[Proc. Roy. Soc. Victoria, **45** (N.S.), Pt. II., 1933.]

Art. XV.—*Ecological Studies in Victoria.—The Cheltenham Flora.*

By R. T. PATTON, D.Sc. (Melb.), D.I.C. (Lond.), M.F. (Harv.), F.R.H.S.

[Read 8th December, 1932; issued separately 1st August, 1933.]

The term Cheltenham Flora has been given temporarily to this very well-defined association as I have hesitated to use the type of nomenclature at present finding favour in the ecological world. The addition of the suffix "*etum*" to the stem of the generic name of one of the dominants to designate an association implies that the ultimate classification of associations must be based on taxonomic principles, a view to which I cannot give any adherence. Associations owe their particular or peculiar physiognomy to the environment, physical, and biotic, and not to the taxonomic relationships of the constituent members of the association. In the classification of plants we are concerned particularly with their floral parts, but in ecology we are only to a minor degree affected by such considerations, but we do concern ourselves with the vegetative appearance of the plants in the association.

In this particular association one must be struck with the very great vegetative similarity of the dominants and subdominants. Yet they belong to the most diverse families. If we were to follow the present vogue of nomenclature this association might equally be named Acacietum, Leptospermetum, or Casuarinetum. There are other associations where species of *Acacia* are dominant, and they would also fall into the generic group Acacietum, yet ecologically such associations are not allied. The use of such terminology can, in the ultimate, only lead to confusion. Thus the term Cheltenham Flora is to be regarded as temporary only. Whatever nomenclature is applied must necessarily link this very striking association to similar associations in other parts of the world.

As pointed out by Sutton(10) this association was very widespread, extending over extensive areas to the east of Port Phillip Bay, but now has become very restricted owing to the growth of settlement.

Physiognomy.

This association is of very great interest because of its undoubtedly close relationship, ecologically and taxonomically, to similar areas in other parts of the world, particularly Europe and South Africa. One of the important families in this association is Epacridaceae, which is closely allied to Ericaceae, which is the important family in the European heaths. This association consists essentially, so far as the dominants are concerned, of scrub species, 3 to 5 feet high, which bear small, narrow, usually coriaceous leaves. The stems are never robust, but are always thin, even as thin as wire in the case of *Platylobium obtusangulum.* Spinescence is a feature, spines being found on leaves, stipules and phyllodes. The ericoid type of leaf is perhaps the most outstanding feature of the association, and this type is found not only among the dominants, but among the subdominants, and even on the very dwarf members such as *Acrotriche serrulata.*

Although there are several species in the dominant class, none is particularly conspicuous owing to the uniformity of leaf size, the grey green colour and the completeness of the ground cover. There are no really large leaves, the largest being those of *Banksia marginata.* Even these, however, are not conspicuous. Although during the flowering season a large number of species other than the dominants and subdominants make themselves evident, these do not alter the general physiognomy of the association, with the possible exception of *Stipa semibarbata,* which among other grasses raises its inflorescence above the surrounding vegetation. The association is distinctly xerophytic, and while in the northern hemisphere there may be some considerable doubt as to the xerophytism of the heath associations, since for one reason the climate is not conducive to xerophytic habitats, here in a much warmer latitude (Lat. 38° S.) with rather scanty summer rainfall, hot dry winds, and with a low water content in the soil there can be no doubt.

Composition.

Although there is an extraordinary similarity in the vegetative characters of the chief members of this association, the flora is an exceedingly rich one, of very diverse families. The general similarity may be regarded as evidence of the moulding influence of the environment. Owing to the very widespread character of the association, there is an amount of variation in the presence or absence of the subordinate members. Since an association is characterized by the physiognomy of its dominants and subdominants, and it may be by other life forms as well, the categorical setting out of all plants occurring, as is usually practised, is of no material value. Ecology is a study of the relationship of the plants to their environment, and their physiognomy is an expression of that relationship. The species present are of secondary consideration, and the presence or absence of species which do not contribute to the general physiognomy of the association is not of any particular moment. In this particular study only those which are of common occurrence have been studied, first at Caulfield over some years, later at Cheltenham and lastly at Frankston. Sutton(10) has given a complete list of plants found on the particular geological formation which gives rise to this association.

In Table I is given a list of evergreen species, all of which are common, and which have been kept constantly under observation for some years. Appended to species of the Dicotyledons is their leaf size according to Raunkaier(8).

TABLE I.

L = Leptophyll. N = Nanophyll. M = Microphyll. D = Dominant.

		Leaf Size.
ARCHICHLAMYDEAE		
Casuarineae	Casuarina distyla. D	L
Proteaceae	Isopogon ceratophyllus	N
	Banksia marginata. D	N—M
Lauraceae	Cassytha glabella	L
Pittosporaceae	Billardiera scandens	N
Leguminosae	Acacia Oxycedrus. D	N
	A. armata	N
	Gompholobium Huegelii	L
	Daviesia ulicina	L
	Aotus villosa	L
	Dillwynia ericifolia	L
	Platylobium obtusangulum	N
	Bossiaea cinerea	N
	Kennedya prostrata	N
Geraniaceae	Geranium pilosum	N
Oxalidaceae	Oxalis corniculatus	N
Rutaceae	Correa rubra var. virens	N
Tremandraceae	Tetratheca ciliata	N
Polygalaceae	Bredemeyera volubile	N
Euphorbiaceae	Amperea spartioides	L
	Ricinocarpus pinifolius. D	L
Dilleniaceae	Hibbertia sericea	L—N
	H. stricta	L
	H. fasciculata	L
Thymeleaceae	Pimelea humilis	N
	P. phylicoides	L
Myrtaceae	Leptospermum myrsinoides. D	L
	L. scoparium. D	N
Halorrhagidaceae	Halorrhagis tetragyna	N
Umbelliferae	Hydrocotyle laxiflora	N
	Trachymene heterophylla	L
	Xanthosia pusilla	L
METACHLAMYDEAE		
Epacridaceae	Astroloma humifusum	L
	Leucopogon virgatus	L
	Acrotriche serrulata	L
	Monotoca scoparia	L
	Epacris impressa	L
Campanulaceae	Wahlenbergia gracilis	L
Goodeniaceae	Goodenia geniculata	N
Stylidiaceae	Stylidium graminifolium	N
Compositae	Olearia ramulosa. D.	L
	Craspedia uniflora	N
	Helichrysum apiculatum	N
	H. scorpioides	N

MONOCOTYLEDONAE	
Gramineae	Themeda triandra
	Microlaena stipoides
	Stipa semibarbata
	Calamagrostis quadriseta
	Dichelachne crinita
	Poa caespitosa
Cyperaceae	Lepidosperma concavum
Restionaceae	Hypolaena fastigiata
Liliaceae	Xanthorrhoea australis
Iridaceae	Patersonia glauca
FILICALES	Lindsaya linearis
	Pteridium aquilinum.

From Table I. it will be observed that the Monocotyledons form only an insignificant part of the evergreen vegetation.

During the spring months the families Liliaceae and Orchidaceae are abundantly represented. These, however, while contributing to the spring aspect, do not alter the physiognomy of the association. The Metachlamydeae also contribute insignificantly to the physiognomy. It is somewhat surprising to find that the characteristic Australian families Myrtaceae and Proteaceae are so poorly represented. In particular is this the case with Proteaceae, which has in general a very xeromorphic structure. The family Epacridaceae is excellently represented. The association is exceedingly rich in species, particularly when those members are added which are only seasonal in appearance. It is worthy of note that the average number of species per family is only 2.2.

Structure.

In the dominant class there are several species which have been indicated by the letter D in Table I. It is somewhat unusual perhaps to find so many. The subdominants are much more numerous, and here the family Leguminosae is particularly prominent, both in species and in numbers of individuals. The majority of the dominants and subdominants belong to the Archichlamydeae, there being only one dominant, *Olearia ramulosa*, belonging to the Metachlamydeae while three species of Epacridaceae belong to the subdominants. The dominants and subdominants together practically give a complete covering to the soil. According to the numerical scheme laid down by Braun Blanquet(2), the value of the covering is 5. Beneath the subdominants there is still a layer of vegetation, consisting partly of dwarf shrubs and partly of creeping plants. *Acrotriche serrulata* is quite dwarf, and tends to form large mats. Among the legumes, *Kennedya prostrata* and *Gompholobium Huegelii* form prostrate plants. *Platylobium obtusangulum* has thin weak wiry stems, which may be prostrate or ascending according to the proximity of other plants.

In such a low scrub association it is not to be expected that lianes would occur, but two, *Bredemeyera volubile* and *Billardiera scandens*, do occur, these two belonging to families in which the climbing habit is not pronounced. Covering large areas of the vegetation is the creeping parasite, one might call it a liane, *Cassytha glabella*.

Environmental Factors.

The evergreen members of this association are decidedly xeromorphic. This is shown by the smallness of the leaves, their coriaceous character, the generally small area of leaf surface, and the thinness of the stems. The total leaf area does not compensate for the generally small size of the leaves as suggested by Thoday (11). For example a bush of *Leptospermum myrsinoides*, four feet high, had seven shoots, and these covered approximately sixteen square feet of ground. The leaves which averaged 7.5 mm. in length numbered approximately 18,000, and were estimated to have a total area of three square feet. The area of the leaves does not equal the area of soil occupied by the plant. The physiognomy is related to the environment of the association, and this generally may be said to be twofold, soil and climate.

A. Climate.

The chief problem of these plants is the availability of water during the hot summer and autumn months. By November (Fig. 1) conditions have become fairly unfavorable for growth, and this is accentuated by the porosity of the soil. Growth does not commence again until after the autumn rains. The rainfall is fairly evenly distributed over the year and, as a matter of fact, the six summer months, October to March, actually receive more rain than the six winter months, April to September, the amounts being 12.91 inches and 12.60 respectively. However, the slightly higher rainfall in the warmer period has no appreciable effect on the vegetation, since the evaporation during these months rises so high. It is the rapid increase in the evaporation rate that so materially affects the flowering period. Conditions for growth are favorable from late autumn to late spring or early summer. Temperatures during the winter period are not low, frosts rarely occurring. It is of interest to note in this connexion that Brockmann Jerosch in his ideal continent (4) suggests that heath is due to oceanic influences. This Australian ericoid type of vegetation is likewise close to the seaboard. October is the wettest month (Fig. 1) of the year, but during November climatic conditions are dry, due to the increase in evaporation. During the six winter months evaporation from a free water surface is lower than the rainfall received, but during the six summer months (October to March) evaporation greatly exceeds precipitation. Maximum floral activity is reached, however, before evaporation reaches a maximum, October being the most active month (Fig. 1). Despite the exceedingly dry conditions which exist in the late summer, however, floral activity is not inhibited. Some plants bloom more or less right through the year, as for instance, *Billardiera scandens*, which has been found in flower in every month of the

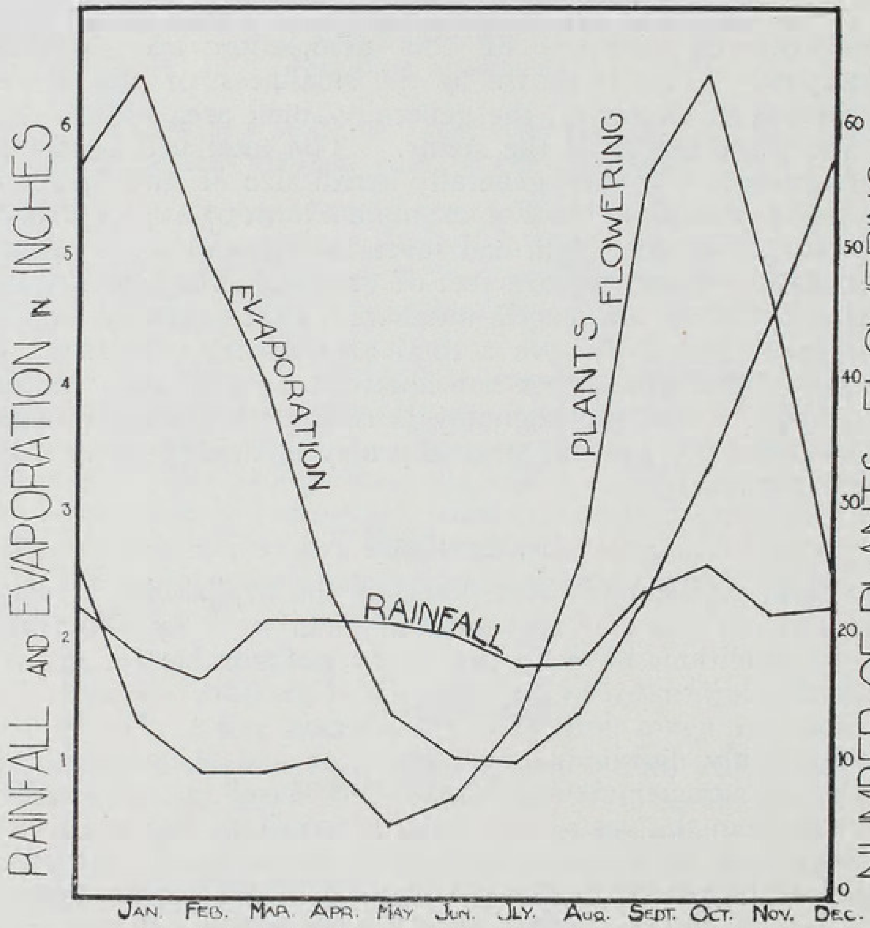

Fig. 1. Rainfall, Evaporation, and number of Plants flowering each month.

year, and which does not appear to have a definite maximum flowering period. On the other hand, *Olearia ramulosa* has its optimum during the hottest months, January to February, but it may be found flowering in a spasmodic manner for the remainder of the year. *Hibbertia fasciculata* also flowers throughout the year. Very localized as regards its flowering period is *Monotoca scoparia*, which is in full bloom during March and April. Other species which flower during the most unfavorable period of the year are two species of Umbelliferae, *Trachymene heterophylla* and *Didiscus Benthamii*, and also the parasite *Cassytha glabella*. The behaviour of such plants raises the question as to how they obtain their water supplies for such an active period. *Monotoca scoparia* and *Olearia ramulosa* are typical ericoid plants. The majority of the evergreen plants have passed into a state of rest while these are most active. In contrast to these dry period flowering plants are those that flower during the coldest period of the year, as for example, *Acrotriche serrulata.* This is a very dwarf shrub bearing small inconspicuous greenish flowers which are borne on the older parts of the stem. This is a rather remarkable case of cauliflory.

In Fig. 1 are shown graphs of rainfall, evaporation, and the number of plants which have been observed flowering during each month of the year.

The total number of flowering plants kept under observation was 85, in which are included all the plants given in Table 1. This has been enriched chiefly by monocotyledonous species which give colour to the spring aspect of the association, but do not affect its physiognomy. The 85 species listed belong to 32 families, giving an average 2.7 species per family, the richest being Gramineae, Orchidaceae, Liliaceae, and Droseraceae, almost all of which flower in the spring period. All of the species observed are common in the association. In Table II. is given a classification of the species according to the Life Forms of Raunkaier(8).

TABLE II.

Nanophanerophytes	23
Lianes	3
Chamaephytes	22
Hemikryptophytes	15
Geophytes	20
Therophytes	2

It is remarkable that Therophytes (Annuals) are so few. It is generally accepted that annuals are a feature of a xerophytic habitat. The geophytes (tuberous or bulbous plants) are abundantly present, but are not conspicuous vegetatively, and none appear in Table I. Another remarkable fact is the absence of succulents. *Mesembrianthemum aequilaterale* occurs in places in this association, but its natural occurrence is doubtful. It will be seen from Fig. 1 that the maximum flowering period occurs just after the time when the evaporation curve passes above that of the rainfall. This marks the onset of very dry conditions which are reflected in the very xerophytic character of the association.

B. Soil.

Sutton(10) has already pointed out that here the soil is a more important actor than climate, for although it is true that evaporation greatly exceeds rainfall in early summer, the xerophytic nature of the habitat is greatly accentuated by the inability of the soil to retain much water. In the Northern Hemisphere the heaths also occur on sandy soils(1) which appear to be generally the same type as those occurring here. The soil is exceedingly sandy with a water-holding capacity generally of from 20 to 25 per cent. The top soil Horizon A_1, containing a fair quantity of organic matter, is dark to grey coloured, and fades gradually into Horizon A_2, which is very light in colour and devoid of humus. This latter is just as sandy as A_1.

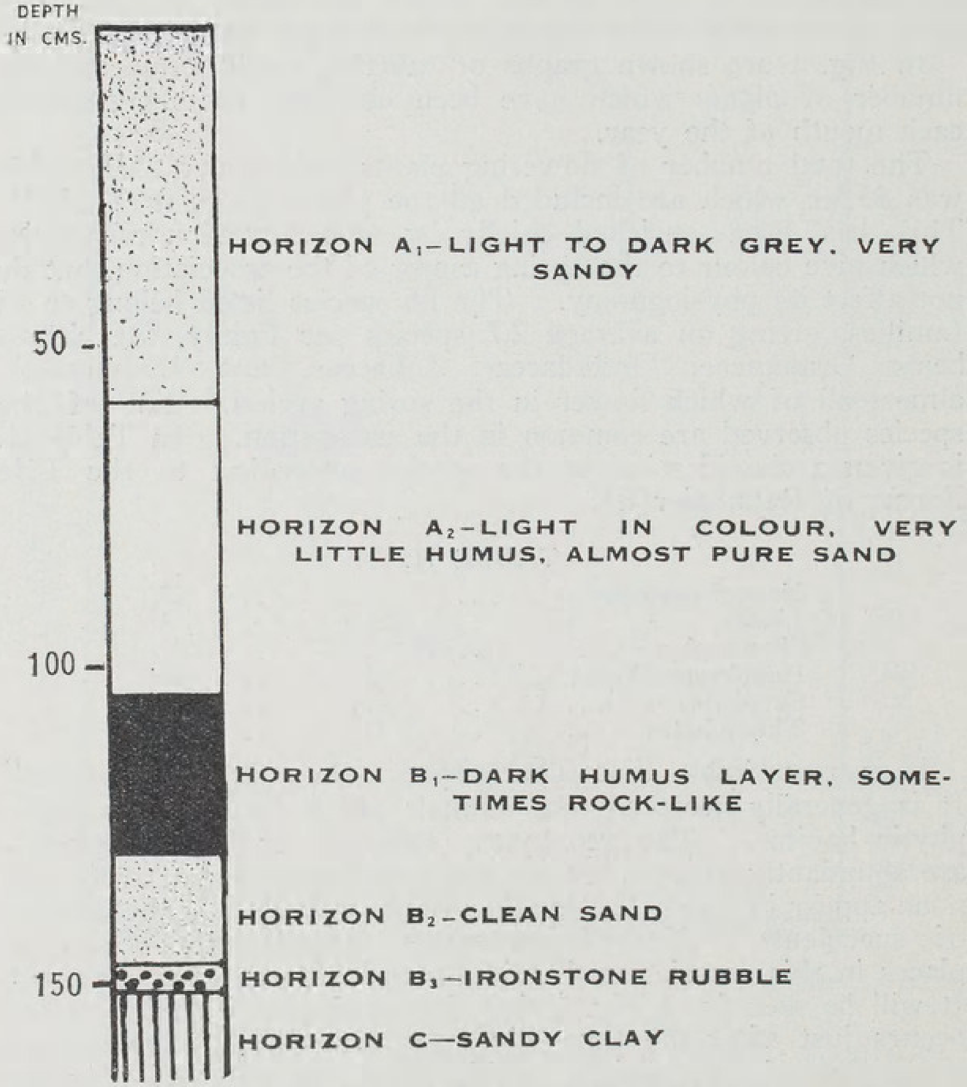

FIG. 2. Typical Profile of Heath Soil.

Generally throughout the widespread occurrence of this heath flora, these horizons remain the same except that A_2 may contain at times some clay. Below A_2 there is a great amount of variation. Very commonly there is a humus layer, Horizon B_1, which is a zone of deposition. The humus material may amount to 10 per cent. In places it cements the sand particles together, and forms almost a solid rock. It will be seen that in Fig. 2, beneath Horizon B_1, there is a layer of pure sand B_2, and beneath this lies an ironstone rubble B_3 which rests on the original rock, Horizon C. The ironstone rubble is very widespread. Roots penetrate very deeply, and in such types as shown in Fig. 2, the roots will be found in B_1, and when this is not too dense will penetrate into B_2, but cannot penetrate the rubble, B_3.

In such a profile as shown in Fig. 2, where there are two zones of deposition B_1 and B_3, there can be little doubt that when Horizon B_3 was formed, B_2 was continuous with A_2. Profiles occur where A_2 is adjacent to the ironstone concretionary layer, and in such cases it is probable that this horizon is formed from the downward movement of moisture from the surface to the unweathered rock. All the ferruginous content has been removed from A_1 and A_2 leaving only the sandy base, and it has been deposited to form the ironstone rubble. Later, if from any cause, and it may be the formation of the humus itself, the downward movement of water is interfered with, the humus layer is formed, and this in itself becomes a barrier to the percolation of water and B_2 becomes cut off from A_2. No further deposition takes place in B_3, and the further weathering of the bedrock is prevented.

In other places, however, the development of such a profile is feeble, and there is no real Horizon B. Beneath A_2 may be a layer, varying from a few centimetres to several metres in depth, of almost pure sand. In Fig. 2 is given a profile of a typical area.

It is probable that the difference in profile is due to the fact that these soils, similar in nature as regards Horizons A_1 and A_2, have different origins. In those soils where the ferruginous concretionary layer exists there is no doubt that they were directly derived from the bedrock on which they immediately rest. The bedrock is of a sandstone nature, varying from a ferruginous sandstone to a sandy clay. The bedrock itself is of primary importance as regards the character of the soil. The term podzol is applied to such a soil, and according to Glinka(3) and Ramann(7), such a soil is the result of a particular type of climate. In the Northern Hemisphere it is essentially a soil of the colder parts. Here, however, the soil exists under totally different climatic conditions. It is difficult to see how any other type of soil could have been developed from such a rock type no matter what the climatic conditions were. Where the Horizon B is wanting, and where there occurs a very deep deposit of sand beneath A_2, there can be little doubt that such areas are really old dunes which have become covered by the migration of the vegetation of the sandstone areas. The sandy soil derived from the weathering of the sandstone would offer the same root environment as the sand dune. Hence the different origin of the two soils is not necessarily indicated in the vegetation. On these old dunes, however, trees frequently occur. They are those that naturally occur on the innermost dunes along the shore. *Banksia marginata* occurs as a shrub on sandstone areas, but as a small tree on the old dunes. The sandy soil, owing to its low water-holding capacity, adds to the problem of the plants in maintaining themselves over the summer period with its high evaporation. After a prolonged period of drought, the following percentages of moisture were found at the depths given:—

Depth, inches.	Moisture, per cent.
1	0.97
6	1.25
12	1.07
18	1.27

The effect of the low percentage is shown in the germination of seeds. For months insufficient moisture exists for seed germination. Experiments with germination of seeds, particularly with peas, show that the necessary percentage of water for germination is about 1.5 per cent., and this may be regarded as a critical moisture content for germination. Since the moisture present is much below this, for some months it necessarily follows that the roots are incapable of absorbing moisture. Seeds have an enormous suction force as shown by Shull(9), and if seeds are unable to obtain sufficient moisture for germination, it must be still more impossible for roots with their much lower suction force to obtain moisture. This is reflected in the physiognomy of the vegetation.

This association is a closed one, and, therefore, there is not the room for root development as is suggested by Maximov(5). The soil not being necessarily deep, there is not the opportunity for depth development, and being in a closed community there can not be much lateral development. Nor are there underground supplies of water.

Morphological Adaptations.

Since the conditions for life become very unfavorable for plants at certain periods of the year, these must, if they are to persist, be provided with some means of withstanding this very unfavorable season. There are two main types of drought-resistant plants in this area; those, particularly members of the Monocotyledons, which persist by means of underground parts, and whose aerial parts are present only during the most favorable period of the year; and those which give this particular association its physiognomy, and which possess the ericoid type of leaf. These latter are evergreen, and they are truly xeromorphic. Not only is there a restriction in the area of the individual leaves, but there is also a decided restriction of the total leaf area.

Reference to Table I. will show that all the great majority of the leaves are either Leptophyll (less than 25 sq. mm. in area) or Nanophyll (between 25 sq. mm. and 9 $\times$ 25 sq. mm. in area).

Truly xeromorphic plants are not necessarily the inhabitants of desert areas as appears to be suggested by Maximov(6). In this association there is a deficiency of water for several months. The roots do not necessarily penetrate deeply, but in any case they do not reach a supply of water. These plants must economize water during the regularly recurring drought period. Maximov(6) regards such plants as the most complicated group among the xerophytes. The restriction of transpiration is accomplished not only by the reduced size of leaves, but also by the reduction of total leaf area. These plants do not bear out the contention of Thoday(11) that although ericoid in size, their extraordinary development as regards number offsets the smallness of the individual leaf. This latter conception is true no doubt of such plants as Spruce and Pine, but these plants are not xerophytic. Such Northern Hemisphere plants have a high rate of growth, and this cannot be true of a xerophyte.

Although the leaves of most of the plants are ericoid in form, only the members of the family Epacridaceae possess leaves which may be regarded as truly ericoid. The leaves of the associated species must be regarded as derived forms, and are not typical of leaves of the family to which the particular species belongs. Thus ericoid leaves are not found as a rule in Leguminosae, nor in Myrtaceae, where in the genera *Eucalyptus, Tristania, Angophora,* we find very large leaves. Yet in the two species of Myrtaceae found in this association, the leaves are very reduced. The great diversity of families from which the constituent evergreen species are derived is reflected in the morphology of the leaves. Although there is similarity in size and indeed of form (Fig. 3), this similarity is superficial only, and has been reached by many diverse paths.

While these leaves do possess in a general way many of the characters usually attributed to xerophytes, there is, nevertheless, no absolute uniformity of structure, and they differ from one another appreciably in several important features; thickness and distribution of cuticle, presence or absence of hypodermis and hairs, type of hairs, development of palisade tissue, decreased development of spongy mesophyll, number and disposition of stomata, development of sclerenchyma and veins, and rolling of the leaf.

The structures of the leaves of *Monotoca scoparia* and *Leucopogon virgatus,* both members of Epacridaceae, show similar features of xeromorphy, although the former has recurved leaves and the latter incurved. The leaves of *Leucopogon virgatus* fold upon the stem during the driest period, but

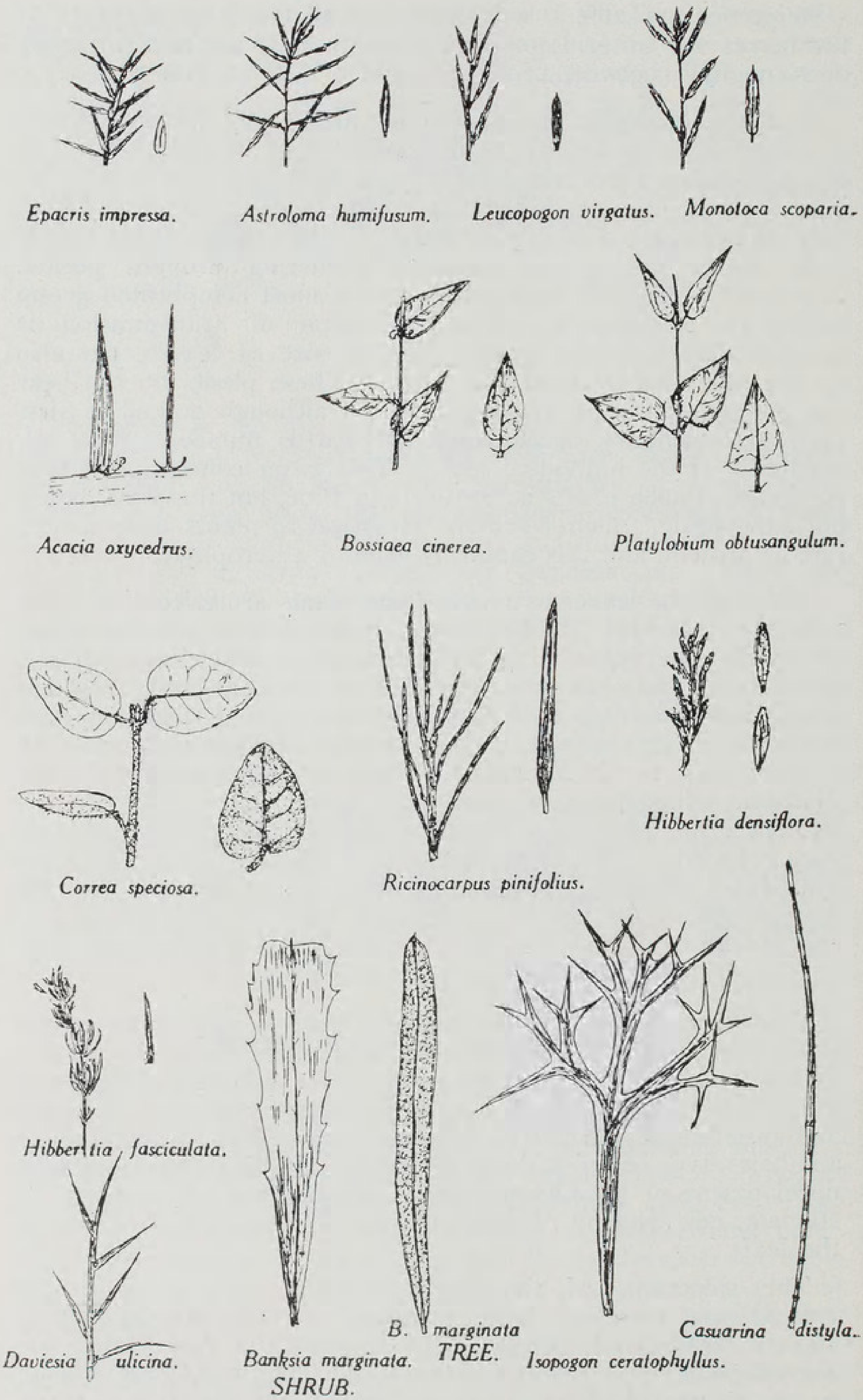

FIG. 3. Types of leaves of the Heath Association.

this does not protect the stomata, because they occur only on the under surface. In both leaves the inner epidermal wall (Fig. 4) is considerably more thickened than the outer, being usually about twice as thick. Palisade tissue is strongly developed, and consists of more than one layer of cells. The spongy mesophyll is poorly developed, really consisting of modified palisade tissue. Each leaf is traversed by several veins, each of these being bounded on the lower side by a strong mass of sclerenchyma. These leaves are both xeromorphic and sclerophyllous. Very similar to these are the leaves of *Leptospermum scoparium.* Equally sclerophyllous and xeromorphic are the leaves of *Banksia marginata,* but the structure is very different. Not only is there a hypodermis, but beneath this again (Fig. 4) there is a very well developed layer of sclerenchyma. The hypodermal cells are much larger than the epidermal, and they possess

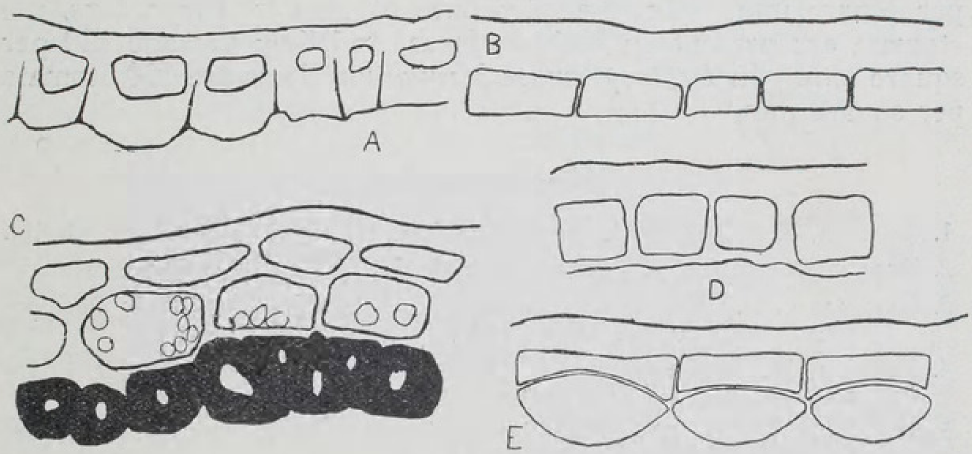

FIG. 4.—A. Leucopogon virgatus. B. Leptospermum scoparium. C. Banksia marginata. D. Hibbertia sericea. E. Platylobium obtusangulum.

a layer of starch grains on the inner wall (Fig. 4). The cuticle is very well developed, but only the outer epidermal wall is thickened. The palisade layer is only one cell thick, and the spongy mesophyll is normally developed. The lower surface of the leaf is covered with a dense mass of appressed coiled hairs. Hairs are not commonly found on leaves of this association, but stellate hairs occur on both surfaces of *Hibbertia sericea,* more abundantly, however, on the under surface. This leaf is xeromorphic, but it is not sclerophyllous. The palisade layer is only one cell deep, and the spongy mesophyll is abundantly developed. In these leaves sclerenchyma is practically absent. The same is true of *Ricinocarpus pinifolius.* This has recurved leaves as has also *Hibbertia sericea.* The recurving is so great that the lower epidermis is restricted to two grooves formed between the recurved margin and the midrib. In these grooves lie the stomata, and in these also are abundant stellate hairs. The absence of sclerenchyma, the normal development of palisade tissue and spongy mesophyll, and the absence of veins of other than the midrib do not support the contention that xerophilous evergreen plants are in any way necessarily sclerenchymatous. The leaves of these two latter species are in striking contrast to those already mentioned. In *Platylobium obtusangulum* (Fig. 4) the hypodermis consists of lenticular-shaped cells which are larger than the epidermal cells.

There is a great amount of variation in the number of stomata present per square mm. It is not possible to compare all the leaves in this respect, since where leaves are recurved as in *Ricinocarpus pinifolius* the stomata are restricted, while in *Platylobium obtusangulum* the leaf is quite flat. In this latter leaf the number of stomata per square mm. is 280, but in another species of Leguminosae, *Bossiaea cinerea,* there are 600 stomata per square mm. In the phyllodes of *Acacia Oxycedrus,* the stomata are present on both surfaces, and they average 120 per square mm. In *Leptospermum laevigatum* there are 100 stomata per square mm.

Bibliography.

1. Blanck, E. Handbuch der Bodenlehre, III. Julius Sprenger, Berlin.
2. Braun Blanquet, J. Pflanzensoziologie. Julius Sprenger, Berlin.
3. Glinka, K. D. The Great Soil Groups of the World and their Development. Ann Arbor, Mich., 1927.
4. Jerosch, H. Brockmann, and Rubel, E. Die Einteilung der Pflanzengesellschaften. Wilhelm Engelmann, Leipzig.
5. Maximov, N. A. The Plant in relation to Water. George Allen and Unwin Ltd., London.
6. Maximov, N. A. Significance of Xeromorphic Structure. *Jour. Ecol.,* xix., 1931.
7. Ramann, E. The Evolution and Classification of Soils.
8. Raunkaier. Life Forms and Statical Methods. *Jour. Ecol.,* i., 1913.
9. Shull, C. A. Measurement of the Surface Forces in Soils. *Bot. Gaz.,* lxii., 1916.
10. Sutton, C. S. Notes on the Sandringham Flora. *Vic. Nat.,* xxviii., xxix.
11. Thoday, D. The Significance of Reduction in the Size of Leaves *Jour. Ecol.,* xix., 1931.