

# Evolutionary Trends in Ericalean Leaf Structure

By TYGE W. BÖCHER

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## Synopsis

The desire to elucidate and try to understand structure in its relation to function and evolution resulted in some morpho-anatomical studies of leaves from selected species of the *Ericales*. Chromosomal data indicate that the *Epacridaceae*, *Diapensia* and *Calluna* occupy a basal position and that some groups of the *Ericaceae* as well as the *Pyrolaceae-Monotropaceae* are more derived. It is concluded that isolation and adaptive shifts in connection with continental drift at a very early time led to ecological and structural specialization in the *Epacridaceae*. The resulting leaves became sheathing, sclerophyllous, palmately veined and often pungent. In the *Ericales* an ericoid leaf structure was evolved in several presumably independent lineages. This type of adaptional evolution within an order is considered to be an atypical convergence which may be called an inherent or linear convergence. Trichomes are considered in relation to their possible functions and their position in hypothetical sematophyletic sequences. While papillae and simple hairs are ubiquitous, the glands are almost restricted to the *Ericaceae*. The globular and peltate glands in this family represent the most intricate and versatile hair structure. The discussion touches on phylogenetic aspects and concepts such as "ancestor", relicts, rigid and plastic species, types of convergence, leaf margin revolution and fusion.

Keywords: Leaf anatomy, ericoid, chromosome evolution, venation, trichomes, inherent or linear convergence.

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# I. Introduction

Is it possible to elucidate the background and trace the evolution of biological structures? Because of our incomplete knowledge of ecological conditions in the past and the scarcity of fossil records, a task of this kind, although tempting, appears overwhelmingly difficult. In this situation I found it necessary to restrict my efforts to selected leaf structures in a taxonomically fairly well-defined group (*Ericales*) and to present this paper as an approach or a sketch.

Ultimately, all structures, independent of their size are, the results of gene action, and thus of the pattern of atomic sequences in the DNA molecules. As we cannot trace the origin of a structure back to the genes or gene complexes giving rise to it, we must content ourselves with what we can deduce from chromosome studies and from the morphology of species considered to be relicts. This is certainly far from what is desirable for a real understanding.

It seems appropriate, already in the introduction, to distinguish between "ericoid" and "ericalean" leaf structure. Ericoid leaf structure is comprehended as a phyllome-lifeform, a structural type manifested in some ericalean plants and also in leaves from several other groups as, e.g., the *Rhamnaceae* (*Phyllica*, cp. *Leinfellner* 1959), the *Asteraceae* (e.g., *Senecio ericaefolius*, cp. *Espinosa* 1933 fig. 15), and *Retziaceae* (*Dahlgren* et al. 1979). Ericoid leaves are revolute. Inverted ericoid leaves ma-

intain an involute structure also at a mature stage (*Böcher* 1979). Ericalean leaf structure is that of plants belonging to the order *Ericales*. Anatomical features have been studied ever since the morpho-anatomical golden age a hundred years ago (*Ljungström* 1883, *Vesque* 1885, *Breitfeld* 1888, *Nieden zu* 1890, *Simon* 1891). In more recent times taxonomists have pursued and utilized morpho-anatomical characters (*Cox* 1948, *Copeland* 1943, 1953, *Stevens* 1971). Few have focused on structure without casting a glance at taxonomy. Nevertheless papers by *Hagerup* (1946, 1953), *Watson* (1964) and *Stevens* (1970) contain new interpretations and revaluations of morpho-anatomical features. However there are signs of an increased interest in the formulation of problems concerning the coherent research field relating to structure, function, development and evolution, and in their elucidation.

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## 2. Chromosomal evolution

*Stebbins* (1971) discussed basic chromosome numbers of woody plants and suggested that the basic numbers of many genera were derived through ancient polyploidy and that the original basic numbers were = 6, 7, 8 and 9. Thus, he distinguishes between original and secondary or derived basic numbers. In the *Ericales*, *Smith-White* (1955:64) found the basic numbers 4, 6, 7 and 9 in the family *Epacridaceae*. He emphasizes that karyotypes of *Styphelia* and *Leucopogon* with  $n=4$  are symmetrical, whereas those of *Astroloma pinifolius* with  $n=7$ , and other species with  $n=7$  and 9, are highly asymmetrical – suggesting that they are derived. In *Sphenotoma* he found  $x=6$  and 7 from which he suggests a derivation of species with  $n=12$  and 13 resulting from an allopolyploid evolution. According to *Smith-White*, the decreasing series of chromosome numbers (from  $n=12$  to  $n=4$ ) in the *Styphelieae* is probably not a result of structural changes and loss of centromeres. The low numbers are real basic numbers.

In the *Ericales* as a whole the original basic numbers are most likely to be 4, 6 and 7, and such original numbers are encountered in the families *Epacridaceae* (4, 6, 7) and *Diapensiaceae* (6). In *Clethraceae* and *Ericaceae* the lowest known haploid number is 8. It was found by *Hagerup* (1928) in *Calluna vulgaris* and later confirmed by others. *Hagerup* further reported  $n=6$  for *Phyllodoce coerulea*, but this was erroneous and had to be changed to  $n=12$  (*Böcher* 1938).

From fig. 24 in *Hagerup* (1928) and fig. 68, 6–7 in *Beijerinck* (1940), it is possible to distinguish 4 larger and 4 smaller bivalents suggesting that even *Calluna* has a secondary basic number. The karyotype in a species such as *Anemone apennina*

with  $n=8$  also suggests two sets of 4 chromosomes (*Böcher* 1945:228).  $n=8$  is found, too, in *Monotropaceae* which is also referred to the *Ericales*, but all other numbers in this group are derived basic numbers, polyploid numbers, and results of hybridization between primary and secondary polyploids. B-chromosomes were recorded in *Leucopogon revolutus* and *L. oldfeldii* by *Smith-White* (l.c. figs. 31–35, 38–39).

In the *Ericaceae* there are numerous species with  $n=12$  or  $n=13$  and polyploid series of numbers with 11, 12 or 13 as the secondary basic numbers. The number 12 is particularly important. It dominates in large genera such as *Erica* and *Vaccinium* and occurs in many taxa which are considered to be ancient or relicts (e.g., *Oxydendron*, *Daboecia*, *Rhodothamnus*, *Pieris*, *Leiophyllum*, *Lyonia*, *Leucothoë populifolia*, *Loiseleuria* and *Phyllodoce*).

Species with 13 as a basic number may have ancestors among the *Epacridaceae* or be derived from species with  $2n=24$  by tetrasomic development; 13 is a secondary basic number and it occurs in genera such as *Arbutus*, *Arctostaphylos*, *Cassiope*, *Menziesia* and the large genus *Rhododendron*.

A series with  $x=11$  may likewise either have epacridaceous ancestors (e.g., *Leucopogon*) or be nullisomic derivations of ericaceous species with  $2n=24$ . Species with  $x=11$  occur in the genera *Elliottia*, *Enkianthus*, *Gaultheria*, *Pernettya*, *Chamaedaphne* and in *Leucothoë fontanesiana*.

Astonishingly few ericaceous species are derived from  $x=8$ . *Calluna vulgaris* is the only example of a species occupying the diploid (or tetraploid) level, while *Harrimanella hypnoides* is the only representative so far of a tetraploid (octoploid) level. According to *Jørgensen et al.* (1958), it has



$2n=32$ . Still higher numbers with  $2n=48$  are reached in species of *Kalmia* and *Andromeda*, but they could just as well belong to the  $x=12$  series.

*Empetrum* belong to a series with  $x=13$ . In the *Pyrolaceae*  $x=13$  occurs in *Moneses* and *Chimaphila*, but the genus *Pyrola* deviates by the basic number  $x=23$  which is clearly derived; the same is the case with *Orthilia* which has  $x=19$  and meiotic irregularities suggesting hybrid origin in the past (Böcher 1961).

According to *Smith-White* (l.c.), the *Epacridaceae* must be of considerable antiquity, many genera dating back to the Eocene. No doubt ericaceous genera are also very old, some dating back to the Cretaceous period. We are unable to discover what kind of relations the families had in these remote times, but basic chromosome numbers (original and derived) are clearly lower in the *Epacridaceae* compared with the *Ericaceae*, and the *Pyrolaceae*, which includes members that are herbaceous and some that are very specialized ecologically (*Monotropa*) have the highest and most devi-

ant secondary basic chromosome numbers. The cytological data indicate that the *Epacridaceae* and the *Diapensiaceae* might contain species that have preserved comparatively primitive features, but common morpho-anatomical features in these groups are few and difficult to rely on (sheathing leaves and thick walls in some epidermal cells, five stamens). Both families, however, bear the stamp of early isolation from the rest of the *Ericales*. The geological and climatological upheavals in connection with continental drift in the southern hemisphere involved radical ecological changes in the biosphere. Large areas were transformed into steppes and deserts and plants were forced to develop some form of defence through sclerophyllous prickly leaves, as found in the majority of epacridaceous species. Quite different conditions prevailed in the mountains of the northern hemisphere and in the Arctic where the ericaceous plants had to survive and adapt their leaves to colder and damper environments.

### 3. Nature and age of leaf characters

Leaves are usually the most important photosynthetic organs of plants. Hence, they are generally indispensable and their occurrence and structure are firmly founded. During evolution they have been subject to changes, but as they constitute the basis for a production of matter, such changes have been very rarely abrupt or radical, but probably resembled those which we know from studies of clinal ecotypical variation, thus involving, e.g., leaf size, density of hairs, etc. An evolution leading to apophyllous, stem-assimilating plants (cf. Böcher & Lyshede (1968, 1972), Böcher (1975)) must have gone through stages where leaves were present at a juvenile stage or green stems were present together with small or early-shed leaves. A radical change in leaf structure may be imagined in the case of *Monotropa*. However, the loss of chlorophyll and the appearance of scale leaves instead of green foliage leaves are features conditioned by the establishment of mycorrhiza. In *Orthilia secunda* a yellowish-green chlorophyll-less mutant (f. *chlorina*) is able to exist in West Greenland (Böcher 1961:33), thus indicating that mycorrhiza can compensate for photosynthetic activity and perhaps make a sudden change possible. But apart from such deviant and rare cases, green foliage leaves are persistent and imperturbable structures and they deserve recognition no less than do the floral structures. In the case of *Harrimanella-Cassiope*, the two genera were once considered to be one, but leaf structure, phyllotaxis and shoot structure – all vegetative characters – and the very specialized and poor mycoflora (Holm & Holm 1980) clearly show that these two genera are very distinct: in fact the floral agreements are rather few and may be the results of

some kind of convergence. The filaments in *Harrimanella hypnoides* and *Cassiope tetragona* are very different, and *Harrimanella hypnoides* possesses a kind of involucre bracts, cp. fig. 2.

The type of venation undoubtedly belongs among the conservative foliage leaf characters.

In the *Ericaceae* the venation is usually pinnate, but in certain genera of the *Diapensiaceae* (e.g., *Shortia*) and the *Epacridaceae* it is palmate (Fig. 1). Transitions to pinnate venation occur in the *Prionotes-Lebetanthus* group, (Arroyo 1975), but pinnate venation is firmly maintained in *Ericaceous* plants with broad leaves as is palmate venation in the *Epacridaceous*.

From an evolutionary point of view distinguishing characters such as, e.g., pinnate-palmate venation are of particular interest. What kind of adaptational advantage, or what kind of ecological event was involved in their appearance or disappearance? Did they ever disappear? Perhaps they were modified or concealed? But some may have been built up by the addition of new alleles with similar effects; they were “created” and established during evolution. Because of the ecological contrast between the climates where the *Epacridaceae* and the *Ericaceae* arose and evolved, it is perhaps possible to understand why palmate or almost parallel venation was preferred in the narrow, often sheathing, rigid, xeromorphic leaves of the *Epacridaceae* and pinnate venation in the broader mesophytic leaves of the *Ericaceae*. However, the absence of multicellular or glandular hairs in the *Diapensiaceae* and the *Epacridaceae* (apart from the *Prionoteae*) is remarkable when we consider the multitude of hair types existing in the *Ericaceae*. In order to understand the discre-



Fig. 1. Leaf morphology and venation. A. *Wittsteinia vacciniacea* F. Muell. – Mount Baw Baw, Victoria. – B. *Epacris crassifolia* R. Br. – N. S. Wales. White arrow points to bracteoles at base of

inflorescences. Scale in A–B 3 mm. C. *Cosmelia rubra* R. Br. – W. Australia Two flowers on the left Scale 2 mm. – D. *Styphelia triflora* Andr. – Port Jackson. Scale 1 mm.

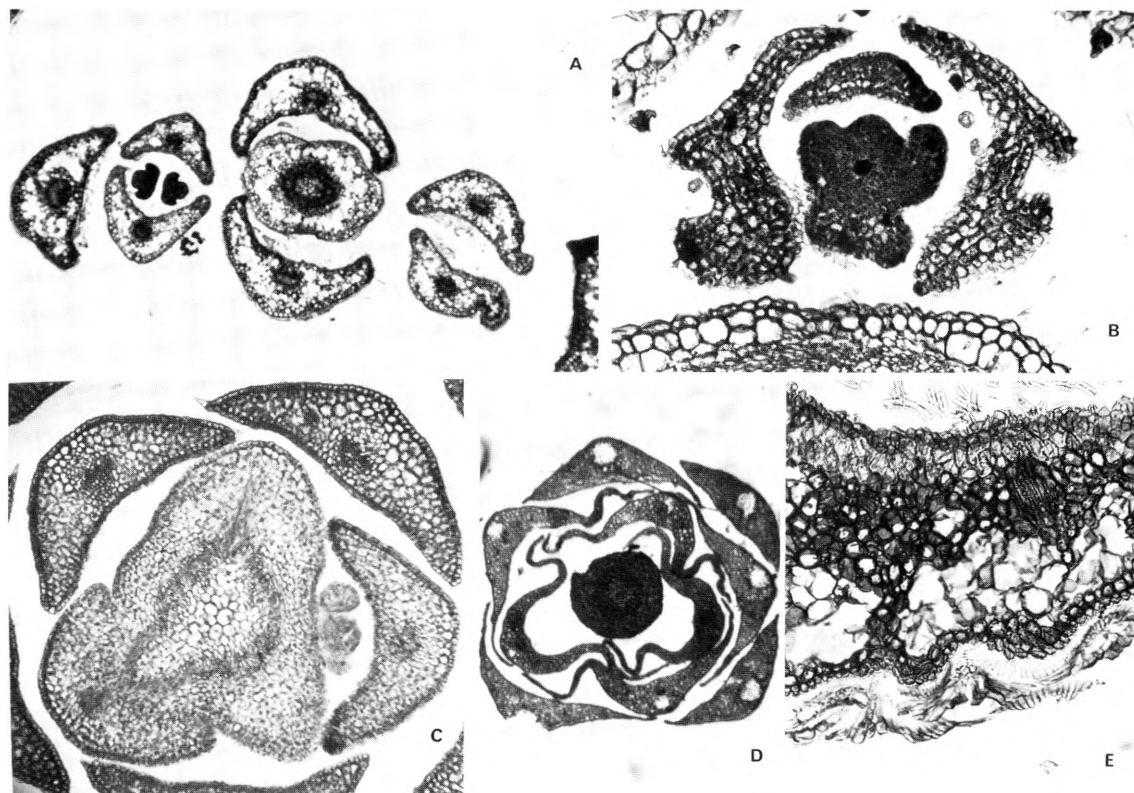


Fig. 2 – A. *Loiseleuria procumbens*. Involute opposite bracts. Left a branch with opposite foliage leaf primordia. The sister branch without primordia but the bracteoles have revolute endings on the right side. Toluidine Blue. x 25 – B. *Cassiope tetragona*. Below: Axis I. Above: Axis II with three pairs of bracteoles. The first pair intermediate between bracteole and foliage leaf. Second and third pair developing. Toluidine Blue. x 160. – C.- D. *Harrimanella hypnoides*. Axis I with one leaf on

the right supporting bud with axis II and two bracteoles. x 100. – Cross section of stem (peduncle); uppermost involucre bracts with scarious curling margins. Fiber strands in central veins showing up in semipolarized light. Fast Green-Safranin (FS) x 25. – E. *Rhododendron lapponicum*. Cross section of bud scale showing adaxial subepidermal sclerenchymatous layer, cavities being formed in parenchyma and abaxial covering of peltate hairs. Fast Green-Safranin (FS). x 100.

pancy with regard to the indumentum it is tempting to reckon that genes for multicellular and glandular hairs emerged from sources other than those in the gene pools of the *Diapensiaceae* and *Epacridaceae*. However, the possible ancestors to the Ericalean families may have had several hair types which perhaps were lost in some groups during later evolutionary stages.

Taxonomists with phylogenetic interests naturally show much interest in ascertaining primitive (ancestral) and advanced characters. Without evidence from fossils, and with little information

about ecological demands and selective pressure in the past, our estimations of the ages of structures are poorly founded. In this situation we may resort to a study of relicts on the Earth and try to utilize living species which, according to their present sporadic occurrences or disrupted geographical ranges, must be assumed to be relicts. Cox (1948:495) states that *Enkianthus* unquestionably represents the most primitive genus of the *Ericaceae*. His opinion is based on wood-anatomical characters which establish its primitiveness. In a diagram Cox places *Enkianthus* near unknown pri-

mitive ancestors. I dare not refute this, but would like to mention that Sax (1960) counted  $2n=22$  and 88 in members of this genus. According to Niedenzu (1890:251), *Enkianthus* comprises 6 species in central Asia and Japan. Niedenzu (l.c.) gives a survey of more than 100 taxa which form circumpolar groups of vicarious and usually rare species. Among the groups are *Pieris*, *Leucothoë*, *Gaultheria* (sect. I) and *Epigaea-Orphanidesia*. Another group of circumpolar relicts is made up of *Rhodothamnus-Kalmiopsis*. Phytogeographical conditions (isolation, odd occurrences) furthermore define many taxa as relicts; e.g., species of *Befaria* (*Bejaria*), cp. Camp (1941), *Elliota*, *Tripetaleia*, *Zenobia* and *Oxydendron*, cp. Wood (1961).

In this connection we should recall the occurrence of *Calluna* in the Middle Pliocene (*van der Burgh* 1978:192). *Calluna vulgaris* is European and monotypic without close relatives. It is polymorphic, its variation being eco-clinal (*Grant & Hunter* 1962). It has, as already mentioned, an almost basic chromosome number and several important distinguishing characters which may be ancient (*Nordhagen* 1937–38). *Watson* (1964) added other characters and joined *Hagerup* (1953) in referring *Calluna* and *Cassiope* to a distinct subgroup of the *Ericoideae*. Later, *Stevens* (1979) described one special tribus for *Calluna* and another for *Cassiope*.

In the light of the tertiary occurrence of *Calluna* and its deviating characters, the question is: Was this microphyllous entity a result of a long, regressive evolution from ancestors with larger leaves, or were the leaves of *Calluna* (and, e.g., *Harrimanella*) derived from another group outside the *Ericaceae* which already had small leaves?

*Niedenzu* (l.c.) holds the opinion that ancient taxa in the *Ericaceae* show the structurally most complicated trichomes. Marginal teeth, too, are better developed, while photosynthetic tissues appear less complicated in the most original forms. He clearly assumes some evolutionary trends to be regressive, others progressive. However, all characters which are products of regressive evolutions and appear more simple, probably imply

adapational advantages and thereby become steps forward. In the section dealing with trichomes some sematophyletic\* trends in trichome structure are dealt with in greater detail.

A demonstration of ancestral characters seems tempting, but it should be emphasized that all genetically stable, distinguishing characters are of interest as tools in evolutionary investigations. Each step involves new gene combinations, and we have to understand the adapational advantages connected with any structural change. However, structural features are manifold and versatile. Some are very complex and genetically almost impossible to unravel because too many genes are involved. The leaf tissue stratification (e.g., dorsiventrality), or the mechanical support of vascular bundles, is probably governed by intricate gene complexes which are often specific and may be restricted to some groups of taxa and thus are important for taxonomy. Other structural characters may be less complex, but they are common to several taxa and appear early during ontogenesis. They may result from comparatively basal genes that recur in several taxa that are obviously not closely related. To focus interest on basal, widespread characters ought to be of value for morphogeneticists trying to understand structural development and to evolutionists studying the distribution of such characters, and perhaps trying to explain their scattered occurrence among the taxa as the results of pleiotropy.

Among the basal leaf characters common to almost all members of the *Ericales* is the absence of deep incisions. All have entire leaves. Another basal character is the lack of stipules. During evolution there has obviously been no need to divide the lamina into lobes, segments or leaflets. Instead, perhaps, leaves with broad lamina were gradually replaced by small, densely spaced leaves (see p. 54).

\*) linguistic correct term for *semophyletic* employed by *Zimmermann*, *Meeuse* and recently myself, *Böcher* (1979).

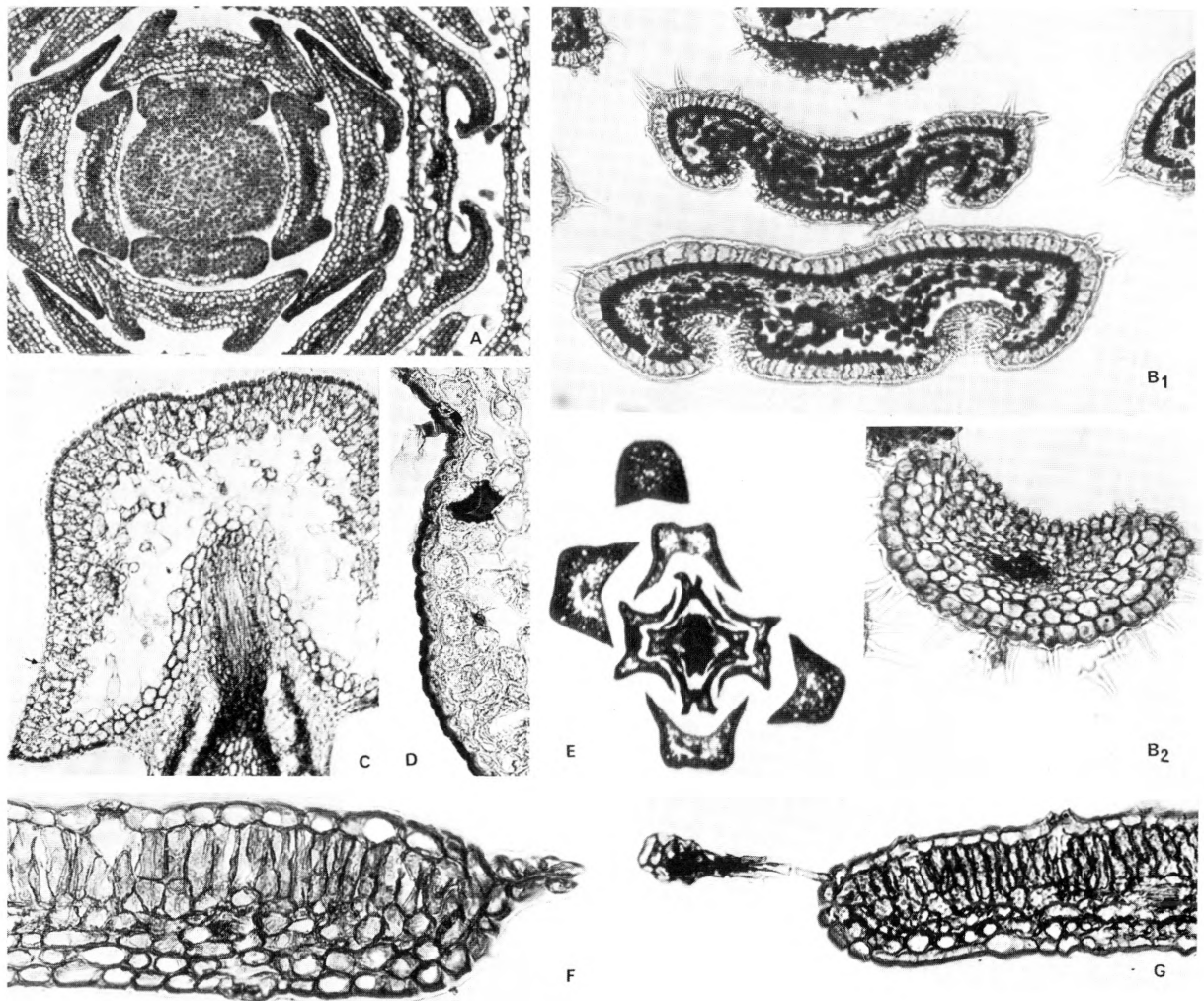


Fig. 3. — A. *Cassiope tetragona* ssp. *saximontana*. Cross section of top of shoot with primordia and young leaves. Active lateral meristems (dark). Johanssen's quadruple staining. x 100. — B<sub>1</sub>–B<sub>2</sub>. *Erica terminalis*. B<sub>1</sub> Young leaves near top of shoot. Leaves arranged in whorls in six rows. Leaves in three whorls cut. Note change from involute to revolute growth. In outer whorl, initials of papillate hairs, cp. fig. 16 Tanniniferous cells dark. Johanssen's quadruple staining. x 100. B<sub>2</sub> Primordium at top of shoot. Adaxial tissues and hairs retarded; involute growth. x 160. — C.–E. *Cassiope mertensiana*. C. Young leaf connected with midvein by short petiole. Arrow points to stomatal

opening and substomatal cavity in young abaxial palisade tissue. Fast Green-Safranin (FS). x 100. D. Central part of abaxial epidermis. Cuticular layer and basal cell in glandular hair stained with Sudan IV. Median shallow groove at the hair. x 250. E. Top of shoot showing deep median grooves in youngest leaves. Quadruple staining. x 32. — F.–G. *Rhodothamnus sessilifolius*. F. Cross section of amphistomatous leaf with palisades and dense spongy parenchyma. Base of glandular appendage. PAS staining. x 250. — G. Adaxial stomata raised. Glandular appendage with head. Fast Green-Safranin (FS). x 160.

A possible pleiotropic effect involving a complex character is discussed in connection with the "ericoid" habit (p. 36 and 59). Abaxial stripes or regions where stomata are concentrated occur in *Cyathodes colensoi* and here independent of leaf margin revolutions on both sides of the midrib (Fig. 7 G–H). Such regions constitute kinds of morphogenetic fields (cp. *Wardlaw* 1952:451), although not primary formative regions, but already localized and approximately specialized. Another morphogenetic pattern showing an example of a common, though sporadically occurring, character of the less complex type may be referred to as the "corner effect". It implies the occurrence of often particularly strong or remarkable trichomes in adaxial edges in the leaves of, e.g., *Cassiope redowskii* and *C. selaginoides* (*Nieden* 1890 fig. 2), *Calluna vulgaris* (Fig. 6), *Erica terminalis* (Fig. 3 B), and many others. In the latter two species the trichomes on the corners are to a great extent shed or shrivel at an early stage.

The many taxa in the *Ericales* constitute an intricate network. Taxa of different rank are in-

terwoven by means of bridging characters. Nevertheless the network is hardly entire. Historical events, extinctions and continental drift have broken it into pieces. Thus, the *Ericales* are more like a number of more or less separate gene-pool networks of very different sizes. One such network concerning the *Andromedeae*, illustrated by a "Wagner tree", was recently treated by *Judd* (1979). The individual networks, however, will never be static. The order and influence of the genes change. Some species are plastic, subject to rapid evolution, others rigid, evolutionarily stagnant. This is the impression we have, and generally it is not based upon genetical evidence resulting from experiments. Such experiments, e.g., on the background of the theory of the plasticity and rigidity of taxa (cp. *Hultén* 1937:22) are much needed.

In the present paper we must confine ourselves to discussing some ericalean character complexes, all relevant to the photosynthetic organs, the foliage leaves.

## 4. Persistent and deciduous leaves

The *Ericales* comprise species belonging to both categories. In the *Ericaceae*, according to *Sleumer* (1966–67:469) most Malesian members have evergreen coriaceous leaves. There are many representatives of both types of leaf in *Rhododendron*, but *Seithe* (1950:378) expresses the view that the genus was originally deciduous. *Stebbins* (1974:253) postulates that the basis for the origin of the deciduous condition in temperate regions was the hardening of the plants prior to the onset of frosts. Selective pressure would be exerted on plants inhabiting moisture-saturated soils “since they would not have been subject to hardening by drought”. The occurrence of deciduous species in arctic-alpine floras hardly gives much support to *Stebbin*’ idea. *Salix herbacea*, *Vaccinium myrtillus*, *Betula nana* and *B. glandulosa* are deciduous, constantly covered in snow during the winter and grow in moist to mesic soils. Other deciduous species, however, are connected with exposed, wind-swept habitats (*Salix uva-ursi*, *Arctous alpina*), while *Vaccinium uliginosum* ssp. *microphyllum* is ubiquitous and without special preferences. Among the evergreen arctic-alpine species, *Arctostaphylos uva-ursi* and *Loiseleuria procumbens* grow on dry soils, *Cassiope tetragona* *Phyllodoce coerulea*, *Vaccinium vitis-idaea*, *Empetrum hermaphroditum*, and *Diapensia lapponica* occur on mesic soils and often in habitats protected by snow while *Harrimanella hypnoides* is at typical snow-bed plant on soil constantly saturated by moisture. Finally, *Oxycoccus* and *Andromeda* are bog plants on wet soils.

An oscillation from the evergreen to the deciduous condition occurs in several ericaceous genera and is usually difficult to connect with changes in the environment. Hybrids between species

belonging to the two categories are very rare and mostly sterile or weak (*Vaccinium vitis-idaea* × *myrtillus* in Sweden, “*Azalerodendrons*”, see *Bowers* 1960:184–86). A species such as *Rhododendron dauricum* is usually deciduous, but sometimes evergreen. The North-east American monotypic *Zenobia pulverulenta* is classified as deciduous to semi-evergreen, and in the *Leucothoë* some sections have evergreen leaves, but species in the section *Eubotrys* are deciduous (*Sleumer* 1959, *Wood* 1961). The majority of ericaceous species supposed to be tertiary relicts have persistent leaves; e.g., *Calluna vulgaris*, but the oscillation between an evergreen and a deciduous condition emerged early. A particularly good example of a deciduous species with many possibly ancient characters is *Arctous alpina* (*Nieden* 1890:179, *H. E. Petersen* 1908 a).

The leaves in the *Epacridaceae* are persistent, entire and coriaceous, plane or curved upwards or downwards, rarely ericoid. Their bases are often broad and sheathing, but can be narrow at the attachment. The shedding of sheathing leaves takes place in a peculiar manner involving the cortex of the internode below (*Dormer* 1945: 149).

The leaves in the *Diapensiaceae* are extremely heterogeneous. *Hutchington* (1969:308) says that the family is probably derived from different basic stocks, the *Diapensieae* resembling the *Ericaceae* and the *Galacineae* resembling the *Pyrolaceae*. *Diapensia lapponica* is evergreen with very thick epidermal cell walls in its leaves (*H. E. Petersen* 1908 b fig. 5C).

If we disregard the herbaceous, problematic *Galacinae*, we will not hesitate to consider *Diapensia lapponica* with  $2n=12$  as ancestral, and if the



*Epacridaceae* are included among those with persistent leaves, it appears convincingly most probable that the evergreen condition is the most original in the *Ericales*. Judd (1979:492) expresses the same view saying that in the *Ericaceae* the generalized condition is coriaceous and with persistent leaves, but cold-adapted species from distantly related genera have evolved deciduous and much

thinner leaves. However, considering the isolated distribution and the monotypic position of *Galax aphylla* and the extremely localized occurrences of *Shortia galacifolia*, both species being herbaceous and with  $2n = 12$  (Baldwin 1939, 1941), it appears more safe to leave open the question about the originality of persistent or deciduous leaves.

## 5. Phyllotaxy, bracteoles, protection of apical meristems

Ericalean leaves are usually alternate or spirally arranged. In some cases (e.g., *Leiophyllum* sp., *Gaultheria* sp., *Pieris* sp. and the epacridaceous *Needhamia pumilia*) transitions to the opposite position are found; a species such as *Chimaphila umbellata* has almost apposite or whorled leaves. In many species there is a clear tendency towards a rosette-like accumulation of leaves towards the top of a year-shoot. However, typical decussate or whorled phyllotaxy occurs in a small number of genera and deserves special attention. The most important examples are found in *Cassiope*, *Calluna*, *Erica*, *Loiseleuria*, and *Kalmia polifolia*. In most cases the leaves are densely spaced, but there is no obvious advantage involved in the opposite decussate or whorled phyllotaxy.

One explanation might be that the action of genes that are responsible for the opposite position of the bracteoles has been altered in some species. In *Cassiope* there are four bracteoles (two opposite pairs) at the base of the flower stalk (Warming 1908: 27–28 and cp. fig. 4B); in *Calluna* the flowers have two to six (opposite) pairs of “Zwischenblätter” above the two normal bracteoles (Nordhagen 1937–38: 15–24). One might suggest that the decussate phyllotaxy has been maintained and extended, becoming applicable to the foliage leaves, too. However, a number of similar bracts placed as “Zwischenblätter” occur in most species of the *Epacridaceae*, and here they are spirally arranged.

Other explanations referring to ecophysiological conditions seem perhaps more probable. In *Calluna*, *Cassiope tetragona* and *Erica dianthifolia*, it is obvious that the position of two or four rows of leaves that approach the direction of the stem affords protection of the stomata in the grooves

on the abaxial sides of the leaves. These grooves are partly covered by the leaves situated just below (Warming l.c., figs 16–17, Beijerinck 1940: figs 2–4). In all such cases a dense spacing of cataphyll-like green leaves results (cp. Böcher 1979:66) and thus long photosynthetic flanks composed by the closely spaced small leaves or fewer elongate, narrow leaves. In the case of *Cassiope* the photosynthetic bodies are tetragonous with four light-exposed sides. They are adapted to utilize radiation from the sun when it is low in the sky, which may be of great importance in high arctic areas where the species is common. *Erica dianthifolia* has long needlelike leaves, which in cross section (fig. 14) anatomically resemble those of *Cassiope tetragona*. They have a more or less upright position on the stems and as the species grows in dry, sunny areas they avoid exposure to sunbeams touching the leaf surface at right angles. The same cannot be said about North Atlantic species such as *Erica tetralix*, which, however, just has more or less spreading, small leaves in whorls of four (or three). But the genes responsible for opposite or whorled phyllotaxy in *Erica* were possibly selected in dry climates of a mediterranean type.

In *Loiseleuria* the bases of two opposite leaves together form a sheath-like body that protects the vegetative and the flowering buds (Warming l.c. p. 14, Rübél 1908 Plate XIV). Otherwise sheathing leaves are rare in the *Ericaceae* but common in the *Epacridaceae* and the *Diapensiaceae*. A spiralled phyllotaxy would not allow a similar type of protection, but densely spaced spirally arranged leaves, which assemble around and cover the apical meristems, are frequently found; e.g. in *Phyllodoce coerulea* (Warming l.c. fig. 10 G–H). In *Phyllodoce glandulifera* the apex is further protected by a

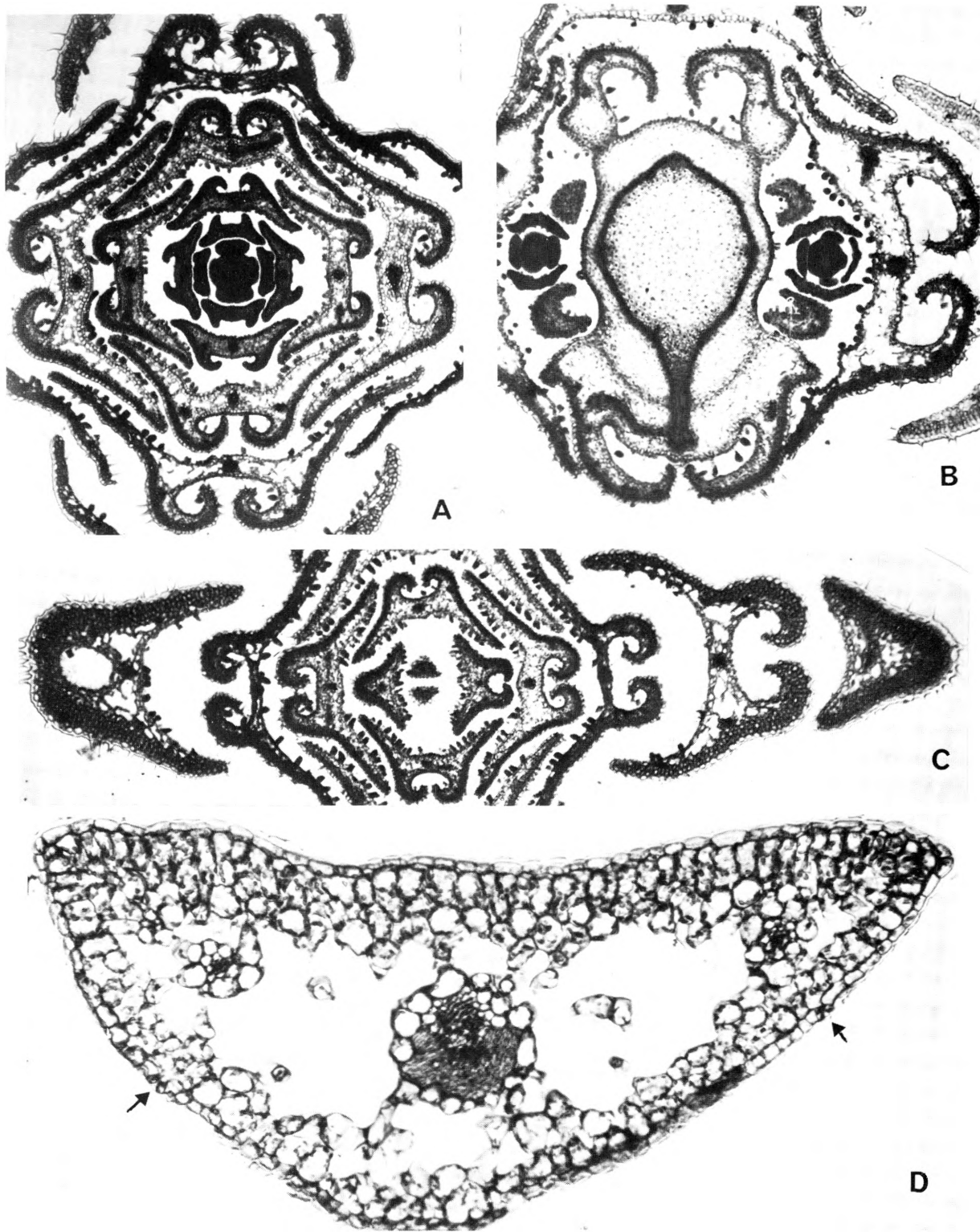


Fig. 4. A-C. *Cassiope tetragona*. Cross sections of shoots. Johannsen's quadruple staining, x 50. A. shoot apex with 9-10 leaf pairs. B. At a short distance from the apex; two opposite branches each with two pairs of bracteoles and basal parts of leaf ears. Commissural strand issuing from leaf trace strand. C. Successive leaf pairs, the youngest in the middle. The

oldest have been cut near the tips of the leaves, where the two flanks have grown together. - D. *Harrimanella stellariana*. Leaf cross section showing three veins and a few trabeculae between the bundle sheath of the midvein and the peripheral chlorenchyma. Arrows point to stomata. FS, x 200.

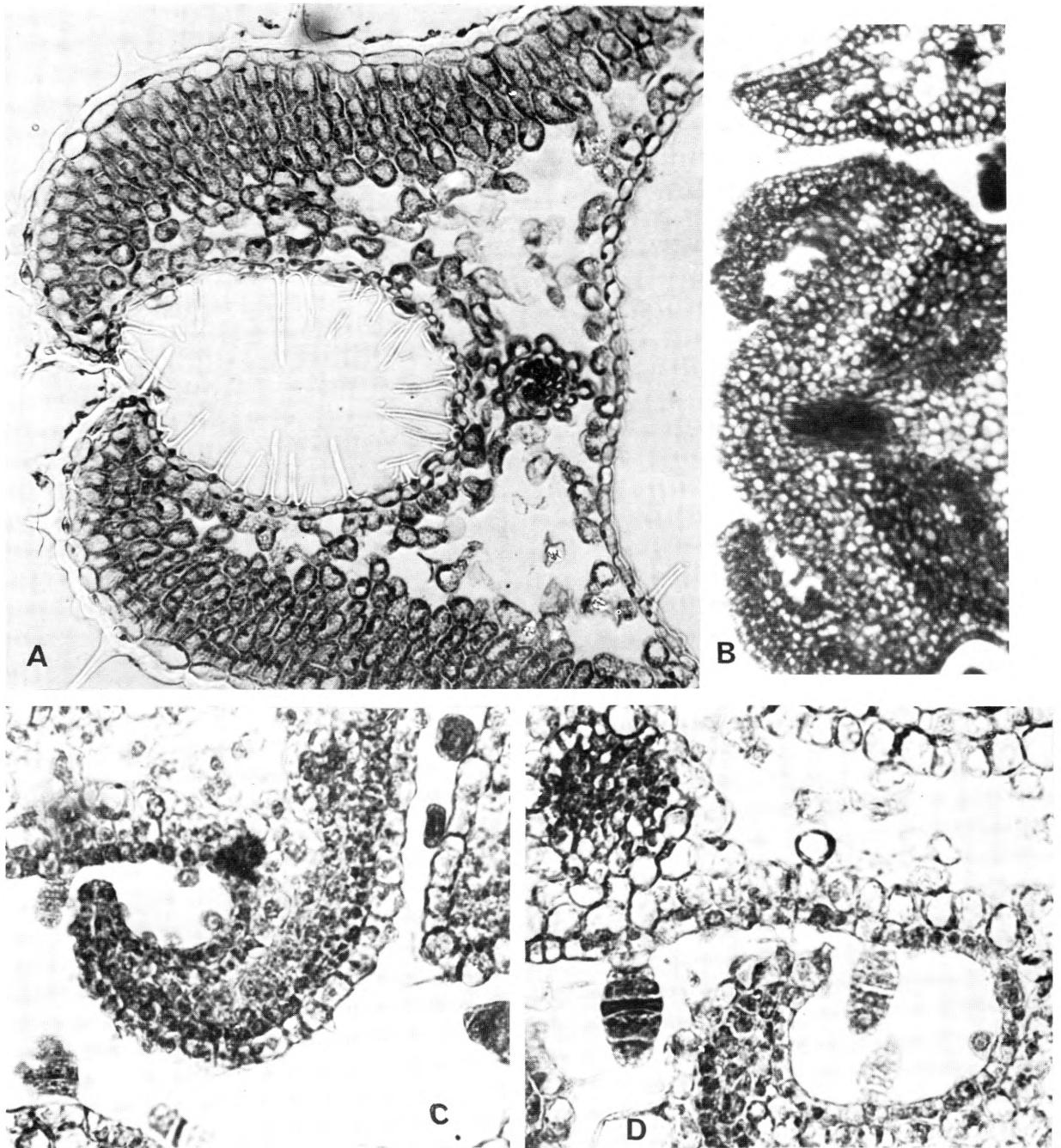


Fig. 5. *Cassiopa tetragona*. Cross section of front part of leaf in semipolarized light. Simple hairs, raised guard cells, midvein with bundle sheath. FS. x 200. – B. Base of leaf, still in connection with main axis. Central leaf trace. Pith in stem. Quadruple

staining, x 200. – C.–D. Details near revolute parts. Leaves from two successive pairs. C. Younger with active lateral meristem and developing glandular hairs. D. Older with larger almost mature hairs. Midvein with bundle sheath. FS. x 640.

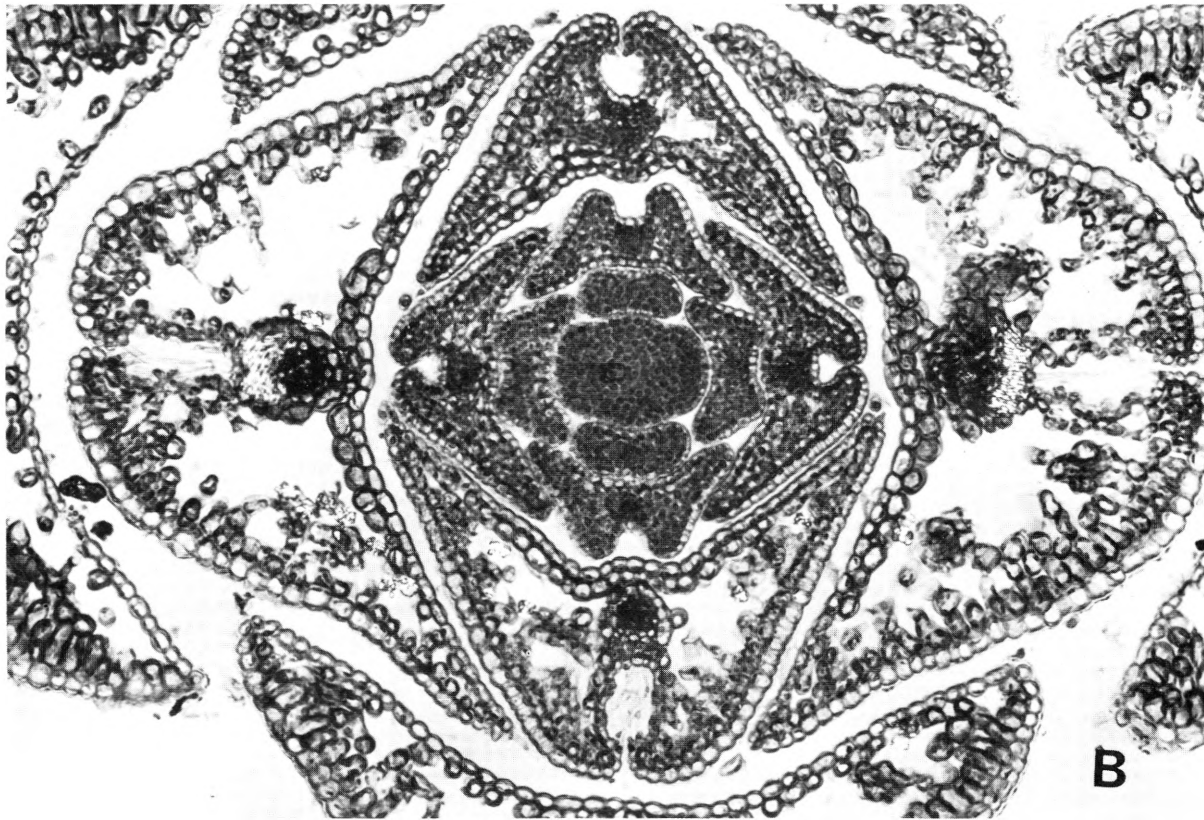


Fig. 6. *Calluna vulgaris*. A. Longitudinal section through shoot apex. A few club-shaped hairs are located in or near the cavities between the uppermost leaf endings near the apical meristem, cp. Fig. 17. the development of the basal ears ap-

pears from a comparison of the opposite successive leaf pairs. – B. Cross section of shoot apex with 8 leaf pairs. Stomatal furrows below midveins. Palisades maturing in leaf pair no. 8. Club-shaped hairs at edges of leaves in sharp corners. FS x 200.

sticky resinous substance produced by glands (see pp. 45–46).

In *Cassiope tetragona* the uppermost leaf pairs protect the apical meristem, but in this species the shoot apex is further protected by resinous material produced by many glands that are particularly dense and active in the youngest parts of the shoots. In *Calluna* the club-hairs described by *Beijerinck* (l.c. fig. 19 and 35) and in the present paper (Fig. 17) may have a similar effect.

*Harrimanella hypnoides* has vegetative terminal buds on many shoots. These buds have no scale-leaves and the dense, spirally arranged, needle-like leaves surrounding the buds alone give some protection. The species is almost confined to habitats with a long-lasting snow cover and it may not need scales on vegetative shoot ends. At the bases of the peduncles, however, the normal leaves are replaced gradually by a kind of involucral bracts, which have scarios, curling margins (fig. 2D) and are shorter and broader than foliage leaves (*Warming* 1908 fig. 14 F). These deviating bracts were already noticed by *Irmisch* (1851:503), who mentions that one such bract sometimes is moved upward on the pedicel. The broader bracts protect the flower-buds.

Scale leaves together with the basal parts of petioles protect the terminal buds in *Andromeda polifolia*, *Arctostaphylos uva-ursi*, *Arctous alpina* and *Lyonia calyculata* (*Warming* l.c.).

*Copeland* (1943:536) published a classification of the degree to which bud scales are differentiated from foliage leaves in the *Rhododendroideae*. His first group contains taxa with winter buds covered by foliage leaves or reduced foliage leaves. It contains, i.a. *Bejaria*, which in many ways is primitive, *Daboecia*, *Rhodothamnus*, *Kalmia*, *Leiophyllum*, as well as *Loiseleuria* and *Phyllodoce* referred to above. In the second group the winter buds are protected by specialized cataphylls. Here *Copeland* mentions *Ledum*, *Rhododendron* and *Menziesia*.

There is nothing about winter buds in the paper by *Holm* (1913) on *Epigaea repens*, but, accor-

ding to *Turrill* (1948), *Orphanidesia* has persistent linear bud scales.

Persistent bud-scales are described in detail in *Empetraceae* by *Hagerup* (1946: 1–15), who also mentions that *Erica tetralix* has persistent bud-scales.

The structure of the protecting scales in *Ledum* was described by *Grevillius & Kirchner* (1923:22). There is an adaxial sclerenchymatous hypodermal layer and wide lysigenous cavities in the mesophyll above the abaxial epidermis. A very similar structure is found in bud-scales of *Rhododendron lapponicum*, which furthermore has a protective layer of peltate hairs on the abaxial sides (Fig. 2E).

In *Rhodothamnus chamaecistus* from the Eastern Alps protective bracts and bracteoles do occur, but there seems no protection of this kind in the East Mediterranean montane *R. sessilifolius*, where, however, the foliage leaves are crowded into terminal rosettes and may initially provide the flower buds with some protection. In *Kalmiopsis leachianus* true bud-scales are illustrated by *Copeland* (l.c. fig. 62, 65, 66), in spite of the fact that the same author places this species in his group I.

According to *H. E. Petersen* (1908), there are no bud-scales in *Diapensia lapponica*, but the buds are deeply hidden among the leaves in the cushion and protect one another by the sheath parts (Fig. 8).

Bud-scales are not recorded in the *Epacridaceae*. But many of the species have sheathing leaves, and densely spaced bracteoles form an involucre around the flowers.

In the *Ericales* a transition from almost open buds without bud scales, as in, e.g., *Calluna* and *Cassiope*, to highly specialized buds with well differentiated bud scales can be ascertained. *Rhododendron* may represent the most advanced step with regard to morphological features affording protection of the buds. However, the vital apical shoot meristem in, e.g., *Calluna*, is protected by leaves issuing below the apical meristem (see fig. 6A).

## 6. Leaf tissue organization and arrangement

### a. Dorsiventrality, isolaterality and derived leaf architectural features.

A typical dorsiventral leaf has palisade parenchyma on one side and spongy parenchyma on the other; usually the palisades are developed at the adaxial side. In rare cases leaves are inversely dorsiventral. This is the case in species of the *Epacridaceae*, e.g., in *Sprengelia sprengelioides* (Copeland 1953 fig. 5) and *Andersonia coerulea* that both have sheathing leaves. In *Asterales* inverse dorsiventrality occurs in *Chuquiraga hystrix* (Böcher 1979 fig. 6–10).

In the *Ericaceae* there are numerous examples of typical dorsiventrality. It is sufficient to refer to *Bejaria racemosa* (Copeland 1943 fig. 1), *Arbutus mollis* (Niedenzu 1890 fig. 1), *Rhodothamnus chamaecistus* (Grevillius & Kirchner 1923 fig. 16) and to examples given in figs. 3, 7–11 of the present paper.

In the *Ericaceae* typical isolateral arrangement was mentioned already by Niedenzu (l.c.), e.g., in *Arctostaphylos nevadensis*. This species occurs, according to Franklin & Dyrness (1969:87), in the xeric type of the *Ponderosa* Pine forests. Another species, *A. patula*, also with isolateral leaves is reported from semi-open brushland, a kind of chaparral (l.c.: 94). In both cases the leaves probably receive much light reflected from the ground, which ecologically makes the isolateral structure easier to understand. In *A. patula* the veins are attached to the two epidermal layers with flanges of fibers (they are what Breitfeld (1888) called “durchgehend”, a common feature in cases of isolateral structure (cp. fig. 10 F and p. 56)).

A similar eco-physiological explanation may be proposed for the leaf blades in *Erica terminalis*

(Figs. 3 and 13). While most species of *Erica*, e.g., *E. tetralix*, have a typical ericoid leaf structure with revolute margins, *E. terminalis* has developed two stomatal furrows along the leaf margins and an intermediate area on both sides of the midvein which has abaxial palisades. This structure may adapt the species to utilize light reflected from the rocks and the ground in the mediterranean maquis. A change from dorsiventral architecture to an almost isolateral one may be considered an ecotypical response to an alteration in light conditions, but the ability to develop abaxial palisades seems deeply rooted in the Ericalean gene pool.

Simon (1891:22), when dealing with the photosynthetic system in the *Epacridaceae*, emphasizes the dependence of palisades on the screening effect of the other leaf tissues. In most cases palisades are developed on the light-exposed adaxial side (e.g. in *Cyathodes*, fig. 9F), but a typical isolateral texture occurs in, e.g., *Brachyloma ericoides* and *Dracophyllum uniflorum* (Fig. 23). Sheathing, more or less upright leaves have palisades to all light-receiving sides (e.g., in *Andersonia* and *Dracophyllum*). There is no large gap between this situation and that in the leaves of *Empetrum* (Hagerup 1946). In *Andersonia* or *Styphelia*, two or more leaves surround the stem and their palisades have an access to the light that is similar to that of the cylindrically arranged palisades in *Empetrum* leaves. Such leaves start as almost flat dorsiventral primordia, but become revolute during maturing. They maintain the dorsiventral tissue arrangement independent of the direction of the leaves in relation to the prevailing angle of incidence of the light.

The margin of the mature *Empetrum* leaf is restricted to a hairy fissure where the two leaf

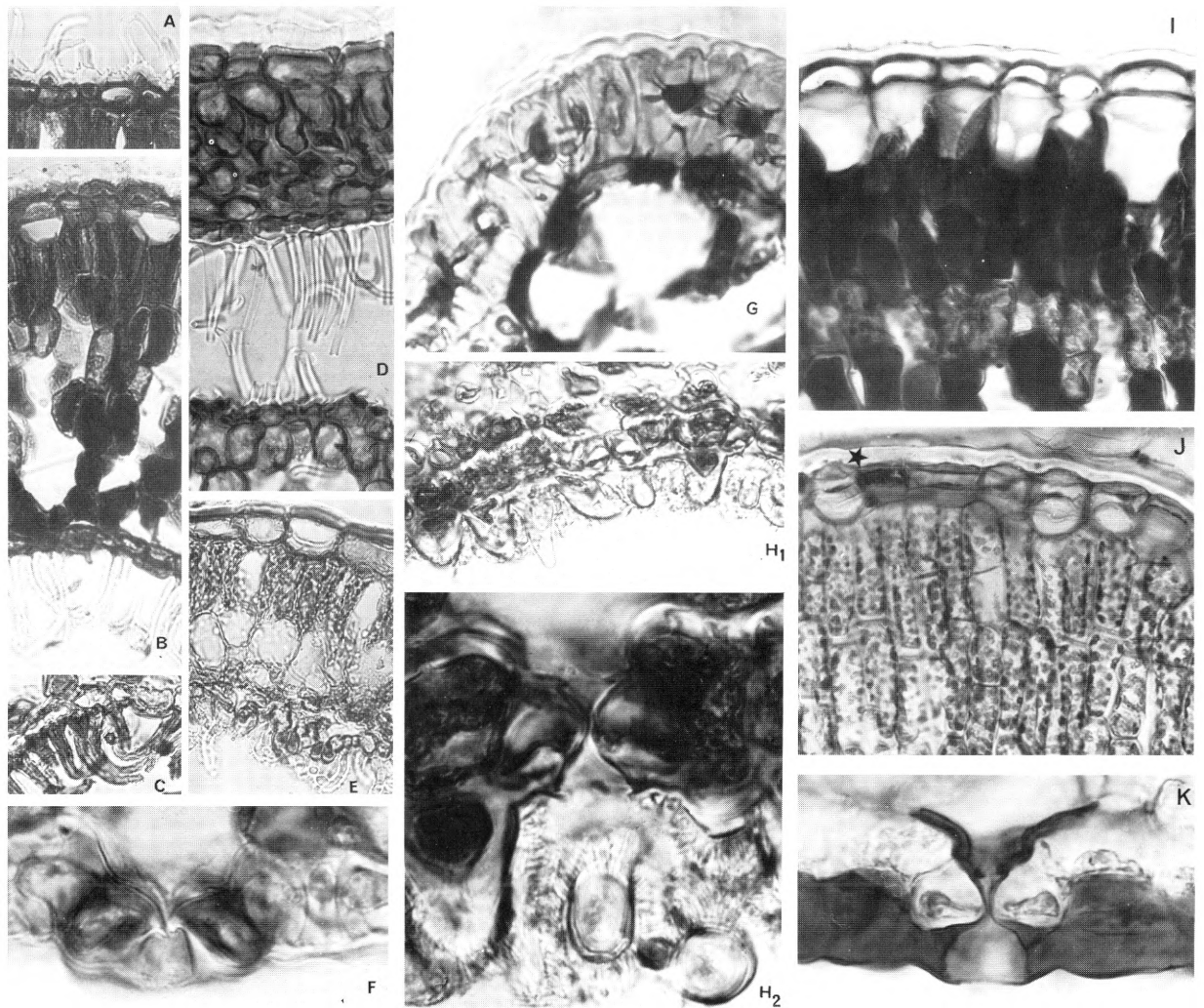


Fig. 7 A.–C. *Kalmia polifolia*. A. Part of adaxial epidermis with cuticular ridges and simple hair without cuticular excrescences. B.–C. Adaxial epidermal cells with mucilaginous interior walls, abaxial epidermal cells with cuticular excrescences on simple hairs. A–B. PAS staining and semipolarized light. C. Sudan IV staining. x 250. – D. *Loiseleuria procumbens*. Transsection from adaxial epidermis through cavity to the recurved part where the abaxial epidermis is turned upwards against the cavity. Fast Green–Safranin (FS) Semipolarized light x 250. – E. *Erica tetralix*. Longitudinal section stained with Ruthenium Red, semipolarized light. Interior pectinaceous epidermal wall intensely stained. Parenchyma beneath palisades of roundish, water-storing cells. Stomata and papillate hairs on abaxial surface. x 250. – F. *Andersonia coerulea*. Guard cells in adaxial epidermis (leaves sheathing). Fast Green –

Safranin. x 1000. – G–H. *Cyathodes colensoi*. G. Adaxial epidermis. Anilin-Blue-Black stains pit canals in very thick walls. x 630. H<sub>1</sub> Cuticular excrescences from papillate hairs surrounding stomatal opening. Semipolarized light x 320. H<sub>2</sub>. Pair of guard cells stained with Sudan IV. Semipolarized light; radiating cuticular excrescences from papillate hairs x 1000. – I. *Leiophyllum buxifolium*. Mucilaginous interior epidermal walls. Pectinaceous layer dark, as is the wall-like borderline of the mucilage. Palisades tanniferous. FS x 320. – J. *Rhododendron lapponicum*. Adaxial epidermal cells with mucilaginous walls, the interior mucilage layers thickest. Black asterisk: Thick birefringent cuticular layer. Mucilage stratified, yellowish green with FS. x 250. – K. *Arctostaphylos uva-ursi*. Sudan IV stains cuticular layer and cuticular coating of substomatal chamber x 630.



halves meet. It is impossible to ascertain a demarcation when the adaxial side terminates and the flanges begin.

In other cases the demarcation can be defined because sharp edges are formed and these are provided with special trichomes (“corner effect”). The flanges take over a considerable part of the photosynthesis in *Calluna* (fig. 6 and *Beijerinck* l.c. figs. 25–29), *Cassiope tetragona* (figs. 3–5 and *H. E. Petersen* 1908 a), *C. selaginoides* (*Nieden zu* l.c. fig. 2 B) and *Erica dianthifolia* (fig. 14).

A morphological sequence in *Cassiope* involves a possible “fusion” of the leaf margins, more precisely the margins of flanges. This was suggested by *Nieden zu* (l.c.: 219) and *Stevens* (1970:1134). *C. redowskii*, an East Asiatic montane species (cp. *Pimenov* 1974), has closed leaves resembling helmets, with openings towards the points of attachment. The palisades cover the abaxial sides and the flanges, *Nieden zu* (l.c. fig. 2A). A sequence terminating with a complete “fusion” is suggested for *C. mertensiana* and *C. lycopodioides*. The process seems to be initiated in *C. tetragona*, in which a fusion of the two sides concerns only the tips of the leaves, *Linsbauer* (1900: 1–2 in Plates I–II). In *C. mertensiana* the area of fusion may be indicated by a low median bulge, *Nieden zu* (l.c. Plate III.4) or – as in my own slides – less typical palisades in the middle of the abaxial side, or after certain preparations in deep incisions here (Fig. 3E). However, it is perhaps unnecessary to envisage a real fusion. The gene pool of the *Ericales* may contain genes which can promote a development of abaxial and lateral palisades. In juvenile leaves of *Calluna* (see *Beijerinck*) (l.c. fig. 28) such genes are clearly active.

Abaxial green parenchyma cells (spongy parenchyma) are heterogeneous. In *Rhodothamnus sessilifolius* such cells are elongate but hardly branched (Fig. 3). The same is the case in *Gaultheria myrsinites* (*Nieden zu* (l.c.:163)). This author further mentions that some species have spongy cells with flattened arms, others have swollen ones. In the *Rhododendroideae* the spaces in the spongy pa-

renchyma are to a great extent formed by the decomposition of entire wide cells. This was already shown by *Breitfeld* (1888 Plates V–VI), who illustrates intercellular lacunae being traversed by pieces of tissue or rows of entire parenchymatous cells. In *Ledum* the wide cells which become disorganized were called transparent cells by *H. E. Petersen* (1908 a, figs. 9–10) *Sifton* (1940) refer to them as swollen cells and studied the series of events resulting in the formation of the wide lysigenous air spaces. A centrally placed tissue with large air spaces traversed by trabeculae of parenchymatous cells occurs in *Harrimanella stellariana* (fig. 42). Similar trabeculae traversing leaves with large lacunae occur in *Calluna* and *Cassiope*. In *Erica tetralix* a layer of swollen spongy parenchyma cells may function as a water-storage tissue (fig. 7E).

*Nieden zu* paid much attention to the cell wall thickness. Spongy parenchyma, but not palisades, with comparatively thick walls are found in most species of *Gaultheria*, in *Pernettya*, the *Vaccinium vitis-idaea* section, and furthermore in *Diapensia lapponica* (fig. 8 and *H. E. Petersen* 1908 b). Palisades with thin walls have few chloroplasts and their main function is probably the storage of water (e.g. *Themistoclesia* leaves, *Nieden zu* l.c. Plate VI 1–2).

*b. Epidermis, hypodermis and other non-photosynthetic tissues.*

A frequently occurring feature is that the adaxial epidermis has larger (wider) cells than those in the abaxial and that stomata are more common here. In *Erica baccans* during leaf ontogenesis *Tetley* (1936) found a rapid increase in size of the adaxial epidermal cells and stagnation in growth of the abaxial ones. The latter finally cover the dorsal grooves with the stomata. Mucilaginous epidermal cell walls are conspicuous numerous. They occur adjacent to palisade cells and sometimes taper into the upper palisade layer, e.g. in *Leiophyllum taxifolium* and *Daboecia polifolia* (figs. 7, 12 and *Copeland* 1943 figs. 82 and 124). The

mucilaginous wall layer is very thick in *Rhododendron lapponicum* (fig. 7J), *R. malayanum* (Breitfeld l.c. Plate V), *Erica tetralix* (fig. 7E) and in *Calluna vulgaris*. In the last-named the mucilaginous layer increases in thickness with the age of the leaves. First when the palisades are fully developed, e.g., in the sixth–seventh leaf pair from the top, does the mucilaginous layer reach its final thickness (fig. 6). The mucilage in *Calluna* stains with alcoholic resorcin blue, a fact which, according to Eschrich (1956:497), indicates that this particular mucilage, exceptionally, is related to callose. The mucilaginous walls are always connected with palisades and may occasionally be of importance for the supply of water to the green cells. Thus they function in the same way as water-storage tissue located near photosynthetic cells. A typical water-storage tissue replacing palisades was described by Niedenzu (l.c. fig. 1 B–C) in *Sophoclesia nummulariifolia*. In *Erica dianthifolia* (Fig. 14) a hypodermal water-storage tissue occurs. The palisades along the flanks and on the adaxial side are protected from excessive light by a dark tanniferous epidermal layer and the water-storing hypodermis, which is exceedingly thick. The cuticular layer is also very thick and shows up in polarized light with a type of refringence opposite to that of cellulose and may thus largely be composed of waxes. In *Arctous alpina* Niedenzu describes wide abaxial epidermal cells, which likewise seem to be water-storing. Finally, *H. E. Petersen* (1908 a) mentions a water-storage tissue in connection with the midrib near the abaxial side in leaves of *Andromeda polifolia*.

A multiple epidermis is rarely developed, but it is described by Niedenzu in *Agarista* (l.c. Plate III 2) and *Vaccinium polystachyum* (in Plate V 9).

In the *Epacridaceae* the epidermal cells are largely sclerenchymetous and of uniform size, see fig. 7G, 22D, Copeland (1943) and Arroyo (1975 figs. 4–5). No similar structure is observed in the *Ericaceae*, but Niedenzu (l.c. Plate VI a) mentions a hypodermal sclerenchymatous layer and a margi-

nal tissue of sclerenchymetous cells in *Macleania cordata*. Marginal sclerenchyma is not common in *Ericaceae* but was found in *Vaccinium vitis-idaea*, *Andromeda glaucophylla* and *Leucothoë axillaris* (fig. 9D). Beijerinck (l.c. fig. 27) reports sclerenchyma in parts of the adaxial epidermis in bracts of *Calluna*.

The thick outer epidermal walls in the leaves of *Diapensia lapponica* appear highly deviating (fig. 8). Their structure was commented upon already by Grevel (1897) and *H. E. Petersen* (1908 b). The adaxial cuticle is abnormally thick and covers a likewise thick pectic-cellulosic wall layer. With Sudan IV the cuticle as a whole stains intensely red, but in polarized light it becomes obvious that it consists of 3–4 layers of wax interrupted by thin layers of isotropic material, presumably cutin. The wax layers show different refractiveness, but generally have a type of birefringence opposite to that of the cellulose in the walls inside. These are very thick and their pronounced capacity to stain with Ruthenium Red indicates that they are to a very great extent built up of pectic substances. The same may be the case with the thick walls in the spongy parenchyma, see fig. 8E.

On account of these chemical properties it is probably correct to regard *Diapensia lapponica* as highly xeromorphic (*H. E. Petersen* l.c. p. 154). This author also mentions elongated, unbranched cells above the abaxial epidermis, which “doubtless form a kind of protective tissue for the spongy parenchyma”. However, they form a rather typical hypodermis and their primary function may be to reduce stomatal transpiration. The substomatal chambers in *Diapensia* are markedly narrow (fig. 8 H).

*H. E. Petersen* (l.c.: 146 and fig. 5 B–C) emphasizes that the cuticular layer has not the same thickness everywhere. It sinks into depressions of the cellulose membrane. There occur, especially towards the lateral walls, canals (gutters) extending outwards towards the cuticle, without, however reaching it. A similar structure was not found in

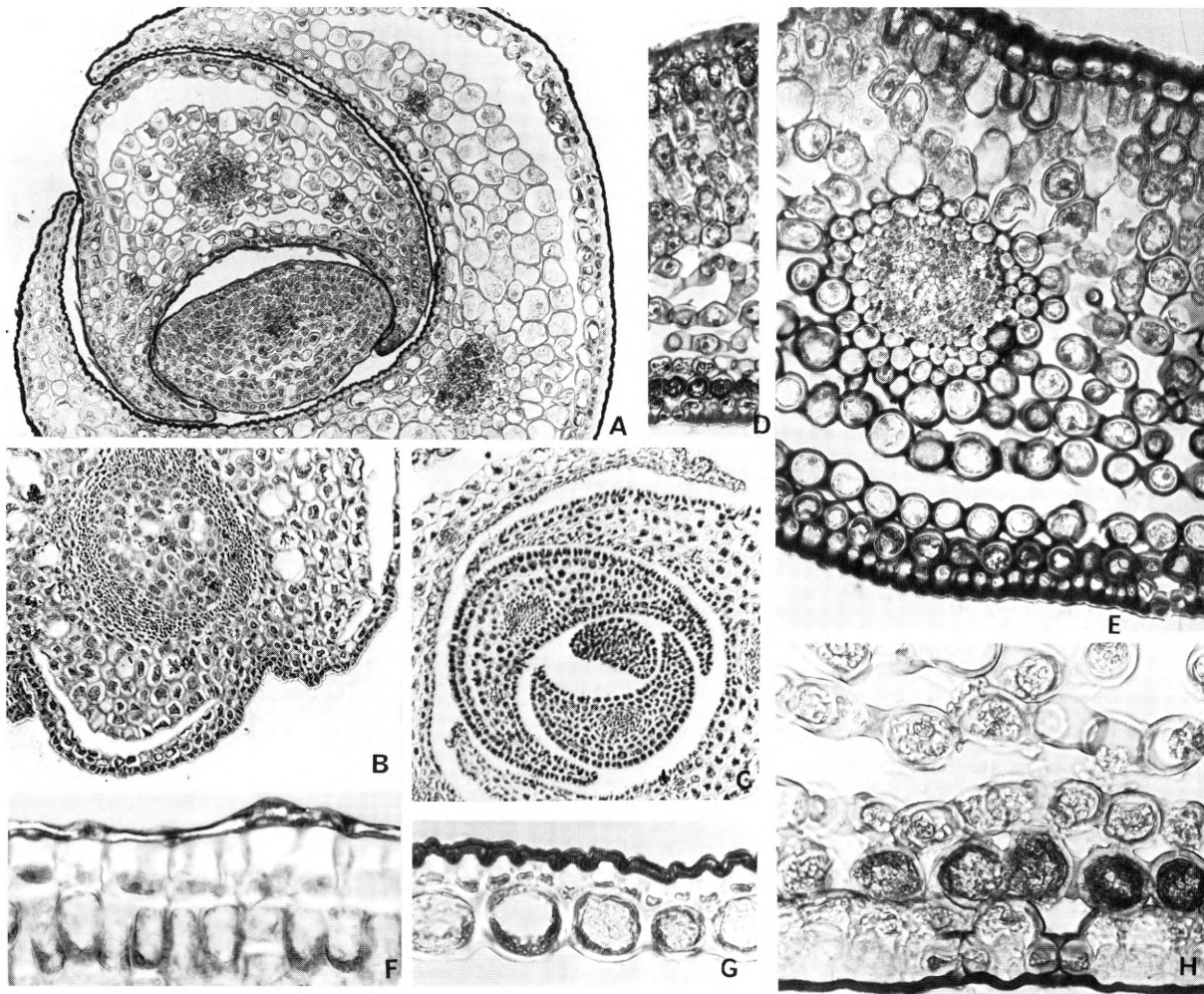


Fig. 8. *Diapensia lapponica*. A–C. Shoot development, in A two sheathing parts and one sheathed primordium already differentiated in palisades and spongy parenchyma. B. Cross section of stem with pith surrounded by vascular tissues and cortex with traces of two successive sheathing leaf parts. Lacunae are formed where the sheathing leaf parts later become disengaged, a large crescent-shaped cavity is usually formed near the abaxial surface. – C. Three successive primordia inside two sheathing parts. – A. Sudan IV x 100. B–C. FS x 100. – D. Cross section of leaf in semipolarized light FS x 128. – E. The same showing abaxial hypodermis and bundle sheath. Ruthenium Red stains pectocellulosic epidermal walls and

walls in bundle sheath and between spongy parenchyma cells. x 160. – F. Adaxial epidermal walls stained with Sudan IV in polarized light. Cuticular lamellae showing up because of wax layers. Interior part of outer walls showing up because of cellulose. x 320. – G. Adaxial epidermal walls in sheath part (cp. fig. 8 A) in polarized light, cuticular layer stained with Sudan IV, wax present. Note very small epidermal cell-lumina. x 320. – H. Abaxial epidermis with two stomatal pores. Sudan IV stains cuticle and cuticular coating of substomatal chamber. Thick wall traversed by pit canals between hypodermal and spongy parenchyma cells x 250.

ericaceous leaves studied by *Petersen* but it occurs clearly in leaves of *Dracophyllum uniflorum* (Fig. 23, D-E).

A typical hypodermis is rarely developed in the *Ericaceae*. It occurs in connection with midveins in, e.g., *Arbutus menziesii* (fig. 10G). *Mansfeld & Sleumer* (1935) mention it from the majority of species of *Bejaria* (except *B. racemosa*). According to *Copeland* (1943), a hypodermis occurs, moreover, in species of *Hymenanthus*. In *Wittsteinia* a hypodermis occurs on the abaxial side, while on the adaxial side it is double-layered and has the character of a water-storing mechanism. According to *Rudall* (1980), the occurrence of a hypodermis is a xeromorphic adaptation.

Most leaves with dorsiventral structure are hypostomatous, an exception being *Rhodothamnus sessilifolius*, which is amphistomatous (fig. 3 F); the same applies to *Bejaria racemosa*. Amphistomatous structure is frequent in typical isolateral leaves; for instance, in *Arctostaphylos patula* and many epacridaceous species. A hyperstomatous structure is rare but is recorded in the primary leaves of *Calluna* seedlings (*Beijerinck* l.c. fig. 28).

The stomata generally occur in the anomocytic type but, in the *Epacridaceae*, *Watson* (1962) report paracytic stomata in the *Styphelieae*. In *Clethra arborea* there are two subsidiary cells on each side of the guard cells (fig. 11 F–G). The shape of the guard cells appears to deviate in several species of the *Epacridaceae*. In transverse sections the guard cells are curved and the pore is placed where they approach one another nearest to the substomatal chamber. There are small outer ledges and front cavities between the outer parts of the guard cells which, where they meet, may cover one another and thereby narrow the pore (fig. 7F–H, 22F).

### c. Venation, mechanical escort of veins.

Broad-leaved members of the *Ericaceae* (e.g., *Arbutus*), as well as those in the *Clethraceae* and *Pyrolaceae*, have pinnate venation. According to the terminology of *Hickey & Wolfe* (1975), the *Ericales* belong to the pinnate *Dilleniidae* with sim-

ple leaves and marginal teeth that are “theoid”. *Bejaria* shows reticulodromous marginal venation. In spite of the fact that the *Ericales* are considered usually to include the *Epacridaceae*, nothing is said about the venation in that family. But already *Simon* (1891:28) pointed out the peculiar venation here which resembles that found in the Monocots. *Copeland* (1954) classifies the venation as palmate; in small-leaved species the veins are nearly parallel, though not genuinely so as there are irregular anastomoses. The margins are entire but in the *Prionoteae* they are minutely dentate and, as shown by *Arroyo* (1975 fig. 4), the venation is almost palmate in *Prionotes* and nearly pinnate in *Lebetanthus*. *Copeland* thinks that the *Epacridaceae* have their origin among the *Andromedeae* and *Gaultherieae*. However the cytological data mentioned earlier make it perhaps more likely that some Ericaceous lines were derived from common ancestors of the *Ericaceae* and *Epacridaceae*.

The *Prionoteae*, as stated by *Stevens* (1971), clearly mark a transition between the two families; this is further manifested by their marginal glands, which are mentioned later. *Arroyo* illustrates a transverse section of a vein showing a bundle sheath and an abaxially arranged strong fiber escort. Bundle sheaths are rare and not typical in leaves of the *Epacridaceae*, but they are common among species of *Ericaceae*, see, e.g., *Rhododendron lapponicum* (fig. 21G), *Calluna vulgaris* (fig. 33a in *Beijerinck* l.c.), and *Wittsteinia vaccinioides*.

The fiber flanges that accompany the veins in *Ericaceae* were mentioned by *Copeland* (1943), but many comments on this character had already been made by *Breitfeld* (1888) and *Niedenzu* (l.c.). Flanges of fibers supporting veins may often extend to the epidermis, as in *Rhododendron arboreum* (*Breitfeld* l.c. Plate V), or they may be important parts of bundle sheath extensions reaching the epidermis as in, e.g., *Arctostaphylos patula* (fig. 10F). However in many species fiber escort is restricted to a crescent-shaped area in cross sections (fig. 9E–F), in fact a trough-shaped band as in the

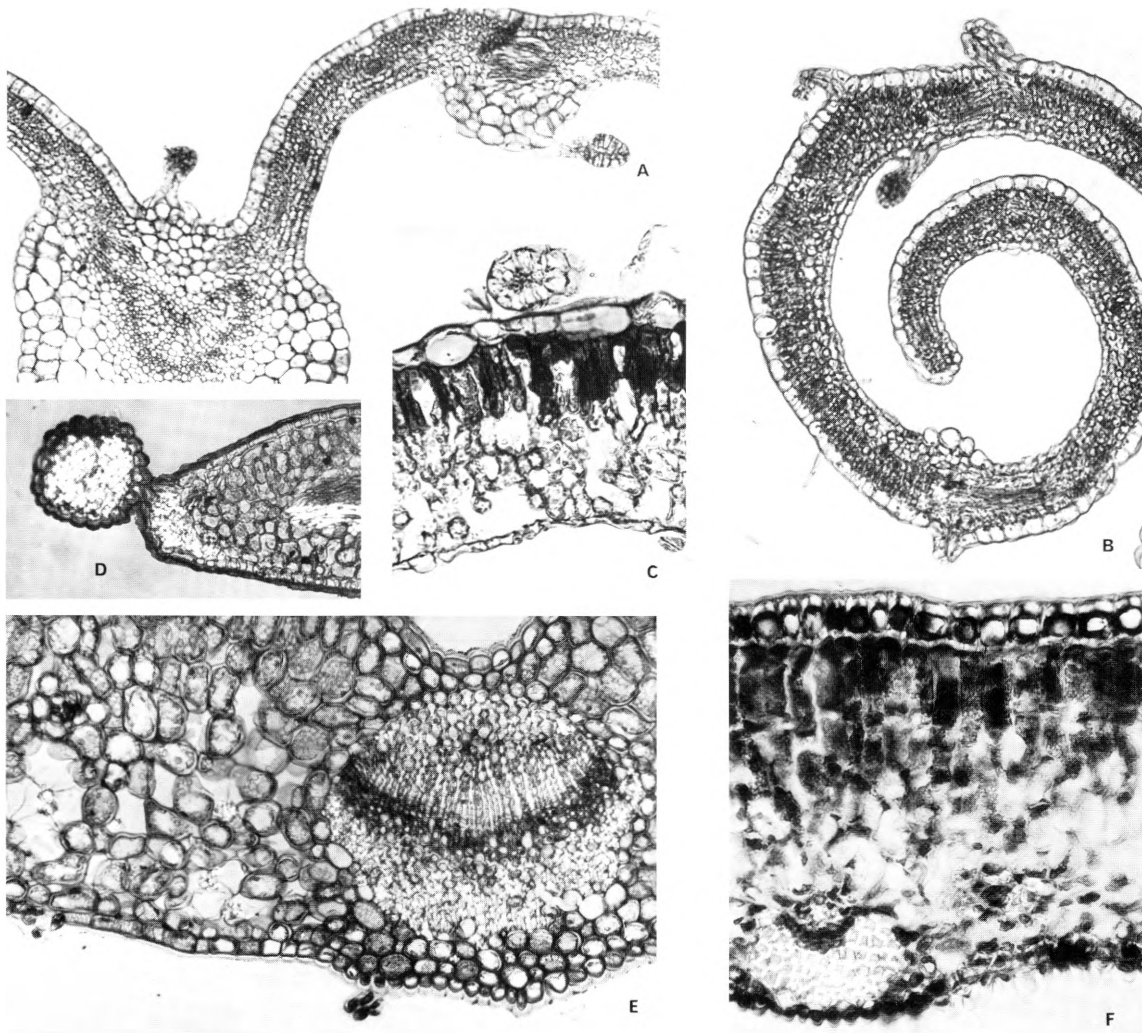


Fig. 9. A–B. *Menziesia pilosa*. A young leaf at the rolling stage and formation of middlewall glands in connection with parenchyma at the veins. FS x 100. – C. *Menziesia pilosa*. Older leaf showing central canal in gland, a few bulbous adaxial epidermal cells and abaxial stoma. Tannin in palisades. FS x 160. – D–E. *Lencothoe axillaris*. D. Margin of leaf in semipolarized light showing bright marginal sclerenchyma and sclerenchyma in

recurved leaf teeth and on abaxial side of vein SF x 100. E. Middle vein with sclerenchymatous support. In spongy parenchyma, clusters of water-storing cells with crystal druses. The foot of two trichomes is seen at abaxial epidermis. Semi-polarized light x 160. – F. *Cyathodes colensoi*. Walls in thick adaxial epidermal cells, in sclerenchyma at vein, in crystals and in the xylem showing up in semipolarized light x 160.

majority of species of the *Epacridaceae*, fig. 22C and Copeland (1954 fig. 5). In *Styphelia longifolia* such fiber bands merge and produce very strong support for the long leaves (fig. 22B).

Lems (1964) made an interesting survey of the venation and leaf anatomy in the *Andromedeae*.

With regard to the vascular tissues of the petiole and the midrib, he distinguishes between three types. In *Oxydendron*, *Epigaea* and *Orphanidesia* the petiole bundle with its fiber escort is cylindrical and encloses pith parenchyma, but in *Lyonia* the bundle is closed and forms a solid core of endarch

xylem, and in the remaining genera (e.g., *Pieris*, *Andromeda* and others) the petiole bundles in cross sections become crescent shaped. *Lems* found characteristic types with regard to the vein endings too. Again *Epigaea* and *Orphanidesia* deviate by their sharply pointed endings.

A comparison of the *Ericales* families unveils a decreasing importance of the supporting tissue systems. The strongest support is found in the *Epacridaceae* which, according to *Simon*, often have fibers of the trough extending to the epidermis (e.g., *Andersonia*), or have veins lying freely in the mesophyll (fig. 22C) but usually near the epidermis.

Within the *Ericaceae* a decrease in fiber support is conspicuous in *Harrimanella* – *Cassiope* and in *Erica*. The two species of *Harrimanella* have needle-like, spirally arranged leaves with strong fiber strands in connection with the midveins. *H. hypnoides* approaches an epacridaceous structure as the midvein with its fiber escort is near the epidermis and the mesophyll is compact. In *H. stelleriana* the midvein with its fibers becomes isolated from the mesophyll at the epidermis because of the wide lacunae surrounding it. In *Cassiope tetragona* and *Calluna* there is no real fiber escort, and in both species the mesophyll contains many wide lacunae at the midveins which, as in *Harrimanella stelleriana*, are connected with the photosynthetic cells by a number of rows of cells arranged as trabeculae. In *Cassiope* and *Calluna* mechanical tissue support is made superfluous because of the leaf size and texture. The well developed leaf flanges are able to resist the bending of the leaves. The midveins in mature flat leaves of *Daboecia cantabrica* become almost encircled by sclerenchyma. In young blades with recurved marginal parts, the sclerenchyma matures first along the abaxial sides.

Some species of *Erica* still possess fiber strands. *Ljungström* (1883) found a single strand at the midvein in the cylindrical leaf of *E. turrigera* (= *E. cupressina*); in *E. vestiflua* and *E. coccifera* there are, furthermore, extravascular sclerenchymatous

strands in the mesophyll. This author regarded *E. vestiflua* and other species with a similar amount of fibers as the best representatives of the “*Erica* leaf type”; thus perhaps the most original. The majority of species have obtained stability or reduced flexibility because of the ericoid structure. Another genus with revolute leaves and also without extravascular fibers is *Phyllodoce* (see fig. 18).

The striking difference between the *Ericaceae* and *Epacridaceae* in stereome development may be viewed in connection with the ecological circumstances where the two groups became distributed. The *Ericaceae* chiefly inhabit montane or cold-temperate, not very arid regions, while the *Epacridaceae* occur in warmer and much drier environments. The production of thick cell walls as in sclerenchymatous, non-photosynthetic cells implies a kind of dissipation which counteracts the production of matter and the building up of reserve materials. The evolutionary advantage achieved through avoiding a production of sclerenchyma seems obvious. On the other hand, the sclerophyllous structure in the *Epacridaceae* is an evolutionary necessity because the leaves must be able to resist herbivorous animals.

Some species of *Dracophyllum*, e.g. *D. filifolium* and *D. uniflorum*, have long, narrow and tapering leaves. Their rigidity depends on the densely spaced sclerenchymatous vein escorts.

#### d. Hydathode position and function

Passive hydathodes with water pores were described in *Azalea indica* by *Neumann-Reichardt* (1917). They occur as light green swellings at the tips of the leaves. The pores are permanently open and older ones sometimes become plugged by dark granular substances. The same type of water-pore hydathode occurs, e.g., in *Epigaea repens* (fig. 11A) and in several other species with toothed leaf margins. In *Arbutus unedo* gutation from the teeth can occur when water is pressed into trunks or stems (*Grevillius* 1923: 64–67). In the species that I studied there was never a typical

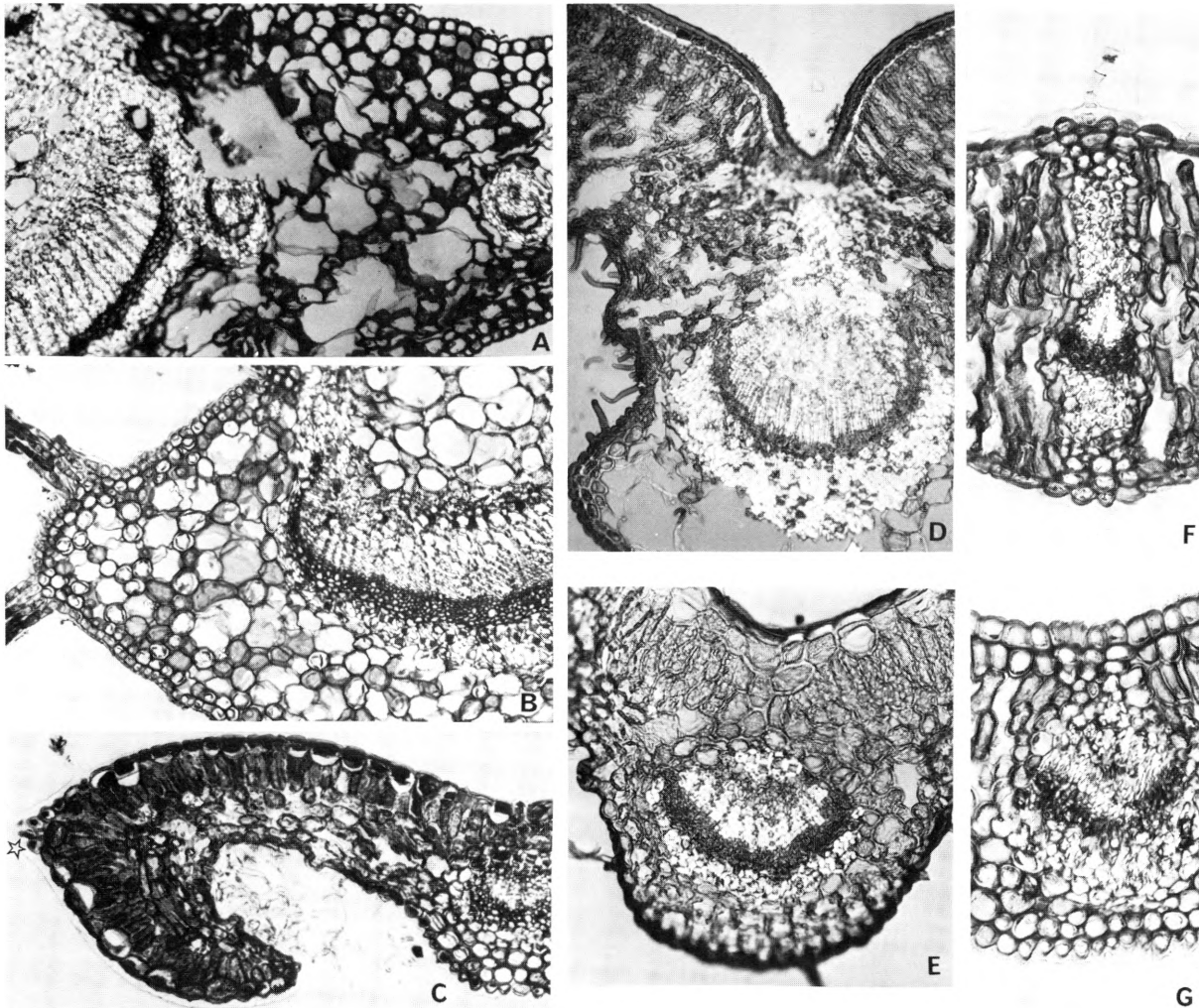


Fig. 10. A. *Orphanidesia gaultherioides*, B. *Epigaea repens* cross sections of base of blade (A) and petiole (B). In B, on the left, bases of two emergences with much anthocyanin. C. *Daboecia cantabrica* cross section of young leaf, small gland and base of large gland ☆ abaxial indumentum of curling hairs, cp. fig. 12, E and H. – D. *Andromeda glucophylla* mid-nerve and adaxial epi-

dermis with crystal sand showing up – E. *Daboecia cantabrica*. Area of mid-nerve. – F. *Arctostaphylos patula* showing isolateral texture. – G. *Arbutus menziesii*, with papillate epidermal layers and adaxial hypoderm. FS or (D–E) Sudan IV, x 100 or (E–F) x 128).

epithem, only loosely packed parenchyma occurring behind the water cavities (substomatal chambers) in connection with the pores. Leaf teeth are mostly furnished with a system of branched tracheid rows which end in loose parenchyma and many water pores (fig. 11–12). A tracheid system and water pores occur in the densely spaced,

small teeth of the East Asiatic *Andromeda ceriua* which has flat leaves. There are no pores in *Andromeda* species with revolute margins.

In mature leaves of *Daboecia* the midveins terminate in a branched system of tracheids and many densely spaced water-pores. The cells surrounding the tracheids appear as short rows of

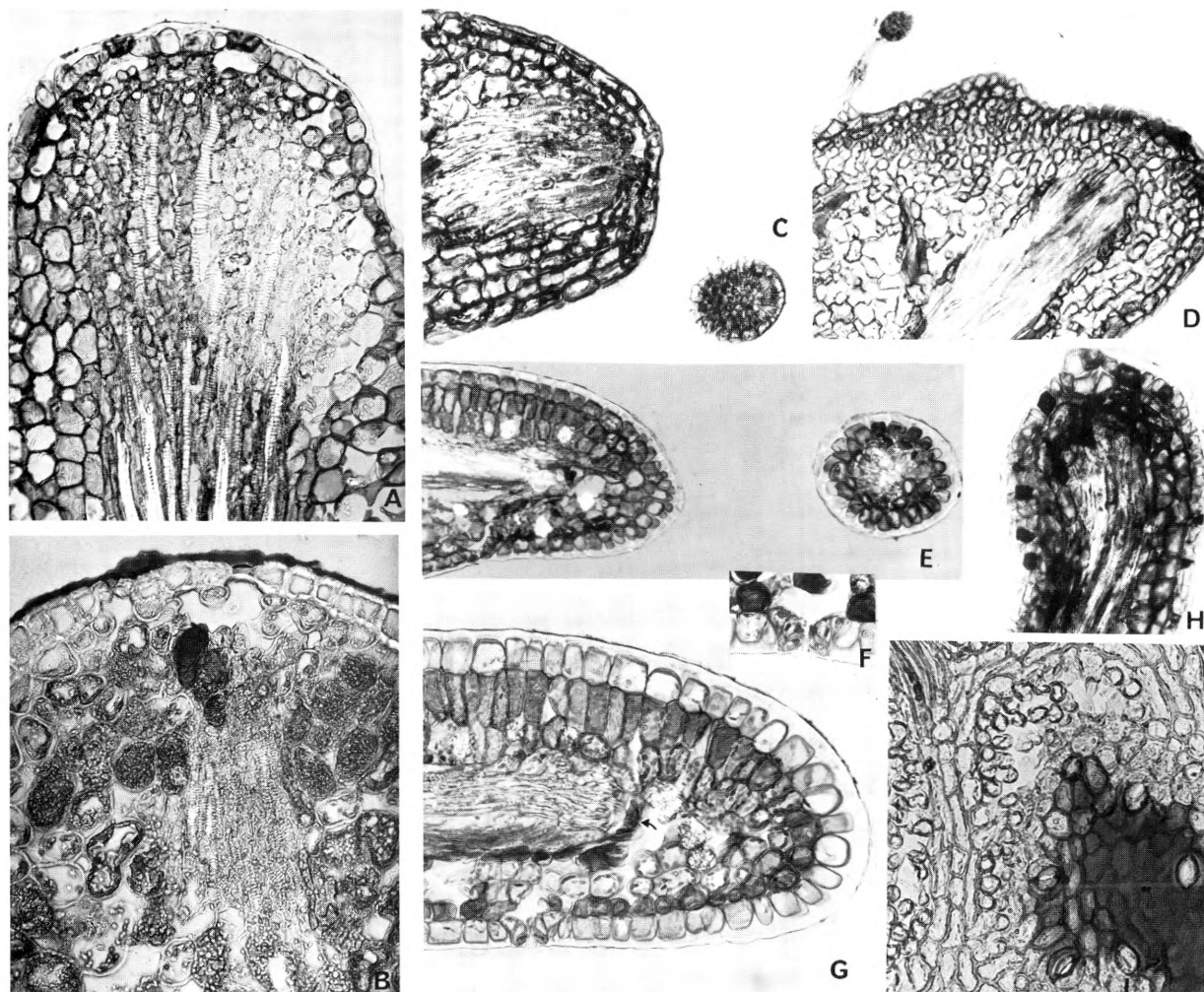


Fig. 11. Water pores. A. *Epigaea repens*. Vein ending in leaf tip. Four water pores (with substomatal chambers) visible. Semipolarized light x 160. – B. *Wittsteinia vacciniacea*. As A, but dark substances (probably tannin) in cells near surface. Large intercellular spaces near vein. Thick wall in epidermis and thick cuticle (stained with Sudan IV) x 160. – C–D. *Rhodothamnus chamaecistus*. C. Vein ending and substomatal chamber. Isolated body is a cross section of the head of the glandular appendage as seen in D., FS, Semipol. light. x 160. D. as C, no vascular supply to glandular appendage. Many intercellular spaces near vein. FS x 100. – E–G. *Clethra arboorea*. E. Sections

through tooth which has a recurved tip containing tracheids (bright) appearing as an isolated body on the right. Semipol. light. Toluidine Blue. x 100. – F. Stoma showing two subsidiary cells on each side FS x 250. – G. as F, but tannin in outer photosynthetic cells and in bundle sheath (arrow). Many crystal druses near bundle. Semipol. light x 160. – H. *Pieris japonica*. Water pore and vein ending, FS, semipol. light. x 160. – I. *Arctostaphylos patula*. Paradermal section through small vein branching and ending at several water pores which are seen in the lower right corner where epidermis and margin of the pores are stained with Sudan IV. x 100.

swellings. Some of them develop into tracheid-like cells which can probably store water. Some less conspicuous water-pores occur at the sharp

fold where the leaf recurves. Glands with long stalks and resinous secretion abound near the pores, see Fig. 12.



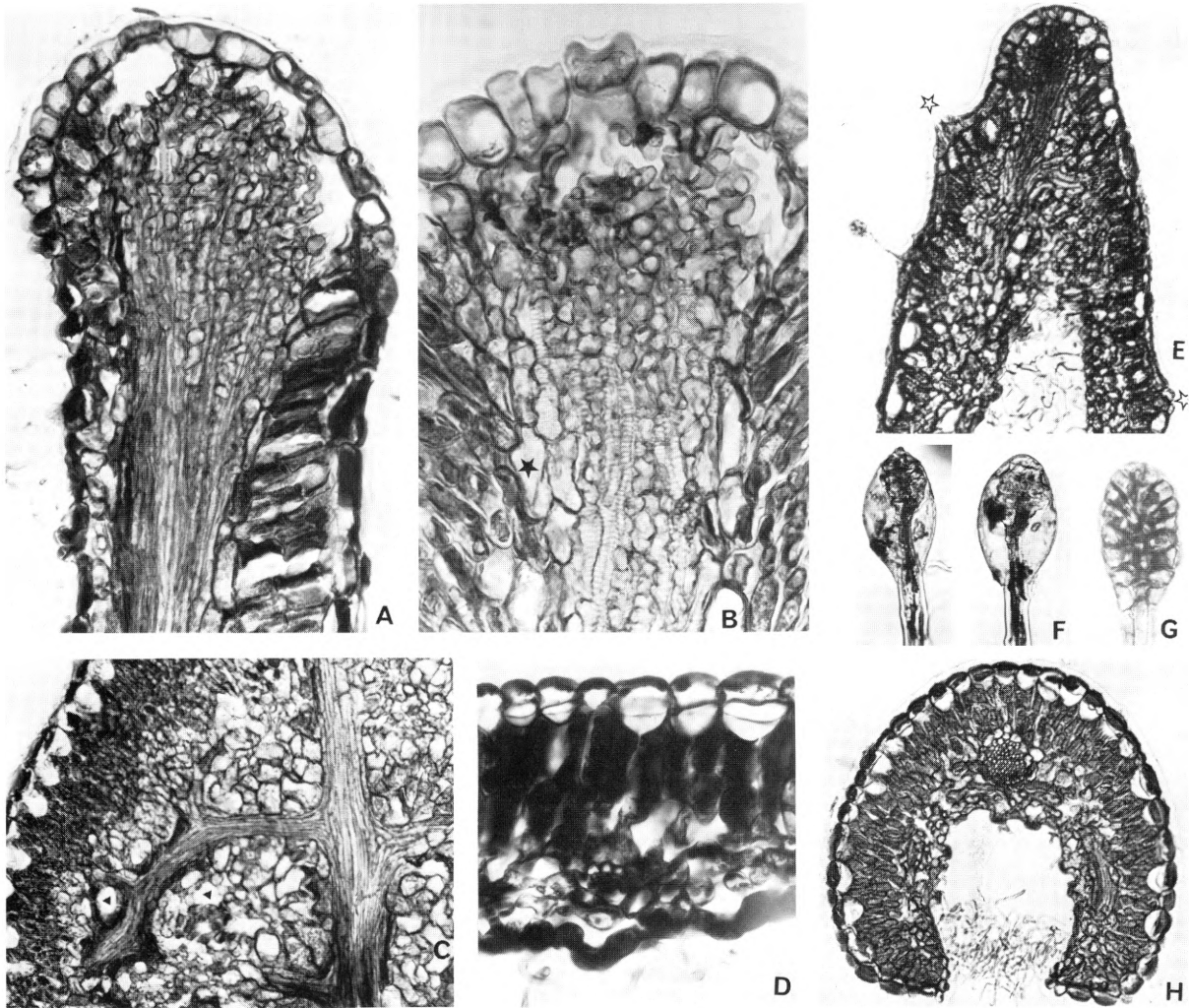


Fig. 12. *Daboecia cantabrica*. A–B. Water pores and vein termination FS. Semipolarised light. In B, water-storing, tracheide-like cells (\*) A x 160, B x 320 – C. Branching of veins near water pores. Lacunae surrounded by bundle sheath parenchyma (small triangles) x FS 128. – D. Cross section of leaf: Johanssen's quadruple staining shows surfaces of lamellae in mucilaginous

interior epidermal walls x 320 – E and H cross sections of leaves; E, with water-pore at sharp fold, small glandular hair and bases of two larger, long-stalked glands (asterisks). FS x 100. F. Heads of larger glands in paraffin oil showing secretion x 160 – G. Head in the quadruple staining showing dark intercellular spaces x 320.

Active hydathodes or water-secreting glands were described by Arroyo (1975) in *Prionotes* and *Lebethanthus*. They are placed in the axils of small marginal teeth in the laminae and have multicellular stalks and heads. They occur outside vein endings and may secrete water or mucilage. A similar position of the glands was found in *Pieris*

*japonica*, but in this case a water-pore occurs in the same notch (Fig. 11H).

As emphasized by Schnepf (1969), it is difficult to make a distinction between the secretion of hydrophilous and lipophilous substances. The secretion is generally a mixture of, e.g. terpenes (ethereal oils, resinous substances), fatty sub-

stances, mucilage and even saline solutions. In *Rhodothamnus chamaecistus* the leaves contain terminal water pores and several marginal emergences with glandular heads (fig. 11C–D). The heads secrete a clear slightly sticky fluid. In several other species the secretion is resinous but its composition and quality vary. A general question is to what extent do glands and hydathodes replace one another physiologically. In the *Ericaceae* it is evident that hydathodes (water-pores) are absent in revolute leaves, whereas different glands are abundant and particularly common in young leaves (and stems), suggesting that the young plants need transpiration and access to water with solutes during their period of growth.

In *Erica* it is obvious that marginal teeth are developed in species with linear-elliptic leaves such as *E. vanheurckii* and *E. ampullacea*, but the genes for tooth development may be absent (or covered) in species with typical ericoid leaves (e.g., *E. tetralix*, *E. glutinosa*) in which, on the other hand, glandular hairs abound.

In the *Diapensiaceae* water-pores are developed at the endings of the middle veins in *Diapensia laponica*. *Shortia galacifolia* and *S. soldanelloides* have rather broad leaves and almost palmate venation and the veins continue into conspicuous marginal teeth, which in the latter species are extended and resemble small spoons.

## 7. Leaf margin development and growth; rolling

The way in which ericaceous leaves develop was commented on by *Hara* (1956) after careful studies; he concludes that there are two types of marginal development, viz.: the revolute (rolled) and the convolute (involute) type. The revolute type includes the ericoid leaves. According to *Hagerup* (1953), typical ericoid leaves are not formed by revolution of the margins of the lamina but by the formation of two coherent pads on the abaxial side along the margins of the lamina. However, *Hara* does not set up a special "ericoid" type and this is because he found some evidence of "ericoid" structure also in leaves of, e.g., *Menziesia* and *Ledum*. He was able to demonstrate periclinal divisions in cells in the abaxial subepidermal layer. They are not true submarginal initials but give rise to such initials and take part in the formation of the rolled part of the leaf.

The margins in *Phyllodoce nipponica*, according to *Hara*, are indicated by glandular emergences. But according to my own observations of the closely related *Phyllodoce glandulifera*, the glandular emergences issue from the leaf edges where the flanges have their limitation towards the up-turned leaf side (fig. 18). The true margins are where the flanges terminate and where the incurved abaxial side begins. The youngest primordia at the top of the spirally arranged leaves are rounded lumpy bodies which, on their abaxial sides, bear several large emergences. Rather soon, however, the young leaves obtain an abaxial incurvation and the central bulging outwards around the midvein (fig. 18C). In this way the "pads" are formed on both sides of this bulge. They become conspicuous near the leaf blade basis (leaf Nos. 1–7 in fig. 60 in *Hagerup* (1946),

but are not developed in the short petioles and narrow bases of the blades (Nos. 12–20 in the same figure which might be compared with figs. 10–11 in *Warming* 1908).

*Hara* places *Cassiope* and *Harrimanella* among species having convolute (involute) leaves at early stages. This is correct in spite of the fact that *Cassiope tetragona*, like *Calluna vulgaris*, achieves flanges and recurving basal ears. The early development in *Cassiope* involves a stage with strong transverse growth and the formation of marginal meristems that divide into one adaxial part producing the two sharp, upper edges and one abaxial part, which becomes responsible for the formation of the recurving ears (fig. 3A, 4A–B). The youngest leaves in *Cassiope* are flat or involute and the development of the edges slightly precedes the formation of basal ears. A similar change from a slight involute curving to the formation of abaxial incurvations occurs in *Erica terminalis*, which also shows a concentration of strong trichomes at or near the "edges" (fig. 3B).

The bud construction in *Rhododendron* was, according to *Sinclair* (1937), investigated by *Balfour* in 1919. *Sinclair* illustrates two constructions which he recognized as the revolute and the convolute type. The revolute type has a chamber at the bottom of which the young leaves develop. The outer bud scales forming the chamber, however, are arranged in the convolute way. In the bud stage *R. lapponicum* is of the convolute type of *Sinclair* and *Hara* (fig. 21A). The marginal meristems consist of four cell tiers, of which two are epidermal. There is no chamber but the dense cover of scales and hairs provides the bud with many air-filled spaces which probably have an

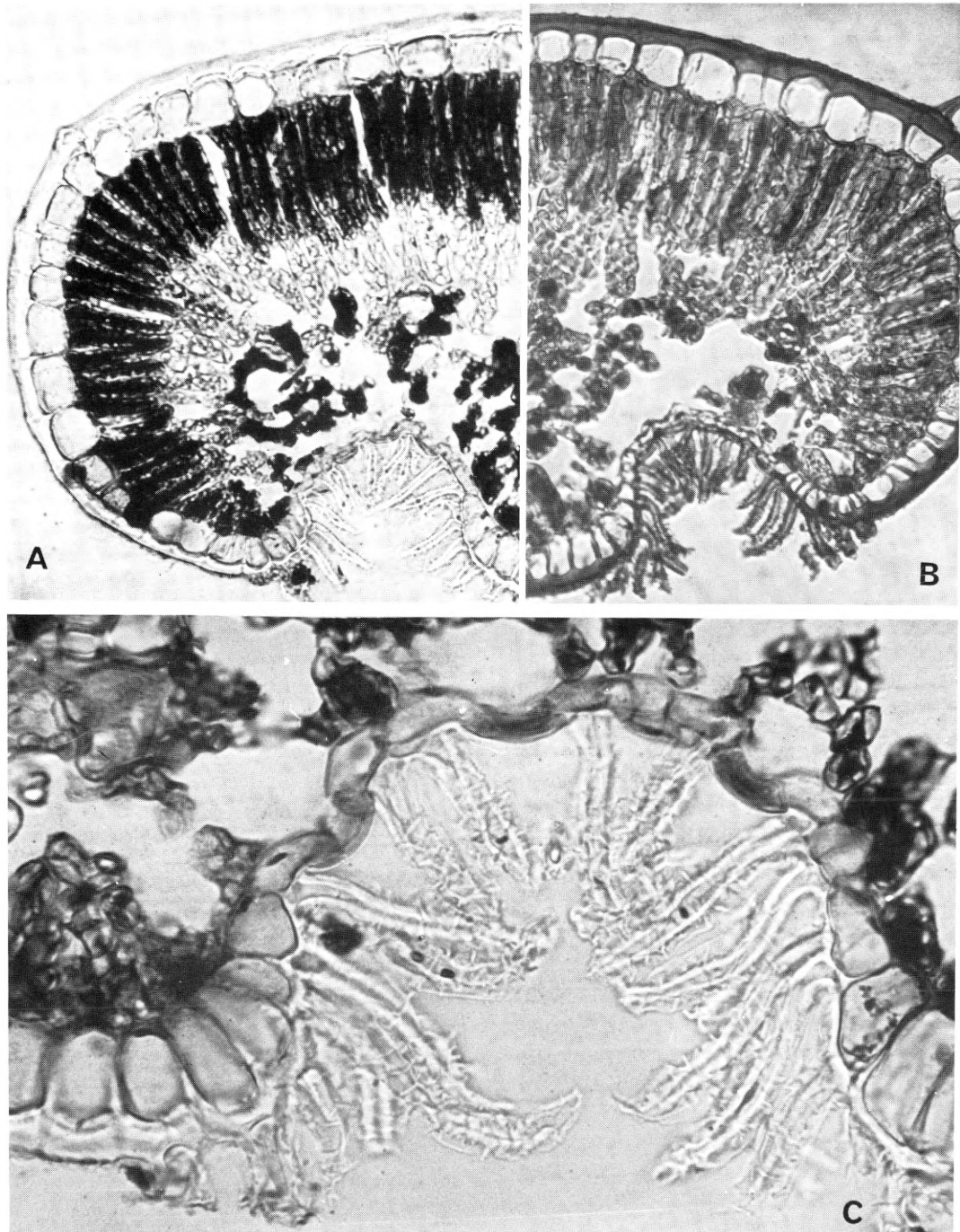


Fig. 13. *Erica terminalis*. Parts of cross sections of mature leaves showing one of the two submarginal stomatal furrows (cp. Fig. 3B) and the cuticular pattern of the unicellular hairs in the furrows. A. Outer palisades dark and tanniferous, but with

light starch grains. FS and semipolarized light. B. Stained with Sudan IV both x 200. – C. Furrow showing three raised stomata and cuticular excrescences on hairs. FS, simipol. light, x 640.

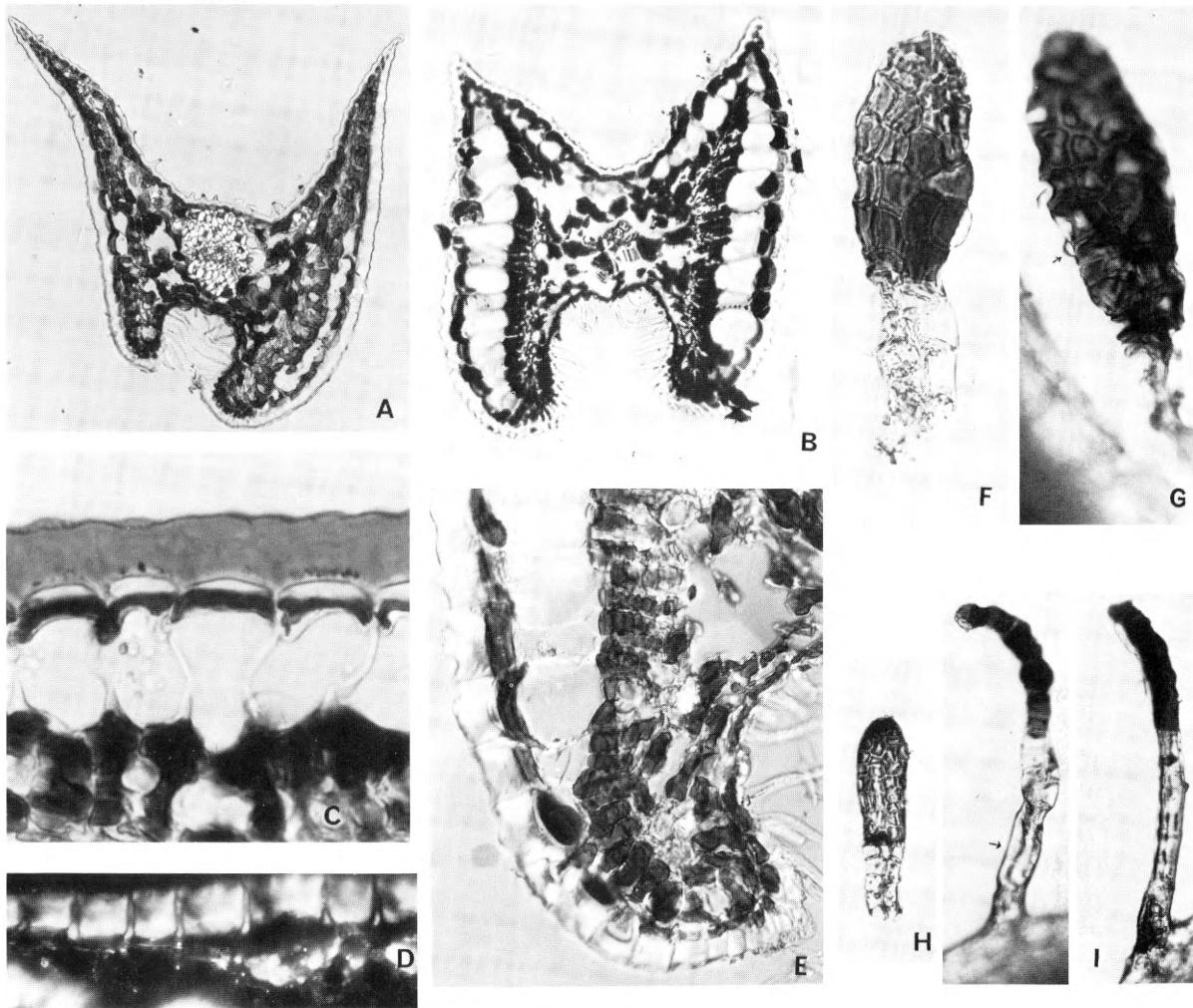


Fig. 14 A–E. *Erica dianthifolia*. A–B. Cross sections of leaves, FS and semipolarized light. Tanniniferous vacuoles dark. x 100 – C. Cross section of cuticular layer (stained with Sudan IV), epidermis with tanniniferous vacuoles, water-storing hypodermis and palisade. FS x 1000 – D. Cuticular layer in polar-

ized light. Birefringence because of contents of wax x 320 – E. Abaxial part x 1000. A–E Material softened with Aerosol OT, according to Peterson et al (1978). – F–I. *Vaccinium vitis idaea* ssp. *minus*. Glandular hairs. F–G. x 1000, H–I. x 205 arrows point to sticky secretions, F and H in glycerin, G and I in paraffin oil.

isolating effect. Hara and Sinclair mention two other species of convolute type, viz., *R. keiskei* and *R. imperator*, but in most species the young leaves are revolute or rolled. Hara also says that *Ledum* is of the revolute type, a statement that can be endorsed with regard to the vegetative buds (fig. 20B). In those containing flower buds, the youngest leaves are clearly involute, the next inter-

mediate, whereas the outermost older ones are revolute (cp. fig. 20A). The first leaves in a vegetative bud show an increasing recurvation and, at the same time, a differentiation between marginal epidermal and subepidermal cells and interior cell layers of which some develop into the larger “transparent” ones already mentioned.

The young leaves in *Menziesia* are typically rolled

(fig. 9A–B). In *M. pilosa* there are a great number of glands emerging from small cell clusters generally formed near the veins and the leaf margins.

*Kalmiopsis leachianus* (cp. Rehder 1932, Copeland 1943) clearly has convolute young leaves (fig. 19H–I), and the same is the case with *Rhodothamnus chamaecistus*. Both species later obtain flat mature leaves.

According to Hara (l.c. Plate XI 5), *Loiseleuria procumbens* has opposite revolute leaves surrounded by opposite bracteoles. The bracteoles in my material are involute and the first foliage leaves are largely transitional between involute bracteoles and normal foliage leaves, which are revolute (fig. 2). Similar transitional leaves occur in young lateral shoots of *Cassiope tetragona*.

In the *Epacridaceae* the leaves in the buds are frequently sheathing and convolute, cp. Copeland (1954 fig. 1–2) Aubreville & Leroy (1975 Plate 6, fig. 4). Sheathing leaves also occur in many species of the *Diapensiaceae*. They were studied in more detail in *Diapensia lapponica*. The sheathing, proximal part of a leaf enclose up to five successive leaves, all convolute and enclosing the following leaf (fig. 8A–C). The distal parts of the leaves, the blades, formed in continuation of the sheath, flatten and the mesophyll soon becomes differentiated in palisades and spongy parenchyma. At a very early time, in fact prior to the disengagement of the sheath part from the stem, long schizogenous transversal cavities are formed in the abaxial parts (fig. 8B).

From the survey by Hara (l.c.:446) it appears that the majority of ericaceous genera have convolute leaves in the bud stage. According to Sinclair (l.c.:270), the convolute type seems to be morphologically simple, whereas the revolute type is more complex in that the ptyxis of the foliage leaves differs from that of the bud scales. The relict species mentioned above (*Kalmiopsis* and *Rhodothamnus*) have convolute young leaves, too. A majority of the facts, therefore, indicates that the convolute type is the most original.

In *Cassiope tetragona* and *Erica terminalis* a de-

velopmental change from convolute to revolute structure takes place. In some genera the revolute type has become stable, so that mature foliage leaves can be characterized as ericoid. Attacks by fungi, e.g., *Exobasidium hypogenum* Nannf. in *Cassiope tetragona*, can counteract leaf recurvation so that the leaves become almost flat and at the same time reddish.

The ericoid structure, so ardently studied by Hagerup (1946, 1953), has been established in members of the *Phyllodoceae*, *Ericineae*, *Calluneae*, *Cassiopeae*, and in certain species of the *Rhodoreae* and *Andromedeae*, e.g., *Leucothoë ericoides* and *L. lycopodioides* (Sleumer 1959). Even in some species of the *Epacridaceae* we find recurved leaf margins; for instance, in *Cyathodes empetrifolia* (fig. 22), in *Styphelia intertexta* (Jackes 1971), and in *Brachyloma ericoides*. We have no knowledge of the nature and number of genes responsible for an ericoid leaf structure, but it is not unlikely that the mutations resulting in the emergence of this structure mainly interrupt the stretching and flattening that take place during the maturing of the leaves in, e.g., *Menziesia pilosa*, *Daboecia polifolia* and many species of *Rhododendron*. A fundamental question is whether the ericoid structure came about independently in several lines, or was pieced together from the ericalean gene pool – perhaps under particular ecological conditions. As the same tribe can contain ericoid and non-ericoid species, we may anticipate the occasional action of modifying genes able to prevent a manifestation of the ericoid habit. In this connection it is worthwhile recalling the variation of the leaves in the *Erica* species that occurs so frequently in South Africa (Baker & Oliver 1967). It appears that the majority of species there have an abaxial, narrow, longitudinal slit and deserve the designation ericoid, but some, e.g., *E. marifolia*, have ovate-elliptical leaves which are “open-backed” almost in the same fashion as found in several cultivated *Rhododendrons*. Obviously closely related species of *Erica* (e.g., *E. filiformis* and *thimifolia*) may differ greatly in the degree of rolling. We see a similar type of

difference between *Ledum groenlandicum* and *L. decumbens*, where the latter is clearly ericoid and the former almost open backed. In both genera the more open abaxial leaf surfaces are connected with a moister habitat or moister climatic conditions, and thus the species with the most markedly rolled leaves occur under relatively xeric conditions. Environmental changes in moisture conditions have almost no influence on the degree of rolling. Since time immemorial the gene pool of the *Ericales* has probably contained gene complexes giving rise to ericoid structure. This occurs in *Calluna* and *Empetrum*, both present in the Middle Pliocene, as well as in certain species of the *Epacridaceae*. However, it appears that the manifestation of an ericoid structure can be sub-

ject to the influence of modifying genes preventing a permanent recurvation. When ericoid leaf structure becomes established in very different tribes, it may be a result of pleiotropy or a genetical repatterning in the ericalean gene pool. It is not a matter of typical convergent evolution but of a deviating type that might be tentatively called linear or inherent convergence. We shall return to this phenomenon in the discussion. The deviating type of convergence recalls that mentioned by Björkman, Troughton & Nobs (1973). They suggest that two evolutionary lines in *Atriplex* – *Obione* evolved species using the C<sub>4</sub> pathway in photosynthesis, and maintain that these lines were developed independently in spite of the fact that the genera belong to the same family.

## 8. Trichome development and distribution

*Copeland* (1943) based his outline on the old accounts of *Vesque* (1885:226) and *Breitfeld* (1888:329) and distinguished between five types of pubescence: (1) unicellular hairs, (2) uniseriate hairs, (3) multiseriate hairs, (4) glandular hairs, and (5) scales. The word “bristles” covers multiseriate excrescences of elongate, often tapering, thick-walled cells, while scales are peltate hairs of different kinds, though often glandular at least when young. *Copeland* does not mention colleters in spite of the fact that multicellular emergences of this kind were described long ago by *Hanstein* 1868 (Plate XII fig. 93–95) in *Azalea indica*. They belong to the category which, e.g., *Kratzmann* (1910) referred to as “Zwischenwanddrüsen”. The largest organs with the function of secreting sticky resinous substances similar to that of the ericaceous colleters are the emergences with a central columella of cells in longitudinal files covered by glandular cells. *Hanstein* (l.c. fig. 37) describes them in *Coffea arabica*. *Ramaya* & *Bahadur* (1968) call them “squamellae”.

*Cowan* (1950) and *Seithe* (1960) produced monographs on the trichomes in the genus *Rhododendron*. The latter author distinguishes between 43 types. Both authors suggest evolutionary trichome successions in a kind of geneological tree.

From old times two main types of trichome have been distinguished, viz., glandular and eglandular (“covering”) hairs. The two types are not well defined nor sufficiently understood with respect to their functions, genetical background and history.

*Niedenzu* (l.c. p. 230) mentions three trichome characters which he estimates to be phylogenetically important. A taxon is considered

more ancient the more complicated the covering hairs are, the stronger the basal tissue of the glandular hairs are, and the more such hairs occur isolated (free). Finally he adds “the more important marginal teeth”.

In a note he remarks that single veins proceed into the teeth in *Oxydendron arboreum*. According to *Wood* (1961: fig. 8), *Oxydendron arboreum* is a typical relict. It is the largest tree in the *Ericales* and has serrulate leaves. I, too, have ascertained veins proceeding into leaf teeth in material of *Arbutus canariensis*, *Andromeda cernua* *Clethra arborea* (Fig. 11E). *Wittsteinia*, cp. pp. 28–31.

### a. Unicellular simple covering hairs

These are often papillate and formed by a single cell. They can be scattered or form a dense cover. This type of hair is the only one in the *Epacridaceae*, if one disregards the tribe *Prionoteae*. Simple, unicellular hairs seem likewise to be the only type in the *Diapensiaceae*. They occur at the margins of the sheath part (*Grevel* 1897:41). Almost all species of the *Ericaceae* have at least scattered simple hairs. In *Elliotia racemosa* the pubescence is composed exclusively of simple hairs which produce a hirsute abaxial cover on the leaves (*Copeland* 1943 fig. 26–27). A similar cover occurs in *Andromeda glaucophylla* and *Kalmia polifolia*, although in the latter the midvein bulge is glabrous. Simple hairs often abound above the midvein on the adaxial side in *Kalmia*. The hairs have slightly granulated cuticular surfaces. Those on the adaxial surfaces, which are without stomatal pores, have glabrous surfaces (Fig. 7A–C). *Loiseleuria procumbens* has a similar dense underside hair cover (Fig. 15H–K), which in foliage



leaves becomes restricted to the revolute parts where the stomata are located, while similar hairs occur abundantly on the involute adaxial surfaces of the bracteoles (Fig. 2A).

The abaxial leaf sides in *Daboecia cantabrica* are covered with curling, twisted, long, generally unicellular hairs. A similar dense indumentum occurs on the abaxial leaf sides in, e.g., *Rhododendron smirnovii* and *R. bureavii*.

A complication of the surface structure of papillate hairs occurs in several species of *Erica*. The ontogenetic development in *E. terminalis* shows that in young, still slightly involute leaves hairs abound on all sides but on the adaxial sides they are generally short, papillate and are shed early. Hairs developed at the edges where the flanges start are larger with ampullaceous base and persist longer. Epidermal cells taking part in the ingrowth at the stomatal grooves have distinct cuticular warts and ridges and many are differentiated into papillate "shaggy" hairs which become empty, but before the protoplasts die the cuticle is modelled into densely spaced, thin, transverse, irregular annular excrescences (fig. 13). Similar hairs were described in stomatal grooves or abaxial surfaces in *E. tetralix*, *E. carnea* and *E. arborea* (Braun 1933 Plate VI). The restriction of the papillate hairs to stomatal grooves is general and probably an adaptional feature which impedes the intrusion of water into the grooves and slows down stomatal transpiration. *Cyathodes colensoi* (*Epacridaceae*) has simple hairs with cuticular excrescences. The hairs tend to curve and shelter the stomatal pores (Fig. 7H). In *Dracophyllum* strong unicellular hairs are forked at the base (Fig. 23B).

Isolated or scattered simple hairs without separate basal cells can be demonstrated in almost all the species that I have studied, even in *Leiophyllum buxifolium*, which has nearly glabrous leaves, and in *Epigaea repens* – a fact which disagrees with information given in the key of Niedenzu (l.c.: 187).

Cuticular excrescences similar to those occur-

ring on simple hairs have been described in several species, e.g., *Rhododendron campylocarpum* (Breitfeld l.c. Plate V, 2), *Bejaria racemosa* (Copeland 1943, fig. 1), *Arbutus petiolaris* and *Agauria buxifolia* (Niedenzu l.c. Plates III–IV). In the *Epacridaceae* they occur in *Leucopogon ericoides* (Copeland 1953 fig. 35).

Densely spaced short papillae or cuticular ridges abound on the abaxial epidermal cells of *Rhododendron lapponicum*, but are absent from the adaxial sides. The cuticular excrescences appear late, at a time when the protective shields of the peltate hairs have almost completed their morphological development and the secretory phase. The papillae or ridges are first covered with a smooth cuticle. The incisions between them are deep but the cuticle remains continuous and also covers the bottoms of the incisions. No papillae occur in the immediate surroundings of the stalks of the peltate hairs where the stomata occur (Fig. 21).

*b. Uniseriate or multiseriate, sometimes branched, eglandular hairs*

Such hairs are appendages separated from the epidermis proper by one (or several) cellwalls. Niedenzu discussed special basal short-cells ("the foot"), which often have thicker walls than the distal hair cells (l.c.: 142–147, Plate III 5–9, V 6). Such thick basal walls are often cutinized and may form a barrier for apoplastic water movement in the hair (cp. Böcher 1979 fig. 7 D). In *Hymenanthes*, Copeland (1943 fig. 222) illustrates a system of branched uniseriate hairs issuing from a foot forming basal tissue. Similar hairs are found among the "Flocken" hairs of Seithe (1960). The brownish, curled and branched hairs on the revolute leaf sides in *Ledum* are of the same type. The foot-cells here are without brownish cell contents and form a lobed or uni-biseriate tissue from which issue the long, twisted hairs. The uncoloured foot consists of rows of 5–10 cells. In leaf primordia the foot part is generally situated on the abaxial side and at the recurving margins.

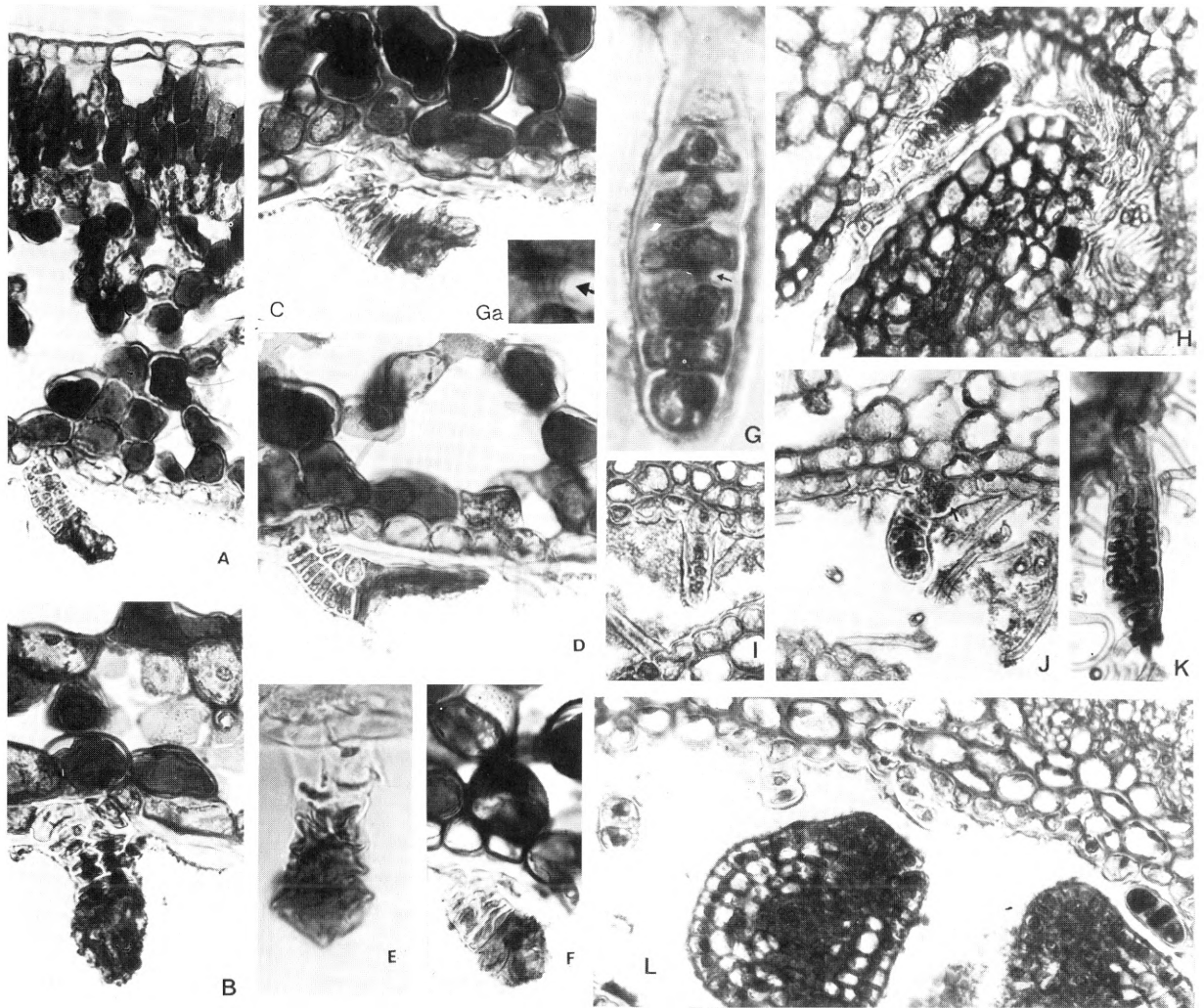


Fig. 15 Glandular hairs. A–F in *Leiophyllum buxifolium*. G–L in *Loiseleuria procumbens*. A. Cross section of leaf x 205. B–F. Single glands on abaxial side x 320 all FS. In A–D, resinous particles on surfaces in C, D, F, the hairs bend towards surface. – G. Young glandular hair with large nuclei, plasmodesmata (Ga, arrows) and pits. x 1000. H–L. Glands on abaxial surfaces

often surrounded by simple hairs, in H, in abaxial cavity, in I–J, imbedded in resinous material. Arrow in J points to small hair initial adjacent to already developed hair. In L, two glands still connected with epidermis, while two (with rows of 2–3 cells) are disengaged – resembling hormogonia. Toluidine Blue (H) or FS. x 320.

There is a smooth transition from the residual marginal meristem to still propagating foot cells. An intercalary growth from initials among the foot cells appears very probable (Fig. 20).

Multiseriate bristles (“Zotten” of *Seithe* l.c. fig. 23–29) are flat, tapering emergences. Their basal part may be composed of several tiers of short,

small foot cells and seems at an early stage to be meristematic. Eglandular bristles are depicted by *Seithe* (l.c. figs. 33, 142) as derived from bristles terminating in glandular heads. According to *Nieden zu* (l.c. Plate III 5), the multiseriate trichomes in *Epigaea repens* are sometimes without heads, or the heads resemble stalk cells. *Seithe*

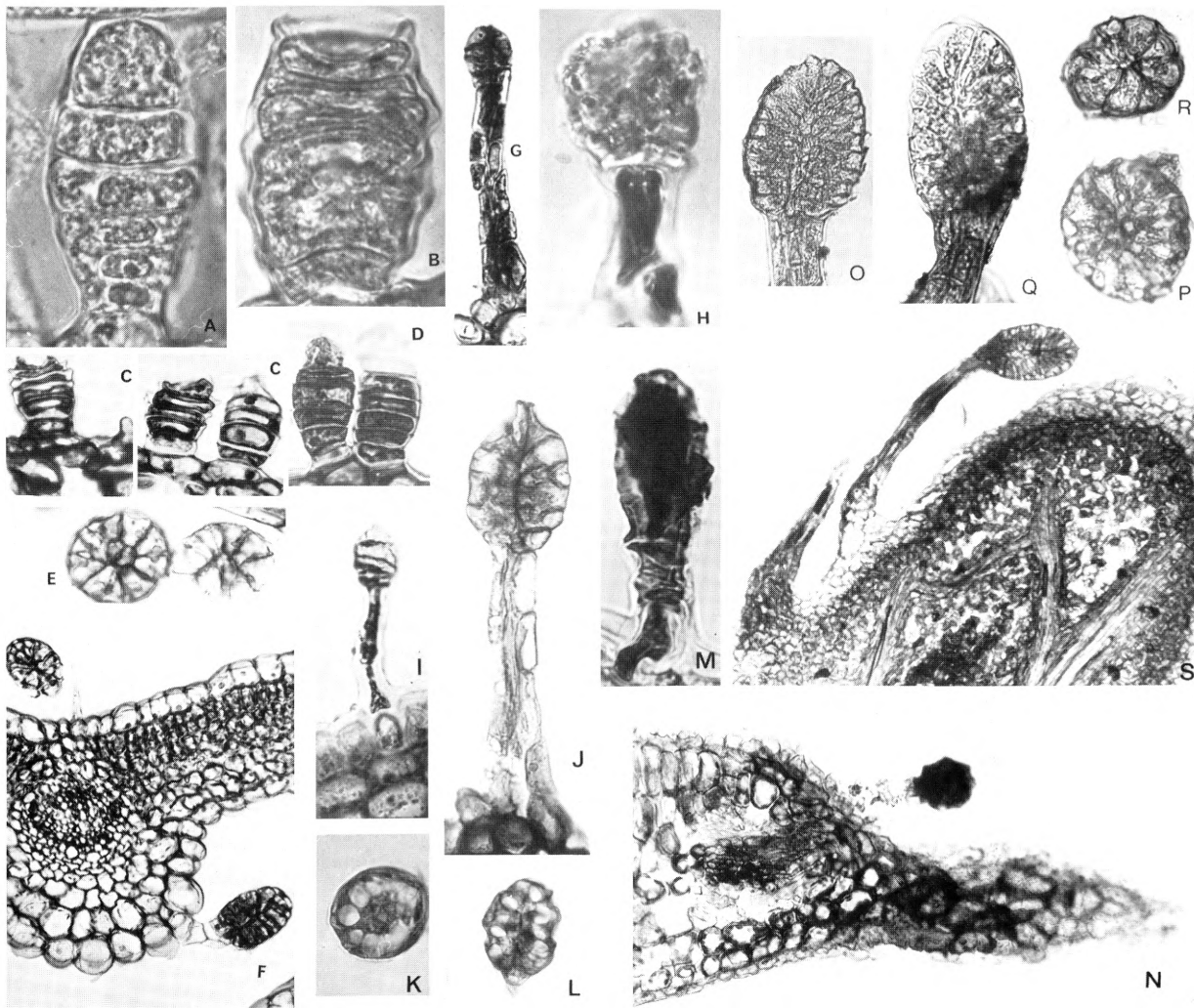


Fig. 16 Glandular hairs or appendages. A–D. Uniseriate glands in *Cassiope tetragona*. A–B. x 1000. A, mature stage; B, after release of material from apical cell, cuticular bulges. C–D. FS x 320. Bulges at transverse walls indicate secretion from subapical cells. In D, uppermost cells emptied of contents. – E–F *Menziesia pilosa*. E. Cross sections of glandular heads with middle cell wall cavities. Toluidine Blue x 320. F. Midvein in young leaf and two glands of the middle wall type, stalk connection is seen in the abaxial one only. FS x 160. – G. *Epigaea repens*. Small glandular hair off abaxial midvein. Stalk with much anthocyanin, head with dark-stained transverse walls FS x 250. – H. *Arctostaphylos uva ursi*. Short glandular hair at margin of young leaf. Head producing lumpy birefringent secretion from six cell stories FS x 1000. – I–L. *Rhodothamnus sessilifolius*. I. Small glandular hair at abaxial midvein, secre-

tion in walls in the head. J. Large marginal emergence with elongate conducting cells in the stalk. In the head, a central channel and several middle wall spaces. – K–L. Transverse and longitudinal sections of head with middle wall cavities and apertures FS x 320. – M–N *Pieris japonica*. M. Glandular hair containing dark resinous masses. In the stalk, tanniferous cell contents. FS x 492. N. Small glandular hair; the reddish head with resinous content. The gland is placed near water pore at small marginal incision. FS x 160. – O–S. *Rhodothamnus chamaecistus* marginal emergences. O and P, heads lengthwise and transversely cut, showing marginal vacuoles and central channel. Ruthenium Red x 250. – Q–R, the same but Sudan IV staining the margin of the channel x 320. – S. Leaf margin with foot and stalk of two emergences. Veins with tracheids leading to water pores. Semipolarized light. FS x 100.

writes of a "Primärdrüse" and this ancient or basal type resembles the hairs in *Epigaea*. In his opinion two sematophyletic lines may be ascertained, one leading to recent eglandular bristles or multiseriate branched trichomes and another terminating in heads with transversally arranged glandular cells, or capitate as in the peltate hairs (scales).

### c. Glandular appendages

There are probably no glandular hairs with a unicellular head producing a secretion between cell wall and cuticle in the *Ericales*. In this group hairs with small heads on long stalks are generally composed of several small glandular cells (e.g., *Gaultheria cordifolia*, c.p. Stevens (1971 fig. 1 D), *Epigaea repens* (Fig. 16G)). Glandular hairs in *Empetrum* have multicellular heads, too. (Gibelli 1876, Plates V–VI).

#### 1. Glands without well demarcated heads.

These are composed of one, two or a few parallel rows of cells and may be related to the "Gliederhaare" of *Seithe* (l.c.). The hair approaches a situation where the major part of it acts as a glandular head because most cells have very large nuclei and appear active in the secretory processes. To this category belong the glandular hairs in *Leucothoë*, illustrated by *Niedenzu* (1890 Plate III, 10 a–b). In *L. axillaris* which I have studied, the mature, elongated narrow head is covered by a sticky, blackish, resinous material. The differentiation of the glandular cells appears rather late. In young hairs the uppermost cells may be slime producing.

A good example is provided by the glands in *Loiseleuria procumbens*, which were thoroughly studied by *Rübel* (1908). They occur mainly on the petioles of leaves that function as bud scales. Microchemical tests show that they secrete a pectinaceous mucilage. My own observations have revealed that one or two rows of glandular cells obtain a terminal part, in which the cells become filled with a brownish, granular substance that is

finally released and may cover large areas of the epidermal surface (fig. 15, I–J). The cells in the glandular cell row are connected through plasmodesmata, which can be detected because they contain precursory material for the secretion (Fig. 15 G). The cell walls in the distal part are thin and the secretion is contained behind thin terminal cell walls and cuticles, which finally burst or are dissolved. The secretion does not ooze out regularly into wall interspaces, but this may happen occasionally. The glandular cell rows often develop in pairs successively from epidermal mother cells (Fig. 15J). Some of them stop their growth early and may be released in a two or few-celled condition after rounding off of the proximal cell walls (cp. Fig. 15L).

*Leiophyllum buxifolium* has similar scattered glandular hairs (Fig. 15A–F). The cells become shorter distally and often have brownish contents; they end in a kind of head consisting of a few thin-walled cells. These cells receive the brownish viscous substance that is released concomitantly with a dissolving of the walls. The hairs may be formed in pairs and curve towards the epidermal surface, which seems to be smeared with the secretion. A gland from *Leiophyllum lyoni* shows a similar curvature *Copeland* (1943 fig. 81).

In *Cassiope tetragona* the glands occur in great quantities on the adaxial surfaces and the revolute undersides of young leaves. They consist of 9–10 cells in a row all with large nuclei. The row is initiated by one hemispherical cell which undergoes several divisions before a stretching and maturing of the resulting cells takes place. Some cells inserted in the row may die early (dark in fig. 5C–D). The dome-shaped terminal cell matures first and after a release of its contents it leaves a collar or circular pad (Fig. 16B). With Sudan IV a very thin, stainable lamella can be ascertained in most of the cell walls. The glandular hairs stain a dark blue colour with Toluidine Blue. The cytoplasm contains large vacuoles and granular masses. *Warming* (1886: 177 and 204) first thought that the glands might be water-absorbing, an idea

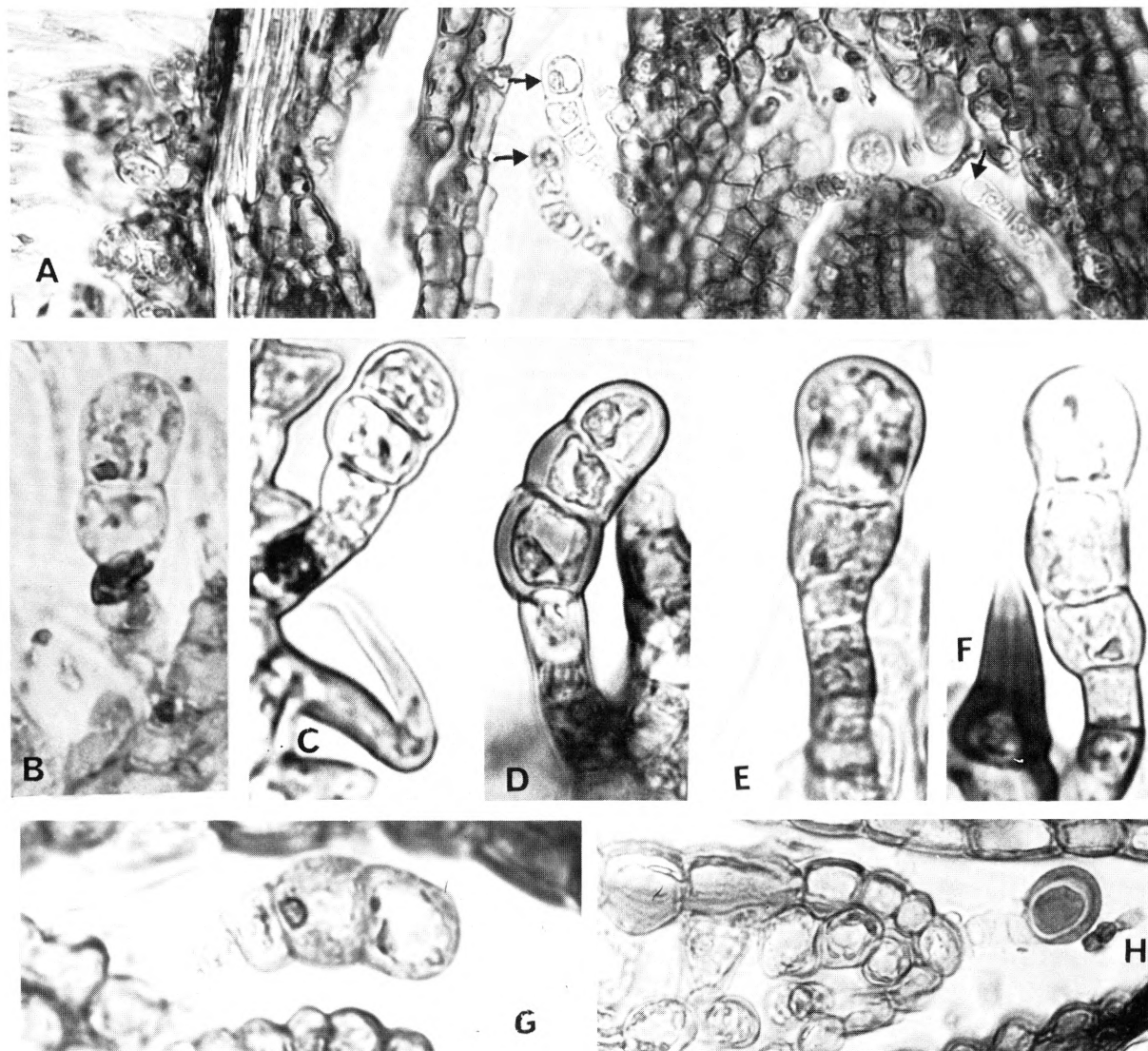


Fig. 17. *Calluna vulgaris*. A. Longitudinal section of shoot apex showing club-shaped hairs (arrows) in cavities near the apical meristem, which occurs just below the leaves on the right: cp. fig. 6 A. FS. x 500. – B–G. F. Single club-shaped hairs. In all cases a darker middle cell is inserted among the stalk cells. The “head” consists of 2–3 cells. Starch is accumulated (C–D) and

the walls thicken (D), but there are irregularly distributed thin areas (E) and finally the contents in the uppermost cell may be released. (F). – H. PAS stains thick wall and contents in terminal cell and laminate, pectinaceous, interior epidermal walls B, E, F, G: FS, C and F: Sudan IV, H: PAS. C–E. Semipolarized light. C–G. x 984. H x 640.

which still cannot be refuted, but later he found that they produce resinous masses that could be removed with alcohol. Young shoots and primordia could be enveloped by the secreted material. It burns under strong crackling. The colleters in

*Helianthemum*, described by Hanstein (l.c.: 734 Plate XII 90–92), resemble in many ways the glands in *Cassiope*; they, too, produce resinous substances and mucilage. In *Cassiope tetragona* bulges of the cuticle outside transverse walls in

the cell row are common (Fig. 16C). Resin, probably together with mucilage, is squeezed out from interspaces in such walls. Bulgings are numerous in alcohol-fixed material. They were formed during the exudation of resin and are now empty bags. Young leaves near the shoot apex have glistening, sticky surfaces. Light microscopy reveals a resinous covering on the adaxial sides and numerous lumps of resin adhering to the simple hairs at the margins. The glands are completely covered up. The basal cell in the glandular cell row is not morphologically distinct and seems inactive in the secretory process. The amount of the mucilage, which appears to be produced together with resin, is unknown.

Uniseriate glands in *Cassiope selaginoides* resembling those in *C. tetragona* were depicted by *Nieden zu*; those in *C. redowskii* deviate by possessing a few lateral cells (*Nieden zu* l.c. fig. 2). The glands in *C. fastigiata* (*Nieden zu* Plate III, 6) consist of rows of elongate cells and have thick-walled basal cells. They resemble the mucilage-producing glands on the ochreae in *Rumex* and *Rheum*, described by *Hanstein* (l.c.: 699 and Plate XI) and *Schnepf* (1968). The glands in *Cassiope fastigiata* and *C. wardii*, another Himalayan species, are said also to be able to collect moisture and to conduct it to the leaves (*Lilley* 1965). A more thorough comparative work including EM observations of all species of *Cassiope* is both tempting and urgent.

In *Calluna vulgaris* the club-shaped hairs (Fig. 17) first described by *Beijerinck* (1940), slightly resemble the glands in *Cassiope*. They are uniseriate, but weakly differentiated in a stalk and a head of 2–3 cells, which when treated with Toluidine Blue retain a blue tint while the stalk cells finally become colourless. The young top cells are usually swollen and their contents are stained with PAS. Their walls gradually become thinner. Starch is accumulated in the cells at early stages, but it seems to disappear at the mature stage. The hairs then have up to 6–8 stalk cells in a row while the head sometimes attains a few lateral ones. The secretion is sticky and brownish. After a drying-

up or emptying, the apical cells shrivel. The club hairs in *Calluna* occur mainly at the sharp edges where the flanks end (corner effect) and they mature on the development of leaf pair No. 4–5 from the top; in pairs initiated later only shrivelled, or sometimes elongated but empty club-shaped hairs are seen on the adaxial edges. In the same way as in *Cassiope*, the function of the club-shaped hairs may be connected with the growth of the shoot apex and the first primordia, which may be kept smooth and protected by the secretion. However, such hairs are moreover considered to act as some kind of trichome hydathode and by their activity to increase the requisite flux of water with solutes to the apical meristems.

Glands without distinct stalk and head can be multicellular, conical or tongue-shaped bodies (see, e.g., *Copeland* 1943: 212). In *Vaccinium ellipticum* they are incorporated in the epidermal tissue and limited towards the chlorenchyma by a special wall layer (*Nieden zu* l.c.: 147, Plate V 2–7). The glands in *Vaccinium vitis idaea* are postulated to be water-absorbing (*Lundström* in *Grevillius* l.c.: 93). According to my observations of glands in the arctic ssp. *minus* they are secretory. They have a short colourless stalk and a multicellular head, somewhat flattened and brownish. They occur in the leaf margin and on the abaxial side where they become stretched along the epidermis. Cuticular bulges encircle a translucent, sticky material, which seems to be exuded between the head cells and seeps down to be deposited at the base of the stalk (Fig. 14, G–J). The glands depicted by *Schroeter* (1908: Fig. 30) are very dissimilar.

## 2. Glands with stalks and distinct secretory heads, but not peltate.

A more specialized type of gland is developed in several of the *Rhododendroideae*. In the *Ericoideae* these glands occur in *Erica*, see *Palser & Murty* (1967 fig. 23, T–W). The glands were first described by *Hanstein* (l.c.: 730, Plate XII 93–95) and *Rauter* (1871 Plate V 1–12) in *Azalea indica* and

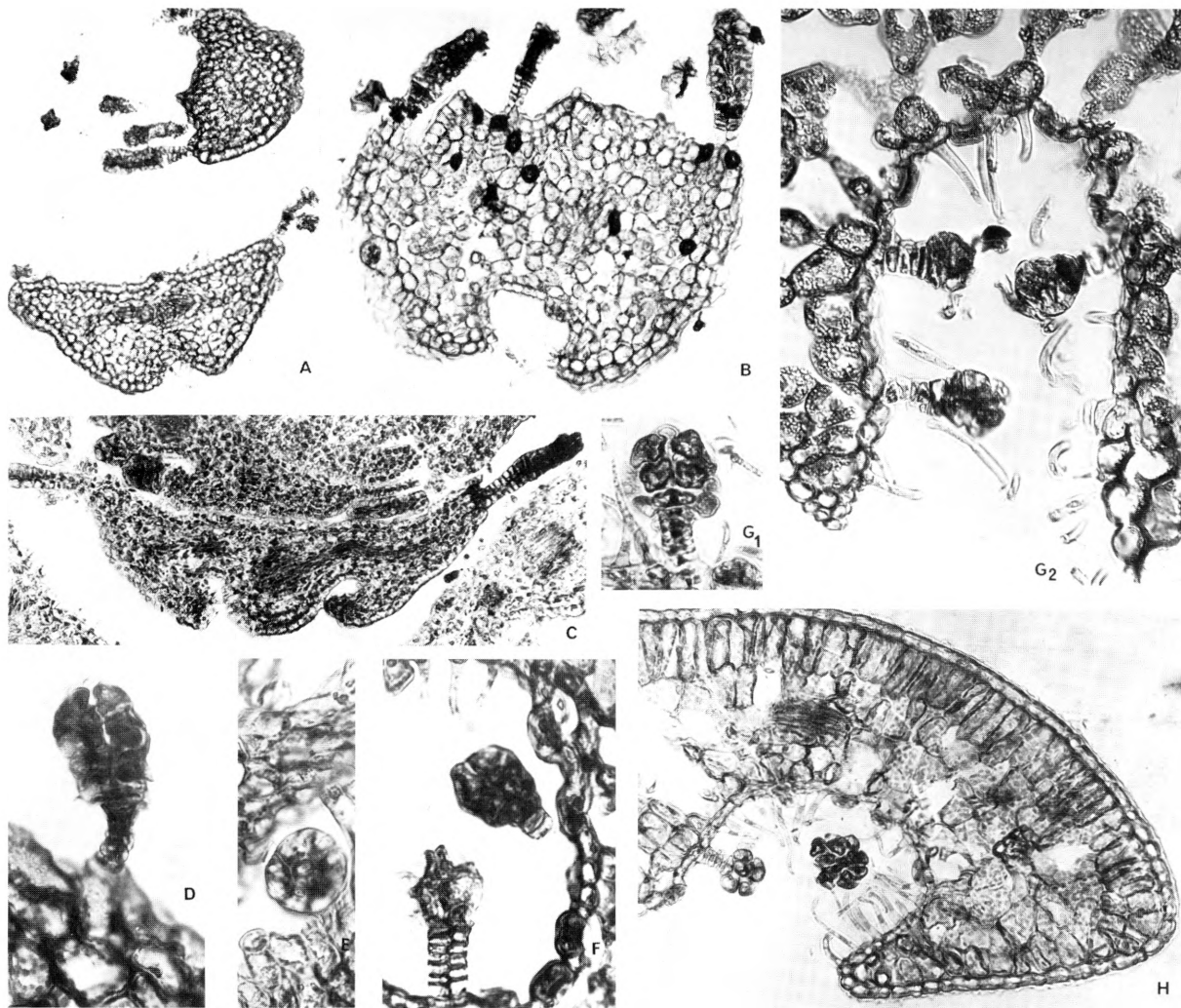


Fig. 18 *Phyllocladus*. A–F. *P. glandulifera*, G. *P. coerulea*, H. *P. empetrifolia*. A–C. Primordia from top of shoot. The adaxial sides bear vigorous elongate middle-wall glands. The abaxial stomatal furrow is formed in A–B, but not yet the bulging at the midvein. Adaxial stoma in A. FS, A x 100, B x 160. – C. Young leaf near top of shoot with long glands in corner position and bulging of midvein. Toluidine Blue x 160. – D–E.

were characterized as colleters or glue-producing glands (“Leimzotten”). The sticky secretion is collected in intercellular spaces between the gland cells forming the head. *De Bary* (1877) referred to this type of gland a “Zwischenwanddrüse”. *Copeland* (l.c.) describes them as consisting of several

Middle wall gland with apical opening and central channel, in E with stained secretion along wall in channel. Quadruple staining x 320. – F. Abaxial stomatal furrow. Glands with heavily stained material along walls, quadruple staining x 492. – G<sub>1</sub>, Single gland and G<sub>2</sub> abaxial stomatal furrow with simple hairs, glands and raised stomata. Interference contrast. FS x 250. – H. Leaf margin and stomatal furrow FS x 160.

superimposed whorls of tack-shaped cells, in contact with each other but separate at the middles at maturity. *Seithe* (l.c.) uses them as a basal type from which he derives peltate or spherical glands which likewise have intercellular spaces between secretory cells. *Börgesen* (1890:31) places the colle-

ters in *Phyllodoce coerulea* among those which lack intercellular spaces, but in mature colleters the cells in the head form clusters with small central spaces. The same is the case with *P. empetriformis*. Both can be derived from those in *P. glandulifera*, which has a more “advanced” glandular structure. Its glands sometimes have long stalks and elongate heads with 6–8 glandular cell rows around an intercellular space or channel which is seen to be coated with brownish resinous material (Fig. 18). The channel ends in an aperture where sticky material is exuded; the remains of this material can be seen to coat young shoots and inflorescences. The shoot apices with the youngest primordia carry a multitude of such glands (Fig. 18 and p. 33).

In *Rhodothamnus chamaecistus* the stalks have up to ten peripheral and a few central cell rows, while the heads have about 14 peripheral glandular cells surrounding a core of a few elongate cells and one or two narrow channels. The glandular cells have conspicuous vacuoles near the periphery, and radial, intercellular spaces between the cells are easy to detect in older glands (Fig. 16O–S). At the top of the colleter the cuticle is extended because of the secretion collected in the channel; finally it bursts. The radial and peripheral walls of the glandular triangular cells have thin Sudan IV-positive lamellae. The stalk cells have thick walls that are heavily stained. The heads react strongly with Toluidine Blue and Ruthenium Red.

In *Rhodothamnus sessilifolius*, cp. *Davis* (1955), there are smaller colleters but they resemble those of the preceding species. However, they occur not only along the leaf margin but also, e.g., on the mid-rib bulge (Fig. 16, I–L). The very similar glandular structures in *Menziesia pilosa* also occur in connection with the veins and particularly as outgrowths from the parenchyma at the veins; further details are seen on figs. 9A–C and 16E–F.

The attractive relict shrub *Kalmiopsis leachiana* (*Rehder* 1932, Plate 40, *Copeland* 1943, fig. 62–66) has two kinds of gland. The most common ones

on stems and leaves are similar to those in *Rhodothamnus* and have the same staining properties. They deviate perhaps by having a narrower opening inside the coating of glandular cells in the head. *Copeland* calls the other type “scale-like”, but it would be better to call them glandular clusters or aggregates. They have a short stalk and a broad multicellular head consisting of several tiers, each of concentric cycles of cells. According to *Copeland*, the heads secrete a firm outer wall of “stain resistant” material and the secreting cells “shrive away from the wall forming a heavily staining amorphous mass”. In the material that I have studied the “wall” is comparable to distended, fused, cuticular layers of several glandular cells in the cluster. With Sudan IV the “wall” is easily stained and exhibits about three concentric Sudan-positive membranes separated by delicate layers of pectinaceous material which stains with Ruthenium Red, Toluidine Blue, or PAS. There is some agreement with the glands described by *Hanstein* (l.c. Plates XI–XII) in *Ribes*, *Salvia* and *Lonicera*. The latter has three glandular tiers and here, as well as in *Salvia*, the distended cuticular layer appears to be thick (tough?). I agree with *Copeland* in regarding the glandular clusters in *Kalmiopsis* as essentially different from the peltate glands in *Rhododendron*. They occur exclusively on abaxial leaf surfaces and resemble in this respect the small globular glands in *Ledum* (see later). Sometimes the cells in the cluster are maintained, no distended common membrane being developed above. Such clusters are rare and may have been checked in their function (Fig. 19C–D). The most common situation is that the basal wall part of the glandular cells remains as a coherent body which, in section, looks like a chain of horse-shoe-shaped projections below the broken common membrane (Fig. 19G). The amorphous mass mentioned by *Copeland* (l.c.: 567, fig. 63) suggests some kind of resinous material, but the strong distension of the membrane points to a production of essential oils.



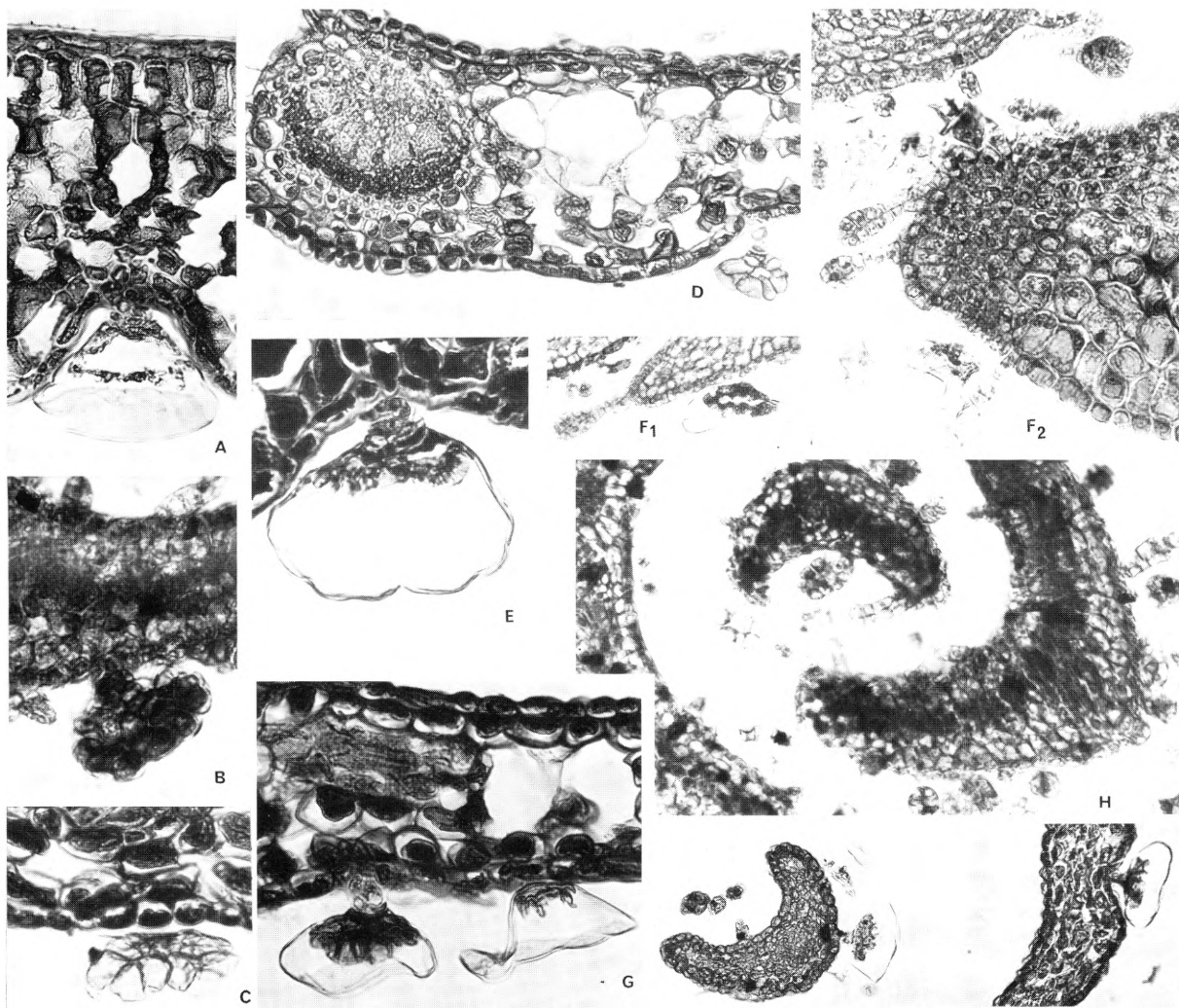


Fig. 19. *Kalmiopsis leachianus*. A. Glandular cluster on abaxial side. Upper, dying secretory cells seem to be lifted towards the expanded outer membrane which has two layers FS.  $\times 320$ . – B. Young cluster. Single secreting cells each with expansion of cuticle. FS  $\times 400$ . – C. Cluster of empty cells. PAS  $\times 320$ . – D. Cross section of leaf with vein, water-storing cells and crystal druses. Deviating cluster probably with empty cells. Toluidine Blue.  $\times 250$ . – E. Cluster stained with PAS. The thick outer

membrane is expanded and appears to be composed of about seven fused membranes and of two layers  $\times 320$ . – F<sub>1</sub> F<sub>2</sub>. Small middle-wall glands and single clusters near leaf margin. PAS  $\times 320$ . – G. Cross section of leaf with two old clusters showing horseshoe-shaped cell wall, remains of glandular cells FS  $\times 160$ . – H–J. Youngest leaves in bud with vigorous middle-wall glands and young abaxial glandular clusters. FS  $\times 250$ .

### 3. Globular and peltate glands.

To this group belong the largest and most diversified trichomes in the *Ericales*. As pointed out by *Seithe*, they may be derived from “Zwischenwanddrüsen” (intercellular or middle wall glands).

*Ledum decumbens* has two kinds of globular gland. This was rightly pointed out by *H. E. Petersen* (1908 a: 93), who also stated that the larger ones occur on both surfaces of the leaves. The smaller glands (Fig. 20G) have longer and more

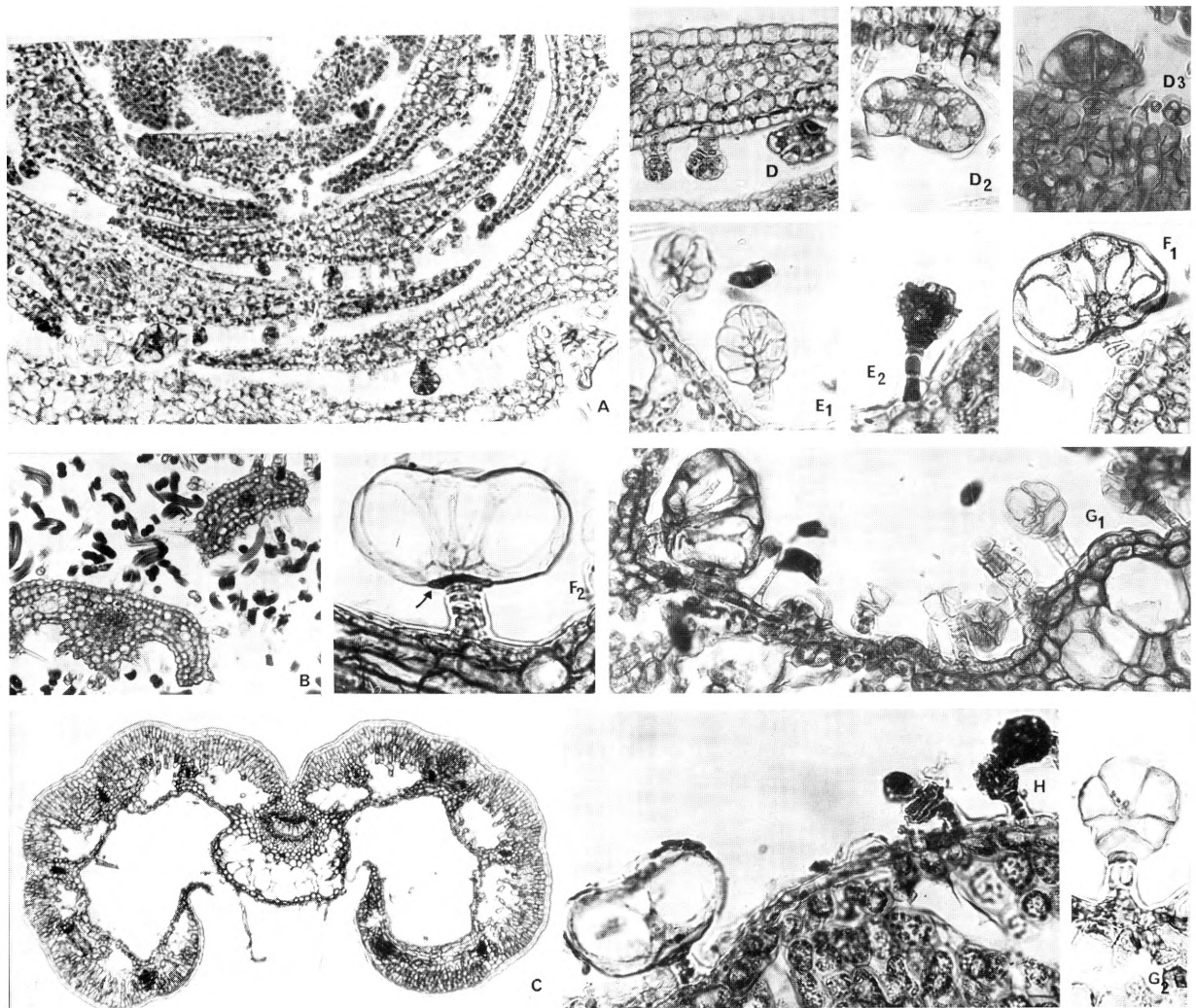


Fig. 20. *Ledum decumbens*. A. Interior involute bud scales in flowering bud. Initial stages of glands. FS x 160. – B. Youngest leaf primordia in vegetative bud. Many brownish branched hairs, revolute leaf margin. FS x 100. – C. Mature leaf. Marginal hairs tend to close openings to the two abaxial cavities formed by the recurving leaf halves. Several cavities in spongy parenchyma and below midvein. FS x 100. – D<sub>1</sub> Early stages in development of large globular glands. FS x 250. – D<sub>2</sub>–D<sub>3</sub>. Young globular glands with cuticular bulges because of secretion FS x 320 and 250. – E<sub>1</sub>–E<sub>2</sub>. Smaller globular glands. E<sub>1</sub> as

slender stalks of 3–7 cells, usually in a single row. The heads consist of five–six cells in a cluster. At an early stage the glandular cells have very thin walls and obtain a thin cytoplasmatic layer enclos-

well as G<sub>2</sub> show the cellular arrangement x 250. E<sub>2</sub> is in the stage of secretion. x 320. – F<sub>1</sub>–F<sub>2</sub>. Large globular glands showing intercellular dark channels and outlet fissures from larger cavities; arrow points to middle cell. x 250 and 100. – G<sub>1</sub>–G<sub>2</sub>. Smaller globular glands, probably emptied, in G<sub>1</sub> also one large gland in abaxial stomatal cavity. FS x 320. – H. Smaller glands (on the right) producing dark resinous material which is deposited on surface of large globular gland (on the left). x 250.

ing a large vacuole. With fast Green-Safranin they remain green with red nuclei, while the uppermost stalk cell attains a red colour. This cell, as well as the other stalk cells, also stains with Sudan

IV. Accordingly, the cell bordering the head may be a “middle cell” (cp. *Schrödter* (1926)) controlling apoplastic liquid movement. At a later stage the walls in the head become thicker. With Ruthenium Red the stalks remain unstained while those in the head and particularly the walls separating them are stained. At a still later stage the secretorial phase is reached. The heads are filled with a dense brownish substance. The separating walls seem to recede and small refractive globules occur in the narrow spaces between the cells. Finally, the globules burst and the brownish material is liberated. Droplets which remain are intensely stained with Sudan IV. The secreted substance appears to be resinous and is found deposited on other cells where it forms a brownish, cracked coating outside the cuticles (Fig. 20H).

The larger globular glands in *Ledum* have shorter stalks of 3–4 cells, often arranged in two rows. The head is built up of 8 peculiarly shaped cells that form a cavity and gradually large open spaces appear between the cells (Fig. 20F). Each cell is widened in its upper part where it borders a similar cell from the other side of the spherical structure. Secretion starts when the intercellular spaces become visible. Bulges appear in the cuticle enclosing the head and these may burst. During the secretory stage the columnar gland cells have dense cytoplasm around the nucleus and wide terminal vacuoles. The first secretion is colourless and may be an odorous essential oil. In aged glands droplets sticking to the walls are interpreted as shrivelled resinous masses that are maintained along the walls of the cavities. Such droplets stain with Sudan IV, as do the stalk cells and the joints between the cells in the head and the thin cuticle. The stalk cells bordering the head stain most intensely and may act as “middle cells”. Ruthenium Red stains droplets inside the gland, the joints and the intercellular, narrow channels that are observed to radiate to the larger intercellular spaces and to the apertures leading from the spaces to the surroundings.

EM studies of *Ledum* glands (*Schnepf* 1972) reveal that a glabrous tubular ER predominates and that the secretion is oily.

The peltate glands in *Rhododendron* have been objects of study even since the papers by *Vesque* (1885: 228–230), *Warming* (1886, 1888) and *Breitfeld* (1888). *Warming* knew that these hairs were resiniferous but he described them mainly as anti-transpiration arrangements. They produce a dense cover which protects the small pits in which the stomata are concentrated. *H. E. Petersen* (1905 a) repeated this opinion, but *Stocker* (1931) found higher transpiration rates in leaves of *Rhododendron lapponicum* than in leaves of *Vaccinium vitis-idaea* and *V. uliginosum*. This author criticizes the views of *Warming* but admits that the suggested xeromorphic structure might be of vital importance during the spring when the soil is frozen. *Stocker* may not have noticed that in nature, *R. lapponicum*, prefers sites where water that is rich in solutes oozes out, e.g., at the foot of slopes. *Krantzmann* (1910), after a study of peltate hairs in the alpine species, concluded that the hairs belong to the “middle wall glands” and produce essential oils that are released through fissures in the shield. *Duncan* (1933) studied the peltate hairs in *R. punctatum*. They start as middle-wall glands but during their development they change their function. The shield enlarges and when full grown its cell walls thicken and the protoplasts disintegrate. *Duncan* assumes that the scales retard transpiration, at this stage, but he adds that they might be water-absorbing in wet periods. Capillarity would draw water back under the scales and water might enter through thin-walled epidermal cells in the pit surrounding the stalk of the hair. In *R. lapponicum* (Fig. 21) the stalk cells are cutinized or suberized, and the thin-walled epidermal cells under the shields have a thin cuticle mostly without cuticular ridges. The most probable period for water-uptake by the peltate hairs is probably when they are young and not full-grown (Fig. 21C, E). *Cowan* (1950) thinks that peltate hairs in *Rhododendrons* show

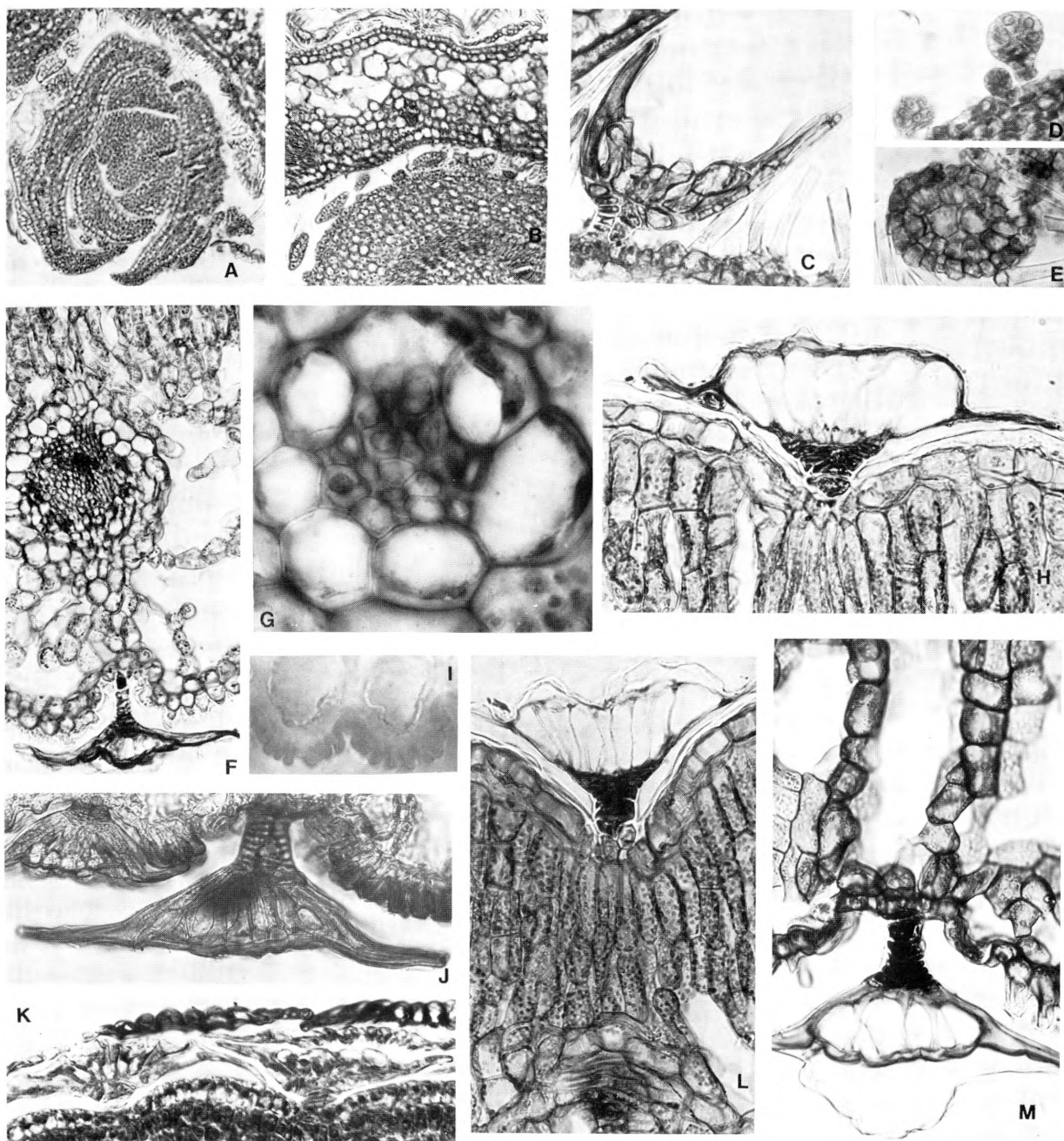


Fig. 21 *Rhododendron lapponicum*. A. Small vegetative bud with involute primordia. – B. Young stem with numerous developing peltate hairs and surrounded by bud scale with abaxial cover of peltate hairs. A–B. FS, x 100. – C. Young peltate hair and simple hairs, intercellular spaces in the shield formed. – D. Young peltate hairs. E. Peltate hair from above, marginal cells not yet expanding, intercellular spaces in central part formed. C–E. FS x 320. – F. Cross section of abaxial part of leaf. Vein with bundle sheath surrounded by trabeculae which traverse schizogenous spaces. Peltate hair in stomatal depression. FS x 160. – G. Bundle sheath with large chloroplasts centrifugally

arranged FS x 1000. – H. Peltate hair on adaxial surface. Elongate narrow green cells continue to vein below (outside picture). Cuticular bulge FS x 250. – I. Cutinized surface of abaxial epidermal papillae. Sudan IV. x 1000. – J. Abaxial epidermis with two peltate hairs. Sudan IV stains stalk cells, papillae and surface of shield. x 250. – K. Cover of peltate hairs on surface of young leaf. Youngest hairs with stalks are covered by older ones. FS x 160. – L.–M. Peltate hairs in depressions in adaxial (L) and abaxial (M) sides. Cuticular bulges. Trabeculae in shields, strongly stained stalks. FS x 320.

adaptations to several physiological activities, thus water absorption and secretion (hydathode-function) and secretion of essential oil. The latter is accompanied by a swelling of the cuticle above interspaces between the cells in the center of the shields (Fig. 21H, L, M). The shield surfaces form flattened "bowls" that may be filled with evaporating oil. The stalk cells remain alive but the cutinized walls make apoplastic water movement impossible. Thus the entire stalk acts as an endodermoid arrangement, similar to single cells in the *Ledum* glands. In *R. lapponicum* the palisade parenchyma below adaxial peltate hairs has the character of a bundle sheath extension, being composed of elongate cells issuing from bundle sheaths which, in this case, contain comparatively

large chloroplasts arranged centrifugally. *Beijerinck* (1940, fig. 33A) illustrates a rather similar arrangement of chloroplasts in bundle sheaths in *Calluna*.

In one locality in West Greenland *Ledum decumbens* ( $2n=52$ ) and *Rhododendron lapponicum* ( $2n=26$ ) have formed a probably sterile hybrid (with defect pollen tetrads), cp. *Abromeit* (1899). The leaf structure in this hybrid is intermediate as, too, the flowers that have pink petals and are arranged in umbels. The large globular glands are slightly flattened (sometimes mainly along their margins) and are closer to *Ledum* than to *Rhododendron* – a fact which may be connected with the chromosomal differences between the parents.

## 9. Discussion and outlooks

### *a. Ancestors, early differentiation and distributional pattern.*

In the previous sections some morpho-anatomical features were presented and provisionally discussed. Many comprise contradictions, e.g., evergreen-deciduous, alternate-opposite (whorled), dorsiventral-isolateral, revolute-involute, pinnate-palmate, etc. These demonstrate the versatility of the leaf structure in the *Ericales* and that very few characters are general. This order thus appears very heterogeneous, but even so botanists usually believe that the *Ericales* are monophyletic. Cox (1948) discussed the primitive ancestors of the *Ericaceae*. One of them, *Oxydendron arboreum*, is monotypic. It is a tree which retains the primitive characteristics of floral and fruit structure, wood type and vessel wall structure. It has  $n=12$  and was described, e.g., by Wood (1962:57). Cox (l.c.: 511) reconstructed a hypothetical ancestor for the five tribes of the *Arbutoideae*, but omitted the *Bejariaceae*. The ancestor, now probably extinct, was envisaged as a shrub with certain wood-anatomical characters and perhaps being a native of South-eastern Asia, the Himalayas in particular. According to Cox, *Bejaria* does not descend from the same ancestor as the other *Rhododendroideae*, which are considered to have a polyphyletic origin.

Nobody seems to have dared to construct a "family tree" for the *Ericales* as a whole. Even the idea of a common ancestor for this huge entity has to be abandoned in advance. It is better to discuss more or less parallel evolutionary lines which need not necessarily go back to single ancestors but may have started from an already differentiated group, which – if we knew it today

– would be referable to several taxa perhaps with generic rank. An opinion of this kind agrees fairly well with that formulated by Stebbins (1974:244).

The differentiation into families and most genera probably took place prior to the Tertiary period. Some ericalean genera are recorded from the Cretaceous epoch. There are many fossil remains from Tertiary times. Gothan & Weyland (1973) mention *Andromeda*, *Kalmia*, *Leucothoë*, *Rhododendron*, *Cassiope*, *Vaccinium* and *Orphanidesia*, but there are also records of *Arctostaphylos*, *Lyonia*, *Menziesia*, *Calluna*, *Erica*, *Arbutus*, *Ledum* and *Empetrum* as well as *Clethra* and epacridaceous genera such as *Leucopogon* and *Epacridicarpum*. This list demonstrates that the *Ericales* were well differentiated at an early stage and that generic evolution hardly takes place in our own time. At the specific level, however, the differentiation continues at least in polymorphic groups such as, e.g. the South African *Ericas* the Asiatic *Rhododendrons* and the New Zealand *Dracophyllum* (cp. Allan 1961).

The *Ericaceae* have reached almost all parts of the world, but they have remarkably few representatives in Australia-New Zealand (*Gaultheria*, *Pernettya*, *Wittsteinia*). The *Epacridaceae* exhibit the opposite behaviour by being concentrated in Australia-New Zealand with radiations to New Caledonia, New Guinea and even to the Hawaiian Islands. These families thus appear to be vicarious. The *Empetraceae* are bipolar and constitute the most dubious members of the order, the *Diapensiaceae* are only found in the northern hemisphere. The *Clethraceae* are tropical-subtropical, but absent from Africa and Eurasia except South-east Asia and the Canary Islands.

The leaf architecture of the *Ericaceae-Empetraceae* is extremely different from that of the *Epacridaceae*. Such a pronounced difference may be a result of geographical isolation, e.g., continental drift, which at a very early time, concomitant to great climatic-ecological changes, brought about two divergent evolutionary lines, the ericaceous and the epacridaceous. As mentioned, the latter radiates out from the Australian continent, but the occurrence of the *Prionoteae*, in Patagonia and Tasmania (cp. Arroyo 1975), and the deviating *Wittsteinia* in Victoria (South Australia), point to former connections between parts of the Australian and South American continents. Stevens (1971:45) referred to *Wittsteinia* as a separate subfamily of the *Ericaceae*. The same author says that the basic chromosome number in *Wittsteinia* is probably 8.

It is exceedingly difficult to envisage a gene pool which would include potentialities for the emergence of both the *Ericaceae* and the *Epacridaceae* and even further families. The evolutionary end-products which we acknowledge nowadays are too far from one another. Let us tentatively suppose that *Calluna vulgaris* would be an ancestor of several lineages. Today it is composed of a series of ecological races which each might give rise to a separate lineage. However, none would develop into taxa that would fall outside the *Calluneeae*, simply because of the conservation of the organization in *Calluna*. If we choose a rare relict species such as *Kalmiopsis leachiana*, we would hardly find any radiation from it, at least not under recent climatic conditions. An ancestor, therefore, would probably have the character of an aggregate taxon, a complex characterized by interbreeding and intercrossing between races and species, and such a swarm which also involved mutations would in size and divergences resemble the evolutionary pattern of the *Ericales*. However, an ancestor of this kind would be diffuse and plastic and at the beginning there would be no real or distinct radiations from it. Plastic taxa in the *Ericales* may be

found in taxonomically difficult aggregates within *Erica*, *Vaccinium* and *Rhododendron*. There are many good examples of "hotbeds" for new taxa in other orders. May I bring to mind a complex such as *Prunella vulgaris-laciniata-grandiflora* or *Campanula rotundifolia-gieseckiana-scheuchzeri*.

*b. Rigid and plastic species, history and fate of taxa, relicts.*

The idea of rigid and plastic species goes back to Turesson (1932) and Hultén (1937). Many of the relict species in the *Ericales* are clearly rigid, but the evolutionary status of such species is not well understood: *Orphanidesia gaultherioides* is a typical relict. It has evergreen, 8–12 cm long and 4–5 cm broad leaves with entire, bristly margins. The petioles are covered with red, glandular bristles (Turrill 1948). It is mesophytic and flourishes in well drained, neutral-acid but fertile soils and prefers protected habitats in not too dense montane subtropical-temperate woodlands. Its rigidity (slight genetic variation, limited range expansion) may be a result of ecological specialization. However, the habitat appears suitable for many species and is not unique. It is an old species on Earth and, together with the related and likewise rare *Epigaea*, it is a member of a complex that once was able to find habitats in North America, Asia Minor and East Asia. Are such relicts the dying "arms" of ancestral breeding centres, or would they under other conditions prosper and produce new branches? The shrivelling of "arms" in rigid species may be due to changes in habitat conditions, combined with biotype depletion. The decline may be caused by the disturbance of suitable ecological niches, but internal factors are more likely to be decisive, e.g., decreasing mutation rates or an irreversible stagnation resulting from incompatibility of new mutations within the gene pool. This brings up the question of the history and fate of taxa. Do they have an incipient reinforcement or youth period, a growth period with increased genetic variability and expansion of range, and then a period of stagnation and

preparation for extermination? Reinforcement might include the establishment of a gene pool and stabilization by the production of additive and multiple genes for vital structures and functions.

Relict species ought to exhibit primitive structural features, but few such characters appear to be evidently primitive. However, some characters are rare in or absent from related taxa, thus, e.g., the glandular clusters in *Kalmiopsis* (Fig. 19). This structure may, however, represent an evolutionary stage on the way to the globular glands in *Ledum*. Another structure, the raised guard cells on the adaxial side of the leaf in *Rhodothamnus sessilifolius*, may be viewed in relation to the replacement of the spongy parenchymatous layer by transversely elongated, hardly branched cells (Fig. 3), and to the fact that the leaves in a bud stage are involute and densely crowded.

*Wittsteinia vacciniacea* has characters that appear to be intermediate between those of the *Ericaceae* (*Vacciniaceae*) and the *Epacridaceae*. This intermediate position also concerns its type of venation. Stevens (l.c. Table 2) classifies the venation as reticulate, but the two lower secondary veins are very strong and bend upwards (Fig. 1). The margins of the thick evergreen leaves tend at the very edge to be revolute but have a few broad teeth containing a network of veins terminating in water pores. The two adaxial hypodermal layers contain many chloroplasts but have the character of a water-storing tissue. The anatomical features recall those of the Andean *Disterigma acuminatum* (*Thibaudieae*) described by Niedenzu (l.c. Plate VI 3).

*Calluna vulgaris* is perhaps not a relict, but being monotypic it deserves attention. Nordhagen (1937–38) attaches importance to its septifragal capsules and the increased number of bracteoles. A similar high number (3–6) of bracteoles (“Zwischenblätter”) was, according to this author, found by Diels in *Shortia galacifolia* (*Diapensiaceae*), and in the *Ericaceae* in species of *Pernettya*, *Gaultheria* and *Disterigma weberbaueri*, in which the

two upper ones suppress the adjacent sepals. An increased number of bracteoles is common in the *Epacridaceae*. In *Calluna*, therefore, this characteristic may be comprehended as an outlived feature without adaptive significance resulting from “neutral” genes that have survived from ancestors common to the *Ericaceae*, *Epacridaceae* and *Diapensiaceae*.

#### c. Variation in leaf blade size.

One of the most striking morpho-anatomical features in the *Ericales* is the enormous differences in leaf blade sizes. If one considers *Calluna*, *Cassiope*, or *Loiseleuria* as primitive, and likewise *Clethra*, *Orphanidesia* or *Arbutus* as primitive, we must admit that the *Ericales* contain both extremes, and they did so at an early stage of evolution into the bargain. It is not easy to imagine a regressive evolution in the past which started with larger, flat, pinnately veined, scattered and petioled leaves and ended with small, densely crowded, opposite, not pinnately veined, revolute, almost sessile, needle-like or scaly leaves. Stebbins (1974: 238), however, assumes that the leaves of the earliest Angiosperms, as a result of marked seasonal drought, were small to medium-sized, undivided, with entire or dentate margins. The two extremes might therefore be products of conflicting evolutions: progressive and regressive.

One circumstance in connection with decreasing leaf size should be emphasized however. There is no clear correlation between increasing climatic dryness or harshness and decreasing leaf size. On the other hand, a coincidence of small leaves, shortening of petioles, and dense leaf spacing is evident. This coincidence may manifest itself as a kind of a syndrome which during evolution was probably selected as a whole, being advantageous under certain ecological conditions. The type of habitat where, e.g., *Empetrum* or *Phylodoce* prefer to grow is, at any rate, open, not deeply shaded and not extremely dry. It is true that *Empetrum nigrum* grows abundantly in sand dunes, but always where sand accumulates on



previously established carpets, and it is abundant in raised bogs. *Phyllodoce* sp. grows particularly in moist heath vegetation protected by constant snow during winter. *Harrimanella hypnoides*, with a habit resembling a *Polytrichum*, is even a dwarfish, snow-patch species. Nonetheless, tropical montane plants, too, may have crowded, small leaves; e.g., *Ledothamnus guyanensis* (cp. *Copeland* 1973: 583). Furthermore, the leaves here have deep grooves on the downward leaf sides, hence a structure similar to that found in *Empetrum*, *Phyllodoce*, *Loiseleuria*, *Cassiope*, *Calluna* and *Erica*. Grooves in ericoid leaves usually have various types of trichome together with stomata, which abound here. The coexistence of grooves, stomata and hairs is part of the syndrome relating to small-leaved taxa. The classical, eco-physiological explanation of this structure is that it serves as an anti-transparent arrangement, but it also protects the stomata against plugging with water.

The coincidence of small leaves and dense spacing has been expounded as a kind of syndrome. In one sense this idea may be legitimate as a dense collection of photosynthetic organs may behave physiologically almost as one unit. Here we should recall the branchlets (short shoots) of *Metasequoia glyptostroboides*, which resemble pinnatifid leaves and are shed as if they were leaves (cp. *Böcher* 1964). But a certain physiological communication between leaves may also exist in a shoot of *Calluna*, *Cassiope* or *Empetrum*, not to mention *Hebe* sect. *flagriformis* and *Tamarix*, which were discussed in *Böcher* (1979: 66).

The trend in *Ericales* to form small, crowded leaves has several parallels. We may put the question: what selective advantage is connected with the combination of small blades, short or no petioles and dense spacing? The combination in itself implies that the leaves shelter one another. At high wind velocities, the shoot will bend but the leaves with their short petioles will not change much in their relative positions. The boundary layer of individual leaves will merge and the shoots will tend physically to be unities. The

shoots or shoot assemblages obtain the character of independent bodies. Being relatively dark, as in *Cassiope tetragona*, they heat up in sunlight and give rise to a local early thawing in their immediate surroundings. The small scaly leaves themselves have short distances from the photosynthetic tissues to the veins, making veins of higher order superfluous. As the petioles are short, the distance from individual leaves to the bundles in the stem is also limited. This reduces the physiological difference between a shoot with many small leaves and, e.g., a pinnatifid leaf, but the latter still has the disadvantage of being exposed to rustling by the wind and thereby of increased transpiration losses.

The division of leaf blades into sections or leaflets occurs repeatedly, particularly among ferns and dicotyledons. However, the eco-physiological advantage connected with this type of morphological change is not evident. Perhaps it is a kind of compartmentalization of the plant body. Many small photosynthetic units, each with their separate water supply system, may be more advantageous than few large ones which, if they were to be destroyed, would imply a more deleterious condition for the plant individual as a whole.

The historical events leading from flat petioled leaves to ericoid small ones may have taken place when a group of species from protected woodland habitats attempted to colonize the open, exposed habitats. The rolling of the leaf margins and the formation of stomatal grooves made it possible to maintain in the grooves an atmospheric situation with high water vapour, similar to that maintained in woodlands. At the same time the rolling made a loss of hydathodes in marginal teeth natural, but it became advantageous to maintain glandular trichomes in the grooves, and they were even maintained in the *Empetrum* leaf that is almost closed.

Guard cells in stomatal grooves are usually raised, as they are in many woodland herbs from humid localities. A picture of a sematophyletic

sequence connecting flat blades, with ericoid ones might be constructed by comparing leaves in, e.g., *Rhodothamnus chamaecistus*, *Daboecia cantabrica*, *Phyllodoce glandulifera*, *Ph. coerulea*, and *Ph. empetrifolia* (cp. Fig. 18). Such a hypothetical sequence starts with a leaf which is flat, dorsiventral, glandularly ciliated and has terminal median hydathodes (water pores), proceeds to a leaf type which is revolute when young and still has terminal water pores, then continues to a leaf with ericoid structure but still with long-stalked, protruding glands, and ends up with typical ericoid leaves having sessile glands situated in stomatal grooves and no typical terminal water pores.

Marginal glandular bristles are not common in the *Ericales*. They occur in *Rhodothamnus* and furthermore in the monotypic *Arctous alpinus* (Niedenzu l.c. Plate IV 5), but in *Ledothamnus* and in *Phyllodoce glandulifera* such glandular appendages presumably issue from false margins as the true ones are the sides of dorsal grooves, see p. 33 and Copeland (1943: 583).

#### d. Arrangement of palisade tissue.

Further structural evolution concerns the transition from a dorsiventral to an isolateral architecture. This is not a simple procedure and it is difficult to find a reasonable starting-point. In certain species of the *Epacridaceae* there are centrally placed sclerenchyma in connection with bundles surrounded by palisade cells, radiating to all sides. A similar central position of a bundle with sclerenchymatous escort and radiating chlorenchyma is found in *Erica turrigera* (p. ) and *Harrimanella*. It is possible to deduce dorsiventral as well as isolateral structure from such cylindrical leaves. But this implies that genes giving rise to both types of development are present in the gene pool. Moreover, the many-sided development of palisade cells is a condition for the leaf structure in *Cassiope tetragona*, *C. mertensiana* and *C. selaginoides*, as well as in *Calluna* and *Erica dianthifolia* (Fig. 14), where the palisade cells chiefly

occur along the flanks. In all cases the occurrence of palisade cells may be a response to the angle of incidence of the light and of its intensity. Low light intensity from many sides (e.g., reflection from melting snow) is connected in the case of *Harrimanella hypnoides* with green cells radiating to all sides, but not formed as palisade cells.

#### e. Evolution of types of venation

The pronounced difference in the type of venation between the *Ericaceae* and the *Epacridaceae* has already been commented upon but it needs an ecological evolutionary explanation. As mentioned, the *Epacridaceae* occur mainly in dry, subtropical climates. The leaves are often sheathing, two succeeding leaves in the bud may even form a thimble-like protection of the shoot apex, but the leaves often become elongate, narrow and may approach a grass-like appearance. If we select the *Wittsteinia* leaf as a hypothetical basal type, an evolution in venation towards the palmate and further on to an almost parallel type might be a matter of adaptation to dry conditions and a defence against grazing animals. However, thick leaves with a rounded apex are also palmately veined (Fig. 1B).

Narrow leaves terminate in spines and the strength of the spines depends on the sclerenchymatous escort of the bundles. The lower secondary veins in *Wittsteinia* tend to be acrodromous (Fig. 1A). In many *Epacridaceae* species with broader leaves all veins are acrodromous but only few reach the tips. In narrow leaves we find the parallel venation. *Dracophyllum filifolium*, one of the New Zealand "grass trees", has sheathing needle-leaves many almost parallel veins with sclerenchymatous escort. When the leaves fall ring scars are left. This transition is not unique within the dicotyledons, and it is paralleled in several families where grass-like leaves have evolved as adaptations to arid conditions. Dahlgren (1971) mentions striking convergences in leaves of *Cliffortia* and *Aspalathus* and illustrates narrow-leaved species with almost parallel veins

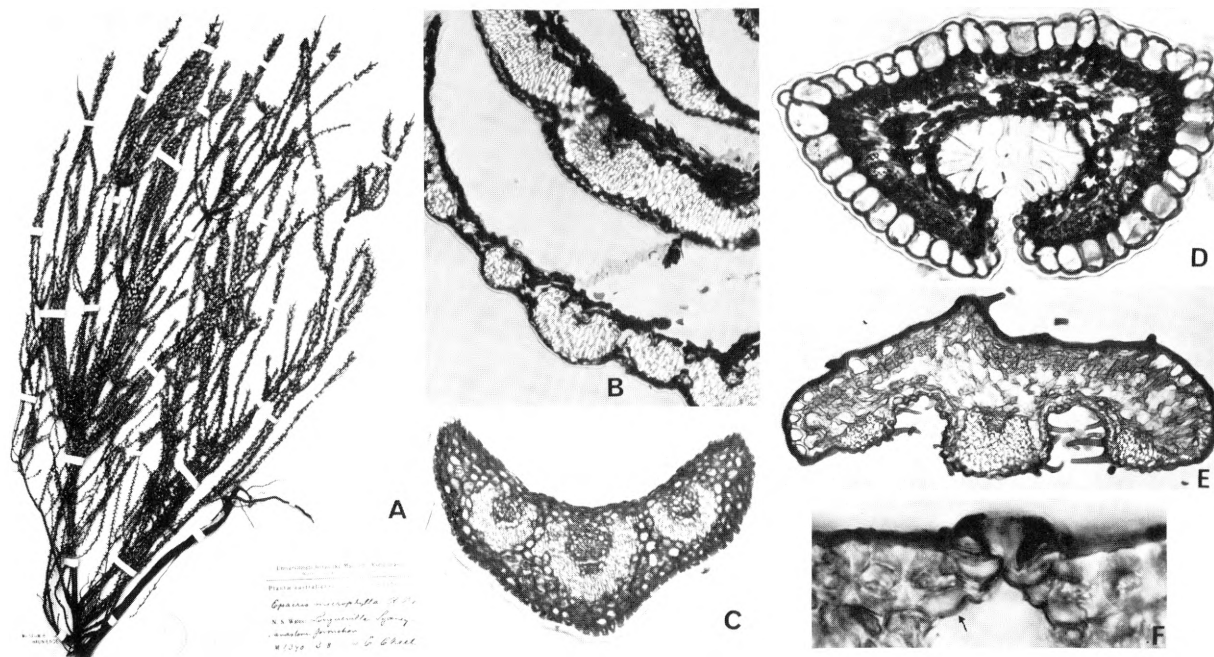


Fig. 22. Leaves in *Epacridaceae* B–F after softening with Aerosol OT, cp. Peterson et al. (1978). A. *Epacris microphylla*. Herbarium specimen showing a general habit resembling that of *Calluna vulgaris*, cp. text. – B. *Stiphelia longifolia* sheathing leaves. Sclerenchyma and xylem showing up. FS x 100. – C. *Brachyloma ericoides* Toluidine Blue x 100. – D. Young leaf of *Cyathodes empetrifolia* Toluidine Blue. Simple abaxial hairs and

papillae showing up. – E. Old leaf of *Cyathodes empetrifolia*. A large bulge along the midvein has divided the abaxial stomatal groove into two, and the three abaxial ridges are all furnished with strong sclerenchymatous escorts of the veins. Sudan IV. x 100. – F. Guard cells in *Sprengelia incana*. Sudan IV stains cuticular coating of upper substomatal chamber (arrow) x 630.

in both genera (*Cliffortia graminea*, *Aspalathus monosperma*, *lancifolia* and *alpestris* (see Dahlgren 1968: Figs. 8 and 18).

*f. Complex and single characters.*

The structure and the function of leaves constitute an entirety. If we select individual characters and discuss their background, we are unfortunately inclined to disregard the function because of our lack of real understanding. Moreover, individual characters are usually difficult to treat as isolated entities, because they constitute an intricate interaction of very different genes. Sometimes it may be possible to estimate the degree of genetical complexity forming the background of a character. A high degree of complexity assigns a character a greater importance as a

tool in phylogeny or sematophylysis. The peltate glandular hairs in *Rhododendron* are very complicated with an intricate structure and several functions. Therefore they constitute an “important” character. Another complicated and particularly important grouping of characters may be the leaf structure and position in *Cassiope tetragona* and *Calluna vulgaris*. The leaves are here decussate and “invo-revolute”, involute adaxially and revolute abaxially, and have basal ears. Such characters which are almost exceptional can hardly be put on the same footing as many others and used e.g. in a computer. The same may be said about the glands in the two species. They consist of an unbranched cell row and are restricted to the area near the shoot apex, which as a result of the activity of the glands is kept moist or greased

during the growing period. *Hagerup* (1953) and *Watson* (1964) find that the two genera are closely related, while *Stevens* (1970) keeps them apart. The problem may be formulated as a question. Is it possible to imagine such a versatile accordance in leaf structure, accompanied by several other structural accordances, to be the result of convergent evolutions or are we forced to acknowledge that a profound genetical relationship exists? If convergence is accepted it must in this case, at any rate, be modified to an instance of inherent convergence (see p. 37).

Among the important complex of not strictly morpho-anatomical characters are the growth forms and the rhythmic involved in shoot structure and the timing of the development of the flower. Conspicuous difference in the phenology of shoots were ascertained in the *Andromedeae* by *Lems* (1962), who distinguishes between three types, or to use a modern expression "strategies". *Oxydendron arboreum* is able to complete one "morphogenetic" cycle within one growing season. *Pieris floribunda*, on the other hand, takes one and a half growing seasons to complete its cycle from bud to fruit maturation, and in *Lyonia mariana* the cycle takes two growing seasons. The number of genes involved in the establishment of such cycles is probably great. Differences in life forms or growth forms ought to be studied much more intensively, not least by comparative cultivations and crossing experiments.

A zonation in shoot structure was mentioned by *Nordhagen* (l.c.: 8–9) in *Calluna vulgaris*. In terminal long-shoots there are three zones, viz., a basal, generally vegetative zone with numerous leaf pairs, a middle zone with few foliage leaves but bracteoles and flowering short shoots, and a distal zone with vegetative shoots only. The middle zone becomes void of leaves during the following winter season. This type of zonation presupposes an intricate, balanced system of phytohormones and is not paralleled in many members of the *Ericales*. It is approached by *Cassiope tetragona* in which the year-shoots have only foliage leaves at

their bases, and these are smaller than the following ones *Warming* (1908 fig. 16). *Hagerup* (1946), moreover, mentions periods in the development of the year-shoots in *Empetrum nigrum* and *Erica cinerea*. *Epacris microphylla* (Fig. 22A) exhibits a remarkable similarity to *Calluna*. It has long shoots with many small, recurved, cordate leaves which, in a middle zone, support dwarf shoots with densely spaced bracteoles and small terminal flowers. The distal zone is vegetative. Again, the similarity invites consideration of the nature of this case of convergence.

#### g. *Convergence or genetical relationship.*

After the introduction of the term "inherent convergence" is a clear demarcation between convergence and genetical relationship impossible to maintain. The problem is to limit the contents of the gene pool which became responsible for the *Ericales* and their precursors in the past. If one agrees that the *Ericales* contain the *Ericaceae*, *Epacridaceae*, *Empetraceae* and others, it is not illogical to imagine that an original gene pool included genes making additional bracteoles and ericoid leaf structure possible, provided that no restraining genes interfered. But, as we go further backwards in time, we find genes established a long time ago that are responsible for, e.g., scalariform vessels, the formation of iridoids, or essential oils. However, such characteristics occur in several orders and the genes involved are common to many of the dicotyledons. It is doubtful or sometimes absurd to utilize accordances in the occurrences of such features to pronounce judgment on relationship or convergence. On the other hand, it is generally believed that there is a genetical background for almost all structural-functional characters, and this implies that even life-forms (e.g., dwarf shrubs, perennials, annual herbs, etc.) may not be the results of convergent evolution alone (cp. *Böcher* 1978), but that the incalculable gene pool of the dicotyledons contains potentialities for the emergence of woody plants as well as ephemerals or water plants.

*h. Xeromorphism in relation to the ericoid leaf structure.*

The much discussed and disputable ericoid leaf structure is not merely a xeromorphic feature. It has developed in a typical xerophyte like *Acantholippia seriphioides* from the Patagonian steppe vegetation, and also in a wet heath or bog plant such as *Erica tetralix* as well as in species from arctic, mesic, snow-protected heaths (*Cassiope*, *Phyllodoce*). It is true that in all these cases the leaf margin recurvation implies the advantage connected with the formation of a humid boundary layer immediately outside the stomatal pores, but the curvature gives the palisades an advantageous position: The distance from the middle vein is short and the palisades with the chloroplasts are not exposed to strong radiation for long periods. The rays of the sun have to pass the epidermis and will, to a great extent, be reflected or attenuated by passing the cuticles and the mucilaginous interior walls. Moreover, a mutual screening of the cells will take place particularly in those occurring along the flanks of the leaves. Another important screening effect is obtained by the dark cell contents, e.g., tanniferous vacuoles in adaxial tiers (see *Erica terminalis* fig. 13). The curvature and the more or less radial orientation of the palisades imply additional advantages which may have contributed to a selection of the revolute structure during evolution. Light reflection and a suitable screening of the photosynthetic cells probably prolong the active period of the chloroplasts. Their fate depends on their position in the leaf. Already *Steemann Nielsen* (1940) held the opinion that the xeromorphic structure in heath and bog plants was primarily an adaptation giving the chloroplasts resistance against too strong radiation.

Anyhow, it is very difficult to estimate the physiological advantages connected with the ericoid leaf structure, but the repeated occurrence in several different taxa favours the point of view that this structure has been selected now and then and it cannot, therefore, be classified as just a case

of the conservation of an organization. An explanation of this kind was proposed in the case of the adaxial groove common to leaflets in all species of *Anarthrophyllum*, independent of the different habitat requirements of the species (*Böcher* 1979).

Bearing in mind experience concerning xeromorphic leaf types among South American xerophytes, it appears doubtful to call any ericaceous leaf typical by xeromorphic. There are clearly some xeromorphic features in, e.g., the epidermal structure of *Arctostaphylos uva ursi* (Fig. 7), but there are no examples of leaves which without hesitation can be placed among any of the xeromorphic leaf types appearing in the South American material. On the other hand, such a designation is easy in the case of the leaves of the *Epacridaceae*. In most cases they are of the sclerophyllous-cutinized type (Type A in *Böcher* 1979). Even epacridaceous species with ericoid leaf architecture possess strong sclerenchymatous abaxial areas, thus *Cyathodes empetrifolia* (Fig. 22). *Diapensia lapponica* with its thick pectinaceous and cellulosic adaxial epidermal walls approaches type C, the non-sclerophyllous xeromorph type, but it is more likely of a separate type not described in the previous paper.

Concluding remarks

Comparative studies of leaf structure in the *Ericales* reveal considerable contradictions that seem inconsistent with the agreement arising from comparisons of floral characters. In this situation the possibilities of misinterpreting the floral characters appears. Floral similarities may be overestimated and thus disguise real coherences. Resemblances of this kind may also be the result of convergent evolutions, which may be more difficult to reveal and understand because the adaptive forces are so intimately connected with the incalculable pollination biology. Several ericaceous lines are unquestionably inherent, but the origin and connections of, e.g., the *Calluneae*, the *Cassiopeae* and the *Ericineae* perhaps need renewed evaluation.

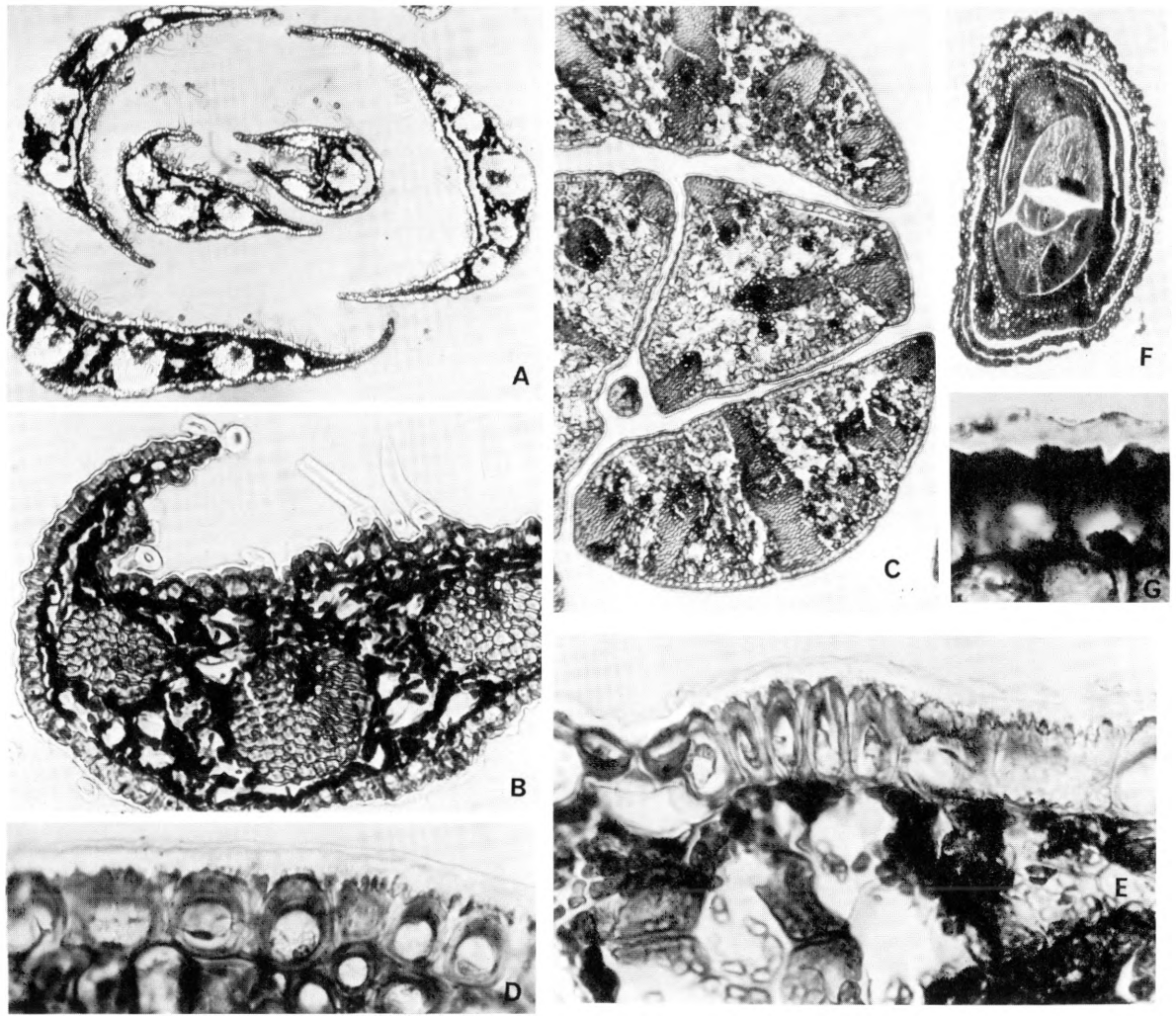


Fig. 23 A–F. Leaves of *Dracophyllum* (*Epacridaceae*). Material from New Zealand forwarded by Dr. M. Philipp. A–B and D–E *Dracophyllum uniflorum*. A. Pairs of successive alternate, but semi-opposite leaves from the same common sheath system. Epidermis and sclerenchymatous vein escorts showing up in semi-polarized light FS x 25. – B. Single leaf showing unicellular, stiff, at the base forking hairs. FS x 100. – D–E. Adaxial epidermis having thick cell walls and a cuticular layer with irregular abaxially tapering surface extensions. Stomatal open-

ning in E on the left. FS x 250. – C. and F. *Dracophyllum prorum*. C. Cross section of leaf aggregate belonging to the same common sheath system (cp. F). The sclerenchyma at the larger veins reaches the epidermis on both sides. – F. A sheath system with two semi-opposite pairs of leaves inside four sheathing leaf bases. FS x 25. – G. *Diapensia lapponica*. Adaxial epidermis with abaxially tapering extensions of the cuticular layer, dark pectinaceous-cellulosic layer and single nucleus, parts of three hypodermal cells. FS x 250.

Among the ericalean families there are conspicuous accordances between the *Diapensiaceae* and the *Epacridaceae*. A morphologically regressive evolution in *Dracophyllum* appears from the illustrations in *More & Irwin* (1978: 114). The reductional series ends with *D. muscoides* from mountain tops in New Zealand. It is said to be one

of the hardest and toughest cushion plants with tightly packed leaves on rigid twigs. It has solitary, flat-faced, white flowers. Although being short-pedicelled the flowers and the structure of the entire plant remind very much on what we find in the cushion plant *Diapensia lapponica*.

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