

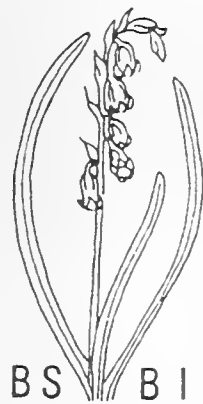


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Preface

BRN 26413

Heathers and heathlands

Edited by S. L. JURY

The eight contributions contained in this issue were presented at a symposium entitled 'Heathers and heathlands', held in the rooms of the Linnean Society of London on Thursday 20 October 1988. The meeting was organized jointly by the Botanical Society of the British Isles (B.S.B.I.) and the Linnean Society as part of the celebrations of the bicentenary of the foundation of the Linnean Society. It was attended by 143 participants, who filled the meeting room, with a significant number of late registrations sadly turned away.

The B.S.B.I. celebrated its own sesquicentenary in 1989 and, like the Linnean Society, has a long and valued tradition of contributions to British and Irish botany. The two Societies have collaborated before, but their coming together on this occasion resulted in a particularly happy and successful day, both socially and scientifically. Other joint meetings are thus likely to be held in the future.

Heathers and heathlands constitute a characteristic community of Atlantic Europe, and constitute a large and important part of the vegetation of the British Isles, perhaps not given the attention deserved by scientists. It was, therefore, a welcome suggestion by Mr David McClintock that they should form the theme of this meeting.

However, it was pleasing to be able to include in the programme a paper by Mr E. G. H. Oliver of Stellenbosch on the Ericoideae and the southern African heathers. This contribution put the impoverished British and European ericaceous flora into context. It is unfortunate that the paper printed here cannot include the spectacular colour photographs that he showed to the conference or convey the impression made by a spectacular display of living plants that he had brought and assembled.

Both Societies wish to pay tribute to Dr F. A. Bisby and Mrs M. Briggs who undertook much of the hard work in putting the programme together, ably assisted by Dr N. K. B. Robson. We are grateful to Cdr J. Fiddian-Green, at the time Executive Secretary of the Linnean Society, who oversaw the administration and domestic arrangements, and to his staff. Thanks are also due to the chairmen, Professor C. A. Stace and Professor C. H. Gimingham.

Reading, May 1989

S. L. JURY



Heather and heathlands

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GIMINGHAM, C. H., 1989. **Heather and heathlands.** Studies of the biology and ecology of heather (*Calluna vulgaris* (L.) Hull) reveal a remarkable combination of characteristics, accounting for its success as a heathland dominant and its ability to persist under traditional forms of use and management. New work on the life history and physiology of the species is helping to explain recent changes in heathlands, and to develop appropriate methods of conservation.

ADDITIONAL KEY WORDS:—*Calluna* – Ericaceae – ecology – life history.

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INTRODUCTION

Heather (*Calluna vulgaris* (L.) Hull) must by now be one of the most intensively studied of British plants. While this gives a remarkable and fascinating insight into the biology and ecology of the species, it is certainly not the case that we know all there is to know about it, or even all we need to know for purposes of using, managing or conserving it. It is quite a long time since the first comprehensive monographs and accounts of *Calluna vulgaris* were being published (Nordhagen, 1937; Beijerinck, 1940; Gimingham, 1960), but there is still a great deal of extremely interesting research involving this plant in progress at the present time, yielding exciting new information and requiring the revision of preconceived ideas.

Calluna has many claims upon our attention. For example, there can be few sights more rewarding than heather in full flower, whether viewed at close quarters in a garden or from a distance in mass on a hillside. But in addition to its contribution to horticulture and landscape, it also supports wild herbivores of use to man and since Neolithic times has provided valuable grazing on poor soils for his domestic animals. As a dominant of extensive tracts of country, it has given rise to distinctive landscapes and has supported rural communities within which unique customs, implements and breeds of sheep and cattle have evolved. These are the landscapes we know as heathlands. This paper addresses the role of

heather as the leading dominant of west European heathlands, and seeks to identify some of the biological and ecological characteristics of the species on which that role depends.

ATTRIBUTES OF *CALLUNA*

Heather is essentially a European species. Its geographical distribution extends from N. Scandinavia and Iceland to the Mediterranean and from the Atlantic seaboard to the Urals. However, it is only in the more oceanic and montane parts of this range, and only where trees or tall shrubs are lacking, that *Calluna* can become widely dominant of heathlands.

To be sufficiently vigorous to exclude competitors and attain dominance, *Calluna* requires the absence of shade, a moist atmosphere and soil throughout much of the year, and relative freedom from temperature extremes. These conditions can be obtained in oceanic west Europe and at appropriate altitudes in the mountains, and here *Calluna* is the dominant species in a number of distinct plant associations and over quite a wide range of habitats.

Certain general properties of *Calluna* contribute to its 'success' across this range of environmental conditions. One is its capacity to perform effectively on acidic soils which are low in plant nutrients, especially phosphorus and nitrogen—conditions which tend to depress the growth of many of its competitors. It has been suspected that this ability to maintain vigorous growth in oligotrophic habitats relates, in part, to the ericoid type of mycorrhiza in the roots of *Calluna*. The role of this mycorrhizal association has still to be fully explored, but there can be little doubt of its importance. Bajwa & Read (1986), for example, have shown that many amino-nitrogen sources can be utilized by the mycorrhizal fungus of *Calluna*. The subsequent demonstration by Abuarghub & Read (1988) that amino-acids may occur in some quantity in the organic horizons of heathland soils suggests that the ericoid mycorrhiza may be very important for the nitrogen economy of *Calluna* on these soils.

A further relevant attribute of *Calluna* is the freedom with which it produces adventitious roots from stems which are in contact with or become buried in moist litter, humus, peat or even dense vegetation such as *Sphagnum* or other mosses. This capacity is by no means confined to young branches, the first formed of which often trail along the ground and begin to root, but can be seen (or produced experimentally) on quite old, woody stems (Scandrett, 1987). In freely-drained soils, *Calluna* is able to root deeply by the development of its primary root systems, but in moist humus or peat a dense mass of feeding roots is produced adventitiously near the soil surface.

Thirdly, *Calluna* displays remarkable plasticity in its above-ground growth-form. This results largely from the way its branch system is made up primarily of a combination of long-shoots (the main axes of growth) and short-shoots (laterals of limited growth; the chief photosynthetic units). Normally, at the start of a new season's growth each long-shoot apex is replaced by two to four new long-shoots, keeping shoot density at the periphery constant as the bush expands radially. Typically, this produces a dome-shaped shrub, but if at any time a long-shoot apex is destroyed or damaged, any of the short-shoots can grow out into new long-shoots. Although the shape of the bush is then distorted, the plant can continue to grow in various directions depending on the position and frequency of damage.

CALLUNA AS A DOMINANT OF MOUNTAIN HEATHS, AND ON PEAT

These three main attributes help to account for the ability of heather to establish dominance in highly wind-exposed habitats on the one hand, and on growing peat surfaces on the other. On mountains, long-shoots rising above a few centimetres may be killed, confining growth to lateral branches or even basal short-shoots, while destruction of all apices on one side may lead to a trailing type of growth in which extension is always in one direction. This, coupled with adventitious rooting from the trailing stems, enables the plant to form the familiar low mats or 'waves' on mountain plateaux. In addition to this plastic response to environment, Grant & Hunter (1962) have shown that genotypes in which the same pattern of growth is fixed have been selected in high altitude populations.

On peat surfaces at lower altitudes, the behaviour of heather is different, though determined by the same attributes. Here, where the substratum is wet, extension growth of the main frame-branches is active but rather lax and straggly, such that the main stems readily spread outwards and sag, their bases often becoming buried in moss or growing peat. With the development of adventitious roots, this results in a form of 'layering' and may lead to a type of vegetative spread in which one original individual gives rise to a ring (or part ring) of offsets (Keatinge, 1975). This behaviour, which enables *Calluna* to share dominance with *Eriophorum vaginatum*, for example, in a rather stable community (Forrest, 1971) is possible only where the peat surface is aerated for at least a part of the growing season. (*Calluna* cannot withstand continuous waterlogging.)

CALLUNA AS A DOMINANT OF HEATHLANDS

At middle and low altitudes, extensive heathlands with *Calluna* as dominant have occupied freely-drained, often podsollic, soils in many parts of the 'heath region', for example in S. Sweden, Denmark, N. Germany, The Netherlands, Belgium, N. and W. France, N. Spain and the British Isles. Throughout most of this region evidence from pollen analysis, archaeology and historical records shows that the heaths were derived from former forest as a result of human impact. *Calluna* was doubtless a component of forests on acid soils, whether pine forest in the north or broadleaved forests further south. Although the shade cast by tree canopies may inhibit flowering and gradually reduce shoot production until the bushes die (Hester, 1988), *Calluna* is an 'opportunist' species and certainly made use of the many gaps and glades in the natural and semi-natural woods.

The ability of *Calluna* to colonize and dominate extensive areas once trees had been cleared may be related to the fact that it has some of the characteristics of pioneer or 'r-selected' plants. These include a very high reproductive capacity and readily dispersed seeds. Estimates of seed production range from about 250 000 (Mallik, Hobbs & Legg, 1984) to 1 million per square metre in a vigorous stand, the seeds being very small, light and readily dispersed by wind. Viability is high and germination takes place abundantly, given sufficient moisture in the medium and exposure (at least for short periods) to light. A

majority of the seeds can germinate soon after shedding, though some have a dormancy period and this ensures that germination will continue intermittently even if a first crop of seedlings fails to survive. Furthermore, if conditions are unsuitable for germination but suitable for storage, the seeds are long-lived and a large soil seed-bank is set up.

Heather, therefore, is an effective colonist on appropriate soils and this contributes to its ability to initiate the formation of heathland. However, it is not necessarily able to retain dominance in the same way as at the higher altitudes or on certain types of peat surfaces. Although on podsoles the lowermost branches may root adventitiously in damp moss or humus, the plant normally adopts a radiating, dome-shaped form as described above, and lateral spread is limited. A. S. Watt (1947, 1955) showed that in the course of time, often after some 20 years, a *Calluna* bush begins to open up with the formation of a central 'gap' in its canopy, while from the age of about 30 it generally begins to degenerate and may eventually die back completely. Watt took the view that after an intervening period of occupancy by other species, *Calluna* might recolonize the spot it had vacated, so establishing a vegetation cycle. This has been questioned, but recent work has confirmed that it does occur (Scandrett, 1987; Gimingham, 1988), though only in default of the arrival of some other species which will continue the process of succession. In these habitats *Calluna* is essentially a seral plant, giving place to other species: sometimes grasses or bracken (*Pteridium aquilinum*) but often trees such as birch (*Betula* spp.), pine (*Pinus sylvestris*) or oak (*Quercus* spp.). These invaders find regeneration niches where gaps occur in the centres of old *Calluna* bushes, or on the wider areas sometimes vacated by simultaneous die-back of whole stands.

Nevertheless, it remains true that *Calluna* continuously dominated many heathlands over considerable periods of time. This can be explained only in relation to the use and management of these areas by man, and to the properties of *Calluna* which have enabled it to respond favourably to these influences. Three types of use and management will be touched on: grazing (often accompanied by burning), cutting and sod removal.

First, grazing, especially by sheep and cattle, has been a widespread use of heather over thousands of years. Here it is again the growth morphology of the plant that accounts for its ability to withstand the impact of herbivores, for as soon as a young, un lignified long-shoot is bitten off, any of the surviving short-shoots below the cut can resume growth as new long-shoots. Furthermore, because every branch grows from a small lateral bud laid down near the long-shoot apex at the end of the growing season, it retains at its base a group of dormant meristems marking the positions of the leaf axils of that bud. If most of the distal green shoots are eaten off, these meristems can then form new shoots to continue growth. Thus *Calluna* can survive removal of between 40 and 60% of the current year's production of green shoots, although more severe defoliation (especially in summer) may eventually cause death (Grant, 1971). Mild grazing tends to keep the plant in a dense, relatively juvenile form in which rather little new wood is formed.

However, it is not always possible to keep up this level of utilization in the summer, and even when subject to grazing the plants may continue to partition assimilate to wood, and to pass into the mature and degenerate phases. It therefore becomes necessary to supplement grazing management by burning, in

order to remove the old, woody above-ground parts of the plant. If this is done before the plant is too old, it is able to regenerate vegetatively by resprouting from the base where, again, there are dormant buds in the positions from which branches were formed (Mohamed & Gimingham, 1970).

A further point about grazing and burning is that both practices result in the removal of plant nutrients from the system, thus preventing a build-up of nutrients which would be inclined to favour competitors rather than the heather.

Grazing has been practised in many parts of the heath region, often supplemented by burning which, especially in north Britain, became a regular means of management. In southern England, France and elsewhere cutting was the main form of management. Cut heather was used for bedding animals and for roof thatch, and bales of it made a resilient foundation for roads and tracks. The heather plant responded exactly as with burning, and again nutrients were removed from the system in the harvest of the bushes.

Finally, a rather different form of heathland use and management became traditional in The Netherlands and North Germany. Known as 'plaggen', this involved grazing flocks of sheep on the heathland during the daytime and bringing them in to a barn at night where whole sods which had been cut from an area of heath, including the upper organic horizon of the soil and the heather vegetation it carried, were used for bedding. Eventually this material, well trodden and with dung and urine incorporated, was used as fertilizer for fields around the village, giving rise to productive 'plaggen soils'. The areas from which the sods had been removed were allowed to regenerate, and because the newly exposed mineral soil contained a substantial proportion of the soil seed-bank, *Calluna* (or in wetter areas *Erica tetralix*) recolonized vigorously. Furthermore, the combination of grazing and sod removal represented a continuous transfer of nutrients from the heath to the neighbourhood of the village (Gimingham & de Smidt, 1983). Sod cutting was also practised in southern England, though usually as a source of fuel (Webb, 1986).

Although some heathlands are still grazed and burning remains a regular practice on grouse-moors and hill sheep farms in Scotland and N. England, in most areas traditional forms of management have declined or disappeared and now the results of nutrient accumulation are beginning to be seen. To the normal return of nutrients to the soil surface with the deposition of plant litter there is now a considerable addition from polluted rainfall. In Denmark, The Netherlands and Germany, *Calluna* is undoubtedly giving place to competitors such as wavy hair-grass (*Deschampsia flexuosa*) and it may be that the competitive balance has been shifted in favour of the latter by an increase in available nutrients (Heil & Diemont, 1983). It seems also to be the case that in these areas *Calluna* may have become more susceptible to attack by heather beetle (*Lochmaea suturalis*) and it has been shown that there is a correlation between severity of beetle attack and the level of nitrogen in the shoots of *Calluna*. Some very recent results obtained in Germany suggest that senescence in *Calluna* may be hastened by increased availability of nitrogen, which seems to cause detectable changes in both structure and physiology. In this kind of way an increase of nutrients in the rooting region of the soil may simultaneously depress the vigour of heather and improve that of competing grasses. The ecological significance of these ideas has still to be tested, but they appear to indicate a possible mechanism underlying observed changes in the composition of heathlands.

CONCLUSION

The examples discussed above bear out the claim that *Calluna vulgaris* is a remarkable species. It possesses the attributes of an opportunist seral species, but because of certain morphological and life-history traits it responds well to grazing and a variety of other types of management. As a consequence it has, over very long periods of time, remained the dominant of semi-natural heath vegetation under human influence. Currently there are signs that discontinuance of management, coupled in places with high nutrient input from polluted rainfall, may result in the replacement of *Calluna* by other species, such as grasses or bracken. This raises important issues in respect of heathland conservation. To retain *Calluna* dominance in future it will be necessary to manage in such a way as not only to keep the plants in a vigorous condition but also periodically to deplete the stock of nutrients in the system.

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Heathers in Ireland

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NELSON, E. C., 1989. **Heathers in Ireland.**

ADDITIONAL KEY WORDS:—*Calluna* – *Daboecia* – *Erica* – Ericaceae.

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Gaily they grow, the quiet throng,
Fair gems of the realm of sun and wind
The hanging bells of the high crags,
Flowers of the rocks, like cups of honey.

Eifion Wyn (1867–1926).

INTRODUCTION

The poets of our Celtic past, word-smiths that have few modern equals, sang praises to the wild flowers and the wildernesses in which they lived and worshipped (Jackson, 1935; Heaney, 1982). They could not, and did not, ignore such a prevalent plant as heather: “fair gems of the realm of sun and wind” is apt as a metaphor for these shrubs.

Since early Christian times when men began to write words on vellum, heather has been reported as a denizen of Ireland. The seventh century poet who composed the Song of Marban, the hermit, was among the first (Nelson, 1979a):

I have a hut in the wood;
None knows it but my lord.
An ash tree this side, a hazel on the other,
A great fern makes the door.
Two heathery door-post for support,
A lintel of honeysuckle,
Around its close the wood
Sheds it nuts upon fat swine.

The heathers of Ireland were not merely sustenance for the poet's imagination: they had mundane uses too; under the ancient Irish law code, the Brehon Laws, heather was a protected plant codified as *losa fedo* (bushes of the wood) (Kelly, 1976); heather has been used to produce a yellow dye (Mahon, 1982). While not perhaps as widely utilized as, for example, gorse (*Ulex europaeus* L.), heather certainly was used to thatch boliehouses—the milking huts in the summer pastures—and to make the two-ply ropes that were used to fix the thatch to cabins (Evans, 1957). Flowering heather was a source of nectar for bees (Watson, 1981).

Heather was, and is still a most familiar plant to most people in Ireland—it inhabits moorland and bog contributing to the formation of the peat, cut as turf, which to this day is an indispensable indigenous fuel. But the familiar, commonplace heather is not as well-known to scientists, I suggest, as might be thought. There is much that is puzzling, even poetic, many questions that are unanswered about the heathers that have colonized Ireland; in particular, we continue to be puzzled by the imbalance, by the conundrum of species common to Ireland and continental Europe but absent from Britain (Praeger, 1932; Webb, 1972).

There are seven native genera of the Ericaceae in Ireland, and about fourteen species recognized as indigenous, in addition there are a few naturalized aliens (Scannell & Synnott, 1987). The ericaceous taxa not usually classified in the folk-taxonomy as heathers are: *Arbutus unedo* L., *Arctostaphylos uva-ursi* (L.) Sprengel, *Vaccinium myrtillus* L., *V. oxycoccus* L., *V. vitis-idaea* L. and *Andromeda polifolia* L. *Rhododendron*, *Pernettya* and *Gaultheria* are represented by naturalized species. The three native 'heather' genera are *Calluna* (represented by *C. vulgaris* (L.) Hull), *Erica* (with six native species—*E. erigena* R. Ross, *E. cinerea* L., *E. vagans* L., *E. ciliaris* L., *E. tetralix* L., *E. mackaiana* Bab.), and *Daboecia* (represented by *D. cantabrica* (Huds.) Koch).

DABOECIA

Daboecia cantabrica is unquestionably the most beautiful, most spectacular of the native heathers, its handsome 'bells' are much larger than the flowers of any of the heathers native in Britain, and it forms a conspicuous component of the vegetation of parts of Connemara (County Galway) and southern Mayo. Apart from work for *Atlas of the British Flora* (Perring & Walters, 1962), no detailed studies have been undertaken and published on its distribution in Ireland, and no-one has defined the precise limits of its range. Why it should be confined to the Connemara/south Mayo region (cf. Praeger, 1934) is not easy to explain, but then the distribution of most of the indigenous heathers is peculiar. As difficult to explain is the species' absence from Britain. It does inhabit large tracts of south-western Europe, from central Portugal northwards into Galicia and thence through northern Spain, the Pyrenees into western France and on the Azores there is a population which is sometimes regarded as a separate species.

Daboecia cantabrica varies morphologically but within narrow limits. The more remarkable wild variants are all now familiar garden plants—white-flowered ones were reported in the early nineteenth century (Nelson, 1982) and the red-flowered forms in the 1930s (Walsh, Ross & Nelson, 1983), and though not common they are certainly not rare and in certain areas can be relatively easy to

find. A 'double-flowered' plant found in Connemara by the author has a multitude of petaloid structures inside the corolla replacing the stamens, and a series of 'inner corollas' too; this is now in cultivation as *D. cantabrica* cv. Charles Nelson (McClintock, 1983).

Daboecia has a unique connection with Ireland, for the generic name is a misspelt version of the name of one of our ascetic saints. Dabeoc (pronounced Davock) of Lough Derg (County Donegal) certainly had nothing to do with this heather and Linnaeus (1762), in coining the binomial *Erica daboeicii*, based on the polynomial *Erica S[ancti] Dabeoci Hibernis*, itself a Latin translation of the Irish *frych Dabeog* recorded by the Welsh antiquarian and natural historian Edward Lhuyd in 1700, haphazardly reversed the "o" and "e" (cf. Nelson, 1985). Thus we have a name that is unpronounceable gibberish.

Daboecia cantabrica is one of the heathers that contributes to the patchwork of purple and gold which colours the August landscape in Connemara; purple is also provided by *Erica cinerea*, and gold is the gorse (*Ulex gallii* Planchon) (Praeger, 1934). *Daboecia cantabrica* and *E. cinerea* tend to prefer well-drained, acidic habitats—they are not plants of the dampest boglands where *E. tetralix* is prevalent.

ERICA

Erica tetralix is perhaps not as interesting as some of the rarer species; it is ubiquitous throughout Ireland in suitable habitats, easily identified by its densely hirsute ovary, and while occasional strange variants are recorded—for example, one with glabrous foliage and a sparsely hirsute ovary about north Mayo (reported as *Erica* × *stuartii* (= *E.* × *praegeri.*); cf. Lamb, 1964), and prostrate coastal forms—little attention has been paid to morphological variation patterns in this species' Irish populations. Casual observations suggest that it reproduces and spreads principally by seed; seedlings occur most frequently in burnt areas. Vegetative reproduction is rarely observed; infrequently is there regeneration from old rootstocks, so no tufts are seen on the vertical faces of disused turf-banks. This is in sharp contrast to another species, sometimes regarded as a mere sub-species of *E. tetralix*, but one certainly deserving full specific rank, namely *E. mackaiana*.

Erica mackaiana is one of the three heathers found in Ireland and western Europe but not in Britain. Some of its habitats in northern Spain (Nelson & Fraga, 1984; Fraga, 1984) are remarkably like those which it frequents in western Ireland, but this is a superficial judgement based on a brief visit some years ago. In other Spanish haunts it hugs pine wood margins, a habitat not present on the bogs of Connemara and Donegal at the present time.

Quite a lot has been written about this species which is today the least contentious; for example, it was suggested that a single clone was present about Craiggamore in Connemara (McClintock, 1972; Scannell & McClintock, 1974). Again, even casual observations made in the region will reveal several different 'types', with distinct corolla shapes, sizes and colour-shades. The Craiggamore populations have been sampled and plants, propagated from these, have been cultivated together under a uniform regime at the National Botanic Gardens, Glasnevin, for seven years; the morphological differences observed in the field

persist, and can be quantified. Corolla shape, size and shade are not the only characters which vary—plants have different habits and other distinctive traits could be studied under garden regimes.

One of the most enigmatic characteristics of the Irish populations is their apparent sterility (Webb, 1972). In Spain seed is abundant and seedlings are frequent. Under cultivation at Glasnevin, I have found that Irish plants are not fertile, while the Spanish plants can have swollen, seed-laden ovaries. No adequate explanation of this phenomenon has been attempted, because no comparative research has been carried out into the reproductive biology of these plants. A study in progress on the reproductive strategies of *Erica mackaiana* and *E. tetralix* in Connemara, especially their respective abilities to spread by vegetative means, may begin to help us understand the enigma.

Another casual observation which had not been subjected to detailed study is the frequent occurrence of malformed stamens, styles and stigmas in the flowers of Irish *Erica mackaiana*. The extreme example is the well-known cultivar *E. mackaiana* 'Plena' in which all the reproductive organs have been replaced with petaloid bracts. Plants with lesser malformations, ranging from fused filaments (forming a 'second corolla') to slightly broadened filaments, and sometimes with enlarged or truncated styles are often found when random population samples of *E. mackaiana* are studied. I have no precise figures for the prevalence of this syndrome of malformations, but it is present in the two separate Connemara populations (*vide* specimens in DBN); there is no evidence for it occurring in Donegal.

As far as the ecology of *Erica mackaiana* is concerned, nothing useful can be added to the information given by Webb (1955) in his biological flora. *Erica mackaiana* is frequent around lough margins and on cutaways in peatlands; the study in progress will enlarge our store of knowledge about the relative distribution patterns of this species and its close relative, *E. tetralix*, at least in the principal Connemara locations. *Erica mackaiana* is now known to be more widespread than early accounts suggested; the Connemara population has been mapped and it extends from Errisbeg north towards Clifden (Nelson, 1981a). The Carna population was lost and then found again, while the Donegal one is, as recorded by Webb (1954), confined to the immediate environs of Upper Lough Nacung.

Since the beginning of this century, it has been recognized that *Erica mackaiana* and *E. tetralix* cross-pollinate in Ireland, and the siblings of this marriage are now named *E. × stuartii* (MacFarlane) Linton (formerly familiar as *E. × praegeri* Ostenf.) (McClintock, 1979, 1980). This hybrid is abundant in the three Irish stations, but it has not been reported in Spain, even where the two species are sympatric although such a situation is extremely rare (Nelson & Fraga, 1984; Fraga, 1984). *Erica mackaiana* totally displaces *E. tetralix* in the relatively cool, wet habitats on the northern and western sides of the Cantabrian mountains, and during field-work in Spain only four sites were discovered where *E. mackaiana* and *E. tetralix* grew together (Nelson & Fraga, 1984).

In Ireland, given the inability of *Erica mackaiana* to produce seed, except perhaps very infrequently, this hybrid must result from the pollination of *E. tetralix*. Hybrid plants may not be entirely sterile—either a few are capable of producing seed, or some pollen grains are viable—for a swarm in intermediates

between *E. tetralix* and *E. × stuartii* has been collected in Connemara, there is almost a continuum in some areas with plants grading from the typical *E. tetralix* (with a hirsute ovary) to plants with a scarcely pubescent ovary. Webb & Scannell (1983) stated that no back-crossing appears to take place, but my observations suggest that back-crossing (at least against *E. tetralix*) must occur, perhaps frequently. In *E. mackaiana* the ovary is completely devoid of hairs, and a few intermediates have been collected with a few hairs at the summit of the ovary, again suggesting back-crossing against it; these observations have not yet been quantified.

Within the area inhabited by *Erica mackaiana* and *E. × stuartii* in Connemara there are more species of heather to be collected than in any other place in these islands. The heather flora includes the rarest of the indigenous species, *E. ciliaris*, Dorset Heath.

Erica ciliaris is restricted to a small patch beside the road between Clifden and Roundstone where it was first discovered in 1846 (Eager, Nelson & Scannell, 1978). Whether the present minute population is the 'original' one is often discussed and the likelihood is that it is.

In Ireland *Erica ciliaris* is eglandular (McClintock, 1968)—I think it likely that the half-dozen or so clumps which exist represent a clone, so the uniformity is not inexplicable. Furthermore, while a few flowers may be seen in August, the peak of flowering does not occur until late September and the plants continue in bloom through the autumn (Nelson, 1983). Under the climatic regime of western Connemara it is unlikely that *E. ciliaris* has any opportunity to set viable seed in Ireland and the survival of the populations is thus dependent upon its ability to reproduce vegetatively by layering.

As pointed out by Webb (1966) the Irish habitat differs from that occupied by this species in Britain and on the continent where *Erica ciliaris* colonizes 'dry heaths'. In Ireland it grows in a damp hollow although remarkably the best growth is immediately adjacent to the road-filling. The plant is protected by law, although that cannot prevent natural predation by wild animals (Nelson, 1986).

Not as rare, but hardly less puzzling, is *Erica vagans*, Cornish Heath, which has had a chequered history in Ireland being reported from County Waterford early last century, then becoming 'lost', and rediscovered in County Fermanagh in the 1930s (Praeger, 1938, 1946): the Waterford report was always suspicious and may now be discounted as a phantom; the Fermanagh population is thriving. On a moorland site at Carrickbrawn—the rock of sorrows—*E. vagans* grows on a gently sloping hillside not far from a small mountain stream. Its habitat was intensively sampled and a detailed vegetation survey underpinned by soil analyses was carried out in the summer of 1970 (Nelson & Coker, 1974). To summarize those results, the heather was confined to an area through which percolated water enriched with dissolved minerals; significantly higher concentrations of calcium and other bases were recorded within the colony suggesting that *E. vagans* grows there because of a less acidic, nutrient-rich soil. The Carrickbrawn population is uniform in flower colour, white—the pinks and lavender shades seen in Cornwall are absent—so the present population may be a clone although seedlings have been seen in one area.

The principal question still posed by this population is whether it is native or introduced. On the whole, I adhere to the view that it is an indigenous

population, not introduced in recent times, but perhaps sometime, long ago, it was assisted by man to colonize Ireland (Nelson & Coker, 1974). I do not believe Cornish Heath was deliberately planted at Carrickbawn: that is the most improbable of the improbabilities.

Human influence on the composition of the present flora of Ireland has been considerable, but botanists have generally been reluctant to proclaim plants as exotic imports without good historical evidence. Recent remarkable finds, of which *Juncus planifolius* R. Br. (cf. Webb & Scannell, 1983) and *Haloragis micrantha* (Thunb.) Sieb & Zucc. (Green, 1989) are the most celebrated, do indicate that plants can arrive and may flourish unnoticed, spreading rapidly and ousting native species. That particular rush is now found in substantial quantities in Connemara and doubtless its conquest of Ireland is only beginning.

Erica erigena, Irish Heath, is one of the most perplexing plants in the heather flora. It is sometimes described as rare, but its populations range over thousands of hectares of moorland and mountain, generally where there is moving water, although it will grow almost totally submerged in bogs (Foss, Doyle & Nelson, 1987). This species is apparently spreading, occupying new habitats, but not ranging far outside those places whence it has been reported for more than 50 years; the species' distribution in Ireland has been mapped recently, and all the populations previously reported—for example by Robert Lloyd Praeger—were relocated (Foss, Doyle & Nelson, 1987). In the last few years *E. erigena* has been studied by Foss (cf. Foss & Doyle, 1988), and he has answered some questions and provokingly suggested that this is an introduced plant, perhaps brought to Ireland in the fifteenth century from north-western Spain, maybe as packing material for wine-flasks. Pollen profiles from sites now profusely covered with *E. erigena* had its pollen only in the upper levels. In striking contrast to *E. mackaiana*, pollen of this species is not known from Irish sites in the pre-Christian period (cf. Mitchell & Watts, 1970).

Erica erigena is an opportunist: it has colonized old railway embankments in Mayo; it occurs on lazy beds—derelict potato fields abandoned perhaps 150 years ago—on the slopes of Mweelrea; it grows on cut-over bogs throughout Mayo; and inhabits stream banks and lough shores. It reproduces by seed and there is a range of colour forms from pallid cream pinks to dark lavenders and even some with clear pink (Walsh & Nelson, 1988).

In many ways this is a plant that is out of place, spectacularly so, as it blooms in early spring when few other indigenous species are in flower. It is tolerant of salty winds but not so tolerant of heavy frosts, and thus tends to inhabit coastal areas.

Erica cinerea is the last of the indigenous species. Like *E. tetralix* it occurs throughout the island in suitable habitats. Like *E. tetralix* it apparently displays little morphological variation: yet prostrate forms do occur in coastal areas and occasionally white-flowered plants are noticed. Red (not purple) blossomed variants are occasionally reported.

This plant behaves in Ireland as would be expected, frequenting well-drained, acidic habitats. In Connemara it grows on rocky outcrops where there is a shallow peaty soil, associated often—as I have noted—with *Ulex gallii* and *Daboecia cantabrica* (Praeger, 1934). *Calluna vulgaris* will also occur in similar situations.

CALLUNA

Calluna vulgaris, ling or fraoch, is undoubtedly the most abundant of the heathers in Ireland, occupying vast tracts of heathland and peat-bog. It shows relatively little variation in morphology although prostrate variants have been collected in extreme coastal sites. Flower colour ranges within the same band as in Britain and other parts of Europe—white-flowered plants are relatively infrequent and nowhere dominant. From one wild locality, in the early 1930s, a multi-petalled form was gathered and it survives in cultivation as *C. vulgaris* cv. County Wicklow (Nelson, 1981).

This is a plant with a wide tolerance of habitats, from windswept mountain tops to sheltered woodland margins, from sodden peat bogs to apparently well-drained rocky hillsides. There is one habitat in Ireland which perhaps few would immediately regard as a suitable one for *Calluna*, yet in it *Calluna* is not just frequent, it is ubiquitous. The Burren, County Clare, is the archetypal karst landscape in these islands, with limestone pavements and a flora that is usually characterized as calcicole—*Gentiana verna* L., *Dryas octopetala* L. and a host of other lime-tolerant species abound. But again, the casual botanical visitor to The Burren must surely be impressed and intrigued by the presence on the limestone pavements of the heathers, both *Calluna vulgaris* and *Erica cinerea* abound on the little 'islands' of peaty soil which rest on the rock, and are often thereon associated with *Arctostaphylos uva-ursi* and *Empetrum nigrum* L. (Webb, 1962; Webb & Scannell, 1983). *Narthecium ossifragum* L., a distinctly calcifugous species, was added recently (Nelson, 1989) to the flora of The Burren hills. Ivimey-Cook & Proctor (1966) noted the presence of *Calluna vulgaris* and *Erica cinerea* in several associations, and described the progression from species communities typical of calcareous grasslands (*Dryas octopetala*–*Hypericum pulchrum* L. association, for example) through to heather dominated tussocks growing in highly leached soil, the acidity of which was enhanced by the accumulated organic material derived from the heathers. To see *Calluna* and *Erica cinerea* plants apparently thriving on limestone pavement is a weird experience which would surely repay detailed study with modern electronic environmental monitors—Ivimey-Cook & Proctor (1966) only set out to describe and classify species associations and did not provide environmental data. To any botanist wanting to see *Calluna* in Ireland, I would now say that The Burren is one of the best sites—it certainly provides the most provocative situations.

CONCLUSION

Those are the Irish heathers, a group of plants with different ecological propensities and distinctive distribution patterns. They continue to perplex plant geographers. It has been suggested that the so-called "Lusitanian" species—*Erica mackaiana*, *E. erigena*, *E. ciliaris*, *E. vagans*, *Daboecia cantabrica* and *Arbutus unedo*—survived in some refugium on the continental shelf through the last glacial period, and that when the climate ameliorated they recolonized the lands vacated by ice and tundra (Mitchell & Watts, 1970). Such an hypothesis is now regarded as untenable—ocean current patterns changed during the glacial periods (Ruddimann & McIntyre, 1973; Ruddimann, Sancetta & McIntyre,

1977) and the western coastline of northern Europe was not bathed in warm water as it is today. For such frost-sensitive plants to have survived hundreds of thousands of years in any refuge to the west is most unlikely (Watts, 1977; Nelson, 1979b). And there is then another problem: if these plants migrated by way of a landbridge, could they have reached Ireland from Europe before sea-levels swamped the migration route (cf. Nelson, 1979b; Devoy, 1985)? The answer is likely to be 'No' (cf. Moore, 1987).

There is a long way yet to go, I suggest, before we can be certain that each species within this group of Irish plants has a common history. The arguments presented by Foss (Foss & Doyle, 1988) for *Erica erigena* are persuasive, and while I would not suggest that *E. mackaiana* and *Daboecia cantabrica* were brought to Ireland by man, we may keep an open mind about the historical biogeography of these taxa.

Heathers have been an integral part of Irish life for centuries: they have provided bedding for humans and fodder for domestic stock, ready-made whisks for spraying potatoes (cf. Scannell, 1983), thatch for houses, tinder for fire; they have yielded dyes, and honey. Today the heathers have lost most of their mundane uses being replaced by modern fabricated materials and tools, but the poetry remains; the tourist brochures proclaim purple mountains cloaked with heather and the purple prose of advertising agencies trumpets blended liqueurs as 'a classic marriage of heather and honey, exotic herbs and Irish spirits'.

For botanists there is much yet to be discovered about these plants, and the unravelling of the contradictions that characterize the Irish heather flora should provide much to stimulate active minds for many years to come.

And, of course, we plant heathers in our gardens (Nelson, 1984) to brighten the summer.

Summer brings low the little stream,
The swift herd makes of the water
The long hair of the heather spreads out,
The weak white cotton-grass flourishes. . .
Flowers cover the world.

Anonymous, c. 900 AD

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The heathers of Europe and adjacent areas

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McCLINTOCK, D., 1989. **The heathers of Europe and adjacent areas.** *Andromeda polifolia*, *Bruckenthalia spiculifolia*, *Calluna vulgaris*, two species of *Daboecia*, 19 of *Erica* with five subspecies and seven natural hybrids are discussed. Comment is chiefly given on *E. andevalensis*, *E. maderensis* and the group currently denominated: *E. anthura*, *E. manipuliflora*, *E. multiflora* and *E. vagans*. Two new combinations are made.

ADDITIONAL KEY WORDS:—*Andromeda* – *Calluna* – *Daboecia* – *Erica* – Ericaceae – hybrids.

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INTRODUCTION

The 'adjacent areas' discussed in this paper extend from N. America to Siberia, Japan and the Levant in Asia, to Madeira and N. Africa and, for one species, to south of the equator. In this extensive domain, some 36 apparently distinct species, subspecies and hybrids have had their origin and been named, with further hybrids so far unnamed.

Three general comments should be made.

1. Chromosomes. Of these 36, and, of the many hundreds of species in southern Africa, only 24 have ever had their chromosome number ascertained, and five of these are horticultural hybrids of South African species. Only seven plants of British origin have ever been counted (McClintock, 1979; Brandham & McClintock, 1983; Fraga, 1983). The numbers are *Calluna* $2n=16$, *Daboecia* and *Erica* $2n=24$, *Bruckenthalia* $2n=36$ —a polyploid?, while *Andromeda* (including its North American variant, *glaucophylla*) has $2n=48$ and must surely be a polyploid.

2. Until very recently, the thousands of hardy cultivars grown were all completely natural seedlings or sports unaided by man, who did no more than propagate them. Thus, they demonstrate the extent of the genetic store of the taxa in question, in a way no wild population can. The reason for this is that

many of the garden variants lack the robustness or other abilities to compete with more normally adapted plants; for example, plants with yellow foliage, or otherwise masked chlorophyll, are inevitably less vigorous. One is more likely to come across worthwhile variant seedlings on open ground, such as the edges of newly made roads before competition closes in on them. Furthermore, sports are practically incapable of perpetuating themselves, but for a gardener propagation is simple.

3. Attempts have been made on a small scale to produce a key to cultivars, a desirable objective, e.g. Munson, 1984. This is made easier if they can be grouped under some botanical category (since all are basically natural products) which will also cover wild, not yet cultivated, plants (McClintock, 1986). To cite just one example, plants of *Erica tetralix* L. with untypical racemose inflorescences instead of the usual umbel, have been grouped under forma *racemosa* (McClintock, 1982). The cultivar 'Terschelling' fits in here and is the type of this form, of which other unnamed examples exist in herbaria. To have a cultivar as the type makes access to it much easier.

The taxa below are set out in taxonomic sequence, the *Ericas* alphabetically in their sections.

THE HEATHERS

Daboecia

Three aberrations may be briefly mentioned. *Daboecia cantabrica* (Hudson) C. Koch 'Covadonga' has its corolla divided into four, giving it a very different appearance—it came from Asturias, Spain. 'Charles Nelson' from W. Ireland has, basically, double flowers. But these flowers have a curious characteristic in that the first, often all those on the plant, are single, as are occasionally the last ones. 'Bicolor' known in gardens for over a century, a chimaera, with flowers of every combination of purple and white, has produced identical seedlings. All come under var. *bicolor* Dippel.

Daboecia azorica Tutin & E. F. Warburg. This differs morphologically only in the smaller size of its parts and the absence of hairs on the corolla (the hairs are present but can be very hard to find in *D. cantabrica*). It reaches a far greater altitude, carpeting the ground almost to the summit of Pico at 2320 m (Richards, 1976). Pressing personal wishes to the contrary by both the authors of this name previously inhibited me from altering its status. But it does seem that it should be recognized at no more than subspecific level, this specially in view of its markedly distinct distribution—for the hybrids between the two species *D. scotica* D. McClintock, are fully fertile and backcross readily. They are markedly hardier than either parent.

So, *Daboecia cantabrica* (Hudson) C. Koch **subsp. azorica** (Tutin & E. F. Warburg) D. McClintock, **stat. nov.**

BASIONYM: *D. azorica* Tutin & E. F. Warburg, *Bot. J.*, 70: 12 (1932).

Andromeda

Not everyone accepts this as a heather, but it was considered so when the Heather Society was made International Registrar for heathers in 1969.

This almost circumpolar plant changes little through its immense range. Certain plants in N. America are generally cited as *A. glaucophylla* Link. Their characteristics, however, are to be found in varying degree in plants named *A. polifolia*, which also occurs widely in N. America. Varietal status seems the most that these variants merit.

An odd fact is that white-flowered plants seem to be unknown in Europe. They are mentioned for *A. glaucophylla* in N. America, but I have never seen any from there. All the white-flowered plants grown in gardens come from Japan.

Calluna

Scores of infraspecific names have been published (cf. Beijerinck, 1940). The most used is var. *hirsuta* S. F. Gray (predated by var. *hirsuta* Waitz), but opinions vary as to where the dividing line comes between the extremes of glabrous and shaggy plants.

Unambiguous is var. *multibracteata* J. Jansen. There are two groups of very late-flowering Lings. The earlier has normal bracts; the later numerous bracts, which pile up until finally, weather permitting, a flower appears. This clearly separates such plants in both gardens and the wild (Turpin, 1984).

Plants occur with flowers that never open (Turpin, 1980). There are three reasons for this, and names to match, again an essential way of sorting such occurrences. In f. *clistanthes* J. Jansen, the flowers are normal but the style becomes stunted. In the commonest variant f. *diplocalyx* J. Jansen, the plants have no stamens or corolla, but eight sepals, twice the normal number. Forma *polysepala* W. Beijerinck also lacks stamens and corolla, but has more than eight sepals and usually a deformed style and stigma.

Two other features of this species may be mentioned. Two double whites 'Alba Plena' and 'Else Frye' have totally different origins. The former was a sport on a white-flowered plant on a North German moor in 1934, the latter a sport on a pink-flowered plant in Seattle N.W. America in the 1940s—before 'Alba Plena' ever reached that country. Yet the two are indistinguishable. In both double whites some of the lower florets are single and likely to be the source of similar double seedlings that have been found near by.

Finally, on exposed cliffs, e.g. in S.W. Ireland and N.W. Scotland including St Kilda (Brien, 1974), the plants are genetically prostrate. This is an example of outside influences selecting the genes. In some of these areas the majority of these plants have white flowers (Scully, 1916), a fact not yet explained.

Erica

Erica andevalensis Cabezudo & Rivera

The plants long recorded from the Huelva region of S.W. Spain as *E. tetralix* do not belong to that species. In 1980 the name *E. andevalensis* was published for them. Their close similarity to *E. mackaiana* Babington was noted, from which they were differentiated only by having shorter glandular hairs. They even share the tiny knob at the base of the anther opposite the appendage, a feature noted by Mr E. G. H. Oliver. *Erica andevalensis* attains 1 m, bushily, with stout stems, in much the same manner as *E. mackaiana* usually grows in the north of Spain. Their very remarkable habitat as given by these authors was "las escombreras y alrededores de las minas de pirita", and indeed they grow where no other plants

can—but, it seems that the authors did not look in any more natural habitats. However, in 1982 specimens were found in quantity along stretches of the River Odiel near by—where the water was also contaminated; consequently here too the lowest zone of vegetation consisted solely of this species (Nelson, McClintock & Small, 1985).

What status should these have? Glands alone are not enough to justify a distinct species, all the more because at least one plant was found in 1982 with no glands at all (McClintock, 1983a: 36) (a state paralleled in *E. mackaiana*, McClintock, 1983b). 'Lawsoniana' and its white sport 'Dr Ronald Gray' are also eglandular. Because of its very disjunct area and fantastic habitat, subspecific rank seems the most that can be justified, for this species:

***Erica mackaiana* Babington **subsp. andevalensis** (Cabezudo & Rivera) D.**

McClintock & E. C. Nelson, **stat. nov.**

BASIONYM: *E. andevalensis* Cabezudo & Rivera, *Lagasalia*, 9(2): 223–226 (1980).

E. australis L.

A gay species calling for little comment. At one time rather smaller plants from the north of the peninsula were given specific rank as *E. aragonensis*. However, they really differ only in size from typical plants and are at best denominated var. *aragonensis* (Willkomm & Lange) P. Coutinho.

E. cinerea L.

This species, whose easterly limits just reach into W. Italy, S. Holland, W. Germany, and S.W. Norway, has the greatest range of flower colour of any heather of the N. hemisphere—reds and pinks in almost every conceivable hue from palest mauve to dark beetroot, plus whites, and bicolors.

There is a variant, var. *schizopetala* Boulger, in which the corolla is evenly divided into four segments. Not only can this come true from seed, but it has also been found as a sport on 'C. G. Best', in cultivation as 'Yvonne' (McClintock, 1980a). 'C. G. Best' itself is remarkable in frequently producing seedlings of the same flower colour.

E. mackaiana Babington

This perplexing taxon grows in three distinct areas: Co. Donegal in N.W. Ireland, 180 miles further south in Connemara, Co. Galway, and 750 miles further south still, in Asturias, Spain (where it was first found in the same year, 1835, as in Connemara), where it is now known to extend for nearly 300 km east to west (Nelson & Fraga, 1983). In Connemara it is almost sterile, in Spain fertile. Other differences between these two colonies are difficult to find, apart from the fact that most plants in Spain grow taller and stouter. Plants in the colony in N.W. Ireland are markedly larger than those in Connemara, but never as tall as most Spanish plants.

Two variants, both from Connemara, may be mentioned. The fully double 'Plena' has been collected, possibly in the same site each time (but efforts to re-find it, even with directions, have failed) in 1869, 1901 (when it was called *E. crawfordii*), 1965 and 1970. No other double hardy *Erica* is known, and only very few, non-persistent, South African examples. The other variant, in cultivation as 'Maura', has semi-double flowers. These can vary so much that Turpin (personal communication) found the 12 florets on one stem each to differ

significantly from the others. Similar variations in an inflorescence have been found on other species.

E. maderensis (Bentham) Bornmüller

This is endemic to Madeira. At lower altitudes, such as 1000 m, it forms a stout bushy plant 60 cm high or so (Richards, 1976); on exposed rocks at the summit of Pico Ruivo—1863 m, it forms cushions or mats, clearly of considerable age—the species may be a poor competitor.

This used to be considered a variety of *E. cinerea* (the record for which species in Madeira is erroneous) but it differs markedly in its habit and in the fact that its leaves in threes never develop into fascicles as do those of *E. cinerea*. The distinctions are set out by McClintock (1981). Ranking this as a good species is justified.

E. terminalis Salisb.

Briquet & Litardière (1938), as do most authors, give the height of this central Mediterranean species as 0.5–1.0 m, but in 1988 I saw it in Corsica with 2.8 m stems, as indeed it can have in Britain, a true stout tree heath. This was on a search for a white-flowered plant, f. *albiflora* Litardière, greatly desired in gardens, and not on record since 1847. It is the only known species with free pollen grains; all the others have tetrads.

E. tetralix L.

This is widespread, petering out east in the Eastern Baltic, but does not grow further south than N. Spain. The type is glandular (McClintock, 1980b), but since glandular and eglandular plants grow side by side, both flourishing, one wonders what the value of glands is.

On moors in early summer it is not rare to find plants with corollas tattered in a way which suggests mite damage. They have been named var. *fissa* Druce. Despite specialists having searched over many years, no direct evidence of mites has been discovered. Later in the year the damage ceases and the corollas are intact.

E. × stuartii E. F. Linton (*E. × praegeri* Ostenfeld)

This is an unfortunate example of a name given originally to an extreme aberration having to be applied to all forms of the taxon (McClintock, 1980d). The clone 'Stuartii' has highly distinctive, very narrow, small dark corollas, quite unlike the usual normal-shaped pink corollas of this intermediate between *E. mackaiana* and *E. tetralix*. Such plants are almost entirely sterile.

In 1980 Charles Nelson and I collected cuttings in Connemara from numerous examples of *E. mackaiana*, *E. × stuartii* and *E. tetralix* with varying amounts of glands and pubescence on the leaves and ovary. These, grown on at Glasnevin, differed also in height, habit, flower colour and flowering time. Indeed, when these have been fully worked on, they may well show almost every intermediate and combination of characters between the glabrous-ovaryed *E. mackaiana* and the hairy *E. tetralix* (Nelson, 1989).

In assessing the populations of this group of species, from Southern Spain northwards, wise folk have pondered how to account for their 'distribution', notably for *E. mackaiana*. To me it is not distribution, but parallel evolution

(McClintock, 1983a: 38). I take *E. tetralix* as the eotaxon, whose genes have combined similarly to produce similar plants in well-separated areas. Since then, the variation has developed naturally by further genetic combination, hybridization and local adaptation. That some of the resultant plants are sterile is no bar to this theory, for there are many examples of sterile forms of good species, not only among heathers. The late Dr C. West agreed that there were similar likely causes to explain apparently identical taxa of *Hieracium* occurring in widely separated areas with no obvious connections. There are analogies elsewhere, such as the double white *Calluna* variants above and single white *E. × darleyensis* below.

The state of affairs has been met by treating the group as consisting of subspecies (Syme, 1872; Macfarlane, 1893), e.g. *E. tetralix* subsp. *tetralix*; subsp. *mackaiana* (Babington) Syme (subsp. *mackayi* (Hooker) Macfarlane); with possibly *E. × stuartii* and *E. × andevalensis*.

The alternative is to group together the taxa with at least some hairs on the ovary, *E. tetralix* and *E. × stuartii*, and those with none, *E. mackaiana* and *E. andevalensis*—as was proposed under *E. andevalensis* above.

E. arborea L.

This species extends further than any other heather, from the Atlantic islands to the Caucasus and down through the Sahara as far as North of Lake Nyassa 9°N 10''S, well south of the equator. In this vast range, dozens of infraspecific names have been published but practically none seem to be of much taxonomic value. The only infraspecific name for any heath in the Mediterranean Check List (Greuter, Burdet & Long, 1986) subsp. *riojana* (Sennen & Elias) Romo was originally given specific rank. Its final character is "Foliis post desicationem persistentibus". The type is at BM and has no leaves at all. Better is var. *alpina* Dieck, an entity which has not been evaluated in the field. 'Alpina' from this population has been grown in our gardens since the end of the last century. This differs in habit, is later flowering, etc. (Turpin, 1981) but its special virtue is greater hardiness, a merit inherited in its superb golden sport 'Albert's Gold'. Pink flowers are mentioned in numerous works, but I have yet to see such a plant. In the Mediterranean area it reaches perhaps 5.5 m, but in Ethiopia and East Africa, where it grows up to 4260 m altitude, its dimensions are far greater, fully tree-size in trunk and height; while in the Atlantic islands it can be greater still, up to 20 m, so far as my records go.

E. lusitanica Rudolph

This is indeed a Lusitanian species, one showing little variation, but the yellow-foliaged 'George Hurst' is markedly tender. In the latter years the species has made itself at home in three areas in S.W. England, and in Brittany. In New Zealand it is a notifiable weed.

E. × veitchii Bean (*E. arborea* L. × *E. lusitanica* Rudolph)

Although there is an allusion to intermediates in Spain in the last century (Laguna, 1890) the two parent species so rarely grow in proximity that a wild hybrid must be a rarity. Hybrids should be looked for where the two species grow on Picoto in the Serra de Monchique, and also where they may meet in N.W. Huelva (B. E. Smythies, personal communication). However, in gardens a

few examples have arisen (Turpin, 1979), the first in the Veitch nursery at Exeter at the end of the last century. Most of these hybrids are more tender than either parent; all have very low or no fertility.

E. carnea L.

The case for the retention of this familiar name appeared in 1987 (Brickell & McClintock, 1987) and has since been recommended for acceptance at the next International Botanical Congress (Brummitt, personal communication). Meanwhile, *E. herbacea* crept in, used by those unaware of the caveats set out by Ross (1967: 68). This is a plant of alkaline areas on the central European mountains. Over 150 cultivars have been named and it is estimated that some 15–20 million plants are sold every year (Brickell & McClintock, 1987). Some are perplexing, such as the largely sterile 'Eileen Porter'. Certain cultivars get pineapple galls, others growing cheek by jowl do not, a useful distinction when selecting garden plants. Yet I have found no record of the galls on wild plants and galls are rare in Britain on any species.

E. erigena R. Ross

Had Rule 69 of the International Code of Botanical Nomenclature made at the last International Botanical Congress existed earlier, it would not have been necessary to disturb the name *E. mediterranea* which had been used unambiguously for this species for nearly 200 years.

This species differs from *E. carnea* in effect only in its natural distribution—the largest colonies are probably those in W. Ireland (Foss, Doyle & Nelson, 1987) and in its height—it has attained almost 4 m, with support, in my own garden. All the other published characters fail, and it is almost impossible to say to which species a young plant belongs. Characters used have included infra-foliar ridges (which rarely seems to work), flowering time (but *E. erigena* can flower before *E. carnea*), length of inflorescence (said to be shorter in *E. erigena*, but 'Brian Proudley' can have inflorescences 30 cm long) and so on. An anomalous, much compacter white cultivar 'W. T. Rackliff' is largely sterile and is in need of investigation.

In view of this similarity, it must be doubtful if *E. erigena* should be regarded as a distinct species; and indeed it has been recognized as *E. carnea* L. subsp. *occidentalis* (Bentham) Lainz. The contrary view is based on the fact that practically all the hybrids between the two species are sterile.

E. × darleyensis Bean

Because the natural distributions of the parents do not come within *c.* 650 km of each other, plants of this hybrid had appeared only in gardens, mostly in England, all as natural seedlings. But lately the hybrid has been made artificially and the parentage confirmed. As stated above, practically all are sterile. But they have the distinguishing feature of hardy hybrids, i.e. the young foliage is discoloured and is yellow, orange or red. A few clones of good species may show this feature too, which means that the converse is not entirely reliable as evidence of hybridity. The white 'Silberschmelze' originated as a sport on the pink 'Darley Dale' in Germany in the 1930s. 'Norman R. Webster' was a seedling in his garden in Scotland in the 1950s. They are indistinguishable (McClintock, 1971).

E. scoparia L.

The typical subspecies grows in the Mediterranean area and is a dull shrub attaining perhaps 4 m.

In the Azores grows *E. scoparia* subsp. *azorica* (Hochstetter) D. A. Webb. This is distinguished by its shorter darker corolla, making the stigma protrude more prominently. But its look is characteristic with the foliage in decorative wavy curls, reminiscent of *Chamacyparis obtusa*, and it "must have reached 30–35 ft" (Guppy, 1917: 395).

In the Canaries is *E. scoparia* subsp. *platycodon* (Webb & Berthelot) Hansen & Kunkel. This is recognizable by its stouter growth with thick spreading leaves, and also by its larger size. It too can grow to 10.7 m (35ft) with a good trunk.

Plants in Madeira come close to subsp. *platycodon*, but have recently been separated as subsp. *madericola* D. McClintock (1989c).

E. vagans L., *E. manipuliflora* Salisb., *E. didyma* Stokes & *E. multiflora* L.

These four species need considering together. It is clear from the lectotype of *E. vagans* L. in LINN and other evidence, that this name refers to what is nowadays called *E. manipuliflora* Salisbury. A case has been put (McClintock, 1989b) for its retention in the sense in which it has been universally used for 200 years or so. Until this is agreed, the plant of Western Europe must take the first valid name given it, viz. *E. didyma* Stokes, which will be used here.

These species grow in distinct areas. *Erica didyma* is in N.W. Ireland (McClintock & Rose, 1970; Nelson & Coker, 1974) S.W. England, W. France, and N. Spain. In central southern France, the Balearics, Italy and the N. Adriatic is *E. multiflora* L., distinct from the other three in its longer and always parallel anthers. *Erica vagans* L. has generally been said to grow in S.E. Italy (cf. Brullo *et al.*, 1986. Minnissala & Spampinato, 1986), the E. Adriatic and in the Aegean and Turkey.

However, the Adriatic and Aegean plants of *E. vagans* are readily separable many of the former very difficult to tell from *E. didyma*. As long ago as 1845 they were distinguished as *E. anthura* Link. A visit to the area around and well to the north of Dubrovnik in October 1988 confirmed the uniformity of the plants in this area, which did not resemble those in the Aegean.

The characters of the Aegean plants, the type of *E. manipuliflora*, are white stems to 3.7 m, short erect leaves and small flowers in a very much interrupted, gappy, inflorescence, and they generally bloom later. In the Adriatic the stems are brown, and not normally over 1.8 m (to 2.3 m rarely), the leaves longer and often all spreading, or at least the lower ones are, and the well-scented inflorescences dense, with negligible or no interruptions. *Erica didyma* can have an even denser, more tapering, inflorescence and longer spreading leaves, but most plants in Dalmatia look very like those of *E. didyma*,

Erica anthura has been placed by Nyman as a variety of *E. vagans* L. (by which he clearly meant *E. didyma*) but it is distinctive enough to warrant specific status, quite apart from the intrusive *E. multiflora* separating their areas.

These four species were well muddled by authors in the last century, so contemporary records should be treated with caution. However, to recognize four species seems to be the clearest way to group them.

A comment on *E. didyma*: there is a curious Cornish variant, grown for nearly 80 years in gardens as 'Viridiflora'. In this the florets are replaced by pale green feathery bracts. These have been proved to be the work of mites, occasionally the

odd pink bell escaping their predation. It comes true from cuttings. Recently analogous forms have been found, also in Cornwall (McClintock, 1989a), and the name f. *viridula* published for them.

E. ciliaris L.

The type is eglandular (McClintock, 1980b), although nearly all the cultivars are glandular. This species has weak stems, but against a spruce tree a plant has reached over 1.8 m on Soussons Downs in Devon (where the colony was planted), and have been seen nearly as tall against a pine tree in Spain.

E. umbellata L.

Anandrous forms exist in most species (cf. Turpin, 1982). In *E. umbellata*. var. *anandra* Lange, the precise deformity has been over-claimed for plants with included anthers such as var. *subcampanulata* DC., which need further study.

E. sicula Gussone

This species was formerly included in the disregarded genus *Pentapera*. It was named from Sicily, its only European station, where it was thought to have become extinct, but has very recently been rediscovered. Elsewhere it can be seen in S. Turkey, Cyprus, Lebanon and Libya. Two subspecies, *libanotica* (Barbey) Yaltirik and *cyrenaica* Brullo & Furnari, have been published, but the validity of their distinctions from subsp. *sicula* needs investigating (McClintock, 1980c; Meikle, 1985). This is a plant of lowland coastal limestone.

E. bocquetii Peşmen

Another plant of limestone but in the mountains, known only at 1750 m in the E. Taurus. It is much smaller in all its parts, with leaves in threes, and anthers without appendages. It has hardly been seen since it was named in 1968 (cf. Browicz, 1983). This species was also included in *Pentapera*.

Hybrids between Erica species in different sections

E. × lazaroana Rivas Goday & Bellot

This was published in 1946 for a cross, said to be frequent in S.E. Spain, between *E. arborea* and *E. umbellata*. No specimens have been seen. Nevertheless, should such a hybrid appear this is the valid name. The authors also called their plant *E. × subcampanulata* (DC.) Goday & Bellot, based on DeCandolle's variety of *umbellata*.

E. watsonii Bentham (*E. ciliaris* L. × *E. tetralix* L.)

This had been long known in England and later in France, but the question to be asked is why is it unknown in Spain (McClintock, 1983a: 37)? The type is glandular (McClintock, 1980b). The inflorescence can differ in shape, but the short appendages to the anthers are the sure key to its identity, plus its almost complete sterility.

E. williamsii Druce (*E. tetralix* L. × *E. vagans* L.)

Still known only from the Lizard with only ten occurrences (cf. Turpin, 1983), yet its parents grow near enough together elsewhere, e.g. in Spain. Is there some sort of incompatibility at work?

The hybrid has recently been produced artificially, notably attempting to get a white one. To this end two white cultivars were crossed and produced an undoubted hybrid, but the flowers were pink. The explanation is to be seen in the minutes of the Royal Horticultural Society Scientific Committee for 7 October 1986 and in Griffiths (1987).

Unsuccessful attempts were made in the past at the fiddling business of crossing heathers. However, in the past ten years or so, Kurt Kramer, a nurseryman of Edewecht—Süddorf in Oldenburg, Germany (McClintock, 1985), independently followed by Dr John Griffiths (1985), a lecturer in colour chemistry at Leeds University and David Wilson, a nurseryman of British Columbia, have had successes. At this stage it is too early to do more than report that this work is going on actively and making worthwhile progress. None of the resultant hybrids, some new to science, including the first successful cross between a European and S. African species, have yet been named.

Bruckenthalia

B. spiculifolia (Salisb.) Reichenb.

This is the counterpart on acid areas of the Balkans of the alkaline *E. carnea* further west. Whether it should be returned to *Erica*, whence it started life, is discussed by Oliver (1989).

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The different types and importance of British heaths

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FARRELL, L., 1989. **The different types and importance of British heaths.** A synopsis of the 22 types of heathland recognized by the National Vegetation Classification is presented. Maps showing their locations are given.

ADDITIONAL KEY WORDS:—*Calluna* – heathland – National Vegetation Classification – Nature Conservancy Council.

The National Vegetation Classification began in 1976. It is based at Lancaster University and the main author of the publication is Dr John Rodwell (Rodwell, 1988). The aim of this Nature Conservancy Council project is to provide a complete description and classification of the range of British plant communities, omitting only those deliberately planted for agriculture or horticulture. This will give us a working scheme enabling us to standardize our approach to habitat and vegetation survey, mapping, monitoring and evaluation. It will also enable a comparison to be made between British and European vegetation.

The heathland chapter was completed in June 1988. It distinguishes 22 types, 12 of these being essentially lowland heath types, usually found occurring on land below 300 m. These 12 types are now described and their distributions in Britain illustrated (Table 1 and Figs 1–13).

Britain is part of the Western Atlantic heathland zone (Fig. 14) distributed along the Atlantic seaboard from Norway in the north, to Portugal in the south and eastwards into Germany. Examples of three European heathland types are found in Britain:

1. Anglo-Norman, NVC type H2 *Calluna/Ulex minor*.
2. Armorican, NVC types H3 *Ulex minor/Agrostis curtisii* and H4 *Ulex gallii/Agrostis curtisii*.
3. Ibero-Atlantic, NVC type H5 *Erica vagans/Schoenus nigricans*.

Because of our oceanic climate, wet and humid heathland types are better developed and more extensive in Britain than in Europe.

In 1976 a report was produced for the Council of Europe on the heathlands of Western Europe (Noirfaise & Vanesse, 1976). Although the facts and figures have changed since then, and the extent of heathland has declined even further, they indicate the decrease in the habitat that was widespread.

TABLE 1. National Vegetation Classification for British heaths

	NVC Type	Community	Distribution
Lowland	H1	<i>Calluna/Festuca ovina</i>	S.E. & E. England (Breckland)
	H2	<i>Calluna/Ulex minor</i>	Weald, Sussex to Dorset
	H3	<i>Ulex minor-Agrostis curtisii</i>	New Forest, W. to Dorset
	H4	<i>Ulex gallii-Agrostis curtisii</i>	S.W. England & S. Wales
	H5	<i>Erica vagans/Schoenus nigricans</i>	The Lizard, Cornwall
	H6	<i>Erica vagans/Ulex europaeus</i>	The Lizard, Cornwall
	H7	<i>Calluna/Scilla verna</i>	Coastal cliffs & islands
	H8	<i>Calluna/Ulex gallii</i>	S.W. England, Wales & N. Midlands
	H9	<i>Calluna/Deschampsia flexuosa</i>	S. Pennines & Midlands
	H10	<i>Calluna/Erica cinerea</i>	Low altitudes in Scotland
	H11	<i>Calluna/Carex arenaria</i>	Coastal dunes & sandy shingle
	H12	<i>Calluna/Vaccinium myrtillus</i>	Lower 'moorland' of S.W. & N. England & Scotland
Upland	H13	<i>Calluna/Cladonia arbuscula</i>	
	H14	<i>Calluna/Rhacomitrium lanuginosum</i>	
	H15	<i>Calluna/Juniperus communis nana</i>	
	H16	<i>Calluna/Arctostaphylos uva-ursi</i>	
	H17	<i>Calluna/Arctostaphylos alpinus</i>	
	H18	<i>Vaccinium myrtillus/Deschampsia flexuosa</i>	
	H19	<i>V. myrtillus/Cladonia arbuscula</i>	
	H20	<i>V. myrtillus/Rhacomitrium lanuginosum</i>	
	H21	<i>Calluna/V. myrtillus/Sphagnum</i>	
	H22	<i>V. myrtillus/Rubus chamaemorus</i>	
Wet Heath	M15	<i>Scirpus cespitosus/Erica tetralix</i>	Upland transition
	M16	<i>E. tetralix/Sphagnum compactum</i>	Widespread

a. In Sweden and Denmark 60–70% was lost between 1860 and 1960. In 1976 13 575 ha remained chiefly in Danish reserves.

b. In N.W. France there were estimated 14 396 ha in 1979 (Nicholson, 1979). This has now declined even further (personal observation).

c. In W. France 200 000 ha remained in 1955, but this represented only one-third of the 1770 total.

d. The Belgo-Dutch Campine used to be covered by vast tracts of heath. It has been reduced by 90%. Most of the 1500 ha left is in nature reserves and military camps.

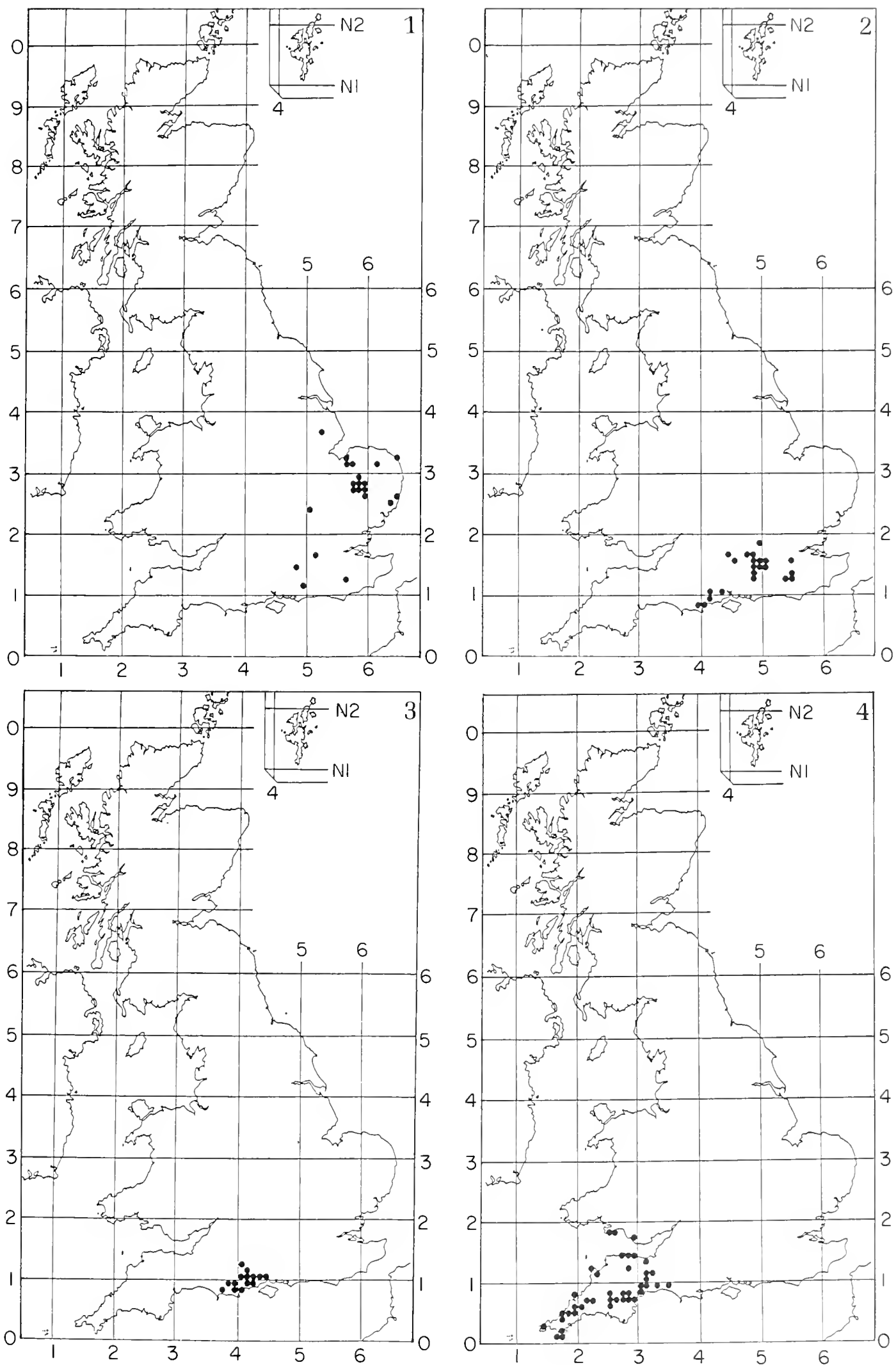
e. Much of the heathland on the German plain has been lost.

f. Friesian coastal heaths have suffered greatly from tourism. In 1970 about 7000 ha remained.

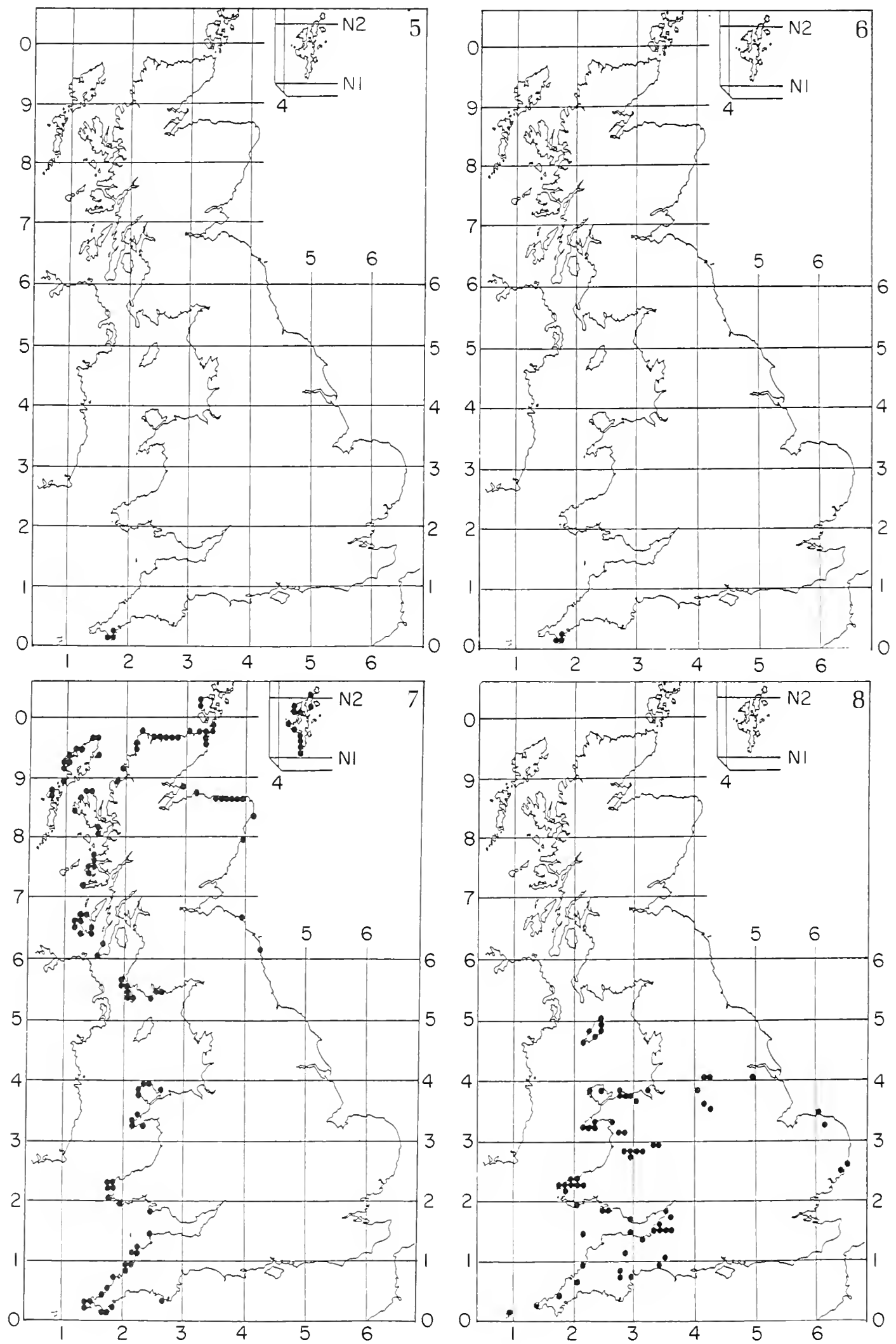
g. Holland now has 42 000 ha left, where previously there were 800 000 ha.

This gives total of approx. 280 000 ha of heathland remaining in the rest of Europe.

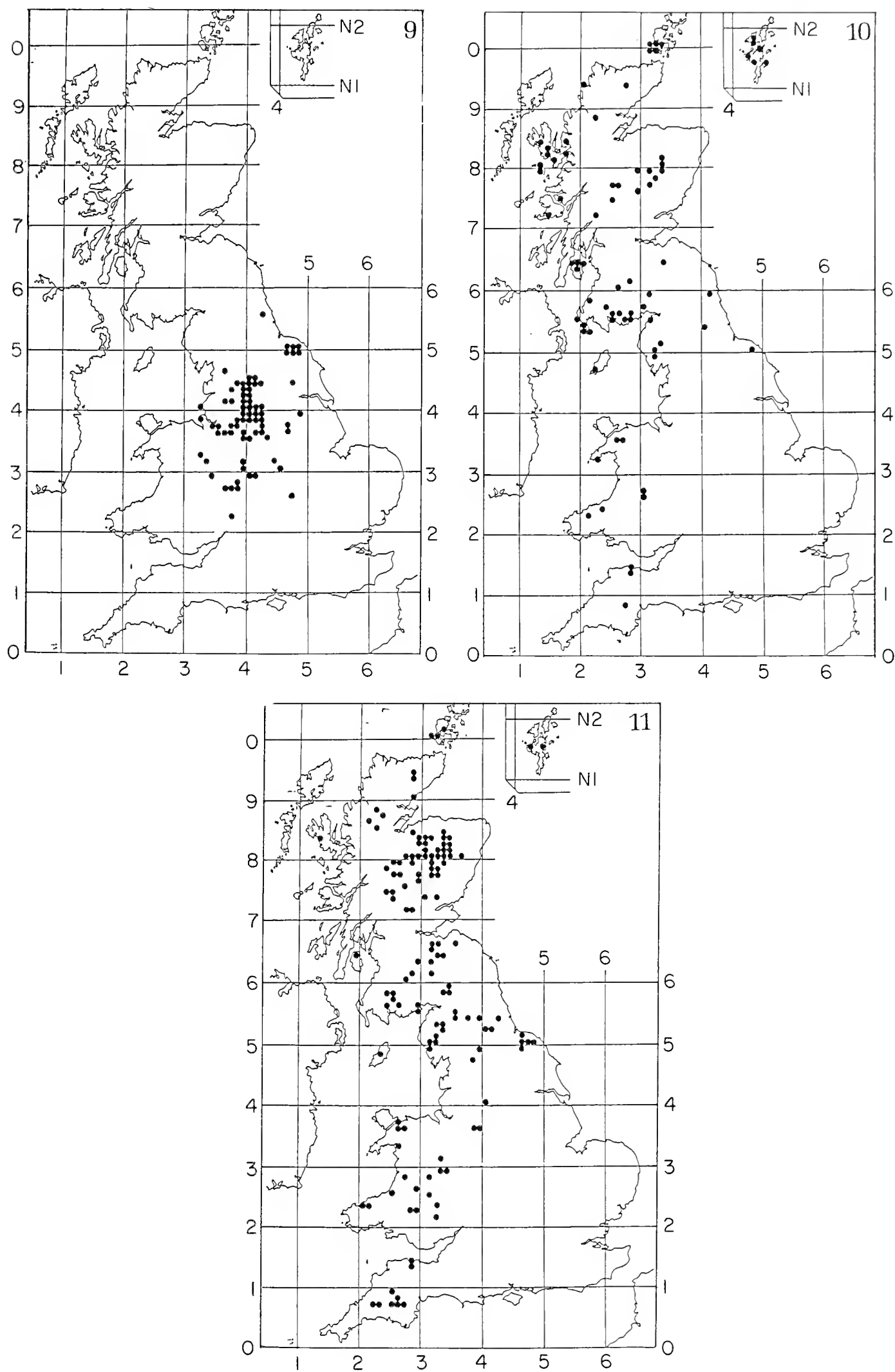
In Britain, the estimated extent in 1980 was 60 000 ha. Figures for England and Wales are reasonably accurate and further survey work is underway in Scotland at the present time. The acreages for different counties are shown in



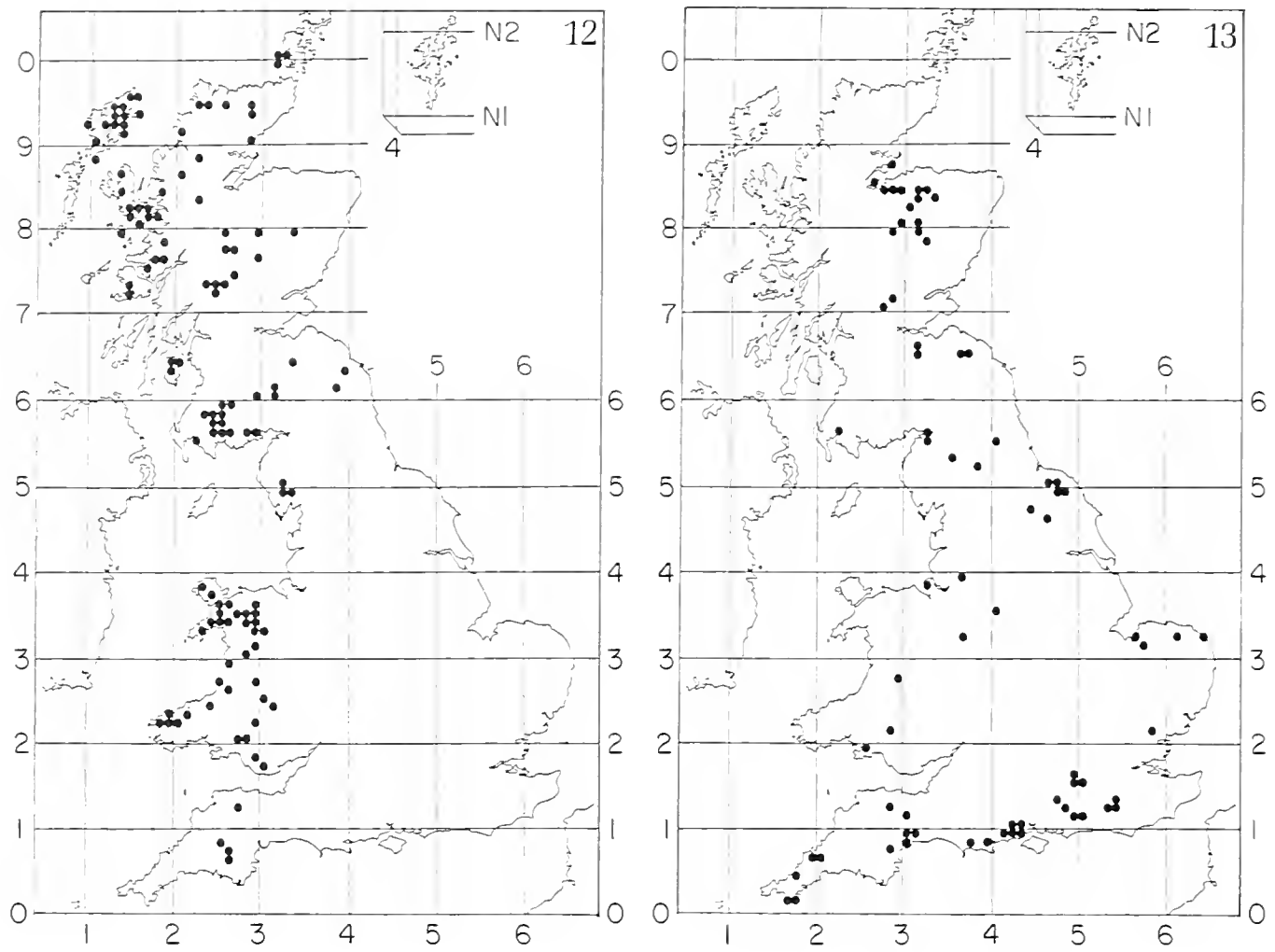
Figures 1-4. Locations of heaths. Fig. 1. H1, *Calluna vulgaris*-*Festuca ovina*. Fig. 2. H2, *Calluna vulgaris*-*Ulex minor*. Fig. 3. H3, *Ulex minor*-*Agrostis curtisii*. Fig. 4. *Ulex gallii*-*Agrostis curtisii*.



Figures 5-8. Locations of heaths. Fig. 5 H5, *Erica vagans*-*Schoenus nigricans*. Fig. 6. H6, *Erica vagans*-*Ulex europaeus*. Fig. 7. H7, *Calluna vulgaris*-*Scilla verna*. Fig. 8. H8, *Calluna vulgaris*-*Ulex gallii*.



Figures 9–11. Locations of heaths. Fig. 9. H9, *Calluna vulgaris*-*Deschampsia flexuosa*. Fig. 10. H10, *Calluna vulgaris*-*Erica cinerea*. Fig. 11. H11, *Calluna vulgaris*-*Carex arenaria*.



Figures 12, 13. Locations of wet heaths. Fig. 12. M15, *Scirpus cespitosus*-*Erica tetralix*. Fig. 13. M16, *Erica tetralix*-*Sphagnum compactum*.



Figure 14. The main areas (hatched) in which lowland heaths occur in Western Europe (from Gimingham, 1972). Limit of Cfb Climate indicates oceanic type climate zone.

TABLE 2. Extent of lowland heathland in Britain in 1980s

Area	Size (ha)
England	
Bedfordshire	<i>c.</i> 20
Berkshire	515
Breckland	4529
Buckinghamshire	5
Cornwall & Scilly Isles (not Lizard)	2080
2080 Cumbria	520
Devon	<i>c.</i> 2000
Dorset	5670
Durham	<i>c.</i> 200
Essex	25
Hampshire	16 845
Humberside	13
Kent	55
Lincolnshire	<i>c.</i> 460
Lizard	2520
Merseyside	103
Norfolk (not Breckland)	729
North Yorkshire	<i>c.</i> 894
Nottinghamshire	<i>c.</i> 50
Oxfordshire	3
Somerset	<i>c.</i> 200
Suffolk Sandlings	1580
Surrey	3149
Sussex	1171
Westmidlands	
	Total
	<i>c.</i> 45 021
Scotland	
Aberdeen	675
Angus	448
Ardnamurchan	261
Argyll	200
Borders	1217
Caithness	486
Central	52
Dumfries	300
Fife	227
Inverness	29
Lothian	771
Orkney	200
Perth & Kinross	202
Ross & Cromarty	100
Shetland	200
Speyside	225
Sutherland	290
Western Isles	100
	Total
	6066
Wales	
Gwynedd	1636
Pembrokeshire & Ceredigion	<i>c.</i> 5000
	<i>c.</i> 6635
	Grand Total
	57 222

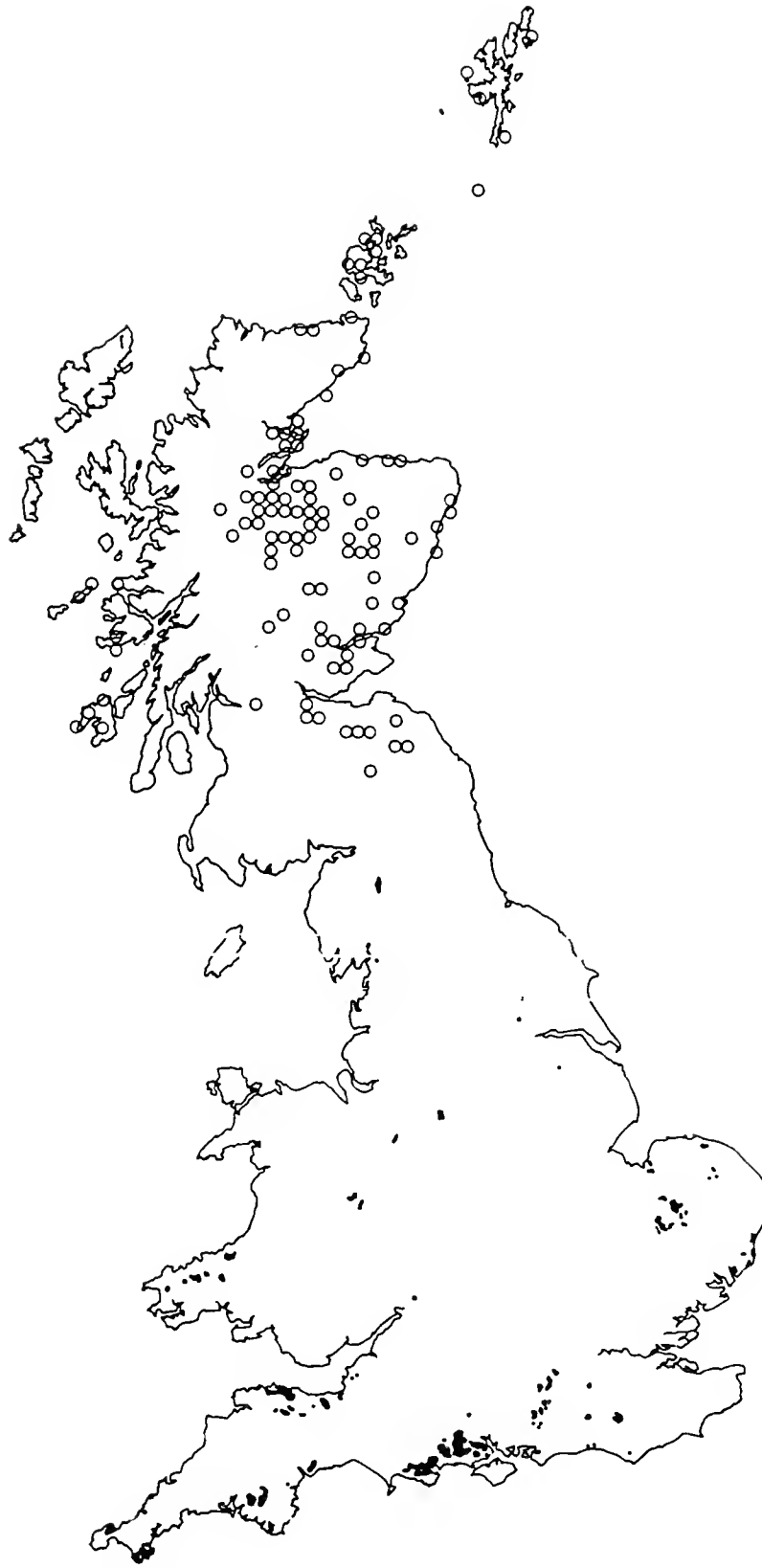


Figure 15. The distribution of lowland heath in the British Isles. Accurate Scottish data still to be collected.

TABLE 3. British heathland sites designated as biogenetic reserves

The Lizard NNR
Studland Heath NNR
Arne NNR and RSPB Reserve
Hartland Moor NNR
Morden Bog NNR
Cavenham Heath NNR
Thursley Common NNR
Sands of Forvie and Ythan Estuary NNR
Rhinog NNR
Muir of Dinnet NNR
Wan Fells SSSI
Lazonby Fells SSSI

TABLE 4. Eight additional heathland sites for possible inclusion in the future

St David's Commons—Wet & dry heath
Pebblebed Commons—Armorican
Lakenheath Warren—Anglo Norman
Bannau Preseli and Chomin Carnigli—Welsh/Irish
New Forest—Anglo Norman
Invernaver—Scottish
North Hoy—Caledonian
Torrs Warren—Dune heath

Table 2 and the distribution by Fig. 15. So Britain represents about 18% of the total European resource.

At the third European Heathland Workshop held in Mols, Denmark, in August 1988, it was agreed by all participants that an updated version of the Council of Europe report should be produced. Representatives of each country were nominated and the author agreed to co-ordinate the data being gathered over the next two years. Each country was clearly of the opinion that a European statement carried more weight when trying to protect the declining heathland resources, than did a statement coming simply from one country.

In 1979 a biogenetic reserves group was set up to distinguish the most important heaths in Europe and to provide them with further protection. Twelve sites have been listed for Britain with recommendations for another eight (Tables 3 & 4).

So why are our British heaths important?

1. They represent a large percentage of the remaining Europe resource.
2. The wet and humid heaths are particularly well represented because of our geographical position in Europe.
3. Maritime heath is geographically widespread in Britain. As Britain has a more extensive coastline than most European countries, so there are more examples of maritime and coastal heath.
4. Mosaics of wet and dry heath as represented in Pembrokeshire are thought to be unique.

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Management of heather for game and livestock

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MOSS, R., 1989. **Management of heather for game and livestock.** Heather provides food and cover for moorland herbivores. Interactions between soils, drainage, climate, muirburn and grazing affect the species composition, structure and growth of moorland swards. Together, these aspects of a sward determine which and how many herbivores it can support. Grazing and burning maintain much heather ground which would otherwise revert to scrub or woodland. Heavy grazing by ungulates can turn a heathery sward into a graminaceous one, so reducing numbers of grouse and mountain hares. On good soils, invading graminoids are usually nutritious grasses and the carrying capacity for ungulates can increase. On poor soils, grazing and frequent burning may lead to swards dominated by poor quality grasses and sedges so that the carrying capacity for ungulates declines. One way of reinstating heather dominance is to remove livestock; where there are no heather plants left, other techniques may be necessary.

ADDITIONAL KEY WORDS:— Grazing — grouse — mountain hares — muirburn — red deer — sheep — upland.

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INTRODUCTION

Heather, Ling (*Calluna vulgaris* (L.) Hull), is, in Britain, a major but declining resource for upland game species, such as red grouse (*Lagopus lagopus scoticus* (L.) Latham), mountain hares (*Lepus timidus* L.), black grouse (*Tetrao tetrix* (L.) Short), and red deer (*Cervus elaphus* L.), and also for hill sheep and cattle. Most heather occurs as dominant or co-dominant in open heath, bog, moorland and summit vegetation. It provides both food and cover but has been little valued by farmers because of its relatively poor nutritive value (Grant *et al.*, 1982). By both design and accident, much management of domestic stock has tended to suppress or eliminate heather and so reduce the range and abundance of heath-dependent small game species such as red grouse, black grouse and mountain hares (Hewson, 1956; Miller, Jenkins & Watson, 1966; Yalden, 1971, 1979, 1986; Hope Jones, 1987; Parr & Watson, 1988).

There have been four main management tools. 1. Fertilizing and reseeded heather ground with grass, often with ploughing. 2. Grazing. 3. Burning. 4. Draining. The response of heather to grazing and burning varies greatly with their intensity and pattern, and also depends upon soil and climate, the species composition and structure of the sward, and the animals doing the grazing. Grazing and burning of moorland prevent regeneration of natural scrub and forest, and can result in heather being replaced by grassy vegetation (Grant & Maxwell, 1988). When combined with trampling and poaching, these practices can also lead to erosion of soils, especially peats. The productivity, species composition and structure of heathery swards are determined partly by the domestic and wild animals using them. In turn, the type of sward affects the species, density and productivity of the animals present.

The possible interactions between soils, plants, grazing animals and climate are many, and poorly understood. Here I shall briefly outline some broad working principles.

IMPACT ON HEATHER OF DIFFERENT ANIMALS

Red grouse eat largely heather all year (Eastman & Jenkins, 1970), though they can benefit from supplements of other foods. Even at high densities, red grouse eat probably less than 10% of a heather sward's annual production of green shoots (Savory, 1978). Young heather can withstand removal of 40% of its annual production of green shoots without affecting its productive capacity the following year (Grant *et al.*, 1978). The only gross effect that grouse are likely to have on a heather sward is to delay very slightly its mean rate of increase in height. Black grouse, although about twice the weight of red grouse (1200 *vs.* 600 g for average adults), eat a smaller proportion of heather (Johnstone, 1969) and do not reach the same high densities. Their impact, therefore, is likely to be negligible.

Mountain hares (2.5–3.0 kg) also eat much heather (Hewson, 1962). Of the small game species, hares have the biggest impact on heather but even when abundant they usually only slow its growth and alter its form (Welch & Scott, 1984; Moss & Hewson, 1985).

Ungulates, unlike red grouse and mountain hares, seem to need a fairly high proportion of graminoid foods in their diet and do not thrive on heather alone (Grant *et al.*, 1982; Mitchell, Staines & Welch, 1977). Hence their impact on heather depends partly upon the availability of palatable grasses and other graminoids. Close by grassy swards, grazing and trampling by red deer, sheep and cattle can lead to reduction or elimination of heather (Welch, 1984). On well-drained moorland soils, heather is often replaced by grasses; these can attract more grazers which eat more heather and cause further expansion of grass. Many of the once-heathery hillsides of north Wales, for example, are now grassy sheep walks for this reason; the heather-dependent red grouse is far scarcer there than it was and there may be only a few hundred black grouse left in Wales (Hope Jones, 1987).

In the Scottish Highlands, numbers of red deer have increased markedly in recent decades (Red Deer Commission, 1987). During this increase, annual variations in deer performance seem to have been density-dependent (Clutton-

Brock, Albon & Guinness, 1987) and related to food supplies and snow cover (Albon & Clutton-Brock, 1988). If food is limiting, as this suggests, numbers of red deer have presumably been approaching the carrying capacity of the Scottish Highlands and one might have expected catastrophic mortality in severe winters. Instead of such mortality, however, the extent of grassy swards has increased in some glens (Watson, 1989). Heavy grazing by red deer, perhaps together with sheep, may have increased the carrying capacity of Scottish hills for red deer by making more grass available. If so, deer as well as sheep may have contributed to a reduced carrying capacity for grouse.

MUIRBURN

The size and frequency of fires in a burning regime depend upon their purpose. Red grouse are territorial, needing relatively short heather for food and tall heather for cover (Watson *et al.*, 1976). Burning moorland heather on a 10–20 year rotation in small patches or narrow (20–35 m) strips increases the amount of edge between tall and short heather. This allows small territories and consequently high densities. Since grouse prefer to feed within a few metres of cover (Savory, 1974), large expanses of very short heather support few grouse. At the other extreme, large areas of tall, old heather usually support lower densities of grouse than patchily-burned areas but higher densities of grouse than large areas of very short heather.

Black grouse are usually associated with taller heather than red grouse but how muirburn affects them is not well understood. Mountain hares are usually associated with short heather and occur widely on the dwarf shrub summit heaths of Scotland, which are not burned but kept short by wind and weather. They also occupy lower ground, particularly where some heather is kept short by muirburn and grazing.

Sheep management usually involves bigger and more frequent fires than grouse management. Young heather, newly regenerating after a fire, is more nutritious than old heather; fire also burns tussocks and mats of dead grass, making room for new, accessible leaves which sheep can graze.

Management of deer forests is generally less intensive than for either red grouse or sheep. Fires of large or moderate size are typically burned, but deer forests generally contain more old heather than sheep walks.

SOILS

The effects of grazing and burning on an initially heathery sward differ considerably with soil and bioclimatic zone. Well-drained, lime-rich soils can attract heavy grazing by sheep and deer, associated with development of herb-rich, grassy swards. Grass swards can develop on many well-drained hill soils, but the more acid soils usually support more of the less palatable grasses. On well-drained acid soils, typical of eastern Scottish moors, heather can tolerate moderate grazing by ungulates without being displaced by grass. In these circumstances, heather regenerates freely following fire and this is ideal for grouse management.

If heather on the more basic moorland soils is not overgrazed, it grows faster, is nutritionally richer and supports higher average densities of grouse than on acid soils (Moss, 1969). Heather can also be enriched by artificial fertilizing, but other grazing animals can eat the fertilized heather, so annihilating potential benefit to grouse (Watson *et al.*, 1977). The growth and nutritive value of heather are generally poorest on deep blanket peats, where the main input of nutrients is from the atmosphere (Moore, Dowding & Healy, 1975).

Where drainage is poor, heather growth and nutritive value can sometimes be improved by draining (Phillips & Moss, 1977). Surface drains may have little effect since lateral percolation of water in peaty soils is often slow. Where drainage is impeded by iron pans, shattering them with a deep subsoiling tine can be effective.

Sward management on wet acid soils and deep peat often involves large, frequent fires aimed at producing new growth for sheep. How grazing and burning interact under such circumstances is not well understood. Some stages which occur, however, are clear. First, heather tends to be replaced by graminoids. Second, more palatable graminoids are grazed preferentially and on poor soils can be replaced by less palatable ones. At the same time, rapidly colonizing graminoids tend to be replaced by slower colonizers. These two processes often act in the same direction since faster colonizing species are generally more palatable. Third, trampling, especially in the fire-induced absence of stabilizing root, mat and tussock, can accelerate erosion, particularly of peat. Fourth, the erosion of peat down to mineral soil can lead eventually to 'islands' of peat remnants separated by erosion channels (D. Henderson, personal communication). This makes further burning impracticable and may in time lead to the establishment of patches increasingly dominated by heather and protected from burning by erosion channels.

SWARD HEIGHT, STRUCTURE AND SCALE

Small-scale patchworks of tall and short heather benefit red grouse (above). Tall heather can also shelter red deer (Mitchell *et al.*, 1977) and sheep. Lance & Triggs (1974) showed that lambs grew better in a patchwork than on large-scale, frequent fires typical of much hill sheep management. Small-scale burning, however, is labour intensive.

The relationship between the height and age of heather varies with local conditions: heather of a given age is taller on low, fertile, sheltered and lightly grazed areas. For feeding, mountain hares (Hewson, 1974) and sheep (Milne, Bagley & Grant, 1979) prefer short, young, pioneer heather; red grouse prefer slightly older and taller heather up to 30 cm (Moss, Miller & Allen, 1972) whilst limited evidence suggests that red deer prefer heather over 25 cm in height (Hewson, 1976).

A main cause of long term declines in red grouse has been the poor management of heather swards by too-frequent burning, underburning and overgrazing, and associated loss of accessible food or cover (Watson *et al.*, 1976). Small-scale patchworks of long and short heather, experimentally created on poorly managed areas of low grouse density in Mull (Watson, Moss & Parr, 1987) and Mayo (Watson & O'Hare, 1979), were accompanied by increases in grouse stocks. A puzzle is that these increased densities were still lower than those

obtained with similar management on traditional grouse moors. This suggests an effect of scale, such that an area of well-managed heather of a hundred hectares or so, set in a large area of poorly managed ground, supports lower densities than much bigger tracts of well-managed heather.

This may help to understand the dramatic decline of red grouse in west Scotland relative to the east. If one starts with a large area of good-quality habitat and allows a small proportion of it to deteriorate, grouse numbers may initially fall in parallel with the proportion of poor habitat. At some point, however, the ratio of poor to good habitat may reach a critical point. The good habitat may be so fragmented that it comprises islands of good habitat in a sea of poor. The effect of scale, above, may then cause an accelerated reduction in grouse stocks disproportionate to the amount of poor habitat.

GROUSE *VERSUS* SHEEP

Heavy grazing by ungulates, especially when combined with overburning, can displace heather, grouse and hares. If a landowner wants both sheep and grouse, for example, he must manage the structure of his sward. This should include a reasonable mixture of long and short heather. Rotational fencing may be a practical way of maintaining some long heather in the face of heavy grazing, particularly where heather regenerates poorly. However, many British uplands have passed the point where heather can be restored by exclusion of livestock. There are too few heather plants left. Where viable heather seeds remain in the soil, regeneration by tillage may be possible, perhaps with the help of selective herbicides to reduce competition from grasses (Reconciliation Project, 1988).

With more food from the lowlands there is less justification for keeping subsidized sheep in the uplands. There is also increasing demand from newly affluent Britons for game shooting. It may be time for more research into improved methods of heather management.

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The invertebrates of heather and heathland

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WEBB, N. R., 1989. **The invertebrates of heather and heathland.** The southern heathlands of Great Britain have long been renowned amongst entomologists. The invertebrates fall into two groups: species which feed on heathland plants—about 40 in the case of *Calluna*—and a second group which depends on the particular physical conditions provided by heathland, such as hot dry sandy areas or the micro-topography of *Sphagnum* bogs. The ecology of representative examples will be described, and the effects of fragmentation and isolation of the heathlands on the distribution and abundance of invertebrates discussed.

ADDITIONAL KEY WORDS:—*Calluna* – Erica – fauna – insects.

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INTRODUCTION

Most of the north-west European heathlands are anthropogenic. They came into existence following forest clearances which commenced three to four thousand years ago, and have been perpetuated by the use of the land (Gimingham, 1972; Webb, 1986). In evolutionary terms this is a relatively short period for a well-defined community to develop.

Changes in the structure and composition of the vegetation through succession need to be controlled by management. Invertebrates generally respond rapidly to small scale changes in their environments, and it is interesting to speculate to what extent the management of the vegetation by man has been a selective force modifying the life cycles and dispersal abilities of many insects.

Invertebrates have complex life cycles. The habitat of each stage—egg, larva, pupa and adult—is different and these habitats must occur correctly in time and space for the life cycle to be completed.

The invertebrate fauna will be reviewed in two sections: first, the fauna which feeds on heather (*Calluna vulgaris*) and second, that which occurs more generally on heathland. Associated with the fauna of *Calluna* is that dependent on species of *Erica*, this is of similar composition but less well known. The presence of

subordinate plant species in the vegetation will also affect the composition of the general fauna. Much of the general fauna of heathland depends on the physical conditions, particularly those accompanying changes in vegetation structure throughout the growth phases of heather (Watt, 1955). Other species require conditions such as hot, dry, sand or acid wetlands.

HERBIVORES OF *CALLUNA*

Calluna is an evergreen sclerophyllous plant well adapted to xeric and nutrient poor conditions. The leaves have a thick cuticle, thick-walled cells, and high content of lignin, tannins, phenolic compounds, resins and essential oils. These features may be a response to nutrient-poor conditions, especially to a deficiency of phosphorus (Specht, 1979) and their presence increases the flammability of the vegetation with important consequences for the community through management by burning.

Theories of plant-herbivore interaction suggest that, in many plants, the production of secondary metabolites has been evolved as a defensive response to invertebrate herbivore attack. Recently, it has been suggested that the accumulation of carbon-based secondary compounds may be a function of the carbon-nutrient balance of the plant and not primarily a response to herbivore attack. If nutrients are not limiting, carbon is used for growth, but under conditions of nutrient stress there is an accumulation of carbon-based secondary compounds. (Tuomi *et al.*, 1988; Edwards, in press.) *Calluna* may be a plant in which secondary compounds have been produced as a result of environmental stress and not as a response to herbivore attack.

About forty species of insect depend on *Calluna* for food and this is approximately the number to be expected from the architecture and geographical distribution of *Calluna* (Lawton & Schroder, 1977). When compared with plants which contain higher levels of nitrogen, the fauna of *Calluna* occurs at low densities. It contains species which tend to be sedentary, often remaining on the same plant, and pass through one generation a season. In some cases, two seasons are required for the completion of the life cycle (McNeill & Prestige, 1982).

Studies on the herbivore fauna of *Calluna* (McNeill & Brown, personal communication) have shown that the density of herbivores depends seasonally on the levels of nitrogen in the shoots and that the number of herbivore species present during the heathland succession is related to spatial and architectural diversity of the plants and the levels of phenolic compounds.

THE FAUNA OF *CALLUNA*

The flowers of *Calluna* contain good numbers of thrips (Thysanoptera), the commonest being *Ceratothrips ericae*. These insects, which feed on pollen, lay their eggs in the nectaries at the base of the flowers. Females moving from plant to plant to oviposit act as important pollinators (Haegerup, 1950).

There are about six species of Hemiptera: Heteroptera and five species of Homoptera associated with heather (Table 1). These have sucking mouthparts and mostly feed on the cell sap but some, such as *Ulopa reticulata*, tap into the phloem and others such as members of the Lygaeidae, feed on seeds. The

Heather Psyllid (*Strophingia ericae*) has been shown to have a lowland race which completes its life cycle in one year and an upland race requiring two years (Parkinson & Whittaker, 1975).

In contrast, the Lepidoptera have biting mouthparts and eat the shoots or foliage (Table 1). Members of the Eupitheciidae eat the flowers. Some of the best-known and attractive heathland insects occur amongst the Lepidoptera such as *Saturnia pavonia* and *Macrothylacia rubi*. *Lycophotia porphyrea* and *Anarta myrtilli* are two very similar-looking noctuid moths which feed on heather, and which may be very abundant. The caterpillars are less easily found, especially those of *L. porphyrea* which feed at night. There are about 17 species of moth which feed on heather of which about eight are monophagous.

Beetles (Coleoptera) associated with heather eat either foliage or in the case of the larvae of some weevils, the roots. The Heather Beetle (*Lochmaea suturalis*) is the most familiar species. Both the adult beetles and the larvae eat heather foliage. The Heather Beetle, which is about 6 mm long, occurs widely on all heathlands, although its abundance varies locally. In the lowlands large outbreaks occur from time to time (approximately ten-yearly), but on the northern grouse moors outbreaks are more frequent and it can be a pest. Severely-attacked plants show a characteristic reddening ('frosted heather') of the foliage and on close inspection the damage caused by the beetles is clear.

The adult beetles swarm in the spring (March/April) when they also mate. The eggs are laid on the heather plants or on the litter surface and hatch in 3–4 weeks. The three larval stages feed on the *Calluna* plants from June until early

TABLE 1. A list of the insects more commonly found feeding on heather (*Calluna vulgaris*). A fuller list appears in Webb (1986). Species marked * do not feed exclusively on *Calluna*

Thysanoptera
Ceratothrips ericae

Hemiptera: Heteroptera
Kleidocerys truncatulus
*Stygnocoris pedestris**
Macrodema micropterum
Ischnocoris angustulus
Scolopostethus decoratus
Orthotylus ericetorum

Lepidoptera
Coleophora juncicolella
Coleophora pyrrhulipennella
Aristotelia ericinella
Lita virgella
Scythris empetrella
Acleris hyemana
*Macrothylacia rubi**
*Saturnia pavonia**
Eupithecia goossensiata
Eupithecia nanata
*Gymnoscelis rufifasciata**
Pachynemia hippocastanaria
*Paradiarsia glareosa**
Lycophotia porphyrea
Xestia castanea
Xestia agathina
Anarta myrtilli

Hemiptera: Homoptera
Ulopa reticulata
Scleroracus corniculus
Scleroracus plutonius
Zygina rubrovittata
Strophingia ericae

Coleoptera
Lochmaea suturalis
Strophosomus sus
*Micrelus ericae**

August when they pupate in the litter. The immature beetles emerge in September and continue to feed on the *Calluna* plants until they start to hibernate in the litter (Cameron, McHardy & Bennett, 1944).

The dynamics of heather beetle populations are poorly understood. Two predators, the pentatomid bug *Rhacognathus punctatus* and the ladybird *Coccinella hieroglyphica* have been suggested as population regulators but these are uncommon on heathland. The eulophid wasp *Aescodes mento* which parasitizes the larvae is sufficiently abundant but its role as a population regulator has yet to be investigated. The parasitoid was first recognized in the north of Britain (Golightly, 1962); levels of parasitism up to 55% have been reported (Waloff, 1987).

In recent years in the Netherlands, defoliation and death of *Calluna* plants through beetle outbreaks have become more frequent and have led to the replacement of dwarf shrub communities by grasslands dominated by *Deschampsia flexuosa* or *Molinia caerulea* (Brunsting, 1982). The increases in fecundity, growth rates and survival of the beetles leading to increases in population have been attributed to increases in deposition of atmospheric nitrogen, particularly ammonia produced by intensive farming operations.

HEATHLAND INVERTEBRATES

Although these invertebrates are considered to be heathland species, they do not depend directly on heather as a food plant. Many can be found in other types of vegetation. They depend on the physical conditions on heaths and the microclimate within dwarf vegetation. This varies with the growth phases of the heather (Table 2), leading to changes in the habitats of many invertebrates within a single heath. The habitat requirements of the Silver-studded Blue (*Plebejus argus*) and the Grayling (*Hipparchia semele*) typify many of these features.

Plebejus argus occurs both on heathland and on calcareous grasslands. Few grassland colonies remain in Britain and those on heathland have decreased

TABLE 2. Characteristics of the heathland microclimate (after Barclay-Estrup, 1971)

	Pioneer	Building	Mature	Degenerate
Age (years)	3-10	7-13	12-28	16-29
Percentage of over-storey	10	85	75	35
Illumination at ground level	High	Reduced to 2% of ambient	Increased to 20% of ambient	Up to 75% of ambient
Surface max.	Highest	Intermediate	Lowest	Second highest
Surface min.	Intermediate	Second highest	Highest	Lowest
Soil max.	High	Lowest	Intermediate	Highest
Soil min.	Low	Lowest	Highest	Intermediate
Saturation deficit	High	Low	Low	Increasing (high on warm clays)
Air movement	Maximal	Negligible	Restricted	Much greater
Throughfall	At a maximum	At a minimum	Still at a low level	Much greater, approaching that of pioneer phase

considerably. The strongholds are now the heaths of Dorset and the New Forest (Heath, Pollard & Thomas, 1984). Its food plants are *Lotus corniculatus*, *Helianthemum nummularium*, *Ulex* spp, *Calluna vulgaris*, *Erica cinerea* and *E. tetralix*. There is a very close association with ants: larvae are tended by *Lasius alienus* or *L. niger*, and the pupa is taken into the ants' nest. This butterfly occurs in discrete colonies on heathland and is one of the most sedentary of British butterflies, adults seldom flying more than five metres from the point where they emerge. Its habitat is fairly short open heath vegetation similar to the building phase or alternatively, humid heath where the presence of *Erica tetralix* in the vegetation provides a similar open structure. The openness of the vegetation and the levels of insolation determine the distribution of the ants, with which the Silver-studded Blue is associated.

Hipparchia semele is a grass-feeding species and occurs over a wide range of soil and vegetation types. Although this species is common on many of the southern heaths, it is not confined to heathland. It prefers sheltered, extremely well-drained sites with sparse vegetation (Heath *et al.*, 1984); a requirement that can be met on grasslands as well as heathlands. However, it has declined considerably at many inland localities and is now rare except on the southern heaths and on the coasts. In this butterfly, cryptic colouration is well developed and at rest the butterfly is difficult to discern against bare sandy soil.

A variety of other notable lepidoptera are associated with the southern heathlands and include *Cleora cinctaria*, *Chlorissa viridata* and the *Pachythelia villosella* with its remarkable life cycle (Heath, 1946).

Bare sandy areas on heathland are important for a variety of insects such as ground beetles, tiger beetles and fossorial wasps. In recent years heath management has tended to favour a uniform cover of dwarf shrubs with few of the bare sandy areas.

The wetlands of the southern heathlands are important habitats for dragonflies (Odonata). The majority of British species are associated with acid waters and the wide variety from small streams, pools and seepages on *Sphagnum* bogs, provide a wide range of habitats.

Studies on the invertebrate community of the Dorset heathlands (Webb, 1989; Webb & Hopkins, 1984; Hopkins & Webb, 1984) have investigated the effects of fragmentation, isolation and surrounding vegetation types. The observed responses of the invertebrates have suggested ways in which heathland can be assessed and how the remaining heathland patches should be viewed within a landscape matrix in which there is interaction between the fauna of heathland patches and their surrounding vegetation.

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An assessment of the importance of heathlands as habitats for reptiles

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SPELLERBERG, I. F., 1989. **An assessment of the importance of heathlands as habitats for reptiles.** Britain has a species-poor reptile fauna of six species. Although they occur in association with various types of plant communities, most species seem to be associated with heathlands. The lizard *Lacerta agilis* is particularly associated with heathlands but data presented here suggests that the vegetation structure of typical, undisturbed, lowland heathlands is less suitable for this species than disturbed heathland with more structural diversity.

ADDITIONAL KEY WORDS:—Vegetation structure – *Lacerta agilis*.

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INTRODUCTION

The reptile fauna of Britain consists of three lizard species (*Anguis fragilis*, *Lacerta agilis*, *Lacerta vivipara*) and three snake species (*Coronella austriaca*, *Natrix natrix*, *Vipera berus*). The habitats of these reptiles are varied and include deciduous woodlands, ride verges in forest plantations, scrub, hedgerows, sand dunes and heathlands. Populations of all six species are found on lowland heathlands but there are few instances of all six species occurring together in any other type of plant community. Ericoid shrub communities seem therefore to be a very important habitat for reptiles, particularly the endangered species (*Lacerta agilis* and *Coronella austriaca*), but as with other plant communities and other animal taxa, the reduction, fragmentation, isolation and change in heathland communities has had a profound effect on reptile habitats and distribution patterns (Nature Conservancy Council, 1983).

Although local populations of all six species have diminished rapidly in Britain (many becoming extinct) over the last few decades and continue to diminish in size, it has been impossible to quantify changes in population levels on a country-

wide basis and difficult, if not impossible, to measure population size of snakes at a local level. This is because the behaviour of snakes prevents complete population counts. However, it has been possible to estimate size and density of some lizard populations, for example House & Spellerberg (1983) estimated the population density of *Lacerta agilis* on heathlands at six localities. The population densities varied from 0.3 to 18.3 lizards per ha and higher densities were found on disturbed heathland, suggesting that either increased plant species richness or vegetation structure could be an important component of the reptile habitat.

The aim of this paper is to assess the value of heathlands as habitats for reptiles with particular reference to vegetation structure.

ENDANGERED REPTILE SPECIES IN BRITAIN

Both *Coronella austriaca* and *Lacerta agilis* are totally protected species under the Wildlife and Countryside Act 1981 and are considered to be endangered in Britain (Nature Conservancy Council, 1983). The distribution of the smooth snake is limited to the southern counties and there they are found in heathlands and other plant communities. The prey of smooth snakes includes lizards and small mammals, and although nestling young of mice and shrews seem to be an important component of the smooth snake diet, this snake is considered to be an opportunistic predator, taking prey according to availability (Goddard, 1984). Results from radio-telemetry studies indicate that although this species is not particularly vagile, there are few barriers preventing dispersal of smooth snakes in heathlands, forests and other plant communities.

The distribution of the *L. agilis* is fragmented, with a small population in the north-west of England and many scattered populations in the south. This lizard is an opportunistic predator, feeding on Coleoptera, Hymenoptera (particularly ant queens), Araneae, Opiliones, insect larvae and Isopoda (woodlice). However, there is both seasonal and site variation in their feeding ecology (Nicholson, 1980). Reproductive requirements of the oviparous *L. agilis* are specialized and in June or July a clutch of about six eggs is laid about 7 cm below the ground surface. The female lizards select nest sites (House & Spellerberg, 1980) but do not protect the nest or care for the young. Large areas of open heathland provide a range of conditions which are suitable for these nest sites and incubation of the eggs.

MATERIAL AND METHODS

Study sites

This research is based partly on a new analysis of data collected by House & Spellerberg (1983), and partly on new field data from two study sites. The study sites were selected to investigate features of heathlands associated with the lizard *L. agilis* but all six species of reptiles occurred on both study sites. The heathland at study site A was very fragmented and occurred as patches (up to 0.3 ha) of all growth phases amongst mature pine (mainly *Pinus sylvestris*), bracken (*Pteridium aquilinum*), rhododendron and other garden shrubs. Most patches of heather contained invasive species and the area supporting *L. agilis* had a complex plant community structure as well as a complex topographic structure, created largely

by sand and clay waste. The area (80 ha) was previously subjected to mineral extraction but is now managed as a nature reserve. By way of contrast, study site B was on typical, wet and dry heathland (building and mature growth phases) and acid bog with only small amounts of the 75 ha site subjected to any disturbance. Plant invasion of the ericoid shrub community was minimal in the central region where *L. agilis* and other reptile species occurred.

Sampling methods

The habitat of *L. agilis* was recorded by way of a 2 m² quadrat centred on each lizard sighted (House & Spellerberg, 1983). Most lizards sighted were basking. The percentage cover (5% steps) of the plant species at six height categories, percentage bare ground and percentage visible litter was recorded in each quadrat. The six height categories were as follows: less than 3 cm, 3–10 cm, 10–30 cm, 30–50 cm, 50–100 cm, greater than 100 cm. A total of 76 quadrats were recorded at site A and 50 at site B.

The following species diversity index (a form of Simpson's or Yule's index) was used to analyse the structural diversity of each quadrat:

$$D = \frac{1}{\sum(P_i)^2}$$

This index is a measure of evenness and P_i is the proportion of the i th species (the higher the index, the more even the proportional distribution of species in the community). The percentage cover of each plant species height category and also percentage bare ground and visible litter was used as a basis for measuring the structural diversity. Scoring of percentage cover was in 5% intervals and so therefore the maximum index was 20 (minimum 1). For example one 2 m² quadrat gave the following results: *Calluna vulgaris* 30–50 cm (20%), *Ulex europaeus* 50–100 cm (10%), *Erica cinerea* 30–50 cm (20%), bare ground (50%). The proportions are therefore 20 : 10 : 20 : 50 and in the equation are expressed as follows:

$$D = \frac{1}{\sum(0.2)^2 + (0.1)^2 + (0.2)^2 + (0.5)^2}$$

$$= 2.9.$$

In this instance, a value of 2.9 indicates an unevenness in the proportional percentage cover of plant species and bare ground or a low value in terms of structural diversity.

RESULTS

The seventy-six 2 m² quadrats at study site A gave 18 species categories (bryophytes, 'various herbs', 'mixed grasses' in addition to plant species identified) and ten species categories resulted from the 50 quadrats at site B. Most quadrats (up to 67%) had three or four plant species and very few had either one or six species. The plant species common to quadrats at both study sites was similar (Table 1) with *Calluna vulgaris*, *Erica cinerea*, bare ground and plant litter being the most common species and features recorded. In terms of the

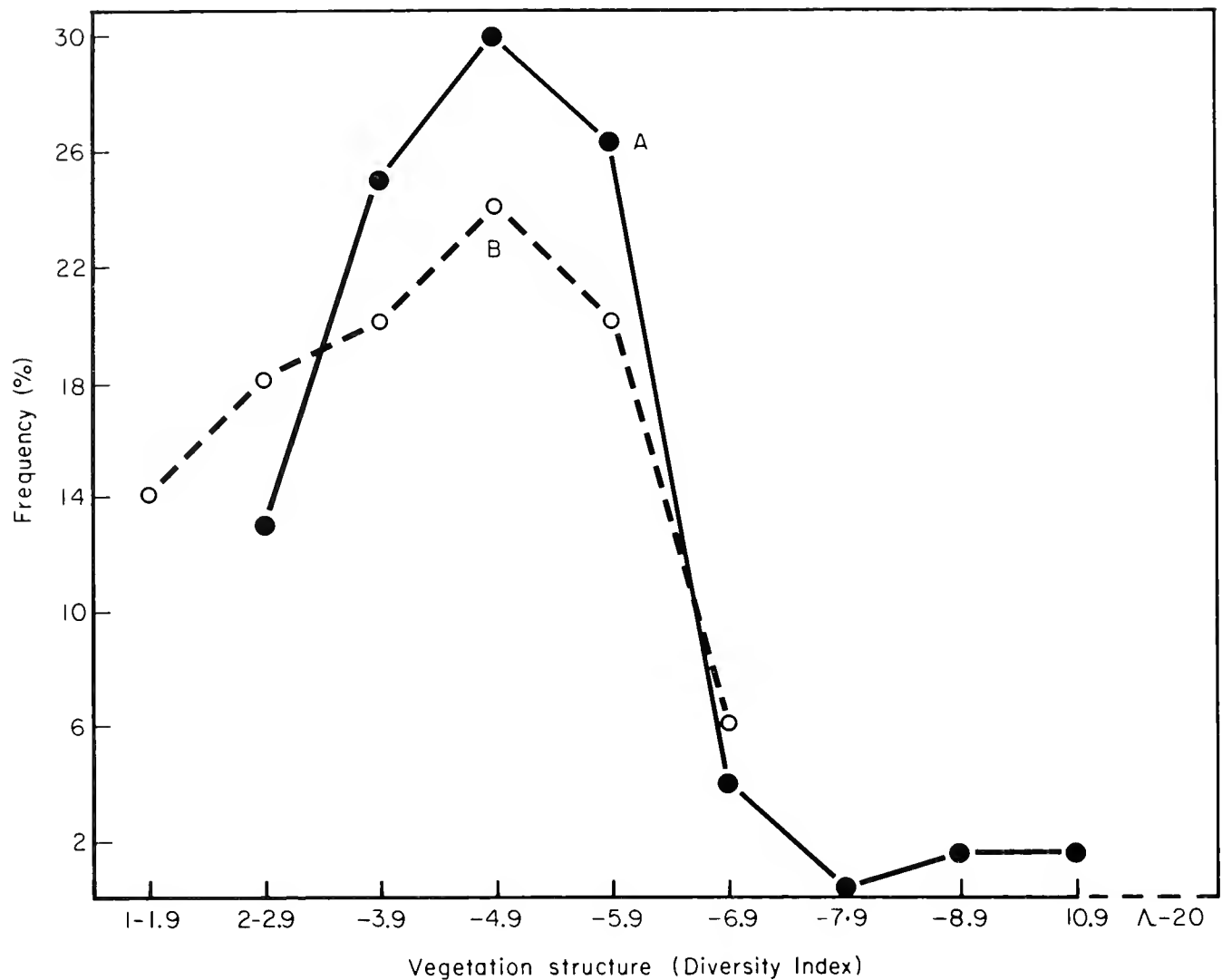


Figure 1. Range and frequency of structural diversity for all quadrats at both sites.

plant species composition of the lizard quadrats, there was little difference between the two sites.

Vegetation structure can be measured and expressed in many ways. The several height categories combined with percentage cover of plant species, bare ground and litter provided a basis for a measure of structure in each quadrat by way of a diversity index. Quadrats with a high structural diversity contained several plant species height categories and quadrats with low structural diversity contained only one or two plant species of uniform height. The range and frequency of structural diversity for all quadrats at both sites is shown in Fig. 1.

TABLE 1. Occurrence of plant species in quadrats

Plant species/feature	Percent occurrence in quadrats	
	Site A (76 quadrats)	Site B (50 quadrats)
<i>Calluna vulgaris</i>	85.5%	100 %
<i>Erica cinera</i>	76.3	62.0
Bare ground	67.1	44.0
Litter	56.5	42.0
<i>Ulex europaeus</i>	48.6	28.0
<i>Molinia caerulea</i>	27.6	16.0
<i>Agrostis</i> sp.	27.6	22.0
Bryophytes	27.6	20.0
<i>Erica tetralix</i>	11.8	18.0
<i>Pteridium aquilinum</i>	9.2	10.0
<i>Pinus</i> spp.	9.2	—
<i>Ulex minor</i>	7.8	40.0

The mean diversity index for site A was 4.4 (S.D. 1.29) and the mean value for site B was 3.8 (S.D. 1.46). These are significantly different ($t=2.47$, $P>.02$).

DISCUSSION

House & Spellerberg (1983) have shown that the basking sites of *L. agilis* in heathlands are not randomly distributed and that this species seems to select basking sites. Two important features of heathland communities providing habitats for *L. agilis* and other reptile species could be plant species richness and vegetation structure. The species composition of the quadrats on the two study sites in this research are very similar but vegetation structure (as measured by a diversity index) was significantly different. Fewer suitable conditions at site B would support a smaller population of lizards and this is supported by the difference in lizard population density: 9.2 ha at site A; 0.3 at site B (House & Spellerberg, 1983).

The main ecological requirements of reptiles include space, food, heat (for maintenance of precise, body temperatures) and protection from both predators and unfavourable weather conditions. In general, snakes are more mobile (vagile) than lizards and therefore space requirements (expressed as home ranges) are much larger than home ranges of lizards (Spellerberg, 1988a). The six species of reptiles eat a range of prey from insects to small mammals (Table 2). Reproduction, digestion, rate of growth, visual acuity, locomotion and other forms of behaviour are temperature dependent and therefore reptiles devote much time to behavioural thermoregulation. The structure of ericoid shrub communities provides protection from some predators but of more importance the structure is particularly suitable for basking and for precise regulation of body temperature. Alternating between sunlit and shaded areas is a basic form of behavioural thermoregulation common amongst reptiles and is a means of control of heat uptake for precise regulation of body temperature. The mosaic of sunlit and shaded areas within heathland communities and within ericoid shrubs enables reptiles to shuttle between these areas, making optimum use of the heathland microclimate.

TABLE 2. Distribution, size, reproduction and some ecological characteristics of Britain's reptiles

	<i>Anguis fragilis</i>	<i>Lacerta agilis</i>	<i>Lacerta vivipara</i>	<i>Coronella austriaca</i>	<i>Natrix natrix</i>	<i>Vipera berus</i>
Distribution	ESW	E	EHSW	E	EW	ESW
Weight (g)	15	9.7	3.6	34	98	76
Length (cm)	16	7.8	5.8	42	60	45
Reproduction	V	O	V	V	O	V
Tb (°C)	23	31	32	27	26	30
C (°C)	2.7	3.0	-0.9	0.3	1.6	-0.5
Prey	Slugs Worms	Insects Spiders	Spiders Insects	Nestlings Small mammals Lizards	Fish Amphibians Small mammals	Small mammals Lizards

E, England; S, Scotland; W, Wales; H, Ireland.

V, Viviparous; O, oviparous; Tb, mean body temperature.

C, Lowest temperature for activity.

From Spellerberg (1988b).

If *L. agilis* is selecting basking sites with a high vegetation structural diversity, the benefits would probably be linked to behavioural thermoregulation and food requirements. Utilization of sites with maximum variation in structure would allow the lizards to alternatively bask and seek shade with minimum costs. As well as providing suitable microclimates for *L. agilis* and other reptiles, a structurally complex heathland site may also support higher levels of invertebrate prey items which in turn could contribute to the presence of higher levels of small mammal communities. Undisturbed, open expanses of lowland heathlands probably support poor populations of small mammals (Webb, 1986) but in areas where the typical ericoid shrub community has been altered with invading plant species and where the ground has been disturbed as a result of the construction of embankments and other earthworks, small mammals may be more abundant. An abundance of small mammals, and structurally complex vegetation and topography would form the basis of habitats suitable for *C. austriaca* and the other two snake species.

Where reptiles do occur on heathlands, management directed at the conservation of heathland plant communities would not be detrimental to the reptile populations. It is suggested that open heathland sites should continue to be managed with a view to the normal considerations and protection of heathland floristics and more importantly structure. Sparse populations of *L. agilis* will survive in such areas but higher densities of lizards can occur if scrub, bracken, trees and various forms of ground disturbance are included in the area. An overriding problem for conservation of wildlife on heathlands is the continual process of reduction in area, fragmentation and isolation of this plant community. The remaining fragments of heathland cannot all be managed to satisfy the conservation needs of all taxa and therefore there seems to be a need for compromise and possibly the establishment of priorities in terms of management strategies. Restoration of heathlands (now well researched; British Gas, 1988) and possibly recreation of this diminishing resource may alleviate such difficulties.

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The Ericoideae and the southern African heathers

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OLIVER, E. G. H., 1989. **The Ericoideae and the southern African heathers.** The subfamily Ericoideae (Ericaceae) containing the true heathers and heaths has been a group long recognized as a sound natural entity. With work on the southern African genera and species which comprise approximately 95% of the subfamily well in progress, a reassessment of the number of genera has become necessary because of the considerable variation recorded in, and the postulated polyphyletic origin of, the capsular genera. Changes envisaged will affect the whole concept of the heaths within Africa. The genus *Philippia* Klotzsch has been reduced to synonymy under *Erica* L. and it is shown that the case for a similar action is very strong for *Blaeria* L. and *Ericinella* Klotzsch. The position of the monotypic European genus, *Bruckenthalia* Reichb., is also affected but remains unresolved.

ADDITIONAL KEY WORDS:— *Blaeria* – *Bruckenthalia* – *Erica* – *Ericinella* – *Philippia* – taxonomy.

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INTRODUCTION

The subdivision of the family Ericaceae *per se* has not received much attention other than as part of a worldwide treatment of families and genera (Don, 1834; Bentham, 1839, 1876; Drude, 1897). Klotzsch (1834) was the first to look at heathers on their own. He divided them into three tribes based on the degree of fusion of the stamens. Bentham in treating the whole family for de Candolle's *Prodromus* (de Candolle, 1839) and later for the *Genera Plantarum* (Bentham, 1876) introduced the subdivisions Euericeae and Salaxideae at subtribal level based on the carpels and their complement. Drude retained Bentham's classification for Engler & Prantl's *Die Natürlichen Pflanzenfamilien* (Drude, 1897), but using the updated terminology as recognized today, i.e. the subfamily Ericoideae with two tribes, Ericaceae and Salaxideae.

This work remained as the standard treatment of the subfamily for the next 80 years until Watson, Williams & Lance (1967) queried this classification. They looked at a fairly wide range of characters but in only a small sample of the family. Using a computer-assisted numerical analysis they suggested a new system which contained two tribes within the subfamily 'Ericoids', tribe 1 containing *Calluna* and, surprisingly, *Cassiope* from the Arbutoideae and tribe 2 with all of the rest of the subfamily. Stevens (1969, 1971) did a world-wide and more detailed assessment of the family. He rejected the inclusion by Watson *et al.* (1967) of *Cassiope* within the heather subfamily even though its members look very heath-like. He proposed the subdivision of the Ericoideae into three tribes, Callunaeae, Ericaeae and Salaxideae. The latter two he retained as construed by Bentham and Drude on the grounds of insufficient data to suggest otherwise. This is the classification of the subfamily most accepted at present.

CALLUNEAE

Calluna is an enigmatic genus because of its numerous bracteoles, sagittate leaves, pith type, adaxial leaf stomata and septicidal capsule. None of these characters occurs within the rest of the genera in the subfamily. Recognition of this very distinct genus at a high level is certainly justifiable. Stevens chose to isolate the genus at tribal level, but it could be argued that *Calluna* should be placed in its own subfamily thus rendering the Ericoideae more uniform.

ERICAEAE

The rest of the heather subfamily can be retained with the subdivision into Ericaeae and Salaxideae, but not based on ovary complement as the sole distinguishing criterion as has been done to date. My investigations suggest the structure of the fruit as the criterion, i.e. dehiscent vs. indehiscent. This will necessitate a reallocation of genera between the tribes. All the genera possessing a dehiscent capsule would belong to the Ericaeae and all are widespread in Africa and Europe (Fig. 1). The indehiscent fruited genera having either a berry or drupe would be placed in the Salaxideae. These are all endemic in the southwestern and southern Cape Province in southern Africa and are more advanced, recently evolved, genera which can be derived from a basic ericoid groundplan by reduction in or fusion of parts of each whorl.

I propose to discuss here only the capsular genera in the Ericaeae as currently accepted in *Flora Europaea* (Webb, 1972; Webb & Rix, 1972), *Flora of West Tropical Africa* (Ross, 1963), *Flore de Cameroun* (Letouzey, 1970), *Flora Zambesiaca* (Ross, 1983), *Flore des Mascareignes* (Friedmann, 1981) and *List of species of southern African plants* (Oliver 1987a). These are of more relevance to a British audience and also exhibit some remarkable variation patterns which will have a considerable effect on our acceptance of these genera. The genera are *Erica* L., *Philippia* Klotzsch, *Blaeria* L., *Ericinella* Klotzsch and *Bruckenthalia* Reichb.

Erica

Erica, by far the largest genus in the subfamily with *c.* 670 species at present, exhibits the basic groundplan of the ericoids with B1,br2,K4,C(4),A8,G(4),S ∞ ,

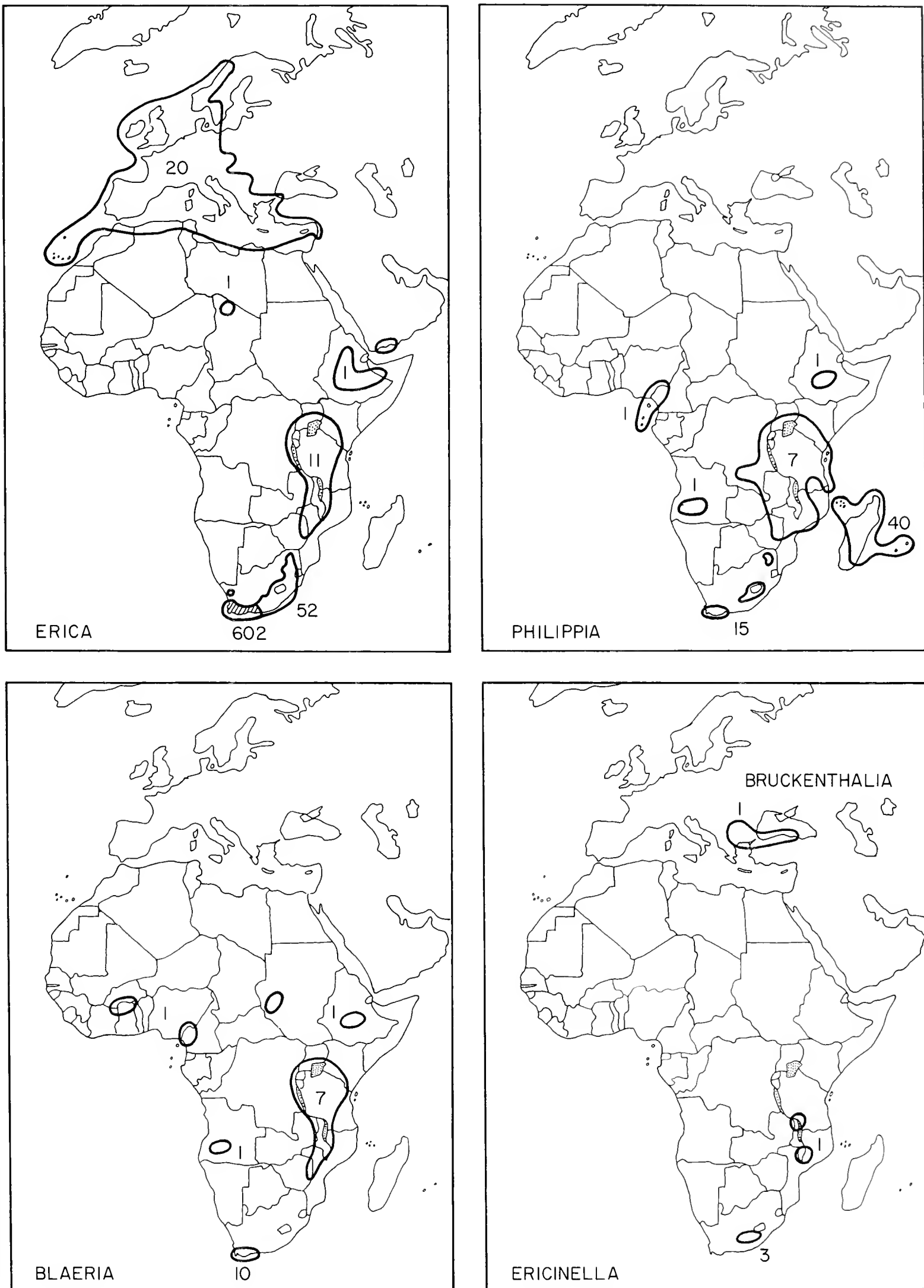


Figure 1. Maps showing the approximate native distribution of the capsular genera, *Erica*, *Philippia*, *Blaeria*, *Ericinella* and *Bruckenthalia*. Figures represent the estimated number of species per region.

i.e. bract 1, bracteoles 2, (K) calyx free 4, corolla fused 4, androecium (stamens) free 8, gynoecium superior 4-locular and seeds numerous, and this with, remarkably, very few exceptions. Most of the variation within the genus occurs in the structure of the inflorescence, in the size, shape and colour of the calyx and of the corolla and in the shape and adornments of the anthers.

The other capsular genera can be regarded as offshoots closely related to *Erica*. These capsular genera are currently being revised for inclusion in the Flora of southern Africa.

Philippia

The results of a detailed study of the southern African species of this pan-African genus have recently been published (Oliver, 1988). However, I will repeat the salient points to emphasize the generic problems within the capsular genera.

Philippia was described by Klotzsch in 1834 and has been maintained as a genus in all subsequent regional African floras and the only complete revision (Alm & Fries, 1927) based on the possession of a fully recaulescent bract and no bracteoles producing a zygomorphic 4-partite or -lobed calyx, a condition found in most of the *c.* 65 species (Fig. 2).

However, problems in the distinction between *Philippia* and *Erica* were noted by Alm & Fries (1927.) They referred on a number of occasions to "übergangsformen, -typen" but proceeded to retain the genus.

Investigations in the southern African material have revealed a complete series of intermediates within a few species, namely *P. pallida* L. Guthrie, *P. stokoei* L. Guthrie, *P. tristis* H. Bol., *E. peltata* Andr., *E. accommodata* Klotzsch var. *ebracteata* H. Bol., *H. caespitosa* Hilliard & Burtt, *E. hispidula* L., *E. inops* H. Bol., *E. ebracteata* H. Bol., *E. anomala* Hilliard & Burtt, *E. sparsa* Lodd., *E. alticola* H. Bol. and *E. dissimulans* Hilliard & Burtt. The most remarkable variation data are shown in Table 1.

The variation recorded was such that either end of the range could be located under two separate species in two separate genera and, depending on the flower looked at, a collection could be placed either in *Erica* or in *Philippia*. There were in fact two places in which to file material in the herbarium! A brief reference to collections of *Philippia* (BOL, MO, PRE) and to literature on the Ericoideae from tropical Africa (Pichi-Sermolli & Heiniger, 1953; Ross, 1957, 1983) and from the Mascarenes (Friedmann, 1981) revealed a similar variation pattern in

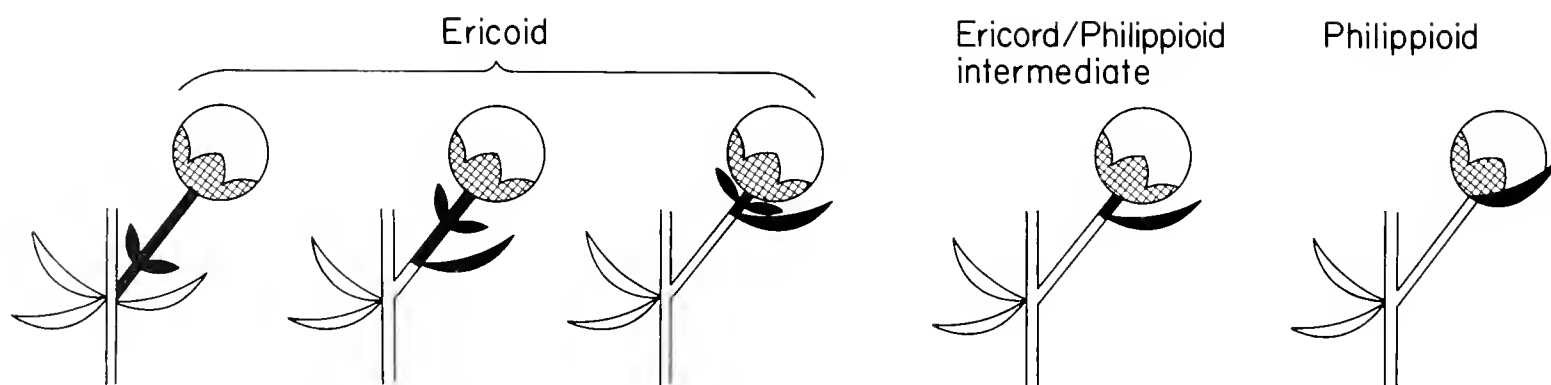


Figure 2. Series of diagrams showing stages in the recaulescence of the bract up the pedicel in the Ericoideae from axial (aB) on the left to totally recaulescent (RB) on the right.

TABLE 1. Distribution of bract/bracteole/calyx characters in six species of *Erica* (Ericoideae) in southern Africa^a

Species	<i>Erica</i> rB, 2br, K4	<i>Erica/Philippia</i> rB, Obr, K4 or 3	<i>Philippia</i> RB, K3
<i>E. anomala</i>	0	40	60
<i>E. dissimulans</i>	2	98	0
<i>E. caespitosa</i>	3	83	14
<i>E. ebracteata</i>	11	46	43
<i>E. peltata</i> ^b (= <i>P. pallida</i>)			
Ashton	16	40	44
Swellendam	0	38	62
Niekerkshek	3	30	67
Others	22	38	40
<i>E. sparsa</i>	2	94	4

^aFigures express the percentage of flowers in the samples examined.

^bAnalysis of three population samples and of 15 collections from the complete range of the species.

the B/br/K arrangement, but perhaps only to the same degree in the East African *P. keniensis* S. Moore and *E. kingaënsis* Engl.

Several additional features are very relevant to the existence of *Philippia*. Most species of *Philippia* have their closest allies within the section *Arsace* in *Erica*. However, some such as *P. pallida/E. peltata* and *P. stokoei/E. lasciva*, are more closely related to ericas in other sections than they are to species of *Philippia*. Similarly, it is clear that the philippias of East Africa are more closely related to East African ericas than to southern African philippias. Alm & Fries (1927: 11) stated clearly that they could not find any close relationship between the Madagascan/Mascarene species and the continental species nor between the tropical African and the Cape species. This clearly points to a polyphyletic origin for the genus.

Blaeria

This genus was created by Linnaeus as early as 1737 and since then has always been recognized in African Floras. It differs from *Erica* in only one character, four *vs.* eight stamens, and since Linnaeus' time any ericoid with four stamens has often been placed in *Blaeria*. Problems with the stamen complement have been known for some time, the classic case being *E. eylesii* L. Bol. var. *blaeriodes* Wild from the Zimbabwean highlands (Wild, 1954). Ross (1980: 137) stated that within the species complex, which includes *E. eylesii*, even the possession of four stamens instead of eight, the feature distinguishing *Blaeria* from *Erica*, could not be used as a distinguishing criterion because of plants with a complete range of stamen number.

In southern Africa I have come across problems in some species of both *Erica* and *Blaeria* (Table 2). From the literature this is clearly the case to the north in tropical Africa (Ross, 1957) where there is a variation in stamen complement that places flowers of a single specimen in either genus. With the inclusion of

TABLE 2. Variation in generic delimiting characters in some species of *Blaeria* and *Erica*

Taxa	Number of stamens
<i>Blaeria</i> (most species)	4
<i>Erica tetragona</i> L. fil.	4 (6) 8
<i>Erica filiformis</i> Salisb.	4 (6) 8
<i>Erica pleiotricha</i> S. Moore	
var. <i>pleiotricha</i>	(7) 8
var. <i>blaeriodes</i> (Wild) R. Ross	4-8
<i>Erica parvula</i> Guth. & Bol. ^a	8
<i>Blaeria campanulata</i>	4-(8)
<i>Blaeria equisetifolia</i> (Salisb.) Don	4-(8)
<i>Erica sensu lato</i> ^b	
<i>Philippia nyassana</i>	4 (5)
<i>Philippia mannii</i>	(5) 6 (7 or 8)
<i>Philippia hexandra</i>	6 (7 or 8)

^aSpecies complex of very closely related taxa.

^bThe genus *Erica* when *Philippia* is reduced to synonymy.

Philippia in *Erica* (Oliver, 1988) the problem is compounded as there is considerable variation in the tropical species. *Philippia nyassana* Alm & Fries has mainly four stamens but occasionally five, *P. mannii* (Hook. fil.) Alm & Fries usually six, occasionally five, seven or eight, *P. benguellensis* (Welw. ex Engl.) Britten eight, occasionally five to nine and *P. hexandra* S. Moore six, occasionally seven or eight stamens. Ross (1957: 735) also mentioned the problem in *Erica* when he noted that some specimens of *E. arborea* L. from East Africa have four or five stamens in most flowers.

Blaeria exhibits a somewhat anomalous distribution compared to *Erica* and *Philippia* (Fig. 1). A few species are widespread in tropical, subtropical and temperate Africa. The genus is absent between the highlands of Zimbabwe and the mountains of the southern Cape Province with no representatives on the Drakensberg where both *Erica* and *Philippia* occur.

Within the Cape it is clearly evident that the species bear close relationships with local species of *Erica* and are in no way closely related to the other species of *Blaeria* far to the north. As was the case with *Philippia* one can again postulate a polyphyletic origin for the genus.

Ericinella

The above discussion then leads on to the last of the African capsular genera, *Ericinella* Klotzsch, described in 1838 and a smaller genus not as widespread as the other two. It has up to now been distinguished by a totally recaulescent bract as in *Philippia* and only four, rarely five stamens as in *Blaeria* and an ovary of G3(4). From the foregoing discussion it is immediately evident that problems must therefore occur in recognizing *Ericinella*.

Ross (1983: 158) could separate the single tropical species only on the anther appendages and the size of the stigma both of which are frequently used as specific characters in the rest of the subfamily. This was because *P. nyassana* and *Ericinella microdonta* (C. H. Wright) Alm & Fries from Mlanje both have a totally recaulescent bract and four stamens. *Philippia mannii* widespread in tropical

Africa, has five to eight stamens and an ovary of G3 or G4. Ross (1980: 126) also noted that in *B. kingaënsis* the bracteoles can often be absent as occurs in the *Erica/Philippia* intermediate state (Fig. 2).

In the Cape Province the three species of *Ericinella* appeared to be quite distinct from the other capsular ericoids in having four stamens and an ovary complement of G3. However, recent studies in the Cape blaerias brought to light variation within *B. campanulata* Benth. with four, five or six stamens and an ovary of G3. So here again there is an overlap in generic diagnostic features. As with *Blaeria* the genus *Ericinella* has an anomalous distribution with a large gap occurring between the three Cape species and the single species, *E. microdonta*, from Malawi and south-western Tanzania. This latter species appears to be more closely related to the tropical *Erica/Philippia/Blaeria* complex than to the Cape species of *Ericinella* suggesting again polyphyly.

Bruckenthalia

The last of the capsular genera in the Ericoideae is another enigmatic European genus, namely *Bruckenthalia*. This monotypic genus is confined to Europe, in the south-eastern parts only and northern Turkey. It is occasionally cultivated in Britain.

The genus is easily distinguishable from *Erica* in Europe (Webb, 1972) by having no bracteoles and a partially-fused calyx. However, working on a global classification of the ericoid genera one encounters problems with the southern African species of *Erica*. There are seven Cape ericas in the section *Gamochlamys* characterized by a partially-fused calyx (Baker & Oliver, 1967) with one species, *E. newdigatei* Dulfer, having a calyx almost identical to that in *Bruckenthalia*. With *Philippia* included within *Erica* an additional approximately 35 species possess a partially-joined calyx.

The absence of the two bracteoles is very much similar to the situation mentioned earlier (Fig. 2) in the *Erica/Philippia* intermediate except that the bract is always in the axial position as aB. However, *E. alticola* H. Bol. in the Transvaal has been found to possess flowers mostly of the aB,Obr type and a very similar inflorescence to that occurring in *Bruckenthalia* which appears invariably to have flowers of the aB,Obr type. Populations of *Bruckenthalia* will need to be examined in detail to ascertain whether this last statement is in fact true.

One interesting feature of *Bruckenthalia* is the chromosome number. The few ericoids, c. 5%, that have been looked at so far have $n=12$ for *Erica*, $n=8$ for *Calluna* and $n=18$ for *Bruckenthalia* (Callan, 1941). A nurseryman near Bremen in West Germany, K. Kramer (personal communication) has managed very recently to produce offspring from a *Bruckenthalia* × *Erica* cross (*B. spiculifolia* (Salisb.) Reichb. × *E. carnea* L.). An investigation of the chromosomes should prove most useful. Material of *Bruckenthalia* is currently being cultivated at the National Botanic Gardens, Kirstenbosch, for further studies.

CONCLUSIONS

From the above discussion it is clearly evident that the current delimitation of genera within the capsular members of the Ericoideae is very unsatisfactory. It is shown that the variation patterns found within certain species of all the genera

produce situations where the degree of overlap between the genera renders their recognition as distinct entities unacceptable or at least very tenuous. The situation is such that certain specific taxa can easily be placed in either of two genera.

In three of the genera, *Philippia*, *Blaeria* and *Ericinella*, the relationships of the species do not all lie within their current generic boundaries, but rather with species alliances in another genus. This situation is compounded by the geographic separation of the species into regional alliances. Polyphyletic origins for the above three genera as presently construed are strongly indicated by all the evidence. The genera are clearly unnatural groupings of species.

The decision to reduce the genus *Philippia* to synonymy under *Erica* for the southern African region has been published and the nomenclatural changes have been made (Oliver, 1987b, 1988). The nomenclatural changes for tropical Africa, Madagascar and the Mascarenes need still to be made. From the brief arguments put forward above, the cases of *Blaeria* and of *Ericinella* are clearly similar. However, more detailed papers setting out each case and dealing with the nomenclature will be published elsewhere.

The situation with *Bruckenthalia* remains unresolved because further studies on any variation in the distinguishing characters and an investigation of the hybrids with ericas should be undertaken before a final decision on the validity of the genus is taken.

As a result of my investigations in the Ericoideae some drastic changes will have to take place to rationalize the classification of the subfamily. The retention of the three tribes listed by Stevens (1971) is endorsed but with a recircumscription of the Ericaceae and Salaxideae and consequent reallocation of genera. The tribe Ericaceae could eventually consist of the single megagenus *Erica*.

KEY TO TRIBES OF THE ERICOIDEAE

Leaves sagittate, bracteoles 6 or more	<i>Calluneae</i>
Leaves not sagittate, bracteoles 0–2	
Fruit a dehiscent capsule	<i>Ericaceae</i>
Fruit an indehiscent drupe or berry	<i>Salaxideae</i>

CONSTITUENTS AND DISTRIBUTION OF TRIBES

Calluneae: one genus, *Calluna*, with one species widespread in Europe up to the Ural Mountains.

Ericaceae: two genera—*Erica* with approximately 735 species widespread in Europe including the Atlantic islands, the Middle East (Turkey, Syria and Lebanon), the Arabian Peninsula (Yemen), the whole of Africa, Madagascar and the Mascarenes, 92% of the species occurring in the Cape Province—*Bruckenthalia* with one species confined to south-eastern Europe and Turkey.

Salaxideae: approximately 14 genera with 130 species all confined to the southern Cape Province.

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