The old forests of Western Europe and their epiphytic lichens

The epiphytic lichen vegetation of British forests is now quite well known, having received much attention in the last 18 years. Accordingly, I have in collaboration with a number of continental lichenologist friends, been attempting to carry out a survey of the lichen flora of as many as possible of the old forests of western continental Europe. This work began in 1968, and in recent years has covered many regions and forests. About 260 individual forests have now been sampled in the epiphyte survey: 105 in most parts of France, 12 in West Germany, 60 in Denmark, 33 in Norway, 10 in Belgium, 2 in Luxembourg, 1 in Holland, 30 in N and central Italy, and 2 in NE Spain.

Since about 1968 Pisut, Wirth and others have drawn attention to the great decline in epiphytic lichens in the forests of central Europe, attributing this change to a combination of increasing air pollution, and in more remote areas, to changes in forest management techniques, including the felling of many of the older stands of hardwoods, and their replacement with conifers. In the Netherlands and Belgium as Barkman pointed out in 1958, such changes have been going on for a long time. These changes have become steadily more serious, so that today little is left of the formerly rich epiphyte floras of those hardwood forests that remain in a great zone of the north European Plain from about Calais eastwards through the Low Countries, across Germany, and far into Poland and Czechoslovakia; the hilly country of central Germany is also severely affected, so that one has to go south to the Black Forest and the Swabian Jura before one finds anything of the old flora surviving.

Nevertheless, recent survey work has revealed that many species and communities of epiphytic lichens, (and bryophytes) survive in extensive areas of western Europe where it had been feared that they were extinct. This is particularly the case in France, where apart from
the industrial region about Lille and Dunkirk in the far north, severe pollution zones are still limited to the immediate neighbourhood of Paris and the lower Seine valley down to Rouen, and to smaller areas about Lyon, St-Etienne, Nantes, North Lorraine, etc., though management practice in many French lowland forests (where trees are regenerated in very dense stands, and trees are cut down when they reach a diameter of 40 to 50cm) has resulted in rather dull epiphyte floras generally of the Parmelion perlatae type (with much P.caperata, P.perlata, P.revoluta, P.glabratula, Evernia, Pertusaria spp etc). Even in the French lowlands, however, Lobarion and Usneion communities survive in a few places in old forests in the relatively oceanic Pas de Calais, e.g. at the Foret de Boulogne and Foret de Montcavnel. In Normandy, and still more in highly oceanic Brittany, rich Lobarion communities of SW British type, are still present in a number of old forests (See B.J. Coppins' account of the BLS Excursion to Brittany in Lichenologist, 1971). Even though there are rather few really large old oaks or beeches such as one finds in comparable sites in SW England, the Lobarion communities seem able to maintain themselves in the moist, clean air on smaller trees than is usual in SW England. What one does notice in Brittany and Normandy (those parts of continental Europe most akin in climate to southern England) is the great rarity, indeed often absence, of the Lecanactidetum premneae, the community that is so uniquely

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developed in southern Britain. *Lecanactis premnea*, *L. lyncea*, and *Rinodina roboris*, for example, are extremely rare in most of lowland west and central France — there just aren't enough old oaks present for it to develop as the normal "post climax" epiphyte community as it still commonly does with us, even into dry East Anglia.

Apart from the oceanic west of France the only other area of lowland north or central France where rich epiphyte communities occur is in a few of the ancient, formerly Royal, forests around Paris. The supreme example here is the great forest of Fontainebleau, some 120 square miles of woodland far enough (38 miles) south of Paris to be little affected by its pollution. Even here, the greater part of the forest is either sandy heathland, colonised by (or planted with) pines, or else rather dull managed oak or beech forest with relatively small trees, or else coppice. But some areas remain — the "Reserves Biologiques" — ironically, owing their original conservation as relics of the ancient hunting-forest structure not to naturalists, but to the artists of the Barbizon school of painters last century. These artists were outraged when the French forest authorities began to clear the old, ancient, irregular open woodlands in order to plant some more economically valuable trees, and managed to save perhaps 200 hectares or so of the old woodlands.
It was much later that the naturalists awoke to the situation and took these areas over. In one of these reserves, an area of very hilly, open-old beech and sessile oak forest with holly etc., and many sandstone outcrops, a remarkable flora persists including a little Lobaria pulmonaria, Nephroma parile, Pannaria conoplea, and Gyalecta ulmi (none of these now occur anywhere else within 100 miles of Paris), while on the moist N facing sandstone cliffs (and on a few nearby birches) there remains an extraordinary relic oceanic flora, including Menegazzia terebrata, Cetreria olivetorum, Parmelia laevigata and P. endochlora. The drier sandstone outcrops at Fontainebleau are of course famous for their saxicolous lichens, including both southern elements like Dimelaena oreina, and boreal ones like several Umbilicaria species.

There is very little forest of any lichenological interest left in the plains of the Netherlands and northern Germany today, until one reaches the northern part of Schleswig-Holstein. Here are oak and oak-beech-holly forests, rather reminiscent of some of eastern Scotland in their lichen epiphytes, with a species poor Lobarian. In Denmark, particularly in Jutland, are the best remaining lichen rich woodlands of the northern European plains. Here species-poor Lobarian (L.pulmonaria only, no Pannariaceae now) occurs quite luxuriantly in several ancient oak and beech forests, with again many of our usual British crustose "old forest" lichens. SW Norway on the other hand, is much more oceanic, and the lichen flora (as well as the oak and ash woods) remind one of western Scotland, though a number of the more strongly oceanic species are rare (Parmelia laevigata) or absent (Parmelia taylorensis, Thelotrema subtile).

However, apart from the more oceanic areas along the Atlantic coastline, the major "oasis" in west and central Europe today where rich lichen epiphyte vegetation (with many old forest relic species) can still be studied, are to be found in the montane massifs. These lie above 350m (in the north) or 500m (further south) up to the tree line about 1500m, and include a number of relatively isolated hill or mountain groups beside the major Alpine and Pyrenean ranges.

Although acid rain is modifying the lichen communities, in more exposed sites from a Lobarian towards a Pseudevernion, extensive forests remain in many of these massifs with little altered lichen vegetation, particularly to the west and south. A clear zonation
of forest communities, unlike anything to be seen now in the British Isles, is characteristic of most montane massifs in western central and central southern Europe. The more central group of upland areas includes the Belgian Ardennes, the Massif Central, the Vosges, and the Jura in France, and the Black Forest, the Swabian Jura, and the Bohmer Wald-Bayrischer Wald in Germany. The greater ranges of the Alps and Pyrenees show similar vegetation patterns at least on their northern sides. One passes from the oak-hornbeam-lime zone (often much modified by management, and so only locally lichen-rich) into the beech zone (with mature sycamore) at about 900 - 1000m (at only c.500 m in Ardennes) and into the silver fir zone (usually with beech still present) at c.1450 m, though on poorer soils this may descend lower.

The oak and beech zones are characterised by a rich Lobario of progressively more continental type as one goes eastward, and the silver fir, though it also carries the Lobario on the better soils, has a rich Usneion of Usneetum filipendulae type on poorer soils and in the higher purer stands.

The Lobario in the west (Pyrenees, Massif central) has a number of more oceanic species present. Lobaria virens, (which does not seem to occur east of the Rhone Valley today), Sticta limbata, Dimerella lutea, (Pyrenees only) and much Nephroma laevigatum; more continental species such as Nephroma resupinatum, N. bellum; and Leptogium saturninum; however occur too, as does Catillaria globosa, and these extend right to the east of central Europe, with the addition of Menegazzia terebrata, which (besides occurring in the hyper-oceanic western British Isles) is very much a feature of the central and east European Lobario, together with Cetraria olivetorum, Lobaria pulmonaria, Lobaria amplissima, L. scrobiculata and Parmeliella triptophylla. Thelopsis rubella is rare, but widespread throughout the European Lobario, S. into Italy and N. into Norway. The Usneion of the higher silver fir (and spruce, where native further east) zones is characterised by Usnea filipendula, Alectoria sarmentosa, Ramalina thrausta, Bryoria fuscescens, B. capillaris, B. bicolor, B. nadvornikiana, and from the Vosges eastwards, by Bryoria setacea and Evernia illyrica. Letharia vulpina is essentially a species of the Alps. Pseudevernia communities (with Cetraria pinastri, Hypogymnia bifurcata and H. vittata) come in more to the east.
Natural Quercus pubescens and Pinus halepensis forest, Aragon, Northern Spain.

The general decline in oceanic elements eastwards is, however, interrupted by the occurrence in warmer, humid Austrian valleys, such as by Almsee, of such surprising species as Parmelia crinita, P. laevigata, P. sinuosa and Heterodermia obscurata. Parmeliella plumbea and Nephroma laevigatum do not seem now at least, to extend north of the Alps, east of the Wutach valley in SW Germany.

Further south in Europe, the zonation of the forests and their lichen communities is more complex at lower levels, but essentially the same higher up. In Provence in SW France, for example, and generally in the Mediterranean lowlands up to 300 or sometimes 500m, the remaining fragments of native forest (usually much modified by man) of evergreen oak (Quercus ilex) on more calcareous soils and of cork oak (Q. suber) or Pinus halepensis on more siliceous soils; carry a Xanthorion community rich in Physconia species (including P. servitii, P. venusta, P. pulverulacea) and "southern" mosses like Leptodon smithii and Leucodon morensis. From 160 m upwards in humid spots (Les Mayons, near Le Lac) but more generally from 400 to 800m, ancient Castanea forests, managed as pasture woodland and
often with many old pollards, represent the main type of forest climax at the present time. Though there is still argument about whether the chestnut is really native here, it certainly carries a superb Lobarion, which may be evidence for indigenous status. This Lobarion contains three Lobaria species (no L. virans) and much Parmeliella plumbea, together with a wealth of other blue-green photobiont species of Pannariaceae and Collemataceae such as Pannaria mediterranea, P. ignobilis, P. conoplea, P. rubiginosa, P. olivacea (confined to the Mediterranean zone), Parmeliella atlantica, Collema furfuracea and C. subflaccidum. These are intermixed with what in N Europe we would regard as Xanthorion species, including Physconia venusta, P. pulverulacea, Physcia semipinnata, Anaptychia ciliaris, and Parmelia acetabulum, plus an abundance of the very southern Parmelia quercina. This community should perhaps be described as an Anaptychio-lobarion and is rich in southern basicole mosses.

The beech zone is only reached in a few places in Provence, as on Mont Ventoux at over 1400m, where a species poor Lobarion (Nephroma resupinatum and Peltigera collina abundant) occur with a little Lobaria pulmonaria and Leptogium saturninum and bryophytes only from ground level to about 1m up on the trunks of the ancient beeches, corresponding to the zone protected by snow in winter, while above this level there is a rather austere Xanthorion (with Parmelia acetabulum, P. sulcata, Anaptychia ciliaris, Physconia spp. and Phaeophyscia labrata) in the trunk zone exposed to the mistral wind at all times. Fruticose species, other than Ramalina, are almost absent.

A very remarkable forest is that of St. Baume in Provence, where an ancient religious tradition that Mary Magdalene spent her last years in a cave here has preserved this forest as virtually a sacred grove. Here on a humid N slope on limestone the Quercus pubescens forest gives way gradually to beech-holly-yew forest (apparently wholly natural) at the low altitude of 700m. The Anaptychio-lobarion (with Gyalecta ulmi) of the Quercus zone gives way to a rather British, oceanic type of Lobaria (with Pachyphiale carneola and Thelopsis rubella) in the beech forest.

The Apennine mountains in central Italy, N. of Lucca and N & E of Florence, display similar zonations to those in Provence, with Xanthorion in the lower, mostly much-modified evergreen and downy
oak (*Quercus pubescens*) woods up to about 500m; above this the mosaic of chestnut and *Quercus pubescens* forests has a Lobarion even richer than in Provence, with an even greater wealth of *Collema* spp. including *C. nigrescens*, *C. fasciculare*, *C. faccidum*, and *Leptogium* spp such as *L. brebissonii*, *L. lichenoides*, *L. cyaneascens*, and *L. teretiusculum*. Fruticose species are even rarer than in Provence - even *Evernia prunastri* is very rare, as are calcifuge species like *Hypogymnia physodes* and *Parmelia saxatilis*, but many of the small crustose species associated with ancient forests in Britain (e.g. *Pachyphiale carneola*, *Thelopsis rubella*, *Thelotrema lepadinum*, *Catillaria atropurpurea*, and even *Rinodina isidioides* and *Pachyphiale arbuti*) occur, also much *Pannaria sampaiana*. The beech-silver fir zone begins at about 1200 - 1300 m, (e.g. Abetone, Vallombrosa) and besides carrying on trunks of both species a Lobarion of more northern, British type, has luxuriant festoons of *Bryoria fuscescens*, *B. capillaris*, and *Usnea filipendula*, besides other *Usnea* spp. - so far unnamed. The epiphyte flora in the central Italian mountains seems unaltered over the last 100 years, and is probably the most intact in Europe, apart from those of west Scotland and parts of Norway.

The questions that the epiphyte communities pose are these. Why does one find the Xanthorion as the forest climax epiphyte community in the lower altitude areas in southern Europe, even on trees with bark that would be acid in Britain or north France, such as pines? Why, higher up, is the Lobarion so interpenetrated by species that in N Europe we would regard as members of the Xanthorion, and so lacking in fruticose genera like *Usnea*? The answers seem to be that in the Mediterranean zone the summer is long, hot and dusty; the bark of trees becomes thus impregnated with base-rich dust, producing a high pH and eutrophication. Hence Xanthorion type species are able to thrive. Lower down it is probably too dry for too long for Lobarion species to survive at all, except in a few sheltered long-undisturbed sites; higher up, the winter rains and October to April humidity are evidently adequate for the more hygrophytic Lobarion communities, but dusty enough in summer for some Xanthorion elements to become established.

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