0	–	–	–	–	–	–
Haematomma ochroleucum var. *porphyrium*	–	–	–	–	–	–	+.0	–
Lecanora chlarotera	–	–	+.0	–	–	–	–	+.0
L. conizaeoides	2.2	–	–	+.0	–	–	–	–
L. dispersa	–	–	+.0	–	–	–	–	+.0
L. expallens	2.2	–	+.0	1.2	2.3	+.2	2.2	+.0
Lecidea quernea	–	–	+.0	+.2	–	–	–	–
Lecidella elaeochroma	–	–	+.0	–	–	–	–	+.0
Lepraria candelaris	–	–	+.0	–	–	–	–	–
L. incana	–	–	–	–	–	+.0	+.0	–
Ochrolechia turneri	–	–	+.0	–	–	–	–	3.2
O. yasudae	–	–	+.0	2.3	–	–	+.0	–
Opegrapha varia s.l.	–	+.0	–	–	–	+.0	–	–
Parmelia acetabulum	2.2	2.5	2.3	+.2	5.5	+.0	1.2	+.0
P. caperata	–	–	1.3	–	–	–	–	+.2
P. elegantula	–	–	+.0	+.0	–	–	–	–
P. glabratula	–	–	+.0	–	–	–	–	–
P. laciniatula	–	–	+.2	–	–	–	–	–
P. perlata	–	–	2.2	–	–	–	–	1.3
P. saxatilis	–	–	+.0	–	–	–	+.0	–
P. subaurifera	–	–	+.0	–	–	–	–	1.3
P. subrudecta	+.0	–	+.2	+.2	2.2	+.0	+.0	+.2
P. sulcata	–	–	4.3	1.3	1.2	+.0	1.2	+.0
P. tiliacea s.l.	–	–	1.3	–	–	–	–	–
Pertusaria albescens var. *corallina*	–	–	+.0	–	–	–	+.0	–
P. amara	–	–	–	2.2	–	1.2	–	–
P. coccodes	–	–	+.0	1.3	–	–	–	+.0
P. hymenea	–	1.2	–	–	–	–	–	2.3
P. pertusa	–	–	+.0	–	–	–	–	–
Physcia adscendens	+.0	1.2	+.2	1.2	+.1	–	–	2.3
P. aipolia	–	–	2.2	2.2	–	1.2	–	1.2
P. leptalea	–	–	+.3	–	–	–	–	–
P. orbicularis	1.2	+.1	+.0	+.2	+.1	+.0	–	–
P. tenella	+.2	–	–	–	1.3	–	–	–
Physciopsis adglutinata	–	–	+.0	–	–	–	–	–
Physconia enteroxantha	–	–	–	–	–	+.0	–	–
P. grisea	+.0	2.2	+.0	+.0	+.2	4.3	–	–
P. pulverulenta	–	–	+.2	1.2	–	–	1.2	1.2
Ramalina baltica	–	–	+.0	–	–	+.0	–	–
R. farinacea	–	–	+.0	+.0	–	–	+.0	+.0
R. fastigiata	–	–	+.0	–	–	–	–	+.0
Rinodina roboris	–	–	–	–	–	–	–	2.3
Schismatomma decolorans	–	–	–	–	–	–	+.0	+.0
Xanthoria parietina	–	2.3	1.3	1.2	+.0	+.2	–	1.3
Camptothecium sericeum	–	1.4	+.2	1.3	–	–	2.4	–
Hypnum cupressiforme	–	–	–	2.3	1.2	+.2	–	–
Leucodon sciuroides	–	–	–	–	–	2.3	–	–
Orthotrichum diaphanum	+.0	–	–	–	–	–	–	–
Porella platyphylla	–	–	–	1.3	–	–	–	–
Tortula laevipila	–	+.1	+.2	1.2	–	–	+.0	–
Zygodon viridissimus	–	1.2	–	–	–	–	–	–

1. Hertfordshire, North Mymms Park (52/2 – – 0 – –): *Ulmus procera* in open park, 1·5 m diam, incl. 85°, aspect W, 1·0 × 0·5 m, cover 30%, 26 October 1968, F.R.
2. E. Kent, Bourne Park (61/1 – – 5 – –): *Ulmus procera*, 0·8 m diam, incl. 90°, aspect SW, 0·3 × 0·3 m, cover 70%, 16 March 1967, F.R.
3. E. Kent, Denton Court Park (61/2 – – 4 – –): *Fraxinus*, 0·8 m diam, incl. 90°, aspect S, 1·0 × 0·3 m, cover not indicated, 8 June 1968, F.R.
4. E. Kent, NE of "Tudor House" roadhouse E of Bearsted (51/8 – – 5 – –): *Fraxinus* in parkland, 1·5 m diam, incl. 90°, aspect S, 2·0 × 1·0 m, cover 75%, 4 September 1968, F.R.
5. E. Kent, Maidstone, Mote Park (51/7 – – 5 – –): *Acer campestre*, 0·6 m diam, incl. 90°, aspect SW, 1·0 × 0·5 m, cover not indicated, 10 September 1968, F.R.
6. W. Norfolk, Hilborough Park (53/8 – – 0 – –): *Fraxinus* in parkland, 0·7 m diam, incl. 90°, aspect SW, 0·5 × 0·5 m, cover 80%, 5 June 1970, F.R.
7. W. Suffolk, Ickworth Park (52/8 – – 6 – –): *Acer campestre* in open parkland, 0·6 m diam, incl. 90°, aspect N, 1·0 × 0·5 m, cover 60%, 28 September 1968, F.R.
8. E. Sussex, Udimore (51/8 – – 1 – –): *Acer campestre*, 0·6 m diam, incl. 90°, aspect S, 1·0 × 0·5 m, cover not indicated, 15 April 1968, F.R.

Mediterranean association and thus it is not surprising to note that, in the British Isles, it appears to be most frequent in southern England. Although Barkman regarded *Physcia clementei* as an important component of this association, communities including that species in the British Isles seem sufficiently distinctive to warrant treatment as a distinct association, the *Teloschistetum flavicantis*.

Teloschistetum flavicantis ass. nov. (Table VII)

This previously unrecognized association recalls, and may eventually prove to be identical to, Barkman's (1958) unnamed southern Atlantic and montane-Mediterranean variant of the *Physcietum ascendentis* subass. *physciosum leptaleae* Klem. which he considered to occur in Brittany, near Fontainebleau, Provence and the Central Atlas Mountains. The association is closely allied to the *Physcietum ascendentis* but is differentiated primarily by the abundance of *Teloschistes* species (*T. chrysophthalmus* or *T. villosus* in France; usually only *T. flavicans* in Britain). *Physcia clementei*, *P.*

TABLE VII.

Teloschistetum flavicantis ass. nov.

Species	Stands 1	Stands 2	Species	Stands 1	Stands 2
Anaptychia ciliaris	–	+	*Parmelia subaurifera*	2	+
A. fusca	+	–	*P. subrudecta*	–	+
Evernia prunastri	2	–	*P. sulcata*	3	4
Ochrolechia parella	+	2	*Ramalina farinacea*	3	3
O. yasudae	4	–	*R. fastigiata*	3	–
Parmelia caperata	3	3	*Teloschistes flavicans*	4	5
P. perlata	3	4	Bryophyta	–	2

Additional species present in this community in the type locality but outside the areas of the quadrats were: *Buellia canescens*, *Lecanora chlarotera*, *L. expallens*, *Lecidea quernea*, *Lepraria candelaris*, *Opegrapha atra*, *Phlyctis argena*, *Physcia aipolia*, *P. adscendens*, *P. clementei*, *P. leptalea*, *P. tenella*, *P. tribacia*, *P. tribacioides*, *Physconia pulverulenta*, *Physciopsis adglutinata*, *Ramalina baltica*, *R. calicaris* and *Xanthoria parietina*. A colour photograph of this community in the type locality appeared on the front cover of *Environment and Change* **2** (6), February 1974.

1. S. Devon, Torcross, Widdicombe House (20/811417): mature *Acer pseudoplatanus* in pasture, 30 cm diam, incl. 85°, aspect 290°, 20 × 20 cm, cover 87%, 11 August 1973, D.L.H.
2. S. Devon, Torcross, Widdicombe House (20/811417): mature *Acer pseudoplatanus* in pasture, 40 cm diam, incl. 87°, aspect 265°, 20 × 20 cm, cover 90%, 11 August 1973, D.L.H.; *type record*.

leptalea and *P. tribacioides*, which can form extensive stands in the sunniest and driest parts of southern England, are very closely associated with it. This community appears to have been formerly widespread in southern England but is now largely restricted to the south-west (where it is now much rarer than it was last century) from Dorset to Cornwall and is more rarely found in Pembrokeshire (S. Wales). The twig facies (with *T. chrysophthalmus*) is still common in the Mediterranean area and in south-west France (from southern Brittany southwards), where it is largely found on twigs in very well lit situations. In south-west England today it occurs both on twigs and on well lit, well ventilated nutrient-enriched tree trunks, but *T. chrysophthalmus* seems now to be extinct in Britain outside the Channel Islands (Hawksworth *et al.*, 1974).

This community is not identical to the *Teloschistetum chrysophthalmae* Ochsn. (see p. 344), the type record of which lacked any *Teloschistes* species and is referable to the *Physcietum ascendentis*.

IV. Limestone Communities

Hard limestones (e.g. Carboniferous and Devonian) support several distinct lichen communities in the British Isles. Most of these are able to spread on to softer calcareous rocks and a wide range of basic man-made substrates (e.g. asbestos-cement, concrete, basic brickwork and mortar), but then occur essentially as species-poor variants.

The communities developed on coastal limestones are essentially species-poor facies of associations of inland limestone rocks and so are not recognized separately here. Some elements of the *Caloplacetum marinae* and *Verrucarietum maurae*, normally well developed on siliceous rocks, may be encountered on hard coastal limestones, e.g. marine *Caloplaca*, *Verrucaria* and rarely *Lichina* species (see Fletcher, 1975b). *Arthopyrenia halodytes* can also occur on softer limestones and chalk as well as its more usual habitat of barnacles and other intertidal mollusc shells.

Species on soil and humus in crevices, soil and turf around limestone, chalk, pebbles etc., are treated separately on pp. 393–407, while intermediate communities on other basic rocks are discussed on pp. 361–364.

All. 12. *Aspicilion calcareae*

Aspicilion calcareae (Alberts.) comb. nov.—*Lecanorion calcareae* Alberts., *Acta phytogeogr. suec.* **20,** 34 (1946), basionym.—*Caloplacion decipientis* Klem., *Ber. bayer. bot. Ges.* **28,** 263 (1950).—*Gyalection cupularis* Matt., *Bot. Jb.* **75,** 420

(1951) [*nom. nud.*].—*Lecanactinion stenhammari* Matt., *Bot. Jb.* **75,** 415 (1951) [*nom. nud.*].—*Collemation tunaeformis* Degel. (1950) *fide* Degel., *Symb. bot. upsal.* **13** (2), 127 (1954).—*Caloplacion pyraceae* Klem., *Beih. Feddes Repert.* **135,** 72 (1955).—*Collemion rupestris* Klem., *Beih. Feddes Repert.* **135,** 89 (1955).—*Lecanorion galactinae* Laund., *in* Kettering and District Field Club, *First Fifty Years*, 95 (1956).—*Lecanorion dispersae* Laund., *Lichenologist* **3,** 294 (1967).

Although numerous syntaxa have been described for lichen communities on limestones mainly dominated by various *Caloplaca*, *Collema*, *Lecanora* and *Verrucaria* species, in view of the number of species which are, or are sometimes, common to all of them it seems preferable to recognize a restricted number of associations within a single alliance*. Diversity in this alliance is very wide and many of the species indicated in Table VIII as present in it predominate from time to time. To recognize all such facies would in our view be an unwarranted inflation of lichen syntaxonomy, particularly as a very wide range of variation can be seen to occur in apparently uniform habitats with similar moisture and light regimes at a single site; this diversity, basically one of varying local dominants, may well arise from a combination of four factors: (1) the first species that

TABLE VIII.

Lichens characteristic of limestone in the British Isles and the associations in which they usually occur.

Acarospora glaucocarpa[e]	*C. decipiens*[a]
A. heppii[e]	*C. heppiana*[a]
A. macrospora[e]	*C. holocarpa*[a f]
Acrocordia conoidea[b e]	*C. lactea*[a]
A. salweyi[e]	*C. ruderum*[a]
Arthopyrenia saxicola[a]	*C. saxicola*[c]
Aspicilia calcarea[a e]	*C. teicholyta*[a]
A. contorta[a]	*C. tetrasticha*[a c e]
A. prevostii[e]	*C. variabilis*[a e]
Bacidia cuprea[b]	*C. velana*[a]
B. sabuletorum[e]	*Candelariella aurella*[a]
Buellia canescens[f]	*C. medians*[a f]
B. epipolea[a]	*Catillaria lenticularis*[a e]
Caloplaca aurantia[a]	*Clathroporina calcarea*[b]
C. chalybaea[e]	*Collema auriculatum*[e]
C. cirrochroa[b]	*C. crispum*[e]
C. citrina[a e f]	*C. cristatum*[a e]

* Apart from the *Physcietum caesiae* discussed on p. 360.

TABLE VIII—*continued*

C. multipartitum[a e]	*Physconia enteroxantha*[b]
C. polycarpon[a e]	*P. grisea*[f]
C. tenax[a e]	*P. pulverulenta*[f]
C. tuniforme[a e]	*Placynthium nigrum*[e]
C. undulatum[a]	*P. subradiatum*[a]
Dermatocarpon miniatum[b e]	*P. tremniacum*[b]
Diploschistes gypsaceus[b]	*Polyblastia albida*[a]
Dirina repanda[c]	*P. cupularis*[a e]
D. stenhammari[c]	*P. schraderi*[a]
Encephalographa cerebrina[?a]	*Porina chlorotica* var. *persicina*[b]
Gyalecta jenensis[b]	*Protoblastenia immersa*[a e]
Ionaspis epulotica[b]	*P. incrustans*[e]
Lecania erysibe[a e]	*P. metzleri*[e]
Lecanora crenulata[a]	*P. monticola*[a]
L. dispersa[a]	*P. rupestris*[a b e]
L. muralis[f]	*Psorotichia schaereri*[e]
Lecidea jurana[a b]	*Rhizocarpon umbilicatum*[a]
Lecidella stigmatea[a e f]	*Rinodina bischoffii*[a e]
Lempholemma botryosum[e]	*Sarcogyne regularis*[a]
Lepraria crassissima[d]	*Solenopsora candicans*[a e]
L. incana[d]	*Staurothele caesia*[a]
L. sp. (bright green)[d]	*S. hymenogonia*[e]
Leproplaca chrysodeta[d]	*S. rupifraga*[e]
L. xantholyta[d]	*S. succedens*[e]
Leptogium lichenoides[e]	*Synalissa symphorea*[e]
L. plicatile[e]	*Thelidium decipiens*[a b e]
Opegrapha calcarea[c]	*T. incavatum*[a]
O. chevallieri[a]	*T. papulare*[e]
O. mougeotii[c]	*T. pyrenophorum*[e]
O. persoonii[a]	*Toninia aromatica*[e]
O. saxatilis[b]	*Verrucaria coerulea*[a e]
O. saxicola[b]	*V. dufourii*[a e]
Petractis clausa[b]	*V. glaucina*[a e]
Physcia adscendens[f]	*V. hochstetteri*[a]
P. caesia[f]	*V. muralis*[a]
P. dubia[f]	*V. nigrescens*[a]
P. nigricans[f]	*V. sphinctrina*[a]
P. orbicularis[f]	*V. viridula*[a e]
P. tenella[f]	*Xanthoria aureola*[f]
P. wainioi[f]	*X. parietina*[f]

[a] *Caloplacetum heppianae* (p. 353)
[b] *Gyalectetum jenensis* (p. 355)
[c] *Dirinetum stenhammariae* (p. 356)
[d] *Leproplacetum chrysodetae* (p. 357)
[e] *Placynthietum nigri* (p. 357)
[f] *Physcietum caesiae* (p. 360)

chances to establish itself at a site, (2) successional and competition effects between the species present, (3) the softness (e.g. the calcium–silica ratio) and texture of the rock, and (4) the chemical composition of the rock (e.g. magnesium–calcium ratios).

The associations accepted within this alliance here all occupy distinctive microhabitats (Fig. 7) as well as having characteristic floristic compositions

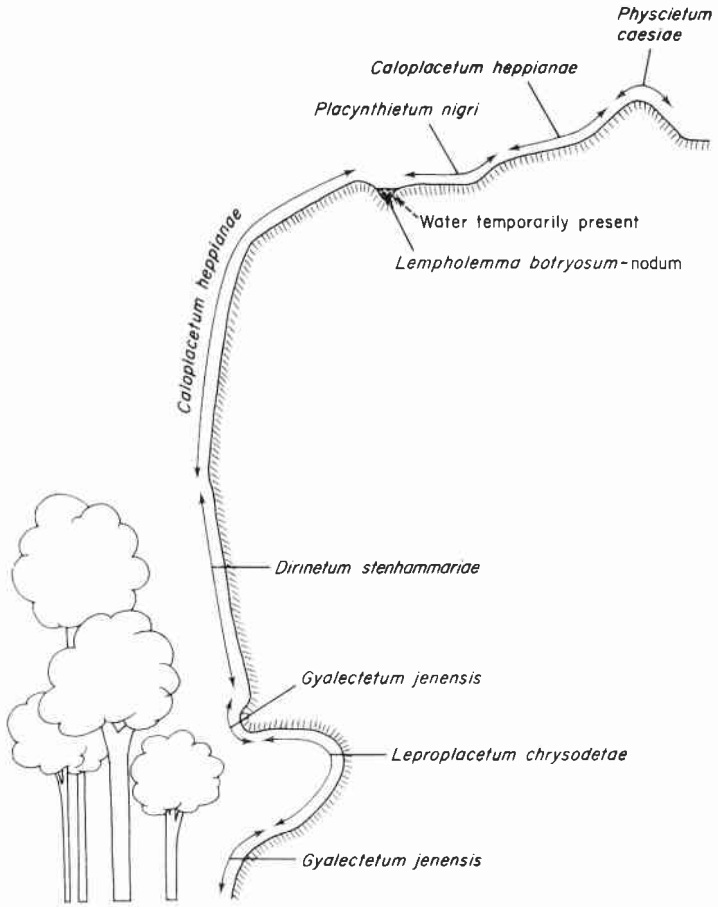

FIG. 7. Diagrammatic section through a limestone bluff to illustrate the microhabitats occupied by the principal lichen communities on limestone.

and so appear to be of greater syntaxonomic importance than communities in similar microhabitats differing only in dominant species. It must, however, be stressed that of the lichen communities treated in this chapter, those which occur on limestones are currently the least understood from the phytosociological standpoint. For this reason it is possible that future

studies may be able to justify a larger number of associations than is accepted here.

The correct nomenclature of this alliance, like that of two of the main associations treated below, is not entirely clear at the present time. For this reason no attempt has been made to typify the names in the rank of alliance cited as synonyms above.

Caloplacetum heppianae DR.

Svensk. växtsociol. Sällsk. Handl. **2,** 47 (1925) [as "*Caloplaca heppiana*-Ass."].

"Synonyms"*: *Aspicilietum calcareae* "(DR.)" Klem.; *Aspicilietum contortae* "(Kaiser)" Klem.; *Caloplacetum aurantiae* Klem.; *Caloplacetum citrinae* "(Gallé)" Beschel; *Caloplacetum murorum* "(DR.)" Kaiser; *Caloplacetum variabilis* Klem.; *Lecanoretum calcareae* Alberts.; ? *Lecanoretum campestris* Massé; *Lecanoretum dispersae* Beschel.

This association, which further study may show does indeed merit subdivision as has been the practice to various degrees of most phytosociologists since Du Rietz (1925) and Kaiser (1926), is essentially that of exposed well lit dry limestones. It is characterized by *Aspicilia calcarea*, foveolate *Verrucaria* species (e.g. *V. hochstetteri*, *V. muralis* and particularly *V. sphinctrina*) and, to a lesser extent, species of *Polyblastia* (e.g. *P. albida*, *P. cupularis* and *P. dermatodes*) and *Thelidium* (*T. decipiens* and *T. incavatum*), but has many facies of which those dominated by one or more placodioid, orange *Caloplaca* species (e.g. *C. aurantia* and *C. heppiana*, both becoming rare in Scotland) are the most spectacular (Fig. 8) and so have most commonly been treated as distinct associations. Facies in which *C. teicholyta* (eastern) and *Solenopsora candicans* (western) are generally abundant also occur, particularly in the south. In the driest sites *Caloplaca aurantia* and *C. heppiana* become rarer and the frequency of *Rhizocarpon umbilicatum* increases; *Caloplaca variabilis*, *Polyblastia deminuta*, *Protoblastenia incrustans* and foveolate *Verrucaria* species are generally present in such reduced communities. Many lichens which occur in this association are, however, small and easily overlooked (particularly the pyrenocarpous species; see Table VIII).

In particularly high-rainfall areas with low sunshine, especially on

* The nomenclature of this and the *Placynthietum nigri* (p. 357) remain confused and require a very detailed investigation, particularly in view of numerous non-latinized names in the literature (e.g. Kaiser, 1926). Rather than take up unfamiliar names we have employed the earliest familiar name in this case and retained an incorrect but widely used name in that of the *Placynthietum nigri*. Synonyms indicated in both cases are preliminary listings as the citations and the validity of many of these names are in need of a more critical study.

FIG. 8. *Caloplacetum heppianae* on a calcareous tombstone. Predominant species: *Buellia canescens*, *Caloplaca aurantia*, *C. saxicola*, *Lecanora dispersa*, *Physcia adscendens*, *P. orbicularis* and *Xanthoria candelaria*. (Surrey: Cobham churchyard, 1977, F. S. Dobson).

Cambrian limestones, a moss-rich facies poor in *Caloplaca* species is developed, including *C. stillicidiorum* (on mosses), *Collema multipartitum*, *Lecidea templetonii*, *Protoblastenia incrustans*, *Solorina saccata* and *Squamarina crassa*.

The species-poor, air pollution-tolerant *Lecanora dispersa*-dominated facies, which is very abundant on concrete, is viewed here as a pioneer phase of this association; that it now often lacks placodioid *Caloplaca* species in urban areas is almost certainly due to pollution effects (see Laundon, 1967). *Candelariella aurella–L. dispersa* communities are very rapid colonizers of fresh concrete and gravestones, and can provide very high cover values within about 5 years (Hawksworth, 1969; Seaward, 1975). On mortar in eastern Scotland *Caloplaca decipiens* and *Xanthoria elegans* (?*X. resendei*) are particularly frequent.

Temporal relationships within this association are evidently complex and have been investigated in Britain only by Syers (1964) who demonstrated, for example, that the foveolate *Verrucaria* element of this community might be a pioneer stage in that it could be overgrown by placodioid *Caloplaca* species or crustose species with epilithic thalli.

Some relevé data for this association in the British Isles are included in Laundon (1967) and Hawksworth (1969) but extensive surveys of it on naturally occurring limestones have not been carried out. In areas of the British Isles that lack naturally occurring limestones, the *Caloplacetum heppianae* is widespread on artificial substrates, particularly on well lit vertical calcareous gravestones and walls in churchyards.

Gyalectetum jenensis Klem.

Beih. Feddes Repert. **135,** 76 (1955).—*Gyalectetum cupularis* Matt., *Bot. Jb.* **75,** 420 (1951) [as "Gesellschaft von *Gyalecta cupularis*"], *nom. nud.*—*Lecideetum juranae* Klem., *Beih. Feddes Repert.* **135,** 75 (1955) [as "(Kaiser 1926) Klement"].—*Caloplacetum cirrochroae* Poelt ex Klem., *Beih. Feddes Repert.* **135,** 88 (1955) [as "Poelt (*in litt.* 1952)"], *nom. inval.* [no frequency values].—*Caloplacetum cirrochroae* Poelt ex Klem. ex Wirth, *Diss. Bot., Lehre* **17,** 258 (1972) [table with frequency values].

A shade and prolonged moisture-loving community which tends to prefer damp limestone where, for example, water also runs over or drips on to it during periods of heavy rain or where it is shaded by trees and herbage. Although *Gyalecta jenensis* is often dominant in this association, it may sometimes be replaced in this role by *Petractis clausa*. Other species characteristic and often extremely well developed in this community include *Acrocordia* (*Arthopyrenia*) *conoidea*, *Caloplaca cirrochroa*, *Diploschistes gypsaceus*, *Lecidea jurana*, *Opegrapha saxatilis*, *O. saxicola*, *Porina*

chlorotica var. *persicina* and *Protoblastenia metzleri*. *Clathroporina calcarea*, an often overlooked but locally abundant species in the British Isles, is probably faithful to this association (communities including it are particularly well developed in the limestone dales of the Peak District, and at Symond's Yat, Ross-on-Wye, but it also occurs on mortar in churchyards in south-west England).

Klement (1955) included *Leproplaca xantholyta* as a characteristic species of his *Caloplacetum cirrochroae* but no *Lepraria* species were cited by him or Wirth (1972); this thus appears to be a more moisture-requiring community than the *Leproplacetum chrysodetae*. It is consequently placed as a synonym of the *Gyalectetum jenensis* rather than of the *Leproplacetum* here.

Wirth (1972) also mentions *Dermatocarpon miniatum* and this is also usually encountered in the *Gyalectetum jenensis* in the British Isles although it can also be well developed in slightly shaded facies of the moisture-requiring *Placynthietum nigri*. The *Opegraphetum saxicolae* Mot. (Motyka, 1926, p. 224) may perhaps be the earliest name for this association but is not taken up here as *Opegrapha saxicola* is rarely dominant in the British Isles.

Dirinetum stenhammariae (DR.) comb. nov.

Lecanactinetum stenhammariae DR., *Svensk. växtsociol. Sällsk. Handl.* **2,** 47 (1925) [as "*Lecanactis stenhammari* Ass."].

The *Dirina stenhammari*-dominated communities on limestone have many lichens in common with the *Caloplacetum heppianae* but tend to be rather poor in placodioid *Caloplaca* species although *C. tetrasticha* (including *C. ochracea*) may be abundant. The *Dirinetum stenhammariae*, first recorded in Britain by Hawksworth (1973a), occupies a distinctive ecological niche on both naturally occurring limestones and calcareous church walls which are slightly shaded, usually north-facing, vertical or almost vertical, and receive little or no direct rainfall. Rather flaky surfaces are perhaps also preferred. In its environmental requirements this association is not unlike the corticolous *Lecanactidetum premneae* (p. 309). In southern England this association occurs far from natural limestone outcrops on church walls. Other species encountered in this community in the British Isles include *Dirina repanda*, *Lecanactis grumulosa*, *Opegrapha calcarea*, *O. mougeotii* and *O. subelevata*. This association, which clearly has Mediterranean or Lusitanian affinities, is, however, generally rather poor in species in the British Isles.

Leproplacetum chrysodetae ass. nov. (Table IX)

This previously unrecognized association is restricted to moderately shaded dry underhangs, recesses, cave entrances and sheltered sides of mortar-stone walls where the substrate is never directly wetted by rain or water run-off; presumably the component species obtain their moisture from the atmosphere (which is often particularly humid in such habitats). The abundance of *Lepraria crassissima*, *L. incana*, *Leproplaca chrysodeta* and *L. xantholyta* characterize this association although the frequencies of these four species may vary markedly from recess to recess and all may not be present in each site. A further species encountered in this community is an apparently undescribed bright green *Lepraria* which is widespread in this habitat in the British Isles; this lichen is probably faithful to the *Leproplacetum chrysodetae*.

As the specialized niche occupied by this association (Fig. 7) is unfavourable to most species of its alliance, this community tends to be rather poor in species although components of the *Gyalectetum jenensis* may occur in it occasionally at low cover values.

The *Leproplaca*-absent but *Lepraria*-rich *Arthopyrenietum conoideae* Codr. has some affinity with the *Leproplacetum chrysodetae* but appears somewhat intermediate between the present association and the *Gyalectetum jenensis*; for this reason it is not treated as identical to either here. In Britain *Acrocordia conoidea–Lepraria* communities occur where stands of the *Gyalectetum jenensis* and *Leproplacetum chrysodetae* adjoin one another and appear to be of little syntaxonomic importance.

Placynthietum nigri Klem.*

Beih. Feddes Repert. **135,** 89 (1955) [as "(DR. 1925) Klem."].—*Placynthieto-Verrucarietum nigrescentis* DR., *Svensk. växtsociol. Sällsk. Handl.* **2,** 44 (1925) [as "*Placynthium nigrum-Verrucaria nigrescens*-Assoziation"].

"Synonyms"*: *Collematetum crispi-Verrucarietum muralis* Gallé; *Collematetum pulposi* Kaiser; *Collematetum multipartitis* DR.; *Collematetum tunaeformis* Alberts.

This association, under a variety of names, has often been treated as forming an alliance distinct from the *Aspicilion calcareae* (by, for example, Klement, 1955; Degelius, 1954; Hawksworth, 1969) but, in view of the large number of species it has in common with that alliance, it seems preferable to regard it as a distinct association in the same alliance as that

* See footnote on p. 353. For other synonyms or possible synonyms see Kaiser (1926) and Klement (1955).

comprising the *Aspicilia calcarea*- and placodioid *Caloplaca*-containing communities (i.e. the *Aspicilion calcareae*).

The *Placynthietum nigri* prefers damper situations than the *Caloplacetum*

TABLE IX.

Leproplacetum chrysodetae ass. nov.

Species	Stand					
	1	2	3	4	5	6
Acrocordia conoidea	2	–	–	–	–	–
Caloplaca cirrochroa	–	–	–	–	–	1.–
C. heppiana	2	–	–	–	2	–
C. saxicola	–	2	–	–	–	–
Catillaria lenticularis	2	–	–	–	–	–
Clathroporina calcarea	2	4	3	3	–	–
Dirina stenhammari	–	–	4	–	–	–
Gyalecta jenensis	–	–	–	–	–	1.–
Lecanora dispersa	–	2	–	–	–	–
Lepraria crassissima	4	+	5	–	8	2.2
L. incana	–	–	–	–	–	0.2
L. sp. (bright green)	–	–	–	–	–	1.1
Leproplaca chrysodeta	–	6	5	+	–	–
L. xantholyta	6	7	7	7	–	2.2
Porina chlorotica var. *persicina*	–	–	–	–	5	2.2
Protoblastenia rupestris	–	–	–	–	2	–
Verrucaria muralis	2	–	–	3	–	–
V. nigrescens	2	–	–	–	–	–
Bryophytes	–	–	–	–	–	1.1

1. Derbyshire, Lathkill Dale (43/165660): Carboniferous limestone underhang, incl. 87°, aspect 30°, 10 × 10 cm, cover 100%, 25 April 1975, D.L.H.
2. Derbyshire, Lathkill Dale (43/160661): Carboniferous limestone underhang, incl. 101°, aspect 120°, 10 × 10 cm, cover 100%, 25 April 1975, D.L.H.
3. Derbyshire, Lathkill Dale (43/160661): Carboniferous limestone underhang, incl. 95°, aspect 55°, 10 × 10 cm, cover 100%, 25 April 1975, D.L.H.; *type record*.
4. Derbyshire, Lathkill Dale (43/160661): Carboniferous limestone underhang, incl. 92°, aspect 50°, 10 × 10 cm, cover 80%, 25 April 1975, D.L.H.
5. Derbyshire, Lathkill Dale (43/165660): Carboniferous limestone underhang, incl. 90°, aspect 120°, 20 × 10 cm, cover 100%, 25 April 1975, D.L.H.
6. West Yorkshire, Settle, Malham Cove (44/903678): Carboniferous limestone underhang, incl. 90°, aspect 270°, 1·0 × 2·0 m, cover 65%, 1970, P.W.J.

heppianae but, like it, requires light although it is rather more tolerant of slight shading. This association thus tends to occur in rather less quickly draining microhabitats, such as damp vertical faces, undulating limestone surfaces and slopes where water run-off keeps them moist. Some facies of the association are rich in bryophytes whilst others may have the large thalli of *Dermatocarpon miniatum* (see also p. 356) abundant, but it is essentially characterized by the abundance of cyanophilous lichens and shade-loving pyrenocarpous species (see Fig. 9). *Placynthium nigrum* is

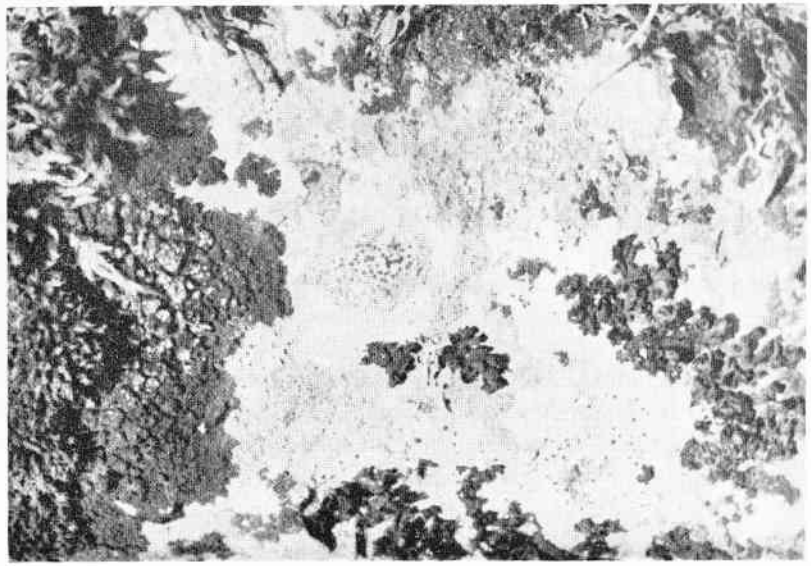

FIG. 9. *Placynthietum nigri* on limestone. Species present include: *Collema multipartitum*, *Placynthium lismorense*, *P. nigrum*, *Protoblastenia rupestris*, *Verrucaria dufourii*, *V. hochstetteri*, and *V. sphinctrina* (Argyllshire: Island of Lismore, 1971, P. W. James).

almost invariably present and often luxuriantly developed in this community; one or more *Collema* species also occur of which the most commonly encountered are *C. auriculatum*, *C. crispum* and *C. cristatum*, although other members of this genus may be abundant in it in some localities (e.g. *C. multipartitum*, *C. polycarpon*, *C. tuniforme* and *C. undulatum*); *Leptogium lichenoides*, saxicolous morphotypes of *L. teretiusculum* as well as *Psorotichia schaereri*, are other regularly occurring cyanophilous species. The rare *Synalissa symphorea* is also probably faithful to this association. Of the pyrenocarpous species, *Thelidium decipiens*, *T.*

papulare, *T. pyrenophorum*, *Verrucaria coerulea* and *V. dufourii* are particularly characteristic of the association. A facies not unlike the *Toninietum candidae* Kaiser but in which *Toninia candida* is replaced by *T. aromatica* occurs but scarcely merits recognition at the association level as it is rather poorly delimited. On mossy limestone rocks in woodland, a facies with abundant *Collema auriculatum*, *C. crispum*, *Cladonia pocillum*, *Polyblastia tristicula* and *Squamarina crassa* can also be recognized. For further species encountered in this species-rich association see Table VIII.

Like the *Caloplacetum heppianae*, the *Placynthietum nigri* is able to extend from natural limestone outcrops on to limestone tombstones and calcareous walls. In churchyards its different ecological requirements can easily be seen by, for example, comparing the lichen communities on the driest and dampest walls of the church, or those on vertical tombstones and around the basal parts of horizontal tops of chest-tombs. Similar contrasts can be seen in comparing limestone boulders in turf and wide expanses of limestone rock faces. The *Placynthietum nigri* is conspicuously rarer in churchyards in the low-rainfall areas of East Anglia than in south and west England.

Allied to this community is one sometimes encountered in depressions in limestone which often hold water for considerable periods of time and in which *Lempholemma botryosum* predominates; this may represent a distinct association but as it is in need of further study it is not formally recognized here but rather treated as a "nodum" (see Fig. 7). Free-living *Nostoc* is often conspicuous in such hollows when it is or has just been raining.

All. 13. *Xanthorion parietinae*

Xanthorion parietinae Ochsn.—see p. 342 for nomenclature.

Physcietum ascendentis Frey & Ochsn.

See p. 344 for nomenclature.

A community not unlike the corticolous association (see p. 344) occasionally occurs on nutrient-enriched calcareous rocks and walls, particularly in farmyards. In this habitat *Buellia canescens*, *Physcia tribacia* and *Ramalina duriaei* are particularly characteristic of it.

Physcietum caesiae Mot.

Bull. int. Acad. pol. Sci. Lett. [*Cracovie*], *sér. B*, **1924,** 843 (1925).

This association is widespread on nutrient-enriched sites (e.g. birds' perching stones) but, while it is particularly frequent on limestones

(especially the horizontal faces on the tops of gravestones and concrete posts), it is less specific to rock type than nutrient availability. In moderately polluted areas the association is especially well developed on asbestos-cement and can extend far into urban areas as a species-poor facies in which *Lecanora muralis* often predominates. Although primarily a community of calcareous substrates, it is also to be encountered on siliceous rocks enriched by bird droppings and, more rarely, on manure-enriched wood near farmyards and limestone dust-enriched bark near limestone-crushing plants and quarries (see p. 345).

The *Physcietum caesiae* is characterized by high frequencies of *Physcia* species (e.g. *P. adscendens*, *P. caesia*, *P. orbicularis*, *P. wainioi*), *Physconia* (e.g. *P. grisea*) and *Xanthoria* (*X. aureola* and/or *X. parietina*); in eastern Britain *Physcia dubia* and *P. nigricans* also enter into this association and the predominance of *Xanthoria aureola* should be noted. *Caloplaca citrina*, *Candelariella medians* and *Lecanora muralis* are amongst the numerous other species frequently found in this community (see also Table VIII). Relevé data from stands of this association in London are included in Laundon (1967).

It is probable that this association has a number of synonyms (e.g. *Caloplacetum elegantis* Mot., *Physcietum dubiae* R. Sant., *P. teretiusculae* Hil., *Xanthorietum aureolae* Beschel) but the status and application of these names has not been studied by us. The *Physcietum caesiae* has clear affinities with the *Physcietum ascendentis* (see p. 344) on the basis of its species composition but characterizes particularly nutrient-enriched sites where fresh bird droppings are often present. There is also a strong affinity with the *Candelarielletum corallizae* (see p. 378).

V. Other Basic Rock Communities

In addition to species-poor facies of essentially limestone associations occurring on calcareous man-made substrates and softer calcareous rocks and basic sandstones, two specialized unnamed communities of basic rocks occur in the British Isles and these are discussed here. Maritime and nutrient-enriched siliceous rocks, which are basic due to environmental factors, are treated separately on pp. 384–389 and pp. 378–382, respectively.

Montane epidiorite nodum

An extremely specialized but rare assemblage of lichens is associated with epidiorite and mica schist rocks on several of the higher mountains in

Scotland (e.g. Ben Hope, Ben Lawers, Caenlochan and Glen Clova). The community spreads from rock on to adjacent rock debris, bryophytes and mica schist-rich soils and thus can be treated as both terricolous and saxicolous. Detailed lists of the species of this nodum on Ben Lawers have been provided by James (1965). On Ben Hope the communities are similar but *Pannaria hookeri* is dominant on rock. Many of the lichens in this nodum are extremely rare and restricted to it in the British Isles. The following may be mentioned as characteristic: *Belonia russula*, *Biatorella fossarum*, *Caloplaca stillicidiorum* (on mosses), *Euopsis granatina*, *Gyalidea fritzei*, *Pannaria hookeri*, *Pertusaria glomerata*, *Placynthium dolichoterum*, *P. pannariellum*, *Polyblastia cupularis*, *P. inumbrata*, *P. scotinospora*, *P. theleodes*, *Protoblastenia siebenhaarina*, *Sporopodium fuscoluteum*, *Thelopsis melathelia* and *Thyrea radiata*.

This nodum is apparently distinct from the *Aspicilietum verrucosae* Frey (see Klement, 1955) although it has a number of species in common with it. Its syntaxonomic position is in need of further study but it has clear affinities with some communities of alpine habitats in Norway of which it probably represents a species-poor facies.

Rhizocarpon petraeum nodum (Table X)

Siliceous rocks at the margins of limestone outcrops support a very characteristic assemblage of species (Table X) whose presence is indicative of the site being somewhat calcareous. This is essentially a transitional nodum occurring chiefly in highland Britain and in which "substrate-switch" species are an important component. Some species of this community (e.g. *Caloplaca flavovirescens*, *Buellia alboatra*, *Rhizocarpon petraeum*) occur, for example, on granite stones in a stone and calcareous mortar wall in lowland Britain. Species found in this nodum include *Bacidia sabuletorum*, *B. umbrina*, *Caloplaca aurantiaca*, *Candelariella vitellina*, *Lecanora muralis*, *Lecidea illita*, *L. speirea*, *L. umbonata*, *Lecidella stigmatea*, *Lithographa tesserata*, *Polyblastia theleodes*, *Protoblastenia monticola*, *P. rupestris* (not usually as "var. *calva*"), *Rhizocarpon petraeum* and *Thelidium pyrenophorum*. This community is not accorded the status of an association here as it is essentially transitional between limestone and siliceous rock associations and is usually very limited in extent.

Ability to recognize this nodum is of considerable importance to ecologists as it enables base-rich rocks in essentially siliceous rock areas to be recognized and thus indicates sites of potential importance for their phanerogamic floras.

TABLE X.

Rhizocarpon petraeum nodum.

Species	Stand 1	2	3	4	5	6
Acarospora glaucocarpa	–	–	–	1.2	–	4.0
Bacidia sabuletorum	+.2	+.2	–	–	–	+.2
B. umbrina	+.2	1.3	–	+.2	+.2	1.2
Buellia aethalea	–	+.2	–	–	–	–
Caloplaca aurantiaca	–	1.2	1.3	+.2	–	–
C. citrina	+.0	+.2	–	+.0	–	–
Candelariella vitellina	–	1.2	+.2	1.3	1.3	1.3
Catillaria lenticularis	1.2	+.2	1.2	–	+.0	+.2
Clathroporina calcarea	–	+.2	–	–	–	–
Collema cristatum	+.0	+.2	–	–	+.2	–
C. polycarpon	–	+.0	–	–	+.2	–
Gyalecta jenensis	–	–	+.2	–	–	1.2
Huilia albocaerulescens	–	+.2	–	–	+.2	–
Ionaspis epulotica	–	–	–	+.0	–	–
Lecanora crenulata	–	–	+.2	–	–	–
L. dispersa	–	+.2	1.2	–	+.2	+.2
L. muralis	–	–	–	1.2	1.3	–
Lecidea illita	–	1.2	–	–	1.2	–
L. lithophila	–	–	1.2	–	+.2	–
L. pelobotryon	+.2	+.0	–	–	+.2	–
L. speirea	2.2	–	2.3	–	1.3	–
L. umbonata	–	–	–	1.2	–	–
Lecidella scabra	–	+.0	–	–	–	–
L. stigmatea	1.2	1.3	1.2	–	+.2	1.3
Lithographa tesserata	–	–	+.2	3.3	1.2	–
Pertusaria amara	–	–	–	+.2	–	–
P. pseudocorallina	–	–	–	+.2	–	–
Placynthium lismorense	–	+.2	–	–	–	–
Polyblastia scotinospora	–	+.2	+.0	–	–	–
P. theleodes	+.2	1.2	+.2	–	+.2	–
Protoblastenia monticola	1.2	1.3	+.2	+.2	+.0	+.2
P. rupestris	1.2	2.3	1.3	2.3	3.2	1.3
Rhizocarpon obscuratum	1.2	–	+.2	+.2	–	–
R. petraeum	2.3	1.2	+.2	1.3	+.0	3.2
Thelidium decipiens	+.2	–	–	1.2	–	+.2
T. pyrenophorum	–	–	1.2	–	1.3	–
Trapelia coarctata	–	–	+.2	–	+.2	–
Verrucaria coerulea	+.2	1.3	1.2	–	+.2	2.2

TABLE X—*continued*

Species	Stand 1	2	3	4	5	6
V. glaucina	–	+.0	–	–	–	–
V. hochstetteri	–	+.0	–	–	–	+.0
V. muralis	+.2	+.2	+.2	–	+.2	+.2
V. sphinctrina	1.2	+.2	+.2	+.2	–	1.2
V. viridula	+.2	–	+.0	+.0	+.2	+.2

1. Sutherland, Inchnadamph, lower slopes of Ben More Assynt (29/286205): transition between acid rock and limestone, exposed site, incl. ± 30°, aspect 180°, 0·5 × 0·5 m, cover 75%, 16 June 1961, P.W.J.
2. Argyllshire, Island of Lismore, Port Ramsey (17/892462): transition between acid rock and Dalradian limestone, exposed site, incl. ± 10°, aspect 270°, 1 × 1 m, cover 80%, 12 June 1972, P.W.J.
3. Perthshire, Kinloch Rannoch, lower slopes of Schiehallion above Lochan an Dairn (27/719568): incl. ± 30°, aspect 45°, 1 × 1 m, 14 August 1970, P.W.J.
4. S. Aberdeenshire, Braemar, above Croft of Muicken (37/143903): exposed site, incl. ± 20°, aspect 315°, 1 × 1 m, 16 August 1968, P.W.J.
5. Mid Ebudes, Island of Mull, Ross of Mull, Carsaig, near Nuns' Pass (17/525205): incl. ± 45°, aspect 225°, 1 × 1 m, 10 August 1969, P.W.J.
6. West Yorkshire, Settle, Malham Tarn, Great Close (44/903678): small outcrop in limestone, incl. ± 30°, aspect 225°, 0·5 × 0·5 m, 16 August 1967, P.W.J.

The *Rhizocarpetum concentricae* Mot. (Motyka, 1926, pp. 219, 226) may be synonymous with this nodum but this was poorly circumscribed by Motyka and included the non-British *Lecidea niveoatra* as a main component.

VI. Siliceous Rock Communities

Communities of lichens on siliceous rocks have, with the notable exception of those on rocky shores (pp. 384–389), received scant attention in the British Isles. Siliceous rocks do, however, support more lichen species than any other major habitat in the British Isles. While many communities meriting phytosociological recognition occur, problems of identification of crustose lichens and the relatively little survey work undertaken mean that the treatment presented here is particularly tentative.

Factors controlling the development of these communities parallel those listed for epiphytic communities (see p. 304) with the addition of (1) roughness and fine texture, (2) hardness and friability, and (3) heavy metal contents.

In order to draw similar alliances and associations together, the siliceous rock communities have been grouped into six broad habitat categories: (A) shaded, (B) exposed, (C) nutrient-enriched, (D) mineral-rich, (E) marine and maritime, and (F) aquatic.

A. Shaded

All. 14. *Leprarion chlorinae*

Leprarion chlorinae Šmarda & Hadač, *in* Klika & Hadač, *Příroda, Brno* **36,** 253 (1944).—*Cystocoleion nigri* Wirth, *Diss. Bot., Lehre* **17,** 105 (1972).

An alliance of shaded underhangs and recesses in hard siliceous rocks which are sheltered from direct rain; the acid rock counterpart of communities in dry bark recesses (pp. 306–313) and similar situations on limestone (pp. 349–360). Crustose and leprose species predominate in this alliance and many of these are abundantly sorediate; indeed a high proportion are unknown fertile.

A comprehensive key to the lichens of shaded acid rock crevices and underhangs in Britain is provided by James (1970) and includes information on the distribution of the species.

Some species-poor communities referable to this alliance are also able to occur on upturned tree roots, soil, pebbles in roadside cuttings or in old acid woodlands, as well as in the dry overhangs and recesses in rock of which they are characteristic. The essentially corticolous *Coniocybetum furfuraceae* (p. 308) is also able to spread on to rock and dry soil in suitably shaded sites and form intergrades with both the *Lecideetum lucidae* and the *L. sylvicolae*. The broad ecological amplitude of the *Leprarietum incanae* (p. 312) includes siliceous rocks on which it can form transitions to the *Lecideetum lucidae* and *Racodietum rupestris* in particular.

The *Sclerophytetum circumscriptae* of recesses in maritime rocks, which occupies comparable but more base-rich habitats than the *Leprarion chlorinae*, is discussed separately below (pp. 387–388), while the heavy-metal requiring *Lecanoretum epanorae*, which also has an affinity for dry crevices, is discussed on p. 383.

Mention should also be made here of a community of uncertain syntaxonomic position which is currently poorly known and thus not recognized formally here: the *Lecidea phaeops–L. taylori* nodum. This is essentially a community of damp overhangs or exposed rocks within sheltered woodland sites to which *Gyalidea hyalinescens* may also be faithful; that it requires damp rocks indicates that it should be placed in an alliance other than the *Leprarion chlorinae* and may perhaps be close to the *Aspicilietum lacustris* (p. 391).

Lecideetum lucidae (Schade) Wirth

Diss. Bot., Lehre **17,** 11 (1972).—*Biatoretum lucidae* Schade, *Beih. Feddes Repert.* **76,** 20 (1934).—*Biatoreto-Chaenothecetum* Schade, *Ber. dtsch. bot. Ges.* **41,** (58) (1924).

A species-poor and very widespread association of dry recesses in siliceous rocks, also encountered on stonework, gravestones and brick, and often consisting only of *Lecidea lucida* although *Lepraria incana* may be locally important. It is pollution-tolerant and particularly common in moderately polluted areas on shaded brickwork. This association shows some tendency to merge into the *Micareetum sylvicolae* (p. 366) and is also allied to both the *Coniocybetum furfuraceae* (p. 308) and the *Leprarietum incanae* (p. 312), both of which can also occur on rock.

Lecideetum orostheae (Hil.) Wirth

Diss. Bot., Lehre **17,** 122 (1972).—*Lecanoretum orostheae* Hil., *Čas. nár. Mus.* **1927,** 9 and 15 (1927) [as "Association à *Lecanora orosthea*"].

This association prefers somewhat better lit sites than other members of this alliance and as treated here tends also to be relatively species-rich. It is particularly well developed on the andesitic rocks of the Welsh border counties. *Haematomma ochroleucum* (including var. *porphyrium*), *Lecanora gangaleoides*, *L. subcarnea*, *Lecanactis dilleniana* and *Lecidea orosthea* are particularly characteristic of this community. Other species commonly encountered in it are *Catillaria chalybeia*, *Huilia albocaerulescens*, *Lecanora atra*, *L. grumosa*, *L. rupicola*, *Opegrapha saxatilis*, *O. saxicola*, *Parmelia glabratula* ssp. *fuliginosa* and *Rhizocarpon geographicum* s.l.

Leprarietum chlorinae Schade

Ber. dtsch. bot. Ges. **41,** (57) (1924).

This association is rather rare in Britain and largely confined to the central highlands of Scotland. It may be viewed as an upland counterpart of the *Lecideetum lucidae* and rarely includes species other than *Lepraria chlorina*.

Micareetum sylvicolae ass. nov. (Table XI)

This previously unrecognized association is closely allied to the *Lecideetum lucidae*, of which we were first inclined to treat it as a facies, but appears sufficiently distinct in both species composition and habitat, preferring

TABLE XI.

Micareetum sylvicolae ass. nov.

Species	Stands 1	2	3	4	5	6
Coniocybe furfuracea	–	–	–	–	1.2	–
Cystocoleus niger	1.2	–	–	–	–	1.3
Haematomma ochroleucum	–	1.2	–	+.0	–	–
Lecidea lucida	2.3	3.4	2.3	1.2	2.3	1.2
Lepraria incana	1.2	1.2	1.3	2.3	1.2	1.3
L. membranacea	–	–	–	+.0	1.2	–
Micarea clavulifera	–	1.2	–	–	–	–
M. polioides	–	–	–	–	2.3	–
M. semipallens	–	–	2.3	–	–	1.3
M. sylvicola	2.3	1.2	1.2	3.4	1.2	2.3
Opegrapha gyrocarpa	–	+.0	–	1.2	–	+.2
O. zonata	+.0	+.2	+.0	–	+.0	–
Porina chlorotica	+.0	–	–	–	–	+.2
P. lectissima	–	–	–	1.2	–	–
Racodium rupestre	–	1.2	–	–	–	–

1. Radnorshire, Rhayader, Glam lyn (22/940693): rock outcrop in sheltered old woodland, incl. 60°, aspect 235°, 1·0 × 1·0 m, cover 70%, 16 April 1976, P.W.J.
2. Island of Mull, Tobermory, Aros Woods, Sput Dùbh (17/509545): rock outcrop in dense old *Fagus* wood, incl. 90°, aspect 135°, 1·0 × 1·0 m, cover 60%, 17 October 1970, P.W.J.
3. Somerset, Porlock, Horner Combe, Cloutsham (31/898430): rock outcrop in woods, incl. 60°, aspect 270°, 0·5 × 0·5 m, cover 95%, 18 July 1969, P.W.J.
4. W. Ross, Upper Loch Torridon, Torridon House (18/868575): rock outcrop by woodland path, incl. 100°, aspect 235°, 1·0 × 1·0 m, cover 90%, 12 August 1966, P.W.J.; *type record*.
5. Merionethshire, Dolgellau, Aber Gwynant, near Kings Youth Hostel (23/683161): dry boulders in earth bank by stream, incl. 80°, aspect 270°, 1·0 × 1·0 m, cover 85%, 8 March 1961, P.W.J.
6. Merionethshire, Maentwrog, Llyn Mair (23/647416): sheltered boulder in old wood, incl. 90°, aspect 235°, 1·0 × 1·0 m, cover 80%, 16 April 1965, P.W.J.

particularly humid recesses (e.g. in woods), to merit separate treatment. Characteristic species of the *Micareetum sylvicolae* are *Lecidea lucida*, *Micarea clavulifera*, *M. polioides*, *M. semipallens*, *M. sylvicola* and *Lepraria incana*. It should be noted that the *Micarea sylvicola* species complex is poorly understood in Britain and in need of critical study.

Opegraphetum horistico-gyrocarpae Wirth

Herzogia **1,** 195 (1969).—*Opegrapha zonata* Soz. Degel., *Uppsal. Univ. Årsskr.* **1939** (1), 88 (1939).—*Opegraphetum zonatae* Wirth, *Herzogia* **1,** 195 (1969) [as "Degel. em."].

An association of continuously shaded rock underhangs and recesses in humid situations but preferring somewhat drier niches than the *Racodietum rupestris*. *Opegrapha gyrocarpa* and *O. zonata* are the most characteristic species of the association but may be joined by *O. lithyrga*, *O. saxigena*, *Porina chlorotica* and *P. lectissima*; the latter two species sometimes having high cover values. Two rare species apparently faithful to the *Opegraphetum horistico-gyrocarpae* in the British Isles are *Enterographa hutchinsiae* and *Rinodina oxydata*.

Racodietum rupestris Schade (Table XII)

Ber. dtsch. bot. Ges. **41,** (52) (1924) [as "*Rhacodietum*"], *Beih. Feddes Repert.* **76,** 16 (1934) [as "*Racodietum rupestris*"].—*Coenogonio-Racodietum rupestris* Schade, *Beih. bot. Cbl.* **49,** 436 (1932).—*Pertusario-Racodietum rupestris* Tobol., *Bull. Soc. Amis Sci. Lett. Poznan, sér.* D, **2,** 47 (1961).—*Cystocoleo-Racodietum rupestris* Kalb, *Diss. Bot., Lehre* **9,** 93 (1970).

This distinctive association consists primarily of felted mats of *Cystocoleus niger* and/or *Racodium rupestre* mixed with varying amounts of *Lepraria incana* and/or *L. membranacea*. The *Racodietum rupestris* is confined to vertical or almost vertical hard siliceous rock faces in shaded humid situations and recesses which are not subject to direct rain. A considerable number of species occasionally enter into this association but generally at low frequencies; these include members of the *Opegraphetum horistico-gyrocarpae*, free-living *Trentepohlia* species and shade-loving bryophytes (e.g. *Dicranella heteromalla*, *Diplophyllum albicans*, *Sphenobilus minutus*). Although essentially saxicolous this association can spread on to adjacent compacted earth; in somewhat drier sites *Coniocybe furfuracea* may also

1. Yorkshire, near Goathland, Beck Hole Gorge (45/825028): fine grained sandstone, incl. 90°, aspect 0°, 20 × 20 cm, cover 95%, 29 May 1969, D.L.H.
2. Yorkshire, near Goathland, Mallyan Spout Gorge (45/824009): fine grained sandstone, incl. 90°, aspect 225°, 20 × 30 cm, cover 95%, 29 May 1969, D.L.H.
3. Yorkshire, near Goathland, Mallyan Spout Gorge (45/824009): fine grained sandstone, incl. 90°, aspect 180°, 25 × 30 cm, cover 80%, 29 May 1969, D.L.H.

TABLE XII.

Racodietum rupestris Schade.

Species	Stands 1	2	3	4	5	6	7	8
Baeomyces rufus	–	3	–	–	–	–	–	–
Cladonia coniocraea	–	–	–	–	–	–	–	–
C. macilenta	–	–	–	–	–	3	+	–
C. squamosa	–	–	–	–	–	+	–	–
Cystocoleus niger	8	8	4	–	–	5	8	8
Diploschistes scruposus	–	–	7	–	–	–	–	–
Fuscidea cyathoides	–	–	–	–	–	4	–	–
Huilia albocaerulescens	–	–	–	–	–	4	–	4
Hypogymnia physodes	–	+	–	–	–	–	–	–
Lecidea tumida	–	–	–	–	–	–	4	–
Lepraria incana	–	–	–	5	6	–	2	–
L. membranacea	7	–	4	6	4	3	–	4
Ochrolechia androgyna	–	–	–	–	–	3	–	–
Parmelia saxatilis	–	–	–	–	–	5	–	–
Pertusaria corallina	–	–	–	–	–	3	–	–
Racodium rupestre	–	–	–	7	7	–	–	–
Sphaerophorus globosus	–	–	–	–	–	+	–	–
Trapelia coarctata	–	3	–	–	–	–	–	–
Usnea subfloridana	–	–	–	–	–	+	–	–
Conocephalum conicum	–	3	–	–	–	–	–	–
Diplophyllum albicans	–	–	–	3	3	3	–	–
Frullania dilatata	–	–	–	–	–	3	–	–
Hypnum cupressiforme	–	–	4	–	–	+	–	–
Rhacomitrium heterostichum	–	–	–	–	–	–	–	5
Scapania umbrosa	–	3	–	–	–	+	–	–

4. Yorkshire, near Goathland, Mallyan Spout Gorge (45/824009): sandstone, incl. 90°, aspect 350°, 15 × 20 cm, cover 80%, 29 May 1969, D.L.H.
5. Durham, near Cotherstone, High Shipley Wood (45/014204): fine grained sandstone, incl. 120°, aspect 205°, 20 × 20 cm, cover 80%, 30 May 1969, D.L.H.
6. Cumberland, Buttermere, Scales Wood (35/17 – 16 –): Borrowdale volcanic rocks, incl. 96°, aspect 15°, 10 × 10 cm, cover 80%, 4 June 1969, D.L.H.
7. Derbyshire, Holloway, Lea Hurst (43/320560): millstone grit, incl. 95°, aspect 90°, 20 × 20 cm, cover 95%, 5 August 1967, D.L.H.
8. Cumberland, Keswick, Castle Head Wood (35/269226): Borrowdale volcanic rocks, incl. 88°, aspect 250°, 20 × 15 cm, cover 80%, 3 June 1969, D.L.H.

be present in it producing stands transitional to the mainly corticolous *Coniocybetum furfuraceae* (p. 308).

Mention should also be made here of a particularly interesting community of vertical rock faces in old coniferous woodland which is encountered rarely in central Scotland (e.g. Glen Strathfarrar) and comprises *Arthonia arthonioides*, *Cystocoleus niger*, *Diploschistes scruposus* and *Haematomma ochroleucum*. The syntaxonomy of this community requires further study but it may prove to represent an undescribed association.

B. Exposed

All. 15. *Lecideion tumidae*

Lecideion tumidae Wirth, *Diss. Bot., Lehre* **17,** 131 (1972).

This species-diverse alliance was described by Wirth (1972) to accommodate communities on exposed siliceous rocks, boulder scree and heathland pebbles in inland sites. The communities are dominated by crustose lichens of which *Fuscidea cyathoides*, *Huilia crustulata*, *Lecidea lithophila*, *L. tumida*, and *Rhizocarpon geographicum* aggr. are particularly characteristic. *Stereocaulon dactylophyllum* and *S. evolutum* are also important species in some associations of the alliance of which three are here accepted as British. The alliance, poorly understood in this country, appears to have very close affinities with species-poor facies of both the *Parmelietum glomelliferae* and the *Umbilicarion cylindricae*; the relationship of the *Pertusarietum corallinae* in particular merits detailed investigation.

Huilietum crustulatae (Klem.) comb. nov.

Lecideetum crustulatae Klem., *Ber. bayer. bot. Ges.* **28,** 254 (1950) [as "*Lecanoretum coarctatae* Duvign. 1939 p.p."], basionym.

This is primarily an association of small, more or less firmly anchored pebbles or stones in open tracts of heathland, but it can also occur on larger outcrops and boulders. The characteristic species are *Baeomyces rufus*, *Huilia macrocarpa*, *H. crustulata*, *Lecanora polytropa*, *Lecidea erratica*, *L. plana* (chiefly in Scotland), *L. tumida*, *Rhizocarpon obscuratum* and sometimes *Trapelia coarctata* s.s. Adjacent terricolous communities are frequently rich in the more widespread species of *Cladonia* as well as *Lecidea granulosa* and *L. uliginosa*. Communities dominated by *Baeomyces rufus* and *Trapelia coarctata* s. lat. on shaded rocks and stones are treated here as a species-poor facies of this widespread moorland association which requires particularly humid sites.

Lecideetum lithophilae Wirth

Herzogia **1,** 202 (1969).

This association is essentially one of sunny hillside rock outcrops and screes as well as siliceous walls in well lit situations in western areas of Britain, but is also sometimes encountered in a fragmentary state on acid gravestones in, for example, the least polluted areas of southern England. The *Lecideetum lithophilae* is commonly rich in species, the most frequent of which are *Buellia aethalea*, *Huilia albocaerulescens*, *H. macrocarpa*, *Lecanora intricata* (including var. *soralifera*), *Lecidea fuscoatra*, *L. lithophila*, *L. pantherina*, *L. tumida* and *Rhizocarpon geographicum* aggr.

Lecidea leucophaea, *L. pelobotryon*, *Placopsis gelida*, *Pilophorus strumaticus*, *Trapelia coarctata* s.l., *T. moorei* and *Stereocaulon pileatum* are often associates in a wetter facies of this association, while in nutrient-rich sites *Acarospora fuscata* and *Candelariella vitellina* are often also present. The presence of *Stereocaulon* species characteristic of sites rich in heavy metals, including *S. delisei*, *S. dactylophyllum* and *S. pileatum*, suggests that this association has affinities with the *Acarosporion sinopicae* (p. 382).

Pertusarietum corallinae Frey

Mitt. naturf. Ges. Bern **6,** 163 (1922) [as "*Pertusaria corallina*-Ass."].

This is a widespread species-rich community of well lit siliceous rock outcrops, boulders and walls in sites which are not nutrient-enriched. Important component species of this association in the British Isles include *Cladonia coccifera*, *C. squamosa*, *Diploschistes scruposus*, *Fuscidea cyathoides*, *Lecanora badia*, *L. polytropa*, *Lecidea leucophaea*, *L. tumida*, *Parmelia glabratula* ssp. *fuliginosa*, *P. saxatilis*, *Pertusaria corallina*, *P. dealbata*, *P. lactea*, *P. pseudocorallina*, *Rhizocarpon geographicum*, *R. lecanorinum*, *Schaereria cinereorufa* and *Umbilicaria polyphylla*.

The *Pertusarietum corallinae* tends to prefer moister sites than the *Umbilicarietum cylindricae* and nutrient-poorer sites than the *Lecanoretum sordidae*, preferring, for example, vertical rather than horizontal rock surfaces and walls.

All. 16. *Pseudevernion furfuraceae*

Pseudevernion furfuraceae (Barkm.) P. James *et al.*; see p. 334 for nomenclature.

Pseudevernietum furfuraceae (Hil.) Kalb

See p. 335 for nomenclature and composition.

This primarily corticolous association is widespread as a species-poor variant (see p. 335) on hard acid siliceous rocks and walls subject to moderate air pollution. The *Pseudevernietum furfuraceae* also occurs in the British Isles on walls and rock debris; in this case the association appears to represent a seral stage giving way to associations of the *Lecideion tumidae* or the *Umbilicarietum cylindricae*.

All. 17. *Rhizocarpion alpicolae*

Rhizocarpion alpicolae Frey, *Ber. Geobot. Inst. Rübel* **1932,** 46 (1933).

The *Rhizocarpion alpicolae* is an arctic-alpine alliance of nutrient-poor siliceous rocks. Due to the relatively mild oceanic climatic conditions, the alliance seems to be poorly represented in the British Isles and mainly confined to the summits of mountains in Scotland and northern England. The two associations recognized here are characterized by a variety of crustose species of which *Fuscidea kochiana* and *Rhizocarpon alpicola* are the respective diagnostic components. Crustose lichen elements of the *Umbilicarion cylindricae* are almost invariably present and macrolichens of the same alliance may also be represented.

This alliance is currently poorly understood in Britain due mainly to the lack of information on the lichen flora of the summits of many Scottish mountains. The following two associations are tentatively delimited here as a guide to further study of this interesting alliance.

Fuscideetum kochianae (Wirth) comb. nov.

Lecideetum kochianae Wirth, *Diss. Bot., Lehre* **17,** 190 (1972) [as "Ullrich et Wirth 1969 em. et nom. nov."]; basionym.—*Lecideetum kochiano-aggregatilis* Ullrich & Wirth, *Herzogia* **1,** 199 (1969) [non Tobol. 1961].

The name *Fuscideetum kochianae* is applied to an association dominated by *Fuscidea kochiana* and including *Lecanora atra*, *L. intricata* (including var. *soralifera*), *L. polytropa*, *Lecidea leucophaea*, *L. lithophila*, *L. pantherina*, *L. tenebrosa*, *Parmelia incurva*, *Pertusaria corallina*, *P. pseudocorallina* and *Rhizocarpon geographicum*. Species of *Umbilicaria*, such as *U. polyphylla*, *U. polyrrhiza* and *U. torrefacta*, together with *Lasallia pustulata*, are sometimes also represented but are confined to the apices of slightly nutrient-enriched erratics.

This association is characteristic of very hard siliceous rocks, especially quartzite, granite and gritstones. *Fuscidea kochiana* is usually abundant, the associated species often forming scattered mosaics between the thalli of this dominant species. The *Fuscideetum kochianae* occurs in moderately exposed to relatively sheltered and shaded situations and is particularly well developed on rocks and boulders on the upper slopes of Penyghent and Ingleborough, Yorkshire, and parts of Cairngorm, Scotland.

The *Fuscideetum kochianae* has particularly close affinities with the *Parmelietum omphalodis*.

Rhizocarpetum alpicolae Frey

Verh. naturf. Ges. Basel **35,** 310 (1923).—*Rhizocarpetum geographicae* Frey, *Veröff. Geobot. Inst. Rübel* **4,** 230 (1927) [as "*Rhizocarpon geographicum*-Ass."].

The arctic-alpine *Rhizocarpetum alpicolae* is rare in the British Isles but is locally widespread on rock outcrops and large boulders on the summits of mountains of the Cairngorm range. The association, which is characteristic of rocks rich in silica but very poor in nutrients and calcium, appears to represent a "climax" stage following the *Umbilicarietum cylindricae* but, unlike that association, is dominated by crustose species rather than macrolichens.

The *Rhizocarpetum alpicolae* is best developed on the south- to east-facing vertical sides of rock outcrops which are partially buried in snow for 2 or 3 months. From a distance these sites appear noticeably yellow to pale green in colour due to an abundance of *Lecanora intricata*, *L. polytropa*, *Rhizocarpon alpicola* and *R. geographicum* aggr. The mosses *Andraea alpina*, *A. nivalis* (very rare), *Grimmia doniana*, *Rhacomitrium heterostichum* var. *gracilescens*, and *R. lanuginosum* may enter into the association. Additional lichens characteristic of the association are *Lecidea atrata*, *L. confluens* aggr., *L. lapicida*, *L. pantherina*, *L. tumida* and *Pseudephebe pubescens*. The rare *Lecanora leptacina* (on mosses) and *Ophniospora atrata* may also be present. Elements of the *Umbilicarietum cylindricae* often also occur, particularly *Cornicularia normoerica*, *Haematomma ventosum*, *Lecanora badia*, *Lecidea tenebrosa*, *Parmelia alpicola*, *P. incurva*, *P. omphalodes*, *Umbilicaria cylindrica*, *U. hyperborea*, *U. polyphylla* and *U. torrefacta*.

In wetter sites characteristic of late snow lie, *Rhizocarpon badioatrum* enters as an important species of the association. On Cairngorm mountain itself, *Lecidea pycnocarpa* is abundant on small quartzite pebbles in shallow hollows in wind-eroded plateau sites; *Cetraria delisei*, *C. nivalis* and, more rarely, *Cornicularia divergens* may utilize these pebbles for anchorage.

All. 18. *Umbilicarion cylindricae*

Umbilicarion cylindricae Frey, *Ber. Geobot. Inst. Rübel* **1932,** 40 (1933).—*Umbilicarion hirsutae* Follm., *Hess. flor. Briefe* **2,** 25 (1973).

This alliance is characterized by many species which are strictly montane in the British Isles, including *Cetraria commixta*, *C. hepatizon*, *Cornicularia normoerica*, *Hypogymnia intestiniformis*, *Parmelia alpicola*, *P. stygia*, *Platismatia norvegica*, *Pseudephebe pubescens* and species of *Umbilicaria*, notably *U. crustulosa* (Langdale Pikes, Lake District only), *U. cylindrica*, *U. hyperborea*, *U. polyphylla*, *U. polyrrhiza*, *U. proboscidea* and *U. torrefacta*; *U. deusta* occurs in deep hollows and is characteristic of a moist facies of this alliance.

Many crustose species enter the associations of this alliance of which *Fuscidea cyathoides*, *F. tenebrica*, *Haematomma ventosum*, *Lecanora intricata*, *L. polytropa*, *Lecidea pantherina* aggr., *L. sulphurea*, *Rhizocarpon geographicum* aggr., *R. lecanorinum*, *R. obscuratum* and *R. polycarpon* are particularly characteristic. The alliance tends to occur on nutrient-poor rather than nutrient-enriched siliceous rocks.

The two associations recognized here are distinguished by both their habitats and species composition.

Parmelietum omphalodis DR.

Akad. Abhandl. Uppsala **1921,** 164 (1921) [not seen]; see Delzenne-van Haluwyn (1976) for later usages.

The *Parmelietum omphalodis* has a strong affinity with the saxicolous facies of the *Pseudevernietum furfuraceae* but is richer in species and differs in the abundance of *Parmelia omphalodes* (see Fig. 10) and species of *Cladonia*, especially *C. cervicornis*, *C. chlorophaea* aggr., *C. coccifera*, *C. crispata* var. *cetrariiformis*, *C. furcata*, *C. gracilis*, *C. squamosa*, *C. subcervicornis* and, occasionally, *C. uncialis* ssp. *dicraea*. Other species characteristic of the association, which is widely distributed in the British Isles on nutrient-poor siliceous rock outcrops, boulders and scree, include *Bryoria bicolor*, *B. fuscescens*, *Cetraria chlorophylla*, *Haematomma ventosum*, *Hypogymnia physodes*, *H. tubulosa*, *Lecanora polytropa*, *Lecidea tenebrosa*, *Lepraria neglecta*, *Ochrolechia androgyna*, *O. tartarea*, *Parmelia glabratula* ssp. *fuliginosa*, *P. saxatilis*, *Pertusaria corallina*, *P. lactea*, *P. monogona* (rare), *P. pseudocorallina*, *Platismatia glauca*, *Rhizocarpon hochstetteri*, *Sphaerophorus globosus* and *Usnea flammea*.

FIG. 10. *Parmelietum omphalodis* on siliceous rock; the *Parmelia*-rich facies. Predominant species: *Parmelia omphalodes*, *P. saxatilis* and *Trapelia coarctata* s.l. (Anglesey: 1972, R. O. Millar).

The association is often rich in bryophytes of which *Andraea rothii*, *A. rupestris* (syn. *A. petrophila*), *Cynodontium polycarpum* (rare), *Hypnum cupressiforme*, *Isothecium myosuroides*, *Orthotrichum anomalum*, *Rhacomitrium fasciculare* and *R. heterostichum* may be considered as characteristic. The *Parmelietum omphalodis* occurs at lower altitudes and latitudes than the *Umbilicarietum cylindricae* often occurring even in or near coastal areas in western parts of the British Isles. At higher altitudes it tends to grade into the *Umbilicarietum cylindricae* and species such as *Cornicularia normoerica*, *Rhizocarpon lecanorinum*, *R. polycarpon*, *Sphaerophorus fragilis*, *Umbilicaria polyphylla* and *U. polyrrhiza* become more abundant. As a rule the *Parmelietum omphalodis* prefers more sheltered sites than the *Umbilicarietum cylindricae*.

Klement (1955) treated Du Rietz's name *Parmelion omphalodis* as a synonym of the *Umbilicarion cylindricae* reserving a homonym of the latter name for a different, more upland, community including, for example, *Hypogymnia intestiniformis*. The usage adopted here follows that of Wirth (1972).

Umbilicarietum cylindricae (Frey) Frey

Ber. Geobot. Inst. Rübel **1932,** 40 (1933).—*Gyrophoretum cylindricae* Frey, *Mitt. naturf. Ges. Bern* **6,** 168 (1922) [as "*Gyrophora cylindrica*-Ass."].—*Umbilicarietum deustae* Frey, *Ber. Geobot. Inst. Rübel* **1932,** 49 (1933).

The *Umbilicarietum cylindricae* is a more upland and more light-demanding counterpart of the *Parmelietum omphalodis* characterized by species typical of the alliance (p. 374). Both associations may occur in very close proximity to one another and the relative abundance of the characteristic species may vary considerably in different sites depending on both geographical location and altitude (particularly as its important components are limited climatically in the British Isles). This association is optimally developed on the uppermost slopes of mountains in the Scottish Highlands where it represents a seral stage leading to the *Rhizocarpetum alpicolae*, an association with a very limited distribution in the British Isles.

The synsystematics of the *Umbilicarietum cylindricae* are poorly understood in Britain but our observations suggest that they are very complex. Preliminary studies indicate that there are several distinctive noda (indicated below), some of which may be referable to the *Parmelietum omphalodis*, and others of which may well prove to merit recognition as separate associations when thoroughly investigated.

1. Dominated by *Fuscidea tenebrica* with *F. cyathoides* and *Rhizocarpon geographicum* as associated species, and characteristic of sunny rocks in exposed mountainous situations which are particularly abundant in the Lake District and western Scotland.

2. A shady and rather dry facies dominated by *Fuscidea taeniarum* known in Britain only from Scotland where it is rare and always found on acid, nutrient-poor rock.

3. Dominated by *Fuscidea cyathoides* but including *Lecidea leucophaea*, *L. lithophila*, *L. pantherina*, *Pertusaria corallina* and *Rhizocarpon geographicum* aggr. (often *R. riparium*) as characteristic associates. This nodum tends to occur at lower altitudes and latitudes than the preceding two noda and is particularly well developed in the Southern Pennines and Peak District on millstone grit rocks. This nodum is close to the *Parmelietum omphalodis* but is placed here tentatively as it sometimes includes *Umbilicaria polyphylla*, *U. polyrrhiza* or *U. torrefacta*.

4. A facies on mineral-rich rocks often in rather moist situations as in shallow valleys or near mountain lakes dominated by *Lecidea lithophila* but including *L. lapicida* and *L. leucophaea*; *Alectoria nigricans* and *Cornicularia aculeata* are frequent associates on mosses in such communities. This facies has a clear affinity with the *Acarosporetum sinopicae* (p. 383) but is poor in species restricted to mineral-rich sites while including many mineral-tolerant ones.

5. A sun-loving markedly western community particularly well developed in the Rhinog mountains in Wales dominated by *Lecanora mauroides* and *Rhizocarpon geographicum* but including *Lecidea pantherina* and *L. tenebrosa* at high frequencies.

6. The *Umbilicaria deusta*-dominated nodum treated as a distinct association by many authors (the *Umbilicarietum deustae* Frey, see above) which is well developed by the sides of upland mountain streams.

7. The very high altitude *Umbilicaria hyperborea* nodum.

8. The *Umbilicaria crustulosa*-dominated nodum of almost vertical south-facing, hard volcanic rocks found on the Langdale Pikes in the Lake District (see Brightman, 1962, for lists of associates).

The "typical" *Umbilicarietum cylindricae* is taken here to include high frequencies of *Umbilicaria cylindrica*, *U. polyphylla*, *U. polyrrhiza*, *U. proboscidea* and/or *U. torrefacta*. This nodum has a particular preference for well lit rather coarse-grained rocks in mountainous areas (particularly granite) with *Cornicularia normoerica*, *Pseudephebe pubescens* and the other macrolichens mentioned as characteristic of the alliance on p. 374 occurring in it. Associated bryophytes include *Andraea rupestris*, *Grimmia doniana*, *G. trichophylla*, *Gymnomitrion* spp., *Hedwigia ciliata*, *Ptychomitriun polyphyllum*, *Rhacomitrium fasciculare* and *R. heterostichum* var. *heterostichum*.

C. Nutrient-enriched

All. 19. *Parmelion conspersae*

Parmelion conspersae Hadač, *in* Klika & Hadač, *Příroda, Brno* **36,** 254 (1944), emend. Wirth, *Diss. Bot., Lehre* **17,** 131 (1972).—*Parmelion saxatilis* Klem., *Ber. bayer. bot. Ges.* **28,** 257 (1950).—*Acarosporion fuscatae* Klem., *Ber. bayer. bot. Ges.* **28,** 257 (1950).

The *Parmelion conspersae* comprises associations of well lit and slightly to markedly nutrient-enriched siliceous rocks. It can be considered as the acid rock counterpart of the *Xanthorion parietinae*, differing from that alliance in too many species to be treated as part of the same alliance. Some elements of the *Parmelion conspersae* are well represented in the terrestrial zone in coastal areas (Fletcher, 1973b) and there is thus some affinity with the *Ramalinetum scopularis* (see p. 386).

Candelarielletum corallizae Massé

Vegetatio **12,** 173 (1964).

Essentially an association of nutrient-enriched siliceous rocks such as birds' perching stones, the *Candelarielletum corallizae* is frequent in suitable sites in both coastal and upland parts of the British Isles. The characteristic species of this community include *Acarospora fuscata*, *Anaptychia fusca*, *Aspicilia caesiocinerea*, *Buellia canescens*, *B. punctata*, *Candelariella coralliza*, *C. vitellina*, *Lecanora muralis*, *Physcia caesia*, *P. dubia* (especially on gravestones in eastern and central England), *P. tribacia*, *P. wainioi*, *Ramalina polymorpha*, *R. subfarinacea*, *Rinodina subexigua*, *Xanthoria candelaria* and *X. parietina*. On the sea-shore, additional species entering the association include *Aspicilia leprosescens*, *Caloplaca* sp. (undescribed), *C. verruculifera*, *Lecanora poliophaea* and *Parmelia britannica* as well as the three rare species *Caloplaca scopularis*, *Candelariella arctica* and *Lecanora straminea*. *Lecanora fugiens* and the rarer and related *L. andrewii* may also belong here; *Physcia subobscura* and *Verrucaria fusconigrescens* may be locally abundant also.

In our view the relationship between the *Candelarielletum corallizae* and the *Physcietum caesiae* (see p. 360) is in need of a critical re-investigation. Further study may also indicate that the sea-shore facies of this association is better subsumed under the *Ramalinetum scopularis*.

Lecanoretum sordidae Hil. (Table XIII)

Čas. národ. Mus. **1923,** 4 (1924) [as "asociace *Lecanora sordida*"].—*Lecanoretum rupicolae* Wirth, *Diss. Bot., Lehre* **17,** 166 (1972) [as "Hilitzer 1925"].

Although the *Lecanoretum sordidae* is accepted here in accordance with Wirth (1972), we are not entirely convinced that it is sufficiently distinct from the *Parmelietum glomelliferae* to merit a permanent status. The major difference between these two communities is that the *Lecanoretum sordidae* is richer, in terms of both species number and cover, in crustose lichens. Species which are characteristic of the association include *Acarospora fuscata*, *Buellia stellulata*, *Candelariella vitellina*, *Diploschistes scruposus*, *Huilia albocaerulescens*, *Lasallia pustulata*, *Lecanora atra*, *L. badia*, *L. grumosa* (chiefly confined to Scotland), *L. polytropa*, *L. rupicola*, *Lecidea insularis* (parasitic on *Lecanora rupicola*), *L. sulphurea*, *L. tenebrosa*, *Ochrolechia parella*, *Parmelia conspersa*, *P. glabratula* ssp. *fuliginosa*,

TABLE XIII.

Lecanoretum sordidae Hil.

Species	Stands 1	2	3	4	5
Acarospora fuscata	–	1.2	–	–	1.2
Aspicilia caesiocinerea	+.1	1.2	+.2	1.2	+.2
A. sp.	+.2	–	+.0	–	–
Bacidia umbrina	–	–	1.2	–	–
Buellia stellulata	1.2	1.2	2.3	+.0	1.2
Candelariella vitellina	1.2	1.2	–	2.3	1.2
Catillaria chalybeia	1.2	–	–	–	1.2
Diploschistes scruposus	1.2	–	–	1.2	–
Lasallia pustulata	–	–	1.2	+.2	–
Lecanora atra	1.2	1.2	1.2	+.1	1.4
L. badia	1.2	1.3	2.3	–	2.2
L. gangaleoides	1.3	+.0	1.2	–	–
L. grumosa	–	–	–	–	2.3
L. intricata	+.2	–	–	–	+.0
L. polytropa	1.4	1.2	+.2	1.2	1.4
L. rupicola	3.3	2.3	2.2	1.3	2.3
Lecidea orosthea	–	+.0	–	1.2	–
L. sulphurea	+.2	1.2	–	2.3	1.3
L. tumida	1.4	1.2	1.2	+.2	1.2
Ochrolechia parella	–	–	1.2	–	1.2

TABLE XIII—*continued*

Species	Stands 1	2	3	4	5
Parmelia glabratula ssp. *fuliginosa*	+.2	1.2	1.3	–	+.0
P. conspersa	–	–	–	2.3	3.2
P. verruculifera	–	1.2	–	1.3	+.0
Pertusaria pseudocorallina	1.2	–	3.2	1.2	1.2
Rhizocarpon geographicum	+.2	–	1.2	+.0	–
R. obscuratum	–	–	–	+.2	+.0
R. viridiatrum	1.2	+.0	1.2	2.3	–

1. Radnor, New Radnor, Stanner Rocks (32/262584): rock outcrop (andesite), incl. 45°, aspect SW, 1·0 × 1·0 m, cover 95%, 11 April 1976, P.W.J. and R. Woods.
2. Shropshire, Church Stoke, Roundton (32/291948): rock outcrop (andesite), incl. 30°, aspect S, 1·0 × 1·0 m, cover 98%, 13 April 1976, P.W.J.
3. Radnor, Llandrindod Wells, above Shakey Bridge, Cefnllys (32/087614): rock outcrop, slight shade, incl. 20°, aspect W, 1·0 × 1·0 m, cover 90%, 11 April 1976, P.W.J. and R. Woods.
4. Montgomeryshire, Welshpool, Criggion, Breidden Hill (33/29 – 14 –): large boulder on sunny hillside, incl. *c.* 20°, aspect NW, 1·0 × 1·0 m, cover 100%, 12 April 1963, P.W.J.
5. Kirkcudbrightshire, Dalbeattie, Moyl Peninsula (25/830526): large boulder in sunny situation: incl. 10°, aspect S, 1·5 × 1·5 m, cover 80%, 25 April 1976, P.W.J. and P. Topham.

P. verruculifera, *Pertusaria flavicans*, *P. pseudocorallina*, *Rhizocarpon geographicum* aggr., *R. viridiatrum* and *Rinodina atrocinerea*. In inland sites in the British Isles the *Lecanoretum sordidae* is well developed on andesitic outcrops in the West Midlands.

In addition to the strong affinity of this association with the *Parmelietum glomelliferae*, it also appears to be allied to a crustose lichen-dominated facies of the *Ramalinetum scopularis* on coastal rocks where, in addition to the species listed above, the following exclusively maritime species occur in it: *Diploschistes caesioplumbeus*, *Lecidella subincongrua*, *Pertusaria ceuthocarpoides* and *Rhizocarpon constrictum*.

Parmelietum glomelliferae Hil. (Table XIV)

Čas. národ. Mus. **1923,** 7 (1924) [as "*Parmelia glomellifera* . . . asociaci"].—*Umbilicarietum pustulatae* Hil., *Preslia* **3,** 16 (1925) [as "Asociace *Umbilicaria pustulata*"].—*Lasallietum pustulatae* (Hil.) Wirth, *Diss. Bot., Lehre* **17,** 152 (1972).—*Parmelietum isidiotylae* Frey, *in* Frey & Ochsner, *Arvernia* **2,** 68 (1926).—*Parmelietum conspersae* Hil., *Preslia* **3,** 16 (1925) [as "asociace *Parmelia conspersa*"].

The *Parmelietum glomelliferae* is treated here in a broad sense to include communities of nutrient-enriched rocks dominated by species of *Parmelia* and *Umbilicaria* s.l. The *Parmelietum conspersae* and *Umbilicarietum pustulatae* have frequently been maintained as distinct entities by continental authors but as they commonly appear to intergrade in the British

TABLE XIV.

Parmelietum glomelliferae Hil.

Species	Stands 1	2	3	4	5
Acarospora fuscata	2	3	2	1	–
Candelariella vitellina	2	2	4	–	2
Cladonia coccifera	–	1	–	2	–
Fuscidea cyathoides	2	3	–	4	2
Lasallia pustulata	–	8	–	–	–
Lecanora polytropa	2	2	4	+	2
L. rupicola	–	–	2	–	1
Lecidea sulphurea	–	2	2	–	1
Parmelia conspersa	6	4	5	4	7
P. glabratula ssp. *fuliginosa*	–	1	–	–	3
P. loxodes	6	–	3	3	5
P. mougeotii	–	–	6	–	3
P. omphalodes	4	1	–	2	4
P. saxatilis	2	–	–	3	3
Rhizocarpon geographicum aggr.	2	2	1	2	2
Trapelia coarctata	2	–	2	3	3
Umbilicaria polyrrhiza	–	–	–	5	–
Xanthoria candelaria	–	3	–	–	–

1. South Devonshire, Dartmoor, Harford (20/642601): granite blocks in pasture, ± level, 10 × 10 cm, cover 95%, 3 April 1969, D.L.H.
2. South Devonshire, Dartmoor, near Wistman's Wood (20/613768): granite boulder used as bird perch, uneven, 20 × 20 cm, cover 90%, 15 September 1969, D.L.H.
3. South Devonshire, Dartmoor, Rippon Tor (20/748757): granite boulder in clatter, incl. 160°, aspect 45°, 20 × 20 cm, cover 80%, 30 August 1976, D.L.H.
4. South Devonshire, Dartmoor, Sharp Tor (20/686731): granite boulder in heathland, ± level, 20 × 20 cm, cover 75%, 29 July 1974, D.L.H.
5. South Devonshire, Dartmoor, Crockern Tor (20/616757): granite boulder in clatter near summit, incl. 140°, aspect 165°, 20 × 20 cm, cover 85%, 15 September 1969, D.L.H.

Isles they are treated as a single association here and subsumed under the earliest available name we have been able to locate—the *Parmelietum glomelliferae*.

The characteristic species of this community in the British Isles are *Acarospora fuscata*, *Candelariella vitellina*, *Cladonia coccifera*, *C. pityrea*, *C. squamosa*, *Lasallia pustulata*, *Lecanora polytropa*, *Parmelia britannica*, *P. conspersa*, *P. disjuncta*, *P. loxodes*, *P. mougeotii*, *P. saxatilis*, *P. sulcata*, *P. verruculifera*, *Trapelia ornata*, *Umbilicaria deusta* and *U. polyrrhiza*. A very large number of other species may occasionally enter the association, particularly elements of the *Parmelietum omphalodis* and *Pseudevernietum furfuraceae*; affinities with the *Ramalinetum scopularis* (p. 386) are also marked. The relationship of the present association to the *Lecanoretum sordidae* is discussed under the latter community (p. 380).

All. 20. *Xanthorion parietinae*

Xanthorion parietinae Ochsn. See p. 342 for nomenclature.

Physcietum caesiae Mot.

See p. 360 for composition and nomenclature.

This association, characteristic of extremely nutrient-enriched sites, can occur on suitably modified siliceous rocks, especially near colonial nesting sites of birds, as well as on limestones, man-made substrates and, rarely, trees.

D. Mineral-rich

All. 21. *Acarosporion sinopicae*

Acarosporion sinopicae Wirth, *Diss. Bot., Lehre* **17,** 131 (1972); type: *Acarosporetum sinopicae* Hil.

This distinctive alliance was introduced by Wirth (1972) for associations restricted to rocks rich in heavy metals. The two associations recognized here are rather specialized and frequently contain several species restricted to metal-rich rocks. In Britain they occur (1) on spoil tips from old mine workings for copper, lead, silver and associated metals, (2) on walls contaminated by heavy metals, principally lead derived from car exhausts or particulate fall-out from smelters, (3) on naturally occurring metal-rich

rock outcrops, and (4) occasionally in the vicinity of, or even on, rusted iron rails, worked lead (as in stained-glass windows), or in areas affected by water run-off from corrugated iron roofing. The thalli of several crustose species characteristic of this alliance are often wholly or partially rust red in colour ("oxydated"; see Chapter 2).

A review of heavy metal tolerance in lichens is provided by James (1973).

Acarosporetum sinopicae Hil.

Čas. národ. Mus. **1923,** 8 (1924) [as "*Acarospora sinopica*-asociace"].

Characteristic species of this association in Britain include *Acarospora sinopica*, *A. smaragdula* (including var. *lesdainii*), *Bacidia umbrina*, *Candelariella vitellina*, *Diploschistes scruposus*, *Huilia macrocarpa* (as "f. *oxydata*"), *Lecanora intricata* var. *soralifera*, *L. polytropa*, *L. subaurea*, *Lecidea atrata*, *L. lapicida* (as "f. *oxydata*"), *L. pantherina*, *L. silacea* (confined to upland sites), *Rhizocarpon obscuratum*, *R. oederi*, *Stereocaulon nanodes*, *S. pileatum* and *Toninia leucophaeopsis* (upland sites only). Other species of *Stereocaulon* (*S. dactylophyllum*, *S. delisei*, *S. evolutum* and *S. vesuvianum*) may also be present. In areas subject to moderate to severe sulphur dioxide pollution *Lecanora conizaeoides* enters this community, sometimes becoming an important component of it; in such sites the association becomes species-poor.

Lecanora subaurea is a very significant member of this association in the southern Pennines (Earland-Bennett, 1975).

Lecanoretum epanorae Wirth

Diss. Bot., Lehre **17,** 173 (1972).

This association is closely allied to the *Acarosporetum sinopicae* but tends to prefer more sheltered, dry situations, being found particularly in dry crevices of mineral-rich acid rocks or on the more sheltered sides of old walls. The community, which is rather species-poor, tends to be dominated by *Lecanora epanora*. Other commonly associated species are *Lepraria incana* aggr., *L. membranacea* aggr. and *Rhizocarpon obscuratum*. Details of the ecology and British distribution of *Lecanora epanora* are given by Earland-Bennett (1975). The occasional presence of *Lecanora subaurea* in the *Lecanoretum epanorae* is indicative of the close relationship of this association with the *Acarosporetum sinopicae*.

Hilitzer (1924) regarded *Lecanora epanora* as an important component of the *Acarosporetum sinopicae* but his material was most probably *L. subaurea*.

E. Marine and Maritime Communities

The marine and maritime lichen vegetation of rocky shores of the British Isles has recently been the subject of considerable attention (Fletcher, 1973a, 1975a,b, 1976). On the basis of Fletcher's careful analyses on the ecology and physiology of sea-shore lichens it seems desirable to recognize four associations for maritime lichen communities in Britain. Three of these, broadly corresponding to the zones defined by Fletcher (1973a,b), are the littoral (black) zone (*Verrucarietum maurae*), the mesic- and submesic-supralittoral (orange) zone (*Caloplacetum marinae*), and the xeric-supralittoral (grey) zone (*Ramalinetum scopularis*); the drier more sheltered aspects of the latter zone support the fourth and very distinctive association described here as the *Sclerophytetum circumscriptae*.

Approximately 65 lichen species are more or less exclusively maritime in Britain, the greatest concentration of these ecologically restricted species occurring in the littoral zone and decreasing further up the shore to very few in the terrestrial zone. The terrestrial region above the xeric-supralittoral zone supports an assemblage of diverse elements of basically non-maritime affinities described elsewhere in this contribution; the species occurring there are more or less maritime influence-tolerant or show non-maritime preferences although some species of the *Ramalinetum scopularis* can occur far inland in Britain (p. 386). Some of the nutritional aspects underlying lichen zonation on rocky shores are discussed by Fletcher (1976).

Communities developed on coastal limestones, dunes, and shingle are treated on pp. 349, 400–402 and 394–395, respectively.

The associations recognized in this section are not referred to alliances as their affinities with other communities seem remote; all may merit placing in distinct alliances.

Caloplacetum marinae DR.

Svensk. växtsociol. Sällsk. Handl. **2,** 50 (1925) [as "*Caloplaca marina*-Ass."].

The *Caloplacetum marinae* is the characteristic association of the submesic- and mesic-supralittoral zones on rocky shores around the British Isles. As with the *Ramalinetum scopularis* which occurs higher up the shore, the component species, though rarely, if ever, submerged in sea-water, do nevertheless appear to have a strong requirement for sea-water spray and are related to a moisture source of neutral or alkaline pH. The association is dominated by *Caloplaca* species (Fig. 11), particularly *C. marina*, *C. microthallina*, *C. thallincola* and, in more nutrient-enriched sites,

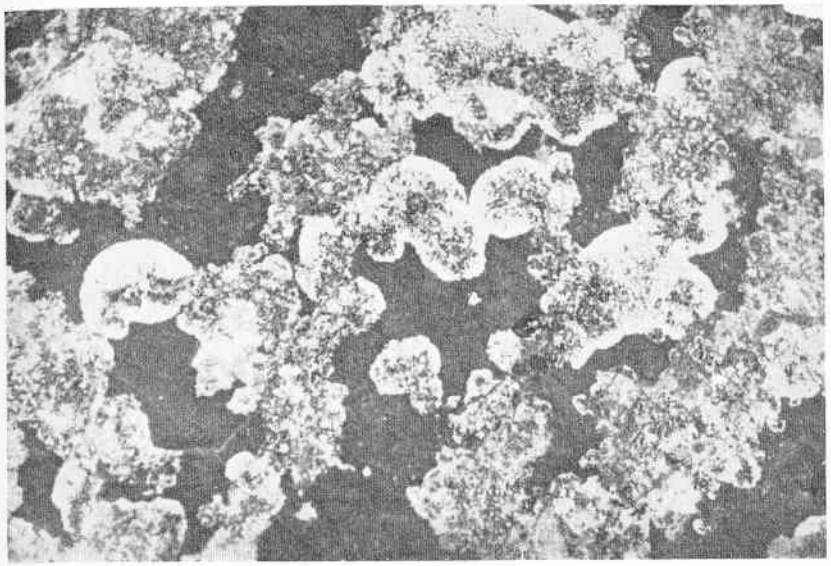

FIG. 11. *Caloplacetum marinae* on maritime siliceous rocks. Predominant species: *Caloplaca marina*, *C. thallincola* and *Verrucaria maura* (Mid-Ebudes: Island of Mull, Ross of Mull, Carsaig Bay. 1972, P. W. James).

C. verruculifera. *Lecanora actophila* and *L. helicopis* are faithful to the association in the British Isles, the former tending to prefer more sunny, well lit situations. *Verrucaria maura* is often present (e.g. Fig. 11), especially on more sheltered shores where it is often overgrown by *Caloplaca thallincola*. In northern and some western areas *Arthonia phaeobaea* and *Lecania aipospila* also form part of this association and may become locally abundant. *Catillaria chalybeia* and *Lecania erysibe* are often common although these species, unlike the others mentioned above, are by no means restricted to coastal rocks. *Lichina confinis*, occurring in the lowest part of the mesic-supralittoral zone, forms a link with the *Verrucarietum maurae*; similarly *Xanthoria parietina*, characteristic of the submesic-supralittoral, interconnects with the *Ramalinetum scopularis* association.

A more nutrient-enriched facies of this association, commonly including *Aspicilia leprosescens*, *Caloplaca verruculifera*, *Lecanora poliophaea*, *Rinodina subexigua* and the alga *Prasiola quadrata* occurs on birds' perching rocks along the shore or near nesting sites. The rare *Caloplaca scopularis*, *Candelariella arctica* and *Lecanora straminea* may also occur in this community. The relationship between this facies and the *Candelarielletum corallizae* is noted on p. 378.

Ramalinetum scopularis Klem.

Beih. Feddes Repert. **135,** 68 (1955) [as "(DR. 1925) Klem."].—*Ramalina scopularis-Anaptychia fusca* Ass. DR., *Svensk bot. Tidskr.* **19,** 333 (1925), *nom. inval.*—*Ramalina scopularis-Lecanora atra-Rhizocarpon constrictum*-Ass. DR., *Svensk bot. Tidskr.* **19,** 333 (1925), *nom. inval.*—*Ramalinetum siliquosae* Follm., *Phillipia* **2,** 8 (1973) [as "(DR.)"].—*Lecanoretum atrae* Massé, *Revue bryol. lichén.* **34,** 889 (1966).

The characteristic association of the xeric-supralittoral (grey) zone of rocky shores in the British Isles is the *Ramalinetum scopularis* (Fig. 12). A species-poor facies of this association may also occasionally be encountered on walls of churches, ancient monuments and stone walls or rock outcrops in inland sites subject to maritime influence, as for instance throughout most of Devonshire and on Avebury Circle and Stonehenge in Wiltshire. This community is exceptionally rich in species (see Fletcher, 1975a) and occupies that part of the sea-shore where moisture derived from the sea and soil from the terrestrial environment are minimal. Amongst the characteristic species of this community are *Acarospora atrata**, *Anaptychia fusca**, *A. mamillata**, *Buellia canescens*, *B. stellulata*, *Caloplaca ferruginea*,

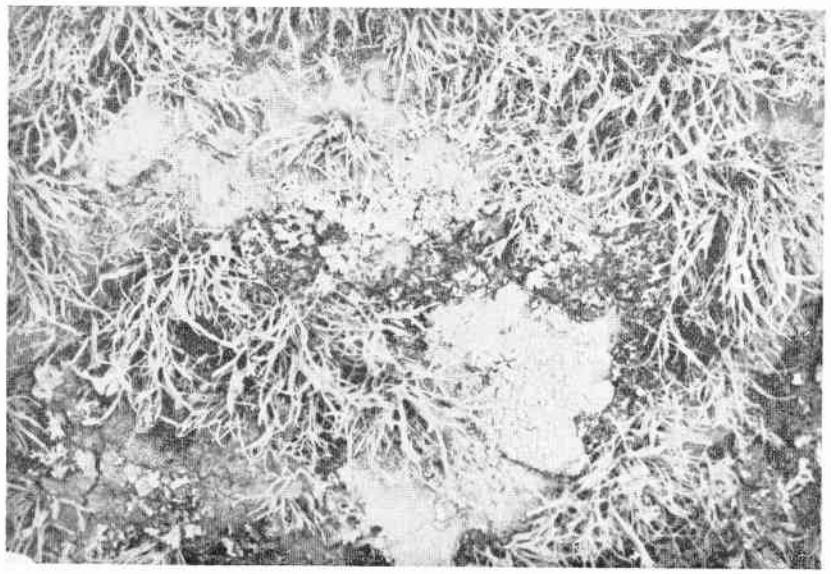

FIG. 12. *Ramalinetum scopularis* on maritime rocks siliceous. Species present include *Anaptychia fusca*, *Ochrolechia parella*, *Parmelia reticulata*, *P. saxatilis* and *Ramalina siliquosa* (Mid-Ebudes: Island of Iona, 1972, P. W. James).

* Species predominantly maritime in the British Isles.

*Diploschistes caesioplumbeus**, *Huilia albocaerulescens*, *Lecanora atra*, *L. fugiens**, *L. gangaleoides*, *Lecidea diducens* (on quartzite), *L. sulphurea*, *L. tumida*, *Lecidella subincongrua**, *Parmelia delisei**, *P. glabratula* ssp. *fuliginosa*, *P. pulla**, *P. loxodes**, *P. verruculifera* (syn. *P. isidiotyla*), *Pertusaria pseudocorallina*, *Physcia subobscura**, *Ramalina cuspidata**, *R. siliquosa**, *R. subfarinacea**, *Rhizocarpon constrictum**, *R. geographicum* aggr., *R. obscuratum*, *Rinodina atrocinerea*, *R. luridescens**, *Verrucaria fusconigrescens** and *Xanthoria parietina*. This association is, however, very variable and other species may be very important components of it locally, for example, *Buellia aethalea*, *B. subdisciformis**, *B. verruculosa*, *Fuscidea cyathoides*, *F. tenebrica*, *Lecanora rupicola*, *Lecidea tenebrosa*, *Pertusaria chiodectonoides*, *P. ceuthocarpoides**, *P. monogona* and *Rinodina confragosa**.

A wetter and more sheltered facies of the *Ramalinetum scopularis* which is optimally developed on friable rocks includes *Acrocordia salweyi*, *Bacidia scopulicola**, *Enterographa hutchinsiae*, *Lecania rupicola**, *Lecanora dispersa*, *Lecidella subincongrua**, *Opegrapha confluens*, *O. gyrocarpa*, *O. lithyrga*, *O. zonata*, *Porina chlorotica*, *P. curnowii**, *Solenopsora holophaea**, *S. vulturiensis**, *Toninia aromatica*, *T. mesoidea**, *Verrucaria internigrescens** and *V. prominula**.

Species characteristic of the *Lobarion*, for example *Lobaria laetevirens*, *Nephroma laevigatum*, *Pannaria microphylla*, *Parmeliella plumbea* and *Sticta canariensis* (both morphotypes) also enter this assemblage on sheltered shores, particularly in western Scotland (e.g. Balnabraid Glen, Campbeltown, Kintyre; near Newton Stewart, Kirkcudbrightshire). Further studies may well show that this facies merits the status of a distinct association.

On rocky coasts, dry sheltered overhangs within the *Ramalinetum scopularis* support the *Sclerophytetum circumscriptae*, discussed below.

Sclerophytetum circumscriptae ass. nov. (Table XV)

The *Sclerophytetum circumscriptae* is a very distinctive association characteristic of dry, often shaded, recesses in siliceous maritime rocks which are not subject to direct rainfall. This association, which is largely restricted to the south and west coasts of the British Isles, includes many rare species often at the northern edges of their distributional ranges. The most characteristic species of this community are *Caloplaca arnoldii*, *C. littorea*, *Arthonia lobata* aggr., *Catillaria littorella*, *Dirina stenhammari*, *Lecanactis dilleniana*, *L. monstrosa*, *Lecanora tenera*, *Opegrapha cesareensis* and *Sclerophyton circumscriptum*. *Lecanora praepostera*, *Rinodina subglaucescens*,

* See footnote on previous page.

TABLE XV.

Sclerophytetum circumscriptae ass. nov.

Species	Stands 1	2
Arthonia lobata aggr.	1.–	–
Buellia leptoclinoides	–	+
Chiodecton petraeum	–	2.2
Lecanactis monstrosa	2.2	–
Lecanora atra	+.1	–
L. gangaleoides	1.–	+
L. praepostera	2.1	3.3
L. tenera	–	3.3
Lecidea orosthea	–	1.2
Pertusaria flavicans	+	–
Ramalina siliquosa	1.1	+.1
Roccella fuciformis	–	1.+
R. phycopsis	–	2.1
Sclerophyton circumscriptum	3.3	2.2

1. Isles of Scilly, St Mary: sheltered dry acid rock, incl. 90°, aspect 315°, 0·5 × 0·5 m, 1968, P.W.J.
2. Channel Islands, Alderney, La Roche peninsula: acid rock, aspect 45°, 1 × 2 m, cover 60%, April, 1975, P.W.J.; *type record*.

Roccella fuciformis and *R. phycopsis* are present as far north as the island of Skomer, Pembrokeshire, whereas *Buellia leptoclinoides*, *Chiodecton myrticola* and *C. petraeum* are restricted to south-west England and the Channel Islands. *Arthonia atlantica* is confined to western Ireland. Further notes on the ranges of many of the species in this association within the British Isles are included in James (1970).

It is of interest to note that in south-west Brittany, northern Spain and Portugal, this association is not confined to crevices but is also able to extend on to exposed rock faces.

Verrucarietum maurae DR.

Svensk. växtsociol. Sällsk. Handl. **2,** 51 (1925) [as "*Verrucaria maura*-Ass."].—*Verrucaria maura-Lichina confinis*-Association DR., *Beih. bot. Cbl.* **49,** 81 (1932)

The *Verrucarietum maurae* is the association of the littoral (black) zone on all siliceous rocky coasts of Britain. The 15 species which comprise it are more or less regularly inundated by sea-water on sheltered shores or lie within the splash zone on more exposed coasts; only *Lichina pygmaea* is regularly submerged by the tide. Although considerable patterns of zonation may occur within the *Verrucarietum maurae* these are often obscured due to variations in shoreline topography and the density of algal cover. This results in the upper and lower elements of this association becoming spatially close as on respectively drier exposed and wetter, seaweed sheltered surfaces in juxtaposition. The *Verrucarietum maurae* is dominated by species of *Verrucaria* the identification of which still presents considerable problems (Fletcher, 1975a). *Verrucaria maura* generally delimits the upper part of the zone and extends into the *Caloplacetum marinae*; on some shores this species is associated with *V. amphibia*. The maximum immersion time for any species in the association is that of 52% of one year recorded for *V. striatula* and *V. mucosa* (Fletcher, 1973a); these two species constitute the lowest extension of the zone. Intermediate species are *Arthopyrenia halodytes*, *Arthopyrenia* sp., *Verrucaria degelii* (northern Scotland only), *V. ditmarsica*, *V. erichsenii*, *V. microspora* auct. and *V. sandstedei*. *Arthopyrenia halodytes* exhibits a very wide range of substrate tolerance, occurring on acid or limestone rocks, on a wide range of shells of molluscs and on soft chalk (as in south-east England).

F. Aquatic Communities

The lichen flora of siliceous rocks in, or at the margins of, lakes and streams includes a small but distinctive assemblage of species, many of which are almost exclusive to the habitat. The horizontal zonation patterns formed by particular lichen associations within or below the splash zone are comparable with those occurring on coastal rocks (see Santesson, 1939; Wirth, 1972). Recently the zonation formed has proved of value even in the determination of river channel capacity (Gregory, 1976). The ecology and phytosociology of the freshwater communities in the British Isles have received little study although the taxonomy of the aquatic species of *Verrucaria* and *Polyblastia*, two of the most difficult genera represented, has been critically reviewed by Swinscow (1968, 1971). According to the information available there appear to be at least four associations which merit consideration. As with the case of the marine and maritime lichen communities, no attempt has been made here to assign the associations of aquatic habitats to alliances.

Some of the ecological factors which account for the delimited distribution of aquatic lichens have been discussed by Ried (1960a,b). Probably the frequency and sum extent of submersion are two important controlling factors for the survival of most species; only *Verrucaria aquatilis*, *V.*

kernstockii and *V. silacea* (the siliceous morphotype of *V. elaeomelaena* according to Wirth, 1972) require prolonged submersion. Several species, for instance, *Porina ahlesiana*, *Verrucaria aethiobola*, *V. hydrela* and *V. margacea*, are markedly tolerant of low illumination and may, in sheltered consistently humid sites, extend to damp rocks some distance from the margins of lakes and streams. Alternatively, a facies of the *Opegraphetum horistico-gyrocarpae*, including *Enterographa hutchinsiae*, *Opegrapha lithyrga*, *O. zonata* and *Porina lectissima*, as well as *Catillaria chalybeia* and *Porina chlorotica*, two species with an extremely wide ecological amplitude, may in similar shaded conditions enter into characteristic aquatic associations.

Both the pH and mineral content of the water may exert an important influence on the composition of the lichen flora. It is noteworthy that intermittently inundated siliceous rocks at the margins of lakes which are fed by streams flowing over basic rocks may develop species-poor facies of the *Gyalectetum jenensis* or the *Rhizocarpon petraeum* nodum (p. 362), including such species as either *Gyalecta jenensis*, *Lecidella stigmatea*, *Placynthium nigrum*, *Polyblastia scotinospora*, *P. theleodes*, *Lecidea speirea*, *Protoblastenia rupestris* or *Rhizocarpon petraeum*, respectively. As with coastal limestone rocks, there are few lichens characteristic of semi-inundated limestones or other types of base-rich rock: in Britain only *Verrucaria elaeomelaena* and the rare species *Placynthium tantaleum* and *Staurothele succedens* seem to belong exclusively to this category. As a rule, semi-inundated limestone supports either moisture-tolerant associations of the *Aspicilion calcareae* or a facies of the communities of dry limestones tolerant of some submersion of which *Thelidium decipiens* can be cited as a notable example.

The communities of lakes and streams seem to be particularly vulnerable to contamination by inorganic fertilizers which find their way into aquatic ecosystems by run-off and seepage from treated agricultural land. The consequent effect is one of more or less intensive hypertrophication which encourages the rapid blanket colonization of swards of blue-green and green algae which rapidly smother the pre-existing lichen communities, nearly all of which are dominated by species with crustose thalli and are unable to compete under such adverse conditions. Damage to aquatic lichen communities in Britain has been accentuated noticeably in the last 5 years, particularly in Wales, south-west Scotland and south-west England, areas where there has been a rigorously applied policy for the extensive reclamation of heathland and moorland for agriculture and forestry; many upland streams have become wholly or partly contaminated due to this cause. This aspect of freshwater pollution is in need of urgent study. To a lesser degree, the lowering or raising of lake levels and the diversion of water from streams and rivers for hydro-electric schemes and the formation of reservoirs has had a notable impact on some of the more interesting aquatic lichen communities.

Aspicilietum lacustris Wirth

Diss. Bot., *Lehre* **17**, 223 (1972).—*Aspicilietum lacustris* Frey, *in* Frey and Ochsner, *Arvernia* **2**, 67 (1926), ? *nom. inval.* as labelled "une fragment".

In the British Isles, the *Aspicilietum lacustris* is the widespread association of the splash zone of lakes and streams subject also to periodic inundation. The characteristic species in well lit sites are *Aspicilia lacustris*, *Dermatocarpon fluviatile*, *D. meiophyllum*, *Rhizocarpon laevatum*, *Staurothele fissa* and *Verrucaria aethiobola*, often in association with *Huilia albocaerulescens*, *H. macrocarpa*, *Lecidea tumida* and *Rhizocarpon obscuratum* in less frequently inundated habitats. With an increase in the degree of shading, a nodum also including *Bacidia inundata*, *Catillaria chalybeia*, *Aspicilia laevata* and *Verrucaria praetermissa* is established; this assemblage of species is perhaps worthy of recognition at association rank. In very shaded and more humid situations the association grades into the *Verrucarietum siliceae* marked by increased frequencies of *Verrucaria hydrela* and *V. margacea*. The *Physcietum caesiae* (p. 360) is not uncommon on the tops of boulders in streams used as bird perches.

Several other noda are discernible in the *Aspicilietum lacustris*, for example, that occurring on very shaded mica schist rocks in small streams in western Scotland and Ireland including *Microglaena larbalestieri* and *Porina guentheri* var. *grandis*; the more widely distributed *Thelidium pyrenophorum* is also often present in this nodum.

Another important nodum mainly confined to Ireland but also represented as a species-poor facies in western Scotland is that characterized by the presence of *Huilia hydrophila*, and which may correspond to the subunion *Haplocarpon hydrophilum* of Wirth (1972). Additional characteristic species of this nodum are *Porina guentheri* var. *lucens*, *P. interjungens* (rare), *Porocyphus kenmorensis* and the ubiquitous *Aspicilia lacustris*, *Catillaria chalybeia*, *Huilia albocaerulescens*, *H. macrocarpa*, and *Rhizocarpon* species.

The *Lecidea phaeops–L. taylori* community discussed on p. 365 might also be placed near here. Most of its characteristic species are markedly euoceanic; the previously "endemic" species *Lecidea phaeops* and *L. taylori* have recently been collected in the Açores (Faial and Santa Maria) where they are dominant in moist woodlands and semi-inundated river valleys similar to those in which they occur in Britain.

Ephebetum lanatae Frey

Mitt. naturf. Ges. Bern **6,** 172 (1922) [as "*Ephebe lanata*-Ass."].

The *Ephebetum lanatae* is a rather local community of lake and stream margins as well as more or less persistent seepage tracks on acid, nutrient-impoverished siliceous rocks. In Britain the association is largely confined to the north and west of the country and is characterized by the presence of *Aspicilia gibbosa* aggr., *A. lacustris*, *Ephebe lanata*, *Rhizocarpon geminatum* (rare), *R. obscuratum* (morphotype), *Scytonema* sp., *Stereocaulon pileatum*, *Stigonema* sp., *Trapelia involuta* and often various Cyanophyceae; *Trapelia moorei* may also be locally abundant as, for instance, on the island of Mull. Cyanophilic algae and the bryophytes *Bryum alpinum* and *Rhacomitrium protensum* are additional important components of the association. When the bryophyte cover is well developed, *Massalongia carnosa* and, more rarely, *Polychidium muscicola*, enter the association.

Ionaspidetum suaveolentis Frey

Mitt. naturf. Ges. Bern **6,** 170 (1922) [as "*Jonaspis suaveolens*-Ass."].—*Ionaspidetum odorae* Wirth, *Diss. Bot., Lehre* **17,** 223 (1972) [as "(Frey 1922) *nom. nov.*"].

A rare and very restricted association in the British Isles, the *Ionaspidetum suaveolentis* includes *Ionaspis suaveolens*, *Placynthium flabellosum* and *Polyblastia cruenta* as its characteristic species. The rare species *Dermatocarpon rivulorum*, *Gyalidea fritzei*, *Polyblastia quartzina* and *Thelidium fumidum* may also belong here. More ubiquitous species recorded are *Aspicilia lacustris*, *Bacidia inundata*, *Catillaria chalybeia*, *Dermatocarpon fluviatile*, *Rhizocarpon laevatum*, *Staurothele fissa* and *Verrucaria margacea*, although these are often present only in small quantities and in direct competition with numerous species of blue-green algae. *Thelidium aeneovinosa* cited by Wirth (1972) as a characteristic species in the association on the Continent has only once been recorded from the British Isles (Durham). The association is best developed in higher mountain areas of Scotland, particularly in the Cairngorm mountains where it seldom occurs below an altitude of 910 m. At lower altitudes the community grades into the *Aspicilietum lacustris* in which *Placynthium pannariellum* and *Polyblastia cruenta*, at least above 200 m, may also be present as subsidiary species.

Verrucarietum siliceae Wirth & Ullrich

In Wirth, *Diss. Bot., Lehre* **17,** 219 (1972).

This association, the *Verrucarietum siliceae*, comprises communities growing on siliceous rocks in streams and lakes where there is a moderate

to rapid water flow, sufficient light and lack of mud and silt. Although the association is frequently submerged throughout the year it may also be found in shaded stream beds which dry out for relatively short periods of the year. *Verrucaria aquatilis*, *V. kernstockii* and *V. silicea* are characteristic of the *Verrucarietum siliceae*. According to Wirth (1972), *V. silicea* is the siliceous rock morphotype of *V. elaeomelaena* which occurs in similar situations on submerged limestones. Various free-living algae of which *Hildenbrandtia* and *Lemanea* merit particular mention are often present as is the moss *Fontinalis antipyretica*. The rare *Collema fluviatile* is faithful to the association in Britain.

A nodum characterized by *Bacidia inundata*, *Staurothele fissa*, *Verrucaria latebrosa* and *V. margacea*, not uncommon in western areas of the British Isles, is also referred to the *Verrucarietum siliceae*. This may be identical to the *Verrucarietum laevato-denudatae* Wirth.

VII. Terricolous Communities

In general, terricolous lichens present much greater problems of phytosociological delimitation than communities characteristic of other substrates, because lichens on soil usually form an intimate and integral part of already designated higher plant associations; they do not form the more or less exclusive stands seen in the case of most corticolous and saxicolous lichen communities. In the case of terricolous communities, lichenologists have often adopted classificatory schemes which pay only minor attention to the vascular plants involved (e.g. Klement, 1955). While this approach can be sympathized with, as those describing higher plant syntaxa have all too frequently ignored lichens in their surveys, in our view an entirely acceptable system for terricolous communities must take a proper account of both phanerogam and cryptogam components.

An outline of the higher plant syntaxa which may be recognized in Britain is included in Shimwell (1971). Those present in Britain as a whole were summarized by Tansley (1939) although he did not adopt the nomenclatural system used by continental workers, and those in Scotland are reviewed in some detail in the work edited by Burnett (1964). A survey of the plant associations of lowland Britain is currently in progress but results from it will not be generally available for some time.

For simplicity, we have separated the terricolous lichen communities into the following four categories, those of pebbles, basic soils, coastal soils and acid soils or peat.

A. Pebbles

Lichens on pebbles may be sporadic within vascular plant-dominated communities or form extensive stands in unstable pebble-dominated situations. Extremely mobile pebbles are scarcely colonized by lichens, perhaps largely due to abrasion of any incipient thalli. Three pebble communities are particularly distinctive in the British Isles and are recognized as associations here as they can occur over large areas with few or no flowering plants.

Huilietum crustulatae (Klem.) P. James *et al.*

This association is discussed under saxicolous communities above (p. 370), as it can also occur on larger rocks and boulders.

Lecideetum erraticae ass. nov. (Table XVI)

This association is particularly well developed on pebbles at Dungeness in East Kent, an area which has a noteworthy facies of the *Lecanoretum subfuscae* on *Sarothamnus* and *Prunus spinosa* (see p. 319) and also *Cladonia*-dominated heathland-like communities on decaying *Sarothamnus*. The characteristic species of the *Lecideetum erraticae* are *Buellia aspersa**, *B. aethalea*, *Lecidea erratica* and *L. tumida*. In a slightly shaded facies, an undetermined *Aspicilia* becomes dominant. Other species occasionally found in this association are *Catillaria chalybeia*, *Buellia verruculosa*, *Lecanora dispersa*, *L. polytropa*, *Rhizocarpon constrictum*, *R. obscuratum* and *Verrucaria nigrescens*. This association is optimally developed on pebbles in small declivities in shingle or where there is partial shading from adjacent scrub. The species present in this community seem able to withstand periodic disturbance; pebbles with the *Aspicilia* mentioned above frequently have their upper and lower sides colonized by this species.

Although best developed at Dungeness, this association has also been recorded in a more fragmentary state from the Chesil Beach, Dorset; Orford Ness, Suffolk; Start Bay, Devon; Pevensey Beach and Pagham, Sussex (Rayner, 1976); and Ballantrae shingle beach, Ayrshire. At Slapton the association occurs on more stabilized shingle, particularly bare patches exposed within the lichen-dominated *Cladonietum alcicornis* (p. 401), and *Buellia punctata* (saxicolous morphotype) is also a rare component there (Hawksworth, 1972a).

* This is a small sterile sorediate species resembling a slightly brown-grey form of *Lecidea tumida* and, as in that species, has a delicately fimbriate dark prothallus; gyrophoric acid is present in the medulla and in the internal part of the soralia.

TABLE XVI.

Lecideetum erraticae ass. nov.

Species	Stands 1	2	3	4	5	6
Aspicilia sp.	+.2	–	3.3	4.3	–	–
Buellia aethalea	2.3	1.2	1.3	1.2	1.2	2.3
B. aspersa	1.2	3.3	2.2	1.2	2.3	1.3
B. stellulata	+.0	–	–	–	+.2	–
B. verruculosa	–	+.0	–	–	+.2	1.2
Catillaria chalybeia	+.0	–	–	–	–	–
Lecanora dispersa	–	+.0	–	–	–	+.2
L. polytropa	–	–	1.1	–	–	–
Lecidea erratica	3.3	1.2	2.2	+.0	1.3	1.3
L. tumida	2.3	2.3	1.3	1.3	2.2	1.2
Rhizocarpon constrictum	–	1.1	–	–	–	2.2
R. obscuratum var. *reductum*	1.2	1.3	1.3	+.2	1.3	1.3
Verrucaria nigrescens	–	–	1.1	–	–	+.0

1. East Kent, Denge Beach, Open Pits (61/073186): pebbles (exposed), level, 1·0 × 1·0 m, cover 40%, 16 July 1976, P.W.J.
2. East Kent, Denge Beach, Open Pits (61/077184): pebbles (exposed), incl. 15°, 1·0 × 1·0 m, cover 55%, 16 July 1976, P.W.J.
3. East Kent, Denge Beach, Open Pits (61/063173): pebbles (shaded), incl. 10°, 1·0 × 1·0 m, cover 35%, 16 July 1976, P.W.J.; *type record.*
4. East Kent, Lydd Ranges (61/015182): pebbles, incl. 25°, 1·0 × 1·0 m, cover 45%, 28 June 1968, P.W.J.
5. Dorset, Isle of Portland, Chesil Beach, Fortuneswell (30/675745): pebbles, level, 1·0 × 1·0 m, 16 April 1970, P.W.J.
6. East Suffolk, Orford, Orford Ness (62/448494): pebbles, incl. 5°, 1·0 × 1·0 m, 25 June 1964, P.W.J.

Lecideetum watsoniae ass. nov. (Table XVII)

Unlike the other two pebble associations recognized here, this association is characteristic of basic situations, particularly calcareous (chalk) slopes of south-east England. The predominant species of the *Lecideetum watsonii* on chalk nodules are *Lecidea watsonii*, *Protoblastenia immersa*, *P. metzleri*, *P. monticola*, *Sarcogyne regularis*, *Staurothele hymenogonia*, *Thelidium decipiens*, *T. incavatum*, *Verrucaria hochstetteri*, *V. muralis*, *V. mutabilis* and *V. viridula*. On flints within the same association *Aspicilia calcarea*, *A. contorta*, *Caloplaca citrina*, *C. holocarpa*, *Lecanora dispersa*, *Lecidella stigmatea*, *Protoblastenia rupestris*, *Verrucaria nigrescens* and *V. viridula*

TABLE XVII.

Lecideetum watsoniae ass. nov.

Species	Stands 1	2	3	4	5
Bacidia muscorum	+.0	–	+.0	–	–
B. sabuletorum	+.2	+.0	+.0	+.0	–
Caloplaca citrina	–	–	+.2	–	–
Collema auriculatum	–	+.0	+.0	–	–
C. tenax	+.2	–	–	+.0	–
Dermatocarpon hepaticum	+.0	–	–	–	–
Lecidea watsonii	1.2	+.2	+.2	+.0	+.2
Lecidella stigmatea	+.0	+.2	–	–	–
Leptogium schraderi	–	–	+.0	–	–
L. cf. *subtile*	–	+.0	–	–	–
Petractis clausa	–	+.0	–	+.0	+.0
Physcia adscendens	–	+.0	–	–	–
Protoblastenia immersa	+.2	–	+.2	–	–
P. metzleri	–	+.0	+.2	–	–
P. monticola	–	+.0	–	–	–
P. rupestris	–	+.2	–	+.0	–
Sarcogyne regularis	+.2	–	–	–	–
Staurothele hymenogonia	+.2	1.2	+.2	+.0	–
Thelidium decipiens	+.2	–	–	+.2	+.2
T. microcarpum	–	–	–	1.2	1.3
Verrucaria hochstetteri	+.2	1.3	1.3	+.0	+.0
V. muralis	1.3	+.2	+.2	+.0	+.0
V. mutabilis	–	–	–	+.2	+.0
V. nigrescens	+.2	+.2	+.0	+.2	+.2
V. viridula	+.2	+.2	+.2	+.0	–
Algae	+.0	+.0	–	+.2	1.2
Bryophytes	1.2	+.2	+.2	+.0	+.0
Phanerogams	+.2	+.2	+.0	+.0	–

1. Surrey, Dorking, Box Hill (51/184525): exposed chalk/flint pebbles, incl. 10°, aspect 180°, cover 65%, 0·5 × 0·5 m, 16 October 1968, P.W.J.
2. West Norfolk, Thetford, Thetford Heath (52/845796): recently exposed chalk/flint pebbles, incl. 5°, aspect 180°, cover 75%, 0·5 × 0·5 m, 12 December 1965, P.W.J.
3. West Sussex, Midhurst, Heyshott (41/902167): chalk/flint nodules in rabbit warren, incl. 35°, aspect 225°, cover 55%, 0·5 × 0·5 m, 6 September 1963, P.W.J.
4. West Sussex, Midhurst, Heyshott (41/902167): chalk/flint nodules in deep shade of *Fagus*, incl. 35°, aspect 225°, cover 70%, 1·0 × 1·0 m, 6 September 1975, P.W.J.
5. Hertfordshire, Tring, Coombe Hill (42/896106): chalk/flint nodules in shade of *Corylus*, incl. 50°, 1·0 × 1·0 m, 3 March 1962, P.W.J. and T. D. V. Swinscow.

can occur. More locally *Petractis clausa* and *Polyblastia dermatodes* on chalk, and *Ochrolechia parella*, *Physcia adscendens*, *P. caesia*, *P. tenella*, *Xanthoria aureola*, *X. elegans* and *X. parietina* on flint may enter the community. A few primarily soil-loving species may also be present, for example *Bacidia sabuletorum*, *Collema tenax*, *Dermatocarpon hepaticum*, *Leptogium lichenoides* and *L. sinuatum*. The chalk nodule–flint communities form a part of those widespread on basic soils in areas such as the Breckland of East Anglia and the Kent and Sussex Downs, and species found in these (see pp. 397–400) may also occur in them occasionally.

The *Lecideetum watsoniae* is optimally developed on dry eroded south-facing hillsides in the downland areas of south-east England. It may have a somewhat transitory nature to judge from its tendency to occur in areas of relatively recent disturbance, as near old rabbit burrows where a fresh supply of chalk nodules suitable for colonization has been disinterred.

A somewhat shaded facies of this association is occasionally encountered, most frequently under *Fagus*, in which *Acrocordia monensis*, *Thelidium macrocarpum* and *Verrucaria muralis* on chalk, and *V. mutabilis* and *V. viridula* on flints become dominant; the moss *Seligeria paucifolia* is also often represented in such communities.

B. Basic Soils

The lichen communities encountered on soil in the immediate vicinity of basic rock outcrops are most appropriately treated as an integral part of those occurring on the rocks themselves (pp. 349–364). For successful colonization in such sites the terricolous lichens require open and sufficiently stable habitats, for example on closely cropped exposed hillsides (particularly those with high rabbit populations) and more especially pockets of soil between and on the outcrops themselves. In such habitats the vascular plant flora is either reduced in height by grazing, or by the overall thinness, and frequently by the dryness of the soil. Some lichens generally treated as terricolous are characteristic of bryophyte-rich communities and are themselves predominantly bryophilous (muscicolous) rather than strictly terricolous.

The ubiquitous indicator lichens of basic soils are *Bacidia sabuletorum*, *Cladonia pocillum*, *Collema tenax* (often a primary colonizer of recently disturbed soils) and *Polyblastia tristicula*; a variety of unicellular and filamentous blue-green algae (Cyanophyceae) are also generally present. Additional species which are frequently present include *Bacidia muscorum*, *Caloplaca citrina* (terricolous morphotypes), *Cladonia rangiformis*, *Collema crispum*, *Dermatocarpon hepaticum*, *Leptogium lichenoides*, *L. sinuatum*, *Microglaena muscorum*, *Placidiopsis custnanii* (in Scotland), *Polyblastia*

gelatinosa, *Squamarina crassa*, *Toninia coeruleonigricans* and *T. lobulata*. Of the rarer or more local species to be found on such soils are *Bacidia herbarum*, *Buellia asterella* (syn. *B. epigaea* auct. angl.), *Fulgensia* sp., *Lecidea decipiens*, *Polyblastia agraria*, *P. wheldonii*, *Squamarina lentigera* and *Verrucaria psammophila*.

In the Breckland of East Anglia, the basic soils support particularly interesting assemblages of species, including *Buellia asterella*, *Lecidea decipiens*, *Fulgensia* sp. and *Squamarina lentigera* (Table XVIII). These communities may well correspond to the *Fulgensietum fulgentis* Gams recognized by many central European authors, but they are in need of further study. *Fulgensietum fulgentis* is a widespread continental community, especially in central and southern France.

TABLE XVIII.

Lichen-rich community of the Breckland, East Anglia (*aff.* Fulgensietum fulgentis *Gams*).

Species	Stands					
	1	2	3	4	5	6
Bacidia muscorum	–	2	1	–	–	–
Buellia asterella	2	2	2	2	–	–
Cladonia foliacea	4	4	2	–	–	–
C. furcata	–	1	–	2	2	–
C. pocillum	–	–	–	2	1	–
C. rangiformis	–	–	–	–	–	5
Collema tenax	1	–	–	–	–	–
Cornicularia aculeata	1	1	–	–	–	–
Dermatocarpon hepaticum	2	2	2	2	–	–
Diploschistes scruposus var. *bryophilus*	1	2	3	–	–	2
Fulgensia aff. *fulgens*	–	3	–	–	–	–
Lecanora dispersa	–	–	–	–	1	–
Lecidea decipiens	6	2	2	–	–	–
Peltigera canina	–	–	–	–	–	2
P. rufescens	–	2	+	–	1	–
Protoblastenia rupestris	–	–	+	–	–	–
Sarcogyne regularis	–	2	+	–	–	–
Squamarina lentigera	2	+	2	–	1	1
Toninia coeruleonigricans	4	4	3	4	4	2
Verrucaria hochstetteri	–	–	1	–	–	–
V. muralis	2	2	–	–	–	–
V. nigrescens	1	–	+	–	1	–
Bryum capillare	–	–	–	–	2	2
Camptothecium lutescens	–	–	+	3	4	–

TABLE XVIII—*continued*

Species	Stands					
	1	2	3	4	5	6
Ditrichum flexicaule	2	4	+	–	–	–
Encalypta streptocarpa	2	4	4	–	–	–
Rhytidium rugosum	–	–	–	–	2	–
Astragalus danicus	3	3	–	–	–	–
Botrychium lunaria	–	–	+	–	–	–
Carex arenaria	–	–	2	–	–	–
C. ericetorum	–	–	+	–	–	–
Carlina vulgaris	3	2	1	–	1	–
Centaurium erythraea	–	+	1	–	–	–
Erigeron acer	2	2	–	–	–	–
Euphrasia officinalis aggr.	2	2	–	–	–	–
Festuca ovina	7	5	3	7	6	4
Galium verum	–	2	–	–	–	–
Gentianella amarella	+	–	–	–	–	–
Koeleria gracilis	4	4	2	3	6	2
Leontodon taraxacoides	2	4	1	–	–	–
Linum catharticum	–	3	2	2	–	–
Lotus corniculatus	–	2	–	–	–	–
Medicago lupulina	–	–	–	+	–	–
Ononis repens	+	–	–	–	–	–
Ornithopus perpusillus	–	3	–	–	–	–
Pilosella officinarum	5	6	2	5	–	5
Pinus sylvestris	+	–	–	–	–	–
Prunella vulgaris	–	–	1	–	–	–
Sedum acre	–	–	–	–	–	2
Senecio jacobaea	1	–	+	–	1	–
Taraxacum laevigatum	–	–	+	–	2	3
Thymus spp.	7	–	2	3	4	5

1. West Suffolk, Lakenheath Warren (52/750805): 1·0 × 1·0 m, cover 90%, 1973, P. W. Lambley.
2. West Suffolk, Lakenheath Warren (52/750805): 1·0 × 1·0 m, cover 90%, 1973, P. W. Lambley.
3. West Suffolk, Lakenheath Warren (52/750805): 1·0 × 1·0 m, cover 100%, 1973, P. W. Lambley.
4. West Suffolk, Deadman's Grave (52/779748): 1·0 × 1·0 m, cover 100%, 1973, P. W. Lambley.
5. West Suffolk, Thetford Warren (52/849796): 1·0 × 1·0 m, cover 100%, 1974, P. W. Lambley.
6. West Norfolk, Weeting Heath (52/757878): 1·0 × 1·0 m, cover 100%, 1973, P. W. Lambley.

Future investigations may indicate that specific habitat preferences shown by particular species are related to the soil chemistry and composition as well as to those climatic factors determining which communities occur on calcareous rocks. *Bacidia sabuletorum* and *Dermatocarpon hepaticum*, for example, both have a wide ecological amplitude and can be both shade- and moisture-tolerant; hence their frequent occurrence with the *Gyalectetum jenensis*. As in the case with dune systems, the amount of calcium carbonate in the soil determines the abundance and species diversity of lichen-dominated communities in calcareous sites. Soils with 100 mg Ca/100 g and a pH usually above 6·2 are the first on which true lichen calcicoles are able to survive and where *Bacidia sabuletorum*, *Cladonia pocillum*, *C. rangiformis* and *Collema tenax* (often in abundance) occur. With increasing pH additional species start to appear but it is only at the highest pH levels (to pH 8·2) where lichens such as *Fulgensia* sp., *Lecidea decipiens* and *Squamarina crassa* are found.

There is little evidence to suggest that certain basiphilous lichens can grow equally well in sites where magnesium replaces calcium as the predominant cation. The lichen flora of the magnesium-rich serpentine outcrops in Shetland, as at Baltasound on Unst, for example, have little in common with that of limestone areas in Sutherland.

Whilst many of the species mentioned above can be expected to occur in most limestone areas of the British Isles, several others appear only with increasing altitude. *Aspicilia verrucosa*, *Caloplaca stillicidiorum*, *Lecidea templetonii*, *Solorina saccata* and *S. spongiosa*, for example, are predominantly montane in England, although they are to be found at sea-level in Scotland where they enter the coastal *Dryas octopetala–Carex rupestris* nodum of McVean and Ratcliffe (1962). A few species are characteristic of basic soils between outcrops of limestones and epidiorites in the Highlands of Scotland; the communities on rocks of the latter type have already been referred to (p. 361). Many of the species in such sites are very rare in the British Isles and the communities they form may be fragments of those more widely distributed in comparable habitats in western Scandinavia; the most important species of these soils in Scotland are *Biatorella fossarum*, *Collema ceraniscum*, *Dermatocarpon cinereum*, *Gyalecta geoica*, *Lopadium fecundum*, *Microglaena sphinctrinoides*, *Polyblastia sendtneri*, *Sagiolechia rhexoblephara* and *Thelopsis melathelia*.

C. Coastal Soils and Dunes

Very few lichens are restricted to coastal soils in the British Isles and, as with most other terrestrial communities, these form an integral but often minor part of vascular plant-dominated communities. Most lichens

found in such situations require open habitats with bare but generally more or less stable soil; exceptions are provided by *Cladonia furcata* and *C. rangiformis* whose erect and relatively fast growing thalli are able to compete in more extensive developments of higher plants.

In coastal sites, terricolous lichens are often most frequent on windswept cliff tops, eroded banks or on thin layers of soil associated with rock outcrops. Small rosette-forming vascular plants such as *Plantago coronopus*, *Pilosella officinarum* and *Rumex acetosella* are commonly present in such sites when the lichens can become almost dominant; when this occurs they can be termed the *Cladonietum alcicornis* Klem. (see Hawksworth, 1972*a*). *Cladonia* species comprise the most important element in such communities and include *C. conistea*, *C. cervicornis* (including *C. verticillata*), *C. chlorophaea*, *C. foliacea*, *C. nylanderi* (rare), *C. pityrea* and *C. pyxidata*, in addition to the ubiquitous *C. furcata* and *C. rangiformis; Peltigera* species are additional important components locally.

On bare soil in exposed situations *Lecidea wallrothii* and *Solenopsora vulturiensis* occur; the latter is also encountered in very sheltered sites or on damp rocks in overhangs. *Lepraria* species (common), small subcrustose *Leptogium* species and *Micarea subviridescens* are also sometimes common in sheltered sites but this shade-loving community is poorly understood. Loose friable soil of banks may support *Moelleropsis nebulosa*, *Vezdaea aestivalis* and *V. leprosa*, and where the soil has become compacted and is more or less basic, pyrenocarpous species may also colonize it (e.g. *Acrocordia salweyi*, *Verrucaria hochstetteri*, *V. muralis*); this latter type of soil is perhaps not unlike the compacted mortar of old walls in some respects, on which such species normally occur.

The lichens in sand-dune systems have been studied in Britain by several workers since the pioneer investigations of Watson (1918a) which were primarily concerned with those in western Britain, emphasis being placed on Braunton Burrows, North Devon. Of the more recent investigations, those of Alvin (1960) on Studland Heath, Dorset, Brown and Brown (1969) on Blakeney Point, Norfolk, and Prince (1974) on the Sands of Forvie, Aberdeenshire, merit particular mention. The extent to which lichens form an important component of the vegetation on sand dunes depends on a variety of factors, such as the stability of the sand, its moisture-retentive properties, the frequency and permanency of dewfall, and the humus and calcium carbonate contents. The calcium carbonate in dunes is responsible for some of our most interesting dune lichen vegetation which includes many calcicolous species; this is derived mainly from the accumulation of mollusc shells but can be supplemented by run-off and erosion of adjacent calcareous outcrops (e.g. Broadhaven, Pembrokeshire). The most consolidated soils of basic dunes have lichen assemblages

similar to those characteristic of limestone crevices (p. 397) and the Breckland (p. 398) in areas where the vascular plants permit their development. The most highly calcareous region in a dune system often corresponds to the transitional zone between the unstable white dunes and the stabilized grey dunes, as in older dunes there is a leaching of the calcium carbonate, a lowering of the pH and an accumulation of surface humus; all these factors favouring the establishment of the acid heathland community types are discussed below (p. 403).

Most species found on calcareous dunes are also known in other lowland calcareous sites; *Squamarina crassa* f. *pseudocrassa*, however, is noteworthy in being exclusively coastal. *Bacidia sabuletorum*, *Cladonia rangiformis*, *C. foliacea*, *C. pocillum*, *Diploschistes scruposus* var. *bryophilus*, *Leptogium lichenoides*, *L. sinuatum* and *Peltigera rufescens* are indicators of very low but perceptible concentrations of calcium carbonate in the dune sand. With increasing pH and calcium carbonate levels, species such as *Dermatocarpon hepaticum*, *Polyblastia gelatinosa*, *P. tristicula*, *P. wheldonii* (rare) and *Toninia coeruleonigricans* appear. *Arthopyrenia subareniseda* and *Polyblastia agraria* are so far confined to this habitat in Britain. In areas where the soil is extremely calcareous, *Fulgensia* sp., *Lecidea decipiens*, *Placynthium nigrum*, *Squamarina crassa*, *Toninia aromatica* and *T. lobulata* may be found.

D. Acid Soils and Peat

Most acid heathlands in Britain are dominated by a single species, *Calluna vulgaris*, which often forms more or less extensive tiered stands over large areas. Gimingham (*in* Burnett, 1964) notes that since dominance by this species is established over such a wide area, there is in consequence a considerable floristic diversity in the communities dominated by *Calluna* in the British Isles; the term "*Callunetum*" thus conveys little ecological information unless qualified in some way. *Calluna* may occur in almost pure stands or form integrated associations with other species indicative of particular habitats, for example *Arctostaphylos uva-ursi* (wetter facies or higher altitudes), *Empetrum nigrum* (high montane but descending to sea-level in Shetland), *Erica cinerea* (dry oceanic moorland), *E. tetralix* (wet moorland), *Vaccinium myrtillus* (dry lowland heaths or heathland under trees) and *V. uliginosum* (high montane heathland). The age of the community and frequency of burning are of considerable importance in relation not only to the diversity of the vascular plant flora but also to that of the cryptogams, including lichens. Open communities show a sequence of lichen development after burning; *Lecidea granulosa*, *L. uliginosa* and sometimes *Baeomyces rufus* are amongst the first species to appear, but in

the following 5–6 years a more species-rich community forms. Eventually the *Calluna* becomes too dense and/or tall, and lichens are gradually excluded from the community, often forming aberrant morphotypes difficult to determine before they are finally lost. In the case of old *Calluna* bushes, the larger *Cladonia* species (e.g. *C. arbuscula*, *C. impexa*) and others (e.g. *C. floerkeana*) can often be seen to colonize the central open dying parts. The various effects of man on acid heathlands are discussed further by Hawksworth *et al.* (1974).

The *Cladonia*-dominated communities of rotting logs, rotting tree stumps and tree bases not uncommonly spread on to adjacent soil provided that this has a very high humus content. These communities, which cannot be regarded as strictly terricolous or corticolous and are treated under the *Cladonion coniocraeae* here (pp. 313–314), include those of the floor of mature pine woods in the Scottish Highlands with several very rare *Cladonia* species (e.g. *C. carneola*, *C. botrytes* and *C. cenotea*).

1. Lowland Heaths

Lowland heathland communities in dry sandy situations support a ubiquitous assemblage of species, most of which belong to the genus *Cladonia* (see Fig. 13): *C. arbuscula*, *C. bacillaris* (rare), *C. cervicornis* (incl. *C. verticillata*), *C. chlorophaea* (all chemotypes), *C. coccifera*, *C. coniocraea*, *C. crispata* var. *cetrariiformis*, *C. floerkeana*, *C. furcata*, *C. glauca*, *C. gracilis*, *C. gonecha* (rare), *C. impexa*, *C. pityrea*, *C. polydactyla*, *C. squamosa* (including var. *allosquamosa*), *C. subulata*, *C. tenuis* and *C. uncialis* ssp. *dicraea*. Additional important species include *Baeomyces roseus*, *B. rufus*, *Cornicularia aculeata*, *C. muricata*, *Icmadophila ericetorum* (rare), *Lecidea granulosa*, *L. oligotropha* (rare), *L. uliginosa* and *Pycnothelia papillaria*. Small siliceous pebbles in lowland heaths often support fragments of the *Huilietum crustulatae* (p. 370).

A particularly wet facies of the above assemblage, whilst retaining *Cladonia crispata*, *C. squamosa* and *C. uncialis* ssp. *dicraea*, may also be partially dominated by *C. strepsilis*; the other species indicated above then tend to be restricted to the crowns of tussocks or other raised areas. This is a particular feature of dying tussocks of *Carex paniculata* and *Molinia coerulea* in bogs where lichens are otherwise absent. Another facies of particular interest is the occurrence of *Cetraria islandica* on lowland heaths of East Yorkshire, Lincolnshire and Norfolk; old records suggest that this species was formerly common in such areas. This facies is almost certainly allied to the richer but comparable communities occurring near sea-level in the Netherlands and west Jutland, Denmark.

Although most lichens in heaths disappear with the increasing density

FIG. 13. Lowland heath community dominated by *Cladonia* species in the centre of an aged *Calluna* tussock. Species present include: *Cladonia chlorophaea*, *C. furcata*, *C. impexa* and *Hypogymnia physodes* (the latter on a *Calluna* stem) (Surrey: Wisley, Ockham Common, 1977, F. S. Dobson).

of the vascular plant vegetation (and sometimes bryophyte cover), *Cladonia arbuscula*, *C. impexa*, *C. tenuis* and, to a lesser extent, *C. furcata* and *C. gracilis* may persist. This tendency is almost certainly due to their upward growth (towards the light) and ability to decay from the base upwards as they grow. Furthermore, these species have a relatively rapid growth rate amongst the lichens (see Chapter 3) and so are more able to compete with the less vigorously growing vascular plants.

2. Blanket Peat

Blanket peat bogs, which cover large tracts of countryside in northern and western Britain, support lichen communities generally similar to those of the more lowland heathlands discussed above but occasionally have species which also occur in upland heaths. As peat becomes exposed either through drainage, river action, peat-cutting by man or erosion, lichen-dominated stands develop on the lips or "hags" which remain. Of particular importance in such sites are *Cladonia coccifera*, *C. bellidiflora*, *C. cervicornis*, *C. gonecha*, *C. polydactyla*, *C. squamosa*, *Icmadophila ericetorum* and *Pycnothelia papillaria*, but several other noteworthy species occur in this type of habitat, for example *Coriscium viride* (with *Thelocarpon epibolum*), *Cladonia fragilissima* (rare oceanic) and *Lecidea glaucolepidea*.

3. Upland Heaths

Detailed surveys of the floristics of upland heaths in the Scottish Highlands have been prepared by McVean and Ratcliffe (1962) and McVean (*in* Burnett, 1964). These authors presented data on the lichens in many of the communities they recognized and in some cases used them in the delimitation of the syntaxa themselves. The lichen-rich heaths as interpreted by McVean and Ratcliffe fall into two main categories, the dwarf shrub heaths and the moss heaths. The former include noda such as the *Arctoeto-Callunetum* of the northern highlands, the *Cladineto-Callunetum* which occurs at high altitudes and includes species such as *Alectoria sarmentosa* ssp. *vexillifera* and *Cetraria nivalis*, and the *Cladonia*-rich *Cladineto-Vaccinetum* which is central and eastern as well as montane in Scotland. Most facies of the moss heaths are dominated by *Rhacomitrium lanuginosum*, but a few associated with patches of late snow-lie lack this species and are dominated by the diverse *Gymnomitrium concinnatum–Salix herbacea* associations. The lichen flora of the mountain tops in the Scottish Highlands is still relatively poorly understood both from the taxonomic and ecological standpoint; indeed many upland areas have not been studied by lichenologists at all in recent decades. For these reasons we have not

attempted here to relate our observations to the communities distinguished by McVean and Ratcliffe (1962).

Some of the rarest and most interesting species in Britain occur in upland heaths, such as those on the summit peaks of the Cairngorm mountains. The lichen-rich communities in montane situations in Scotland appear in general, however, to be species-poor variants or relics of more widespread Scandinavian (particularly Norwegian) communities. The most important lichen species in these communities in Britain are mainly concentrated in sites which are relatively dry and dominated by *Salix herbacea*; wet sites become bryophyte dominated. The low-growing, prostrate, woody stems of *S. herbacea* which shed their leaves in winter provide adequate anchorage for many macrolichens and soil-stabilizing species. The lichen flora developed might perhaps be considered as an oligotrophic counterpart of the lichen assemblage associated with the base-rich mica schist soils of the Ben Lawers range (see p. 362) and includes: *Baeomyces roseus*, *B. rufus*, *Catillaria contristans*, *Cladonia luteoalba*, *Lecanora epibryon*, *Lecidea assimilata*, *L. caesioatra*, *L. granulosa*, *L. stenotera*, *Micarea melaena*, *M. turfosa*, *Ochrolechia androgyna*, *O. frigida*, *O. geminipara*, *O. tartarea*, *Pertusaria oculata*, *Porina mammillosa*, *Thamnolia vermicularis* (var. *subuliformis*), *Toninia havaasii*, *T. tristis*, *T. squalescens* and *T. squalida*.

In bare areas adjacent to *Salix herbacea* (see Fig. 14), colonies of *Cetraria delisei*, *Cornicularia aculeata*, *C. muricata*, *Stereocaulon saxatile*, and, very rarely, *C. divergens* are developed. These species, together with *Alectoria ochroleuca** (very rare), *A. nigricans*, *A. sarmentosa* ssp. *vexillifera*, *Cetraria ericetorum* (rare), *C. islandica*, *C. nivalis*, *Pertusaria dactylina*, *Thamnolia vermicularis* and *Cladonia* species [especially *C. bellidiflora*, *C. coccifera*, *C. deformis* (rare), *C. gonecha*, *C. impexa*, *C. gracilis*, *C. tenuis* and *C. uncialis*] occur in *Rhacomitrium lanuginosum*-dominated areas and all have the ability of either growing on or over this moss, or of vertical growth which enables them to compete successfully with it. The very rare *Nephroma arcticum* and *Platismatia norvegica* occur in the *Polygoneto-Rhacomitretum lanuginosi* and *Arctoeto-Callunetum* respectively of McVean and Ratcliffe (1962).

While emphasis has been placed on the lichen-rich communities of mountain tops in the above, it is important to note that many of the same species also form an integral part of the subalpine *Calluna–Vaccinium uliginosum–Empetrum nigrum* communities which often lie on more inclined adjacent mountain slopes; in such situations the abundance of

* It should be noted that, as pointed out by Hawksworth (1972b), the numerous references to this species by McVean and Ratcliffe (1962) refer to *Alectoria sarmentosa* ssp. *vexillifera*.

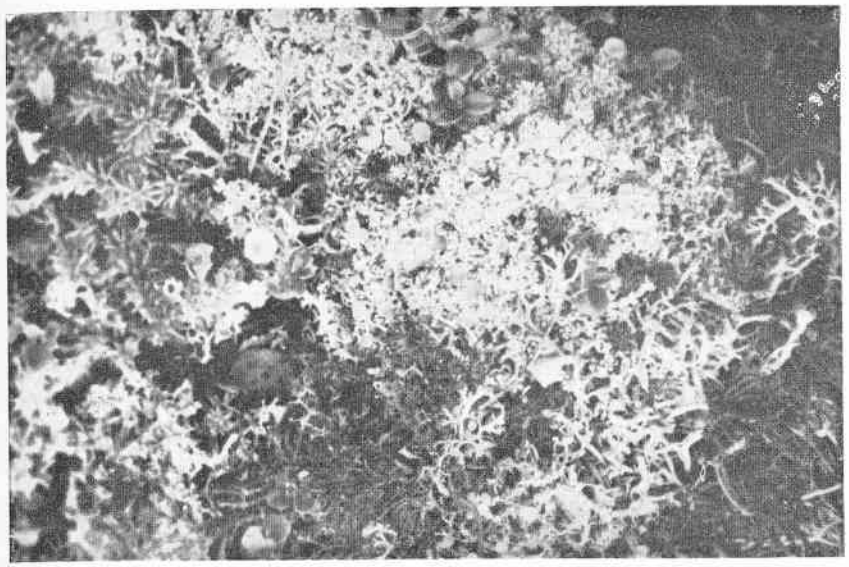

FIG. 14. Upland heath community. Species present include: *Cetraria nivalis*, *Cladonia bellidiflora*, *C. coccifera*, *C. crispata*, *C. impexa*, *C. uncialis* ssp. *dicraea*, *Empetrum nigrum*, *Ochrolechia frigida* (predominant) and *Vaccinium vitis-idaea* (Cairngorm mountains, Cairn Gorm summit plateau, 1974, P. W. James).

Alectoria sarmentosa ssp. *vexillifera*, *Cetraria nivalis*, *C. islandica* and species of *Cladonia* subgen. *Cladina* is particularly striking.

Although the optimal development of upland heaths in the British Isles occurs in the Scottish Highlands, comparable but species-poor communities are to be found on the highest mountains in England (e.g. Cheviot Hills, Lake District) and Wales (e.g. Snowdonia).

VIII. Summary

Following a brief review of previous studies on lichen communities in the British Isles, the value of the phytosociological approach to these is discussed as are the difficulties inherent in such methods. Some of the nomenclatural problems arising in the naming of plant communities are discussed and proposals are made for changes in order both to overcome these and to bring the nomenclatural practice for syntaxa more in line with that for plant taxa (idiotaxa). The major part of the chapter is concerned with a survey of the principal lichen communities in the British Isles. In

the absence of a great deal more field work, an entirely definitive classification cannot be presented, but it is hoped that this preliminary conspectus will serve both as a framework for the future naming of lichen communities in Britain and as a stimulus to further work in this field. Topics requiring more detailed investigation are emphasized throughout.

The epiphytic communities are grouped in eleven alliances, those on limestone in two, and those on siliceous rocks in eight. Some associations, however, have not been referred to any alliances, as in the case of those which occur on moderately basic rock and in marine, maritime and aquatic habitats. Terricolous communities remain mostly unnamed here as they appear to be most appropriately described together with the vascular plants with which they occur. Two new alliance names are introduced (*Parmelion laevigatae*, *P. perlatae*) and three new combinations made at this rank in accordance with changes in the generic names of the species on which their names were based. Eleven new associations are also described and five new combinations made at that rank. A key to the epiphytic alliances is included as are tables of relevé data for most of the main associations treated and synopses of the synonymy of the community names employed.

Note on the Relevé Tables

The relevé data are expressed in the tables of this chapter by one of two methods depending on the recorder: either by the +→10 Domin scale or the Braun-Blanquet +→5 scale, in which case a sociability score on the 0→5 scale is appended after a full-stop. Detailed information on the meaning of these units is included in Shimwell (1971). Data on inclinations, aspects, altitude etc. are included wherever available. Angles of inclination are measured from the horizontal, the recorder facing the substrate (i.e. 90° = vertical, 100° = inclined away from the recorder at 10°).

Acknowledgements

We are very grateful to Mr B. J. Coppins for his constructive comments on our manuscript, to Drs O. Wilmanns and V. Wirth for the loan of copies of several important early publications on lichen phytosociology, and to Mr P. W. Lambley for making available to us his unpublished relevés from the Breckland.

References

Ahti, T. and Vitikainen, O. (1974). *Bacidia chlorococca*, a common toxitolerant lichen in Finland. *Mem. Soc. Fauna Flora fenn.* **49,** 95–100.

Almborn, O. (1948). Distribution and ecology of some south Scandinavian lichens. *Bot. Notiser, Suppl.* **1** (2), 1–252.

Alvin, K. L. (1960). Observations on the lichen ecology of South Haven Peninsula, Studland Heath, Dorset. *J. Ecol.* **48,** 331–339.

Barkman, J. J. (1954). Zur Kenntnis einiger *Usneion*-Assoziationen in Europa. *Vegetatio* **4,** 309–333.

Barkman, J. J. (1958). "Phytosociology and Ecology of Cryptogamic Epiphytes". Van Gorcum, Assen.

Barkman, J. J. (1973). Synusial approaches to classification. *In* "Ordination and Classification of Communities" (R. H. Whittaker, ed.), pp. 435–491. W. Junk, The Hague.

Barkman, J. J., Moravec, J. and Rauschert, S. (1976). Code of Phytosociological Nomenclature. *Vegetatio* **32,** 131–185.

Brightman, F. H. (1962). Field meeting at Arnside. *Lichenologist* **2,** 97–100.

Brodo, I. M. (1974) ["1973"]. Substrate ecology. *In* "The Lichens" (V. Ahmadjian and M. E. Hale, eds), pp. 401–441. Academic Press, New York and London.

Brown, D. H. and Brown, R. M. (1969). Lichen communities at Blakeney Point, Norfolk. *Trans. Norfolk Norwich Nat. Soc.* **21,** 235–250.

Burnett, J. H., ed. (1964). "The Vegetation of Scotland". Oliver and Boyd, Edinburgh and London.

Coker, P. D. (1968). The epiphytic communities of the Ruislip district. *J. Ruislip Distr. nat. Hist. Soc.* **17,** 26–37.

Coppins, B. J. (1976). Distribution patterns shown by epiphytic lichens in the British Isles. *In* "Lichenology: Progress and Problems" (D. H. Brown, D. L. Hawksworth and R. H. Bailey, eds), pp. 249–278. Academic Press, London and New York.

Crespo, A. (1975). Vegetación liquenica epifita de los pisos mediterráneo de Meseta y Montaño Ibero-atlantico de la Sierra de Guadarrama. *An. Inst. bot. A. J. Cavanillo* **32,** 185–197.

Darimont, F. (1975) ["1973"]. "Recherches Mycosociologiques dans les Fôrets de Haute Belgique". 2 vols. Institut Royal des Sciences Naturelles de Belgique, Brussels.

Degelius, G. (1954). The lichen genus *Collema* in Europe. *Symb. bot. upsal.* **13** (2), 1–499.

Delzenne-van Haluwyn, C. (1976). "Bibliographia phytosociologica syntaxonomica" (R. Tüxen, ed.). Supplement I. "Bibliographia societatum lichenorum". J. Cramer, Vaduz.

Dickinson, C. H. and Thorp, T. K. (1968). Epiphytic lichens on *Corylus avellana* in The Burren, County Clare. *Lichenologist* **4,** 66–72.

Du Rietz, G. E. (1925). Götlandische Vegetationsstudien. *Svensk. växtsociol. Sällsk. Handl.* **2,** 1–65.

Earland-Bennett, P. M. (1975). *Lecanora subaurea* Zahlbr., new to the British Isles. *Lichenologist* **7,** 162–167.
Evans, E. P. (1932). Cader Idris: a study of certain plant communities in south-west Merionethshire. *J. Ecol.* **20,** 1–52.
Fabiszewski, J. (1968). Porosty Śnieżnika Kłodzkiego i gór Bialskich. *Monographiae bot.* **26,** 1–116.
Farrow, E. P. (1916). On the ecology of the vegetation of Breckland. I. General description of Breckland and its vegetation. *J. Ecol.* **3,** 211–228.
Fletcher, A. (1973a). The ecology of marine (littoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5,** 368–400.
Fletcher, A. (1973b). The ecology of maritime (supralittoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5,** 401–422.
Fletcher, A. (1975a). Key for the identification of British marine and maritime lichens. I. Siliceous rocky shore species. *Lichenologist* **7,** 1–52.
Fletcher, A. (1975b). Key for the identification of British marine and maritime lichens. II. Calcareous and terricolous species. *Lichenologist* **7,** 73–115.
Fletcher, A. (1976). Nutritional aspects of marine and maritime lichen ecology. *In* "Lichenology: Progress and Problems" (D. H. Brown, D. L. Hawksworth and R. H. Bailey, eds), pp. 359–384. Academic Press, London and New York.
Follmann, G. (1974). Nordhessische Flechtengesellschaften. II. Das *Pseudevernietum furfuraceae* (Hil.) Ochsn. *Hess. flor. Briefe* **23,** 40–47.
Frenkel, R. E. and Harrison, C. M. (1974). An assessment of the usefulness of phytosociological and numerical classificatory methods for the community biogeographer. *J. Biogeogr.* **1,** 27–56.
Frey, E. (1923). Die Berücksichtigung der Lichenen in der soziologischen Pflanzengeographie, speziell in den Alpen. *Ver. naturf. Ges. Basel* **35,** 303–320.
Gilbert, O. L. (1976). An alkaline dust effect on epiphytic lichens. *Lichenologist* **8,** 173–178.
Graham, G. G. (1971). Phytosociological studies of relict woodlands in the north-east of England. M.Sc. thesis, University of Durham.
Gregory, K. J. (1976). Lichens and the determination of river channel capacity. *Earth Surface Processes* **1,** 273–285.
Guinochet, M. (1973). Phytosociologie et systématique. *In* "Taxonomy and Ecology" (V. H. Heywood, ed.), pp. 121–140. Academic Press, London and New York.
Hawksworth, D. L. (1969). The lichen flora of Derbyshire. *Lichenologist* **4,** 105–193.
Hawksworth, D. L. (1972a). The natural history of Slapton Ley Nature Reserve. IV. Lichens. *Fld Stud.* **3,** 535–578.
Hawksworth, D. L. (1972b). Regional studies in *Alectoria* (Lichenes). II. The British species. *Lichenologist* **5,** 181–261.
Hawksworth, D. L. (1973a). The lichen flora and vegetation of Berry Head, South Devonshire. *Trans. Torquay nat. Hist. Soc.* **16,** 55–66.
Hawksworth, D. L. (1973b). Ecological factors and species delimitation in the lichens. *In* "Taxonomy and Ecology" (V. H. Heywood, ed.), pp. 31–69. Academic Press, London and New York.

Hawksworth, D. L. (1974). "Mycologist's Handbook". Commonwealth Mycological Institute, Kew.
Hawksworth, D. L., Rose, F. and Coppins, B. J. (1973). Changes in the lichen flora of England and Wales attributable to pollution of the air by sulphur dioxide. *In* "Air Pollution and Lichens" (B. W. Ferry, M. S. Baddeley and D. L. Hawksworth, eds), pp. 330–367. Athlone Press, London.
Hawksworth, D. L., Coppins, B. J. and Rose, F. (1974). Changes in the British lichen flora. *In* "The Changing Flora and Fauna of Britain" (D. L. Hawksworth, ed.), pp. 47–78. Academic Press, London and New York.
Hilitzer, A. (1924). Příspěvky k lisejnikům šumavy a Pošumaví. *Čas. národ. Mus.* **1923,** 1–14. [Reprint only seen.]
Hilitzer, A. (1925). Étude sur la végétation épiphyte de la Bohême. *Spisy Fac. Sci. Univ. Charles* **41,** 1–202.
James, P. W. (1965). Field meeting in Scotland. *Lichenologist* **3,** 155–172.
James, P. W. (1970). The lichen flora of shaded acid rock crevices and overhangs in Britain. *Lichenologist* **4,** 309–322.
James, P. W. (1973). The effect of air pollutants other than hydrogen fluoride and sulphur dioxide on lichens. *In* "Air Pollution and Lichens" (B. W. Ferry, M. S. Baddeley and D. L. Hawksworth, eds), pp. 143–175. Athlone Press, London.
Kaiser, E. (1926). Die Pflanzenwelt des Hennebergisch-Fränkischen Muschelkalk-Gebietes. *Beih. Rep. spec. nov. regni veg.* **44,** 1–280.
Kalb, K. (1970). Flechtengesellschaften der vorderen Ötztaler Alpen. *Diss. Bot., Lehre* **9,** 1–118.
Kalb, K. (1972). Rindenbewohnende Flechtengesellschaften im Nürnberger Reichswald. II. *Hoppea* [*Denkschr. Regensb. bot. Ges.*] **30,** 73–91.
Klement, O. (1955). Prodromus der mitteleuropäischen Flechtengesellschaften. *Beih. Rep. spec. nov. regni veg.* **135,** 5–194.
Klement, O. (1965). Zur Kenntnis der Flechtenvegetation der Kanarischen Inseln. *Nova Hedwigia* **9,** 503–582.
Knowles, M. C. (1913). The marine and maritime lichens of Howth. *Scient. Proc. R. Dubl. Soc.* **14,** 79–143.
Laundon, J. R. (1956). The lichen ecology of Northamptonshire. *In* "The First Fifty Years. A History of Kettering & District Naturalists Society & Field Club", pp. 89–96. Kettering and District Naturalists Society and Field Club, Kettering.
Laundon, J. R. (1958). The lichen vegetation of Bookham Common. *Lond. Nat.* **37,** 66–79.
Laundon, J. R. (1967). A study of the lichen flora of London. *Lichenologist* **3,** 277–327.
Laundon, J. R. (1970). London's lichens. *Lond. Nat.* **49,** 20–69.
LeBlanc, F. (1963). Quelques sociétés ou unions d'épiphytes du sud du Québec. *Can. J. Bot.* **41,** 591–638.
Mattick, F. (1951). Wuchs- und Lebensformen, Bestand- und Gesellschaftsbildung der Flechten. *Bot. Jb.* **75,** 378–424.
McLean, R. C. (1915). The ecology of the maritime lichens at Blakeney Point, Norfolk. *J. Ecol.* **3,** 129–148.

McVean, D. N. and Ratcliffe, D. A. (1962). "Plant Communities of the Scottish Highlands". H.M.S.O., Edinburgh and London.

Meijer-Drees, E. (1953). A tentative design for rules of phytosociological nomenclature. *Vegetatio* **3,** 205–214.

Motyka, J. (1926). Die Pflanzenassociationen des Tatragebirges. VI. Teil. Studien über epilithischen Flechtengesellschaften. *Bull. int. Acad. pol. Sci. Lett., sér.* **B, 1926,** 189–227.

Ochsner, F. (1928). Studien über die Epiphyten-Vegetation der Schweiz. *Jb. St. Gall. naturw. Ges.* **63** (2), 1–108.

Prince, C. R. (1974). A study of a lichen synusium on the Sands of Forvie, Scotland. *Nova Hedwigia* **25,** 719–736.

Ratcliffe, D. A. (1968). An ecological account of atlantic bryophytes in Britain. *New Phytol.* **67,** 365–439.

Rayner, R. W., ed. (1976) ["1975"]. "The Natural History of Pagham Harbour. Part II". Bognor Regis Natural History Society, Bognor Regis.

Ried, A. (1960a). Stoffwechsel und Verbreitungsgrenzen von Flechten. I. Flechtenzonierung an Bachufern und ihre Beziehungen zur jährlichen Überflutungsdauer und zum Mikroklima. *Flora, Jena* **148,** 612–638.

Ried, A. (1960b). Stoffwechsel und Verbreitungsgrenzen von Flechten. II. Wasser- und Assimilationshaushalt, Entquellungs- und Submersion-resistenz von Krustenflechten. *Flora, Jena* **149,** 345–385.

Rose, F. and James, P. W. (1974). Regional studies on the British lichen flora. I. The corticolous and lignicolous species of the New Forest, Hampshire. *Lichenologist* **6,** 1–72.

Rose, F. and Wallace, E. C. (1974). Changes in the bryophyte flora of Britain. *In* "The Changing Flora and Fauna of Britain" (D. L. Hawksworth, ed.), pp. 27–46. Academic Press, London and New York.

Santesson, R. (1939). Über die Zonationsverhältnisse der lakustrinen Flechten einiger Seen im Angebodagebiet. *Medd. Lunds Univ. Limnol. Inst.* **1939** (1), 1–70.

Seaward, M. R. D. (1975). Lichen flora of the West Yorkshire conurbation. *Proc. Leeds phil. lit. Soc. sci. sect.* **10,** 141–208.

Sheard, J. W. (1968). The zonation of lichens on three rocky shores at Inishowen. *Proc. R. Ir. Acad.*, **B, 66,** 101–112.

Sheard, J. W. and Ferry, B. W. (1967). The lichen flora of the Isle of May. *Trans. Proc. bot. Soc. Edinb.* **40,** 268–282.

Shimwell, D. W. (1971). "The Description and Classification of Vegetation". Sidgwick and Jackson, London.

Stafleu, F. A. *et al.*, eds. (1972). International Code of Botanical Nomenclature adopted by the eleventh International Botanical Congress, Seattle, August 1969. *Regnum Vegetabile* **82,** 1–426.

Swinscow, T. D. V. (1968). Pyrenocarpous lichens: 13. Freshwater species of *Verrucaria* in the British Isles. *Lichenologist* **4,** 34–54.

Swinscow, T. D. V. (1971). Pyrenocarpous lichens: 15. Key to *Polyblastia* Massal. in the British Isles. *Lichenologist* **5,** 92–113.

Syers, J. K. (1964). A study of soil formation on Carboniferous limestone with particular reference to lichens as pedogenic agents. Ph.D. thesis, University of Durham.

Tansley, A. G. (1939). "The British Isles and their Vegetation". Cambridge University Press, Cambridge.

Watson, W. (1918a). Cryptogamic vegetation of the sand-dunes of the west coast of England. *J. Ecol.* **6,** 126–143.

Watson, W. (1918b). The bryophytes and lichens of calcareous soil. *J. Ecol.* **6,** 189–198.

Watson, W. (1919). The bryophytes and lichens of freshwater. *J. Ecol.* **7,** 71–83.

Watson, W. (1925). The bryophytes and lichens of arctic alpine vegetation. *J. Ecol.* **13,** 1–26.

Watson, W. (1932). The bryophytes and lichens of moorland. *J. Ecol.* **20,** 284–313.

Watson, W. (1936a). The bryophytes and lichens of British woods. Part I. Beech woods. *J. Ecol.* **24,** 139–161.

Watson, W. (1936b). The bryophytes and lichens of British woods. Part II. Other woodland types. *J. Ecol.* **24,** 446–478.

Wilmanns, O. (1966). Die Flechten- und Moosvegetation des Spitzbergs. *Spitzb. Tübingen* **3,** 244–277.

Wirth, V. (1968). Soziologie, Standortsökologie und Areal des *Lobarion pulmonariae* im Südschwarzwald. *Bot. Jb.* **88,** 317–365.

Wirth, V. (1972). Die Silikatflechten-Gemeinschaften im außeralpinen Zentraleuropa. *Diss. Bot., Lehre* **17,** 1–306, *1–9.*

Yarranton, G. A. (1967). A quantitative study of the bryophyte and macrolichen vegetation of the Dartmoor granite. *Lichenologist* **3,** 392–408.