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Author(s): Kornelius Lems and Christina M. Holzapfel

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EVOLUTION IN THE CANARY ISLANDS. I. PHYLOGENETIC RELATIONS IN THE GENUS *ECHIUM* (BORAGINACEAE) AS SHOWN BY TRICHOME DEVELOPMENT

KORNELIUS LEMS¹ AND CHRISTINA M. HOLZAPFEL

Department of Biological Sciences, Goucher College, Baltimore, Maryland 21204,
and Department of Zoölogy, University of Michigan, Ann Arbor

ABSTRACT

Twenty-three species of *Echium* from the Canary Islands and Madeira were studied in order to relate growth form to evolutionary status and ecology. As a first step, phylogenetic relationships were approached from the point of view of similarity of trichomes on the leaf epidermis. Trichomes of three basic categories, subdivided into many types, occur in various combinations, as many as six different types to a single adult leaf. The trichome complement of each species was compared with all others, degrees of similarity were calculated, and a chart of relationships was drawn up (fig. 17). Ontogenetic studies of young leaves and of juvenile foliage show that the most highly differentiated trichome complements are found in a group of shrubs with appressed silvery pubescence and a group of shrubs with coarse, glabrescent leaves with pustular spines; a third group containing annuals, perennial herbs, hapaxanth, and shrubs possesses a more generalized and undifferentiated trichome complement. These results are viewed in the light of the neoteny hypothesis of the evolution of annual plants, and of its opposite, the theory of insular woodiness.

Introduction

The Canary Islands have long been known as an archipelago where evolution has produced a flora peculiar not only for its insular endemism but especially for the unusual growth forms exhibited by the plants. Compared with a continental area at the same general latitude, islands such as Tenerife harbor a wider range of forms, some of them clearly adaptive (the cactoid *Euphorbia canariensis* in the coastal dry scrub), others perhaps archaic forms surviving in the equable climate of these island refugia (the dragon tree, *Dracaena draco*; candelabrum shrubs with terminal rosettes). In many of these endemic plant groups the insular isolation and altitudinal climatic zones have provided an opportunity for speciation, often expressed in differences in habit or growth form. In an earlier paper it was shown how the evolution of forms in the genus *Aeonium* (Crassulaceae) could have been the result of

ecological selection by different climates and substrates, resulting in 32 species with different growth forms (LEMS, 1960).

The genus *Echium* is another conspicuous element in the Canarian flora, with 22 species, all but two of them endemic. To European and North American botanists, familiar with the Viper's Bugloss, *Echium vulgare*, it may come as a shock to learn that the majority of the Canarian species are shrubs (fig. 1) and that some of them, including the famous Red "Taginaste" of Pico de Teide (*Echium bourgeauanum*; fig. 2) are woody hapaxanth, that is, they exist for many years as simple vegetative rosettes on short woody trunks, then flower with a single large inflorescence and die. To explain these strange forms there are two hypotheses: the first one proposes that these are recent insular adaptations to the mild oceanic climate, exhibiting the "island syndrome" (CARLQUIST, 1965) of slowly elongating woody stems, rosettes of leaves, loss of dispersal facility (CARLQUIST, 1966), and other presumed adaptive

¹ Deceased March 17, 1968.

phenomena; the second hypothesis claims that these forms are ancestral, surviving wherever competition from more aggressive species has not made them obsolete, for example, on islands and tropical mountains; if the latter view is taken, herbaceous perennials, biennials, and annuals would represent the aggressive, recent descendants of forms resembling these insular relics. This theory was propounded by MEUSEL (1952) with particular reference to the Canary Islands.

The present paper deals with the phylogenetic relations within the Canarian group *Echium*. As was the case in *Aeonium*, floral morphology is helpful only in the separation of a few groups, and one must turn to anatomical criteria to determine which species are most closely related. Trichomes have been used successfully to determine relationships in several genera and families of flowering plants (HEINTZELMANN and HOWARD, 1948; COWAN, 1950; GOODSPEED, 1954; RAMAYYA, 1962). It has long been known that trichomes are sufficiently constant and characteristic to make them useful in the recognition of interspecific hybrids (CANNON, 1909; ROLLINS, 1944; HEISER, 1949). The trichomes of the Boraginaceae have been studied by REVEDIN (1902) and, more extensively, by BIDER (1935). The purpose of the present paper is to examine trichomes in *Echium* from a phylogenetic point of view. Later papers will deal with the evolution of growth forms and cytological evidence.

Material and methods

The species available for this investigation were collected by the authors on all the islands listed in table 1. The three species of *Echium* found on the Cape Verde Islands (*E. stenosphon* Webb,² *E. hypertropicum* de Coincy, and *E. vulcanorum* Chev.) are not included in this paper, but their affinities could be established by study of herbarium material in the Musée d'Histoire Naturelle, Paris. *Echium perezii* Sprague, known only from the type, was studied at the Herbarium of the Royal Botanic Garden, Kew; the material was greenhouse grown and not strictly comparable to the collections made in the field.

In order to study growth forms under controlled conditions, most of the species were raised from seed in a greenhouse. The trichomes of cotyledons and first-formed leaves, and those of later leaves in young condition, were used to elucidate the problem of ontogenetic relationships of different trichome types.

Leaves collected in the field were dried. Free-hand sections were made from these after soaking; com-

parison with fresh material has shown that the trichomes of dried material retain their distinctive characteristics.

Observations

TRICHOME TYPES IN ECHIUM

There are several basic classes of trichomes on the epidermis of *Echium* leaves: glandular trichomes, trichomes whose base is surrounded by rings of stone cells (in this study referred to as "pustular" trichomes), and simple hairs. These groups can be further divided into types on the basis of length, sculpturing of the cell wall, number of cells involved, and curvature of the cells. Each type will be discussed briefly.

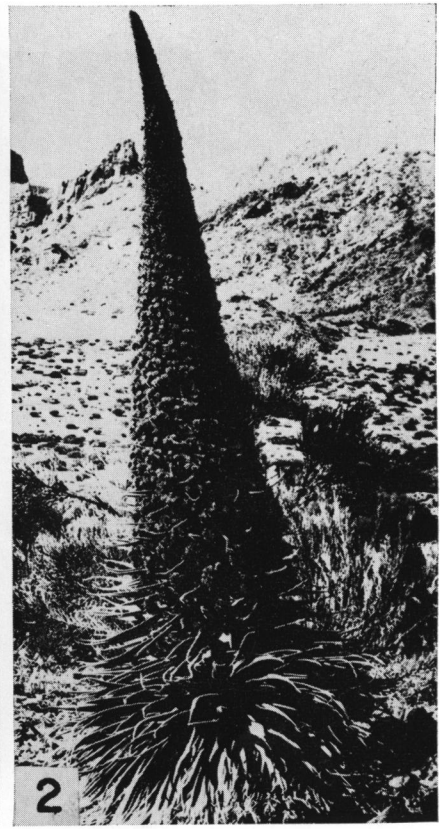
GLANDULAR TRICHOMES.—The least obvious of the trichome types, the glandular trichomes, are located on the lower epidermis of the midrib, occasionally on the upper side of the midrib (*E. leucophaeum*) or the entire lower leaf surface (*E. pininana*, *E. bourgeauanum*, *E. webbii*, etc.). They consist of a single row of cells, differentiated into a rounded or elongate head cell and one or more stalk cells. The shape of the head cell is highly characteristic of the species, most of them having spherical heads (fig. 3), but some are obovoid (*E. simplex*, fig. 4) or ovoid (*E. bonnetii*, fig. 5).

The number of stalk cells in the glands is also characteristic. In most of the shrubby species the number is constant (table 2) but the number tends to vary in the monocarpic and annual plants. In Madeiran material the highest number of stalk cells is two; in species from the Canaries there may be three (*E. webbii*, *E. pininana*, *E. bonnetii*), while material of *E. vulcanorum* and *E. stenosphon* from the Cape Verde Islands has as many as four stalk cells. No glands could be found on the glabrous leaves of *E. gentianoides*.

Sections of young leaves show that glands differentiate from protrusions from the peripheral portion of an epidermal cell. Cell divisions result first in a head cell, then a stalk cell; the latter may or may not divide further. The head cell increases in volume, and its contents differentiate, but no further cell divisions occur in the head. The function of these glands is doubtful, so that the term "gland" is strictly a morphological one based on similarity with other known glandular structures.

SIMPLE TRICHOMES.—Young plants of all *Echium* species possess straight unicellular hairs whose swollen bases are part of the epidermal layer (fig. 11). The surrounding cells are in no way differentiated from the general epidermis. From this simple type, present on cotyledons and juvenile leaves, two different developments may occur both in ontogeny and in the transition from juvenile (first-formed)

² PITARD's report of *E. stenosphon* in the Canaries is based on incorrectly identified specimens of an annual species (PITARD and PROUST, 1908).



FIGS. 1-2.—Growth forms of endemic *Echium*. Fig. 1, *Echium candicans* at Curral, Madeira; fig. 2, *E. bourgeauanum* at Ucanca, Tenerife.

TABLE 1
GEOGRAPHIC DISTRIBUTION OF ECHIUM IN MADEIRA AND THE CANARY ISLANDS^a

Species	Madeira	Porto Santo	Lanzarote	Fuerte-ventura	Gran Canaria	Tenerife	Gomera	La Palma	Hierro	Growth form
<i>Echium giganteum</i> L.f.						+				Shrub
<i>E. aculeatum</i> Poir.						+	+		+	Shrub
<i>E. leucophaeum</i> Webb.						+	+	+	+	Shrub
<i>E. simplex</i> DC.						+				Hapaxanth
<i>E. hierrense</i> Webb.									+	Shrub
<i>E. webbii</i> Coincy								+		Shrub
<i>E. virescens</i> DC.						+				Shrub
<i>E. nervosum</i> Ait. ^b	+	+								Shrub
<i>E. callithyrsum</i> Webb.					+					Shrub
<i>E. bourgeauanum</i> Webb ^c						+		+		Hapaxanth
<i>E. perezii</i> Sprague								+		Hapaxanth
<i>E. pininana</i> W. & B.								+		Hapaxanth
<i>E. auberianum</i> W. & B.						+				Perennial
<i>E. plantagineum</i> L. ^d	+	+	+	+	+	+	+	+	+	Biennial
<i>E. bonnetii</i> Coincy				+	+	+				Annual
<i>E. triste</i> Svent.					+	+	+			Annual
<i>E. candicans</i> L.f. ^e	+	+				+				Shrub
<i>E. handiense</i> Svent.				+						Shrub
<i>E. strictum</i> L.f. ^f					+	+	+	+	+	Shrub
<i>E. onosmaefolium</i> W. & B.					+					Shrub
<i>E. decaisnei</i> W. & B.					+					Shrub
<i>E. famarae</i> Lems ^g			+	+						Shrub
<i>E. gentianoides</i> Webb.								+		Shrub
Species per island.....	3	3	2	4	7	12	5	8	5

^a Voucher specimens to be deposited in the U.S. National Herbarium, Washington, D.C.

^b Syn.: *E. fastuosum* Dryand., a popular cultivated shrub.

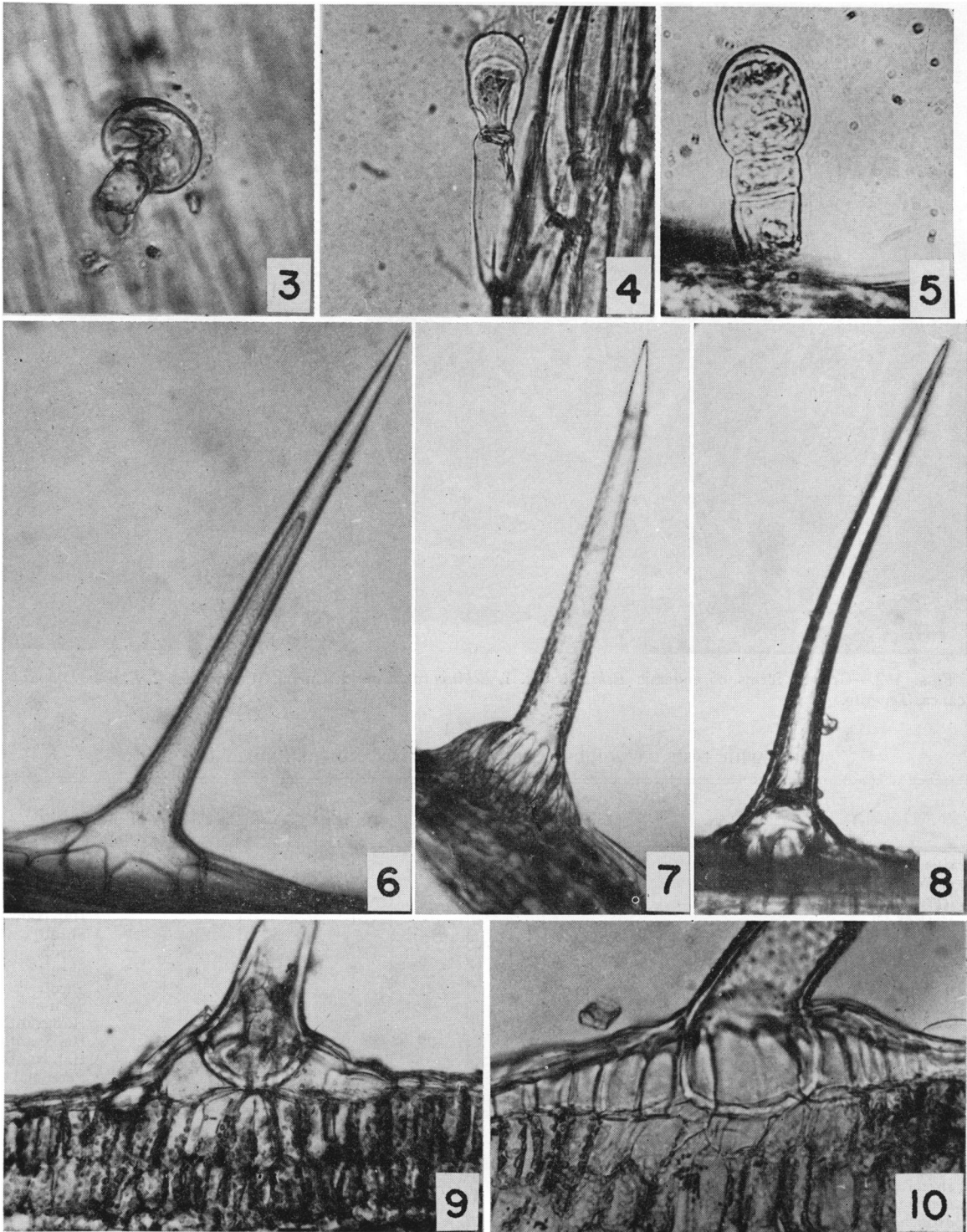
^c Syn.: *E. wildpretii* Hook.

^d Sometimes also annual; found also in North Africa and southern Europe; material from Lanzarote and Fuerteventura subject to revision.

^e Material from Tenerife rather different from typical Madeiran plants.

^f Here including *E. lineolatum* Jacq.

^g A relative of *E. decaisnei* to be described elsewhere.



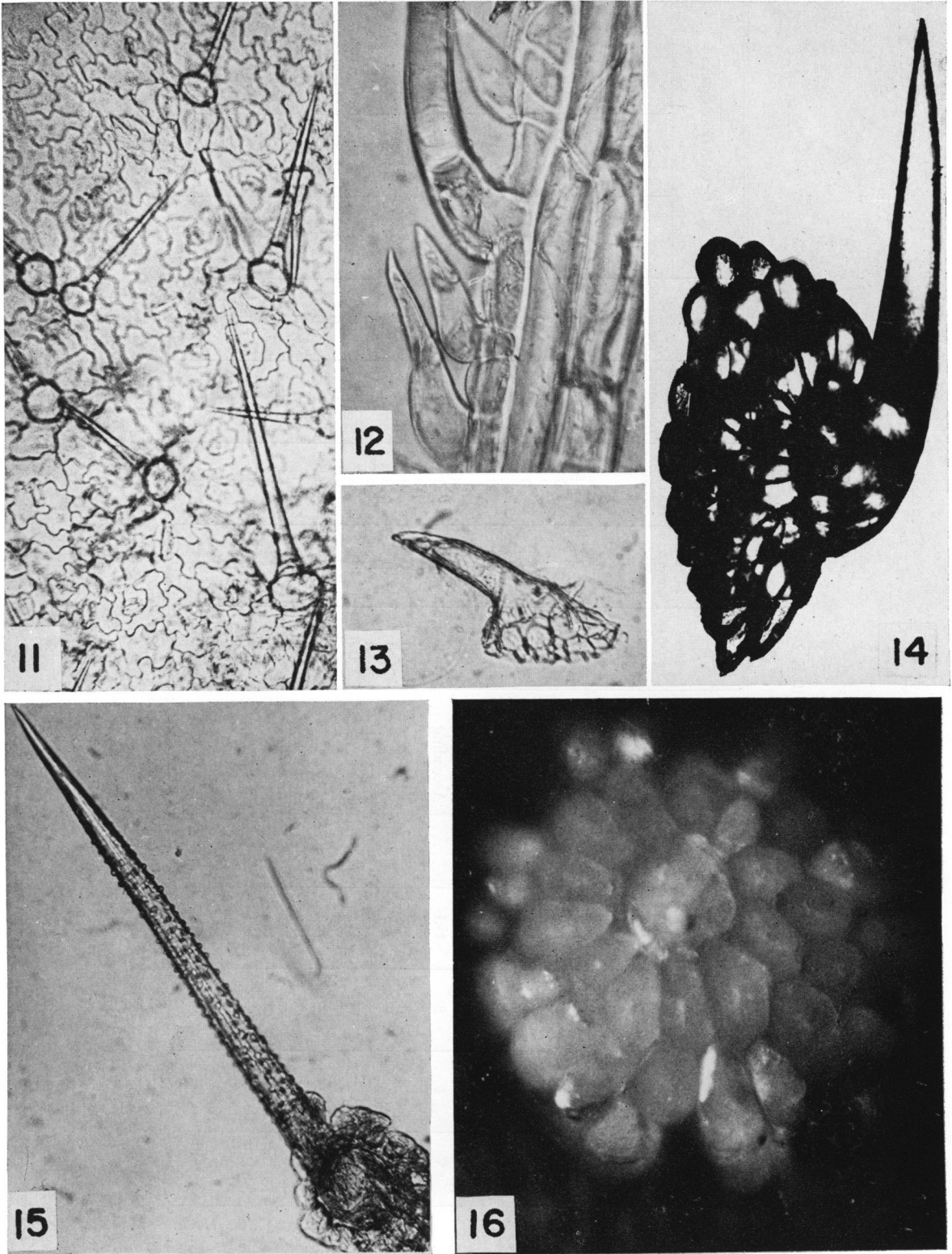
FIGS. 3-10.—Trichomes of *Echium*. Fig. 3, spherical gland of *E. perezii*, $\times 430$; fig. 4, obovoid gland of *E. simplex*, $\times 430$; fig. 5, ovoid gland with two stalk cells of *E. bonnetii*, $\times 860$; fig. 6, early pustule formation, juvenile leaf of *E. onosmaefolium*, $\times 200$; fig. 7, pustule formation, juvenile leaf of *E. aculeatum*, $\times 70$; fig. 8, cross-wall formation in pustular hair of *E. strictum*, $\times 200$; fig. 9, free-hand cross-section showing early pustule formation in juvenile leaf of *E. plantagineum*, $\times 200$; fig. 10, free-hand cross-section of *E. aculeatum* showing pustule formation involving upper palisade layer, $\times 200$.

TABLE 2
TRICHOME CHARACTERISTICS OF 23 SPECIES OF ECHIUM

SPECIES	TOTAL TRICHOME COVERAGE (RANGE)		LONG PUSTULAR TRICHOMES (OVER 400 μ)				SPINY PUSTULES COVERAGE ^a	2-CELLED TRICHOMES COVERAGE ^a	CONICAL TRICHOMES COVERAGE ^a	SHORT PUSTULAR TRICHOMES COVERAGE ^a	SHORT HOOKED TRICHOMES COVERAGE ^a	GLANDULAR TRICHOMES		
	Upper epid. (in %)	Ratio lower to upper	Coverage ^a	No. of rows basal cells	Basal cells elongate	Trichome orientation						Coverage ^a	Cells in stalk	Head shape
<i>Echium giganteum</i>	40-100	1-2.5	2-3	1	Appressed	1	+	+	4	1	Spherical		
<i>E. aculeatum</i>	75-100	1	4-5	1-2	+	Appressed	0	0	+	3	2	Spherical		
<i>E. leucophaeum</i>	95-100	1	3-4	1	Appressed	0-1	0	0	4	2	Spherical		
<i>E. simplex</i>	90-95	1	5	1	+	Appressed	0	1	0	2	1-2	Obovoid		
<i>E. hierrense</i>	95-100	1	4-5	1	Appressed	0	0	+	3	2	Spherical		
<i>E. webbii</i>	95-100	1	4-5	1-2	Appressed	0	0	0	4	2	Spherical		
<i>E. virescens</i>	50-85	1.3	3-4	1-3	Appressed	0	0	0	4	2	Spherical		
<i>E. nervosum</i>	75-85	0.5-1.2	2-3	1-3	Appressed	0-2	0	+	4	1	Sph.-stipitate		
<i>E. callihyrsum</i>	85	1	5	1-3	Ascending	0	0	0	0	1-2	Sph.-stipitate		
<i>E. bourgeanum</i>	80-85	1	5	1-2	Erect	0	0	0	0	2	Spherical		
<i>E. perezi</i>	30	1.3	3	1	+	Erect	0	0	+	0	2	Sph. and oblong		
<i>E. pininana</i>	15-20	0.7	2	2-4	+	Erect	0	0	0	0	2	Spherical		
<i>E. aubertianum</i>	40-70	1	3-4	1	Erect	0	0	0	0	1-3	Spherical		
<i>E. plantagineum</i>	15-45	0.5-1	2-3	1-3	+	Erect	0-1	0	+	1	1	Oblong		
<i>E. bonnetii</i>	20-35	1	2-3	1-3	+	Erect	0-1	0	0	2	1-3	Ovoid		
<i>E. trisle</i>	15	1.3	1	1-3	+	Erect	2	0	0	0	1	Spherical		
<i>E. candicans</i>	20-55	1	3-4	1-3	Erect	0	0	+	1	2	Spherical		
<i>E. handiense</i>	35	1	3	1-3	Ascending	0	0	+	0	1	Spherical		
<i>E. strictum</i>	15-60	0.7	2-3	1-3	Erect	0	0	0	0	1	Spherical		
<i>E. onosmae</i> (oblong)	50-90	0.5-1	2	1-3	Erect-ascend.	2-4	0	0	0	1	Spherical		
<i>E. decaisnei</i>	20-75	0.5-0.8	0	2-4	0	0	0	1	Spherical		
<i>E. famarae</i> ^b	15	0	0	2	0	+	0	0	Spherical		
<i>E. gentianoides</i> ^b	20-30	0	0	2	0	0	0	0		

^a Coverage estimate scale explained in the text.

^b Spiny pustules sometimes reduced to knobs or flat disks.



FIGS. 11-16.—Trichomes of *Echium*. Fig. 11, simple trichomes on cotyledon of *E. giganteum*, $\times 150$; fig. 12, short curved trichomes on free-hand section of *E. aculeatum* leaf, $\times 430$; fig. 13, short conical trichome of *E. nervosum* (*E. fastuosum*, cultivated), $\times 200$; fig. 14, solid spine isolated from leaf of *E. decaisnei*, $\times 200$; fig. 15, sculpturing on pustular hair of *E. virescens*, $\times 160$; fig. 16, surface view of spineless pustule of *E. gentianoides*, $\times 200$.

to adult foliage. In seven of the shrubby taxa and one monocarpic species (*E. simplex*) the adult leaves have a silky appearance which is caused by long and short appressed trichomes; the short ones are unicellular and typically curved (fig. 12). The longer trichomes tend to develop pustular bases, so that on adult, mature leaves one never encounters any trichomes longer than 400 μ without one or more rows of differentiated cells around the base. The only exception to this is the material of *E. perezii*, but it was cultivated and may have retained its juvenile character.

PUSTULAR TRICHOMES.—The term “pustular trichomes” is proposed for those trichomes whose base is surrounded by one to several concentric rows of raised subsidiary cells with calcified walls or contents. It is synonymous with BIDER’s “Hügelborsten” (1935) and METCALFE and CHALK’S “nodular bristles” (1950). They are so characteristic of the family that the term “boraginaceous hair” might well be reserved for this class of trichomes.

On the cotyledons and first-formed foliage leaves, intermediate stages may be encountered between pustular and non-pustular hairs. The cells surrounding the swollen trichome base first become oriented in a circle with straight, thick radial walls. Next, the portions of the epidermal cells adjacent to their base extend upward (figs. 6, 7, 9), forming a definite raised pustule. The cells of the pustule as well as the hair itself are heavily impregnated with calcium carbonate. Treatment with HCl results in the production of CO₂ bubbles; following such treatment the trichomes consist of disorganized fibers of cellulose, as shown by tests with I-KI and H₂SO₄.

The tendency for epidermal cells at the base of the hairs to become organized into pustules extends sometimes to several concentric rows, the number of which is variable within well-defined limits for different species (table 2). In very large pustules the underlying parenchyma also becomes involved. Figure 10 suggests that the first step in this process is the dedifferentiation of the palisade cells. Large mature pustules of *E. decaisnei* show calcification of cells well into the spongy parenchyma. This suggests that trichomes should not be defined as purely epidermal, since many trichome types show the secondary involvement of underlying tissues (cf. FOSTER, 1949; CARLQUIST, 1958).

Several diverging tendencies occur within the group of pustular trichomes, both in ontogeny and in the sequence from juvenile to adult foliage. On long hairs the wall of the shaft develops a sculptured surface, giving the hair a rough appearance (fig. 15). The species differ with respect to the stage at which this occurs: in *E. aculeatum*, *E. virescens*, *E. decaisnei*, and many others, even the cotyledons have rough pustular trichomes, while in *E. plantagineum*, *E.*

strictum, and others, cotyledon trichomes are smooth-walled. *Echium perezii* is the only species in which smooth trichomes were found on “adult” leaves, again casting doubt on the maturity of these cultivated specimens.

Among the short pustular trichomes (less than 400 μ long), several types were found: some trichomes take on a broad cone shape (fig. 13). In some hairs a cross-wall is formed near the base of the shaft; the distal portion is not a functional cell and contains no nucleus; the cross-wall is initiated as a ring which constricts and finally cuts off the shaft, giving the trichome a two-celled appearance (fig. 8).

A final trend in pustular trichomes is the development of spines, resembling inverted thumbtacks with pustular bases of up to five concentric rows of lignified cells and thick, solid points (fig. 14). Such trichomes may be as large as 1 or 2 mm, making the foliage extremely harsh to the touch. The role of these trichomes in the survival of such species as *E. onosmaefolium*, *E. decaisnei*, and *E. aculeatum* (named for its spiny leaves) in the goat-ridden landscape of the Canaries should not be underestimated.

A most interesting development in the line of these pustular spines is the reduction of the trichome to a blunt knob in *E. famarae*, a cliff plant closely related to *E. decaisnei*; and the complete absence of any points at all on some pustules on the leaves of *E. gentianoides*, leaving nothing but round flat disks (fig. 16). It is perhaps significant that both of these species are restricted to cliffs so steep and dangerous that few goats will venture out on them.

A further point of evolutionary interest is that most shrubby species, once they have been browsed by goats, will develop shoots with very spiny leaves, even if the mature foliage did not exhibit spines. This leaf type will persist for a year or more, and mature foliage will reappear if the bush is left undisturbed.

COMPARISON OF THE SPECIES

Each species of *Echium* has its own characteristic trichome complement. There are at least 14 criteria (table 2) which can be applied in comparing the species with one another, including not only the types of trichomes present but their relative abundance, the total coverage of the leaf surface, the size of the pustules, and the orientation of the trichomes. Abundance was estimated by means of a scale of coverage values as follows:

- + = rare, low coverage;
- 1 = common but covering less than 5% of the leaf surface;
- 2 = coverage 5–25%;
- 3 = coverage 25–50%;
- 4 = coverage 50–75%;
- 5 = coverage 75–100%.

VARIABILITY WITHIN THE SPECIES.—Before species can be compared with one another, it must first be established how constant the trichome complement is for members of the same species. It has already been shown that juvenile foliage differs radically from mature leaves and that even on the same adult leaf the number of stalk cells in the glands and the number of rows of pustular cells show some variation. Table 4 shows the extent of variation in the percentage of leaf surfaces covered by all trichomes, by long trichomes (over 400 μ), and by spines. It is clear that there is some intraspecific variation which may

be correlated with insular and climatic-altitudinal zonation. Such variation is limited within the species and is expressed mostly in the degree of coverage, rather than the presence or absence of the trichome types.

SIMILARITY INDEX.—Since there are 14 trichome criteria (table 2), any two species may be rated as to similarity on a scale from 0 to 14. Perfect agreement on every point, including presence or absence, abundance, and range of variation, would result in a score of 14. In compiling scores (table 3) a full point was awarded for each similarity (e.g., the same range of variation, the same abundance estimate, etc.). One-half point was awarded if the ranges showed partial overlap (e.g., coverage 40–80% vs. 60–80%, or pustular cells 1–3 rows vs. 2–4 rows) and also if the abundance estimates for a given trichome type were only one number apart on the coverage scale. However, for trichome types absent in one species and present in the other, and for complete lack of overlap in the range of variation, no points were awarded.

The results of this operation are shown in table 3. Since the most nearly similar species are listed close together, the highest similarity values (bold print) appear near the diagonal, the most dissimilar (*italics*) near the margins of the table. The highest value, 10.5 points, or 75%, was obtained for a few closely related species (*Echium webbii* and *E. hierrense*; *E. hierrense* and *E. leucophaeum*). The only species totally different in every respect are *E. gentianoides* and *E. giganteum*. Not every species has the same cumulative similarity to the rest of the genus, as is shown in the first column of table 3. *Echium gentianoides* has the lowest similarity, which means simply that it has the least in common with its congeners, while *E. auberianum* is more than 50% similar to the other 22 members of the group.

On the basis of these data it is possible to arrange the species into a scheme which reflects relationships (fig. 17).

Discussion

ECOLOGICAL IMPLICATIONS.—The species of *Echium* are found in all the major life zones of the Canary Islands and Madeira. Table 4 distinguishes three broad zones. The subtropical zone is characterized by *Euphorbia* (*E. regis-jubae* in the Canaries, *E. piscatoria* in Madeira) growing in a scrub formation with succulent-stemmed plants ("crassicauletum"), extending to elevations of 300 m on the north coast, 800 m on the south coast of the Canaries, and in Madeira only near sea level. Twelve of the species of *Echium* are found in this zone. The temperate, forested region extends from 300 to about 2,000 m (800 to 2,000 m on south slopes) in the Canaries and practically throughout the island of Madeira. Twelve

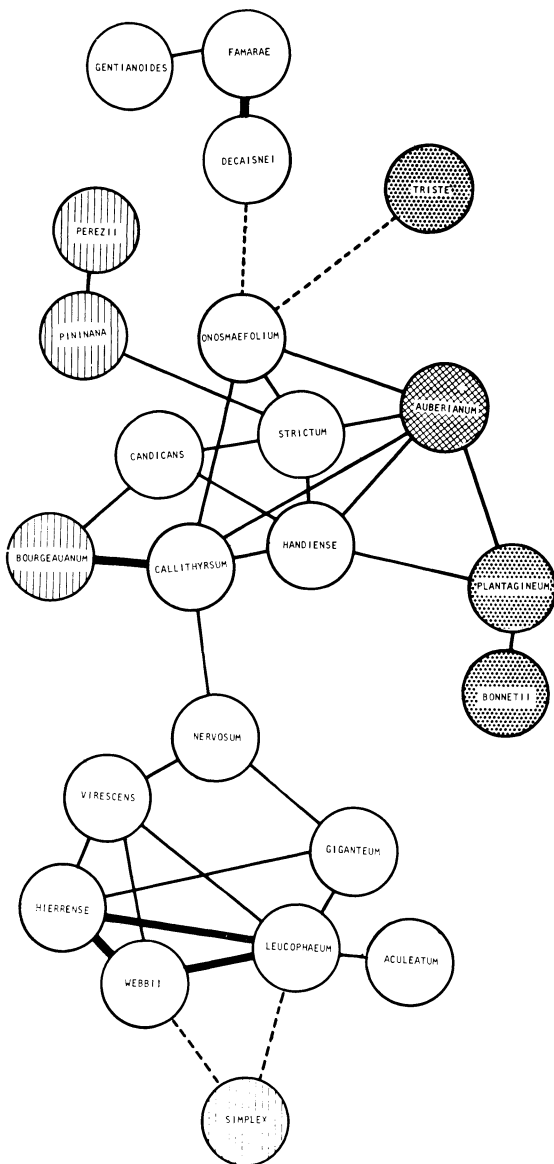


FIG. 17.—Relationships between *Echium* species based upon trichome similarity. Heavy lines: similarity more than 70%; thin lines: similarity 60–70%; dashed lines: affinity of those species lacking close similarity. Based on data from table 3.

TABLE 4
INTRASPECIFIC VARIATION IN TRICHOME COVERAGE

SPECIES	ISLAND	LIFE ZONE	TOTAL COVERAGE (%)		COVERAGE % LONG TRICHOMES		COVERAGE % SPINES	
			Upper epid.	Lower epid.	Upper epid.	Lower epid.	Upper epid.	Lower epid.
<i>Echium giganteum</i>	Tenerife	Subtropical	45	80	25	20	0	0
	Tenerife	Subtropical	75	80	20	15	0	0
	Tenerife	Subtropical	70	100	40	30	0	0
	Tenerife	Subtropical	40	100	30	25	0	0
<i>E. aculeatum</i>	Tenerife	Subtropical	100	100	30	30	0	0
	Gomera	Subtropical	100	100	80	80	1	5
	Tenerife	Subtropical	100	100	50	50	1	5
	Tenerife	Temperate	100	100	75	70	1	5
	Tenerife	Temperate	70	95	40	50	10	15
<i>E. leucophaeum</i>	Hierro	Temperate	100	100	80	80	3	5
	Hierro	Temperate	100	100	90	80	0	5
	Tenerife	Subtropical	95	100	40	30	0	0
	Tenerife	Subtropical	100	100	50	50	0	0
<i>E. simplex</i>	Palma	Subtropical	95	95	40	40	0	2
	Palma	Subtropical	100	100	50	40	0	1
	Hierro	Subtropical	100	100	65	50	5	8
	Tenerife	Subtropical	90	95	80	90	0	0
<i>E. hierrense</i>	Hierro	Temperate	95	100	80	80	0	0
	Hierro	Subtropical	100	100	60	60	0	0
	Hierro	Subtropical	100	100	40	50	0	0
	Hierro	Subtropical	100	100	85	75	0	0
<i>E. webbii</i>	Palma	Subtropical	100	100	60	60	0	0
	Palma	Temperate	100	100	90	80	0	0
	Palma	Temperate	95	95	90	90	0	0
	Palma	Temperate	100	100	90	90	0	0
<i>E. virescens</i>	Tenerife	Temperate	85	100	70	60	0	0
	Tenerife	Temperate	75	95	70	40	0	0
	Tenerife	Temperate	50	60	20	30	0	0
<i>E. nervosum</i>	Tenerife	Subtropical	85	60	45	25	0	0
	Tenerife	Subtropical	80	100	15	20	20	0
	Tenerife	Subtropical	75	40	40	10	20	0
	Tenerife	Subtropical	80	95	20	20	0	0
<i>E. callithyrsum</i>	G. Canaria	Temperate	85	80	85	80	0	0
<i>E. bourgeauanum</i>	Palma	Subalpine	85	80	85	80	0	0
	Tenerife	Subalpine	80	70	80	70	0	0
<i>E. pininana</i>	Tenerife	Subalpine	85	75	85	75	0	0
	Tenerife	Temperate	15	10	15	10	0	0
	Tenerife	Temperate	20	15	20	15	0	0
<i>E. auberianum</i>	Tenerife	Subalpine	70	70	70	70	0	0
	Tenerife	Subalpine	40	50	40	50	0	0
<i>E. plantagineum</i>	Palma	Temperate	45	25	40	23	5	0
	Tenerife	Temperate	15	8	15	8	0	0
	Tenerife	Subtropical	15	15	12	12	3	0
<i>E. bonnetii</i>	Tenerife	Subtropical	25	20	15	15	5	0
	Tenerife	Subtropical	35	35	30	30	0	0
	Tenerife	Subtropical	20	30	15	30	0	0
<i>E. triste</i>	Gomera	Subtropical	15	20	3	4	5	10
<i>E. candicans</i>	Madeira	Temperate	20	25	16	20	0	0
	Madeira	Temperate	55	50	55	50	0	0
<i>E. handiense</i>	Fuerteventura	Temperate	35	30	30	25	0	0
<i>E. strictum</i>	Tenerife	Temperate	15	10	12	8	0	0
	Tenerife	Subtropical	30	20	20	10	0	0
	Tenerife	Subtropical	60	40	40	25	0	0
	Gomera	Subtropical	30	20	25	15	0	0
	Palma	Subtropical	20	20	15	10	0	0
<i>E. onosmaefolium</i>	G. Canaria	Temperate	90	70	0	20	90	40
	G. Canaria	Temperate	50	25	15	10	35	10
	G. Canaria	Temperate	50	50	5	40	40	5
	G. Canaria	Subtropical	50	40	0	0	50	40
<i>E. decaisnei</i>	G. Canaria	Subtropical	55	40	0	0	55	40
	G. Canaria	Subtropical	75	30	0	0	75	30
	G. Canaria	Subtropical	20	10	0	0	20	10
	Fuerteventura	Subtropical	15	0	0	0	15	0
<i>E. famarae</i>	Lanzarote	Subtropical	15	0	0	0	15	0
<i>E. gentianoides</i>	Palma	Subalpine	25	0	0	0	25	0

TABLE 3
SIMILARITY OF TRICHOMES IN ECHIUM: NUMBER OF POINTS OF AGREEMENT (MAXIMUM POSSIBLE = 14)^a

Average Similarity (%)	Species	Gentianoides	Famarae	Decaisnei	Onosmaefolium	Strictum	Handiense	Candicans	Triste	Bonnatii	Plantagineum	Aubertianum	Pinnana	Perezii	Bourgeauanum	Callithyrsum	Nerosum	Virescens	Webbii	Hierrense	Simplex	Leucophaeum	Aculeatum
41.1	<i>Giganteum</i>	0	3	3.5	6	7	7.5	7.5	4.5	4	6.5	8	3	4.5	5.5	4.5	8.5	7.5	7	8.5	5	9	6
38.6	<i>Aculeatum</i>	2.5	4.5	3.5	6	4.5	3	6.5	5	5.5	3	4.5	5	4.5	5.5	5.5	6	7.5	7	7.5	7	9	9
43.3	<i>Leucophaeum</i>	1	2.5	2.5	4	6	5.5	8	4	6.5	4	8	3	4.5	5.5	6	6.5	9	10	10.5	7	9	9
33.9	<i>Simplex</i>	1	1.5	2.5	2.5	4	3.5	4.5	4	6.5	4	5.5	4	6	5.5	6	3.5	4.5	8	7.5	8	7	9
43.5	<i>Hierrense</i>	1	2.5	3.5	4.5	4.5	7.5	7	4	4	5	4	3.5	4.5	8	6.5	7	8.5	10.5
43.2	<i>Webbii</i>	2	3	4	5	5	6	5.5	4.5	5.5	3.5	8	5.5	5	7.5	6.5	5.5	8.5
47.2	<i>Virescens</i>	3	4.5	4	7.5	8	6.5	8	5.5	4	4	5	6	7.5	7	8	8.5
40.9	<i>Nerosum</i>	2.5	4	4	7.5	6	6.5	6.5	4	3.5	6	8	6	4.5	7.5	8	8.5
46.3	<i>Callithyrsum</i>	4	5	4	8.5	7.5	8.5	6.5	5	5.5	5.5	5.5	6	6.5	10	8
46.6	<i>Bourgeauanum</i>	3	4.5	3.5	7.5	7.5	8	8.5	5	5.5	6	7.5	7.5	8
44.3	<i>Perezii</i>	5	5	4.5	6	8	6.5	6	7.5	8	7.5	8	9
41.4	<i>Pinnana</i>	4	6	5	8	9	5	5	8	7	7	6.5
51.8	<i>Aubertianum</i>	3	5.5	7	8.5	9.5	9.5	8	7.5	7	8.5	8.5
41.7	<i>Plantagineum</i>	2.5	4.5	5	6.5	8	8.5	6.5	7.5	9.5
39.1	<i>Bonnatii</i>	3	2.5	4	4	7.5	6	7	6.5
39.8	<i>Triste</i>	4	8	7.5	8	7	5.5	3.5
43.8	<i>Candicans</i>	1.5	2.5	2.5	6.5	9	8.5
45.3	<i>Handiense</i>	2	4.5	5	7.5	8.5
49.2	<i>Strictum</i>	3.5	6	6	9.5
46.6	<i>Onosmaefolium</i>	4.5	7.5	8
34.7	<i>Decaisnei</i>	7	10.5
34.6	<i>Famarae</i>	9
22.4	<i>Gentianoides</i>

^a Bold type = values higher than 70%; italics = values lower than 25%.

species of *Echium* are temperate. The subalpine belt dominated by leguminous shrubs is found above 2,000 m in the Canaries; in Madeira the highest peaks support only a few endemics of subalpine affinity. Only three *Echiums* are native to the subalpine zone (*E. auberianum*, *E. bourgeauanum*, and *E. gentianoides*).

There are considerable climatic differences between these life zones (LEMS, 1960). The mean annual temperature near sea level is about 20 C (68 F), in the temperate belt about 15 C (59 F), and in the subalpine zone less than 10 C (50 F). The rainfall in the three zones depends upon exposure to the trade winds. On the windward slope the three zones receive about 250 mm, 750 mm, and 350 mm, respectively, but this does not take into account the condensation of water on the vegetation in the cloud belt. It is of interest to calculate the effect of these different life zones upon the trichome development in *Echium*.

A study of table 4 reveals that the mean total coverages of trichomes on the upper epidermis are as follows:

Subtropical zone: 64.2% ($N = 36$);
 Temperate zone: 63.3% ($N = 23$);
 Subalpine zone: 64.2% ($N = 6$).

For this calculation, actual individuals rather than species averages were employed, in order to allow for statistical testing. All the above values have standard deviations of about 32%, so we conclude that there is no significant difference in total trichome coverage among the three life zones.

The coverage of the long trichomes alone, calculated in the same manner, shows the following averages and standard deviations:

Subtropical zone: 31.66% \pm 23.7% ($N = 36$);
 Temperate zone: 47.95% \pm 32.3% ($N = 23$);
 Subalpine zone: 60.00% \pm 30.9% ($N = 6$);
 All specimens: 40.97% \pm 29.8% ($N = 65$).

Although this suggests an increase in coverage of long trichomes with increasing altitude, a statistical test shows that such a conclusion is not justified. There is a large probability of getting different means for the different life zones as a result of chance.

A third feature in which the specimens from different zones might show trends is the presence of erect versus appressed trichomes. It should be borne in mind that the first eight species in table 4 have appressed pubescence, the remainder either erect or ascending hairs, or none (in the last three species listed). The distribution of individuals over the three ecological zones is as follows:

Subtropical zone: Appressed = 21, erect or ascending = 9, glabrous = 6;
 Temperate zone: Appressed = 11, erect or ascending = 11, glabrous = 1;
 Subalpine zone: Appressed = 0, erect or ascending = 5, glabrous = 1;
 All specimens: Appressed = 32, erect or ascending = 25, glabrous = 8.

Again, statistical tests show that the conclusion that silky pubescence is correlated with the subtropical zone, the erect pubescence with the temperate zone, is not justified by these data.

The only conclusion to be drawn is that in the genus *Echium* climatic adaptation has not expressed itself in a significant difference in the trichome complements of the species.

TAXONOMIC IMPLICATIONS.—Figure 17 shows that the trichome complement of *Echium* species can make a major contribution to an understanding of relationships in the genus. In the first place, a number of groups which had been defined on the basis of floral morphology (cf. DE COINCY, 1903) can be confirmed: the complex of *E. giganteum*, *E. leucophaeum*, and *E. aculeatum*, shrubs with white zygomorphic flowers; the complex of *E. virescens*, *E. webbiai*, *E. hierrense*, *E. nervosum*, shrubs with bluish actinomorphic corollas; and the complex of *E. plantagineum*, *E. bonnetii*, and other herbaceous species with strongly zygomorphic, purplish flowers. The affinities of certain species had been unknown before and can now be surmised from their trichomes: *E. gentianoides* appears to be a member of the *E. decaisnei* group, although its floral morphology and its geographic location are quite anomalous. *Echium callithyrsum* appears to be intermediate between the members of the *E. strictum*–*E. handiense*–*E. onosmaefolium* line (with which it shares its papery bark) and the *virescens*–*nervosum* group. *Echium triste*, recently discovered by SVENTENIUS (1960), does not have very strong similarities, either in floral or trichome features, but its closest ally might be *E. onosmaefolium*. One group which appears to fall apart is the “simplex group,” supposed to encompass all the monocarpic “hapaxanth” or unbranched woody plants. *Echium simplex* itself is closest to the other silky-leaved species (*E. leucophaeum*, *E. webbiai*), while *E. bourgeauanum* is close to *E. callithyrsum*, and *E. pininana* to *E. strictum*. This parallels the situation in the monocarpic forms of *Aeonium*, which are thought to be polyphyletic (LEMS, 1960).

EVOLUTIONARY IMPLICATIONS.—A major result of the comparison of trichomes is the establishment of different evolutionary lines which at the present time have few characteristics in common. One of these is the line of silky-leaved shrubs. This group

has the following distinctions: (a) they are all woody plants, one of them monocarpic, the others branched; (b) the group includes both actinomorphic and zygomorphic flowers, the latter possibly a specialization; (c) the species are mostly limited to the western islands of the Canarian archipelago (Tenerife, Gomera, Palma, and Hierro) and could be thought of as a local development if it were not for *E. vulcanorum* of the Cape Verde Islands, and *E. nervosum* of Madeira. NETOLITZKY (1932) in his classical treatise on trichomes postulates that the appressed form of trichomes is derived from the erect type, and this fits in well with the concept that the silky-leaved species of *Echium* form a special insular group derived from the more generalized group with hirsute leaves.

Another evolutionary line involves the development of spines and, ultimately, the reduction of these to mere flat pustules. In the sequence *E. strictum*–*E. onosmaefolium*–*E. decaisnei*–*E. famarae*–*E. gentianoides* pustules first become progressively larger, and the hairs thicken into spines and finally disappear entirely. It seems likely that this trend is one of specialization. It may be noted that *E. gentianoides* is the most dissimilar, that is, the most specialized of all the *Echium* species.

There remains a rather large and heterogeneous group of species with erect, hispid pubescence; it includes annuals, biennials, hapaxanth, and shrubs. Among these, *E. auberianum* occupies a special position: it has the largest number of trichome features in common with the largest number of species, and it may therefore be said to be "generalized." At the same time, it is intermediate in growth form in that it is largely herbaceous but has a short woody axis near the ground; and it is variable in longevity, forming lateral offshoots for a number of years before the entire plant dies. All of these would speak for its primitive nature, that is, a plant much like *E. auberianum* may have given rise to the entire endemic group of species. However, the species is found only in one locality in subalpine Tenerife, in a highly specialized environment of recent geological origin.

It is of interest to compare different islands with respect to the types of trichomes. The Canary Islands may be divided into an eastern and a western group,

with the boundary between Gran Canaria and Tenerife. Table 4 summarizes some differences between these. It seems likely that the evolution of spiny, glabrous species was localized largely in the eastern islands, the evolution of silky, pubescent species in the western region.

Finally, we should consider the implications of juvenile and undifferentiated trichome types. There is no doubt that, of all the species, the annuals and biennials show the least amount of change during their maturation: the trichomes on the cotyledons and first leaves are much like those on the flowering specimens. On the other hand, the spiny and silky species undergo a series of changes as the foliage matures; the seedlings of the glabrous, pustular *E. gentianoides* and *E. famarae* have ordinary long trichomes. In *E. leucophaeum*, *E. webbii*, *E. giganteum*, etc., the appressed silky pubescence only develops after the plant has produced 20–50 leaves with sparse, erect pubescence. It seems that in these species the individual goes through a recapitulation of its evolutionary history. The process of recapitulation in trichomes was demonstrated in one other instance by CARLQUIST (1961).

On the other hand, the development of the biennial and annual habit is probably a specialization which came about through the progressive reduction in woodiness and longevity. Exactly what the starting point was for this trend is not certain: it may have been a monocarpic shrub, such as *E. pininana*; a branched shrub, such as *E. strictum*; or a perennial plant with a woody crown, such as *E. auberianum*. In any event, the development of an annual line has evidently resulted in a simplification of the trichome complement: an example of neoteny in the plant kingdom! Such examples have been cited before in the evolution of annuals from perennials involving simplification in vegetative development (PRAT, 1951).

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ANTICLINAL DIVISIONS AND THE ORGANIZATION OF CONIFER CAMBIUM

M. W. BANNAN

Department of Botany, University of Toronto, Toronto 5, Canada

ABSTRACT

The multiplication of radial files of axial elements, which accompanies girth increase, is usually duplicated in xylem and phloem, but sometimes the expansion is temporary and occurs only in the xylem. Because such additions are traceable to anticlinal divisions in the cambium, the deduction follows that permanent changes in cell pattern are due to multiplicative divisions in cambial cells having the initial function, and changes in the xylem only, to divisions in cells on the xylemward side of the initials. A distinction between initial cells and derived tissue mother cells, as proposed by SANIO (1873), is thus confirmed. However, indications of occasional lapses in the initial function cast doubt upon the suitability of restricting the term "cambium" to initials only.

Introduction

Differences of opinion exist with respect to the interpretation of the layers of cells comprising the cambial zone. SANIO (1873) proposed that growth of the xylem and phloem began in a single layer of cambial initials. The initial in each radial file of cells divided periclinally to produce two daughter cells of which one continued as an initial, and the other became a xylem or phloem mother cell. The latter often divided once or twice before maturation to xylem or phloem elements. Support for SANIO's theory was found by later workers, such as MISCHKE (1890), SCHOUTE (1902), and BEIJER (1927), but it was demonstrated that the xylem mother cells in particular often underwent more frequent redivision than SANIO proposed. Certain other investigators (RAATZ, 1892; KLEINMANN, 1923) disagreed with SANIO's hypothesis regarding the existence of a discrete initial. They argued that all cells with capacity for periclinal division were equivalent and that no particular cell could be designated as an initial. Re-

cently, CATESSON (1964) has supported this interpretation.

In a fast-growing tree the cambium, or the cambial zone of some authors (*see* WILSON, WODZICKI, and ZAHNER, 1966), is generally wide, consisting of several layers of dividing cells. In a transection all cells appear similar, and identification of a particular cell as an initial is difficult. In radial sections of conifer cambium, however, the functioning initial may be distinguished by the fact that it is slightly shorter than the adjoining, derived xylem mother cells (BANNAN, 1955). On the other hand, CATESSON (1964) has stated that no such length differences exist in the cambium of *Acer*.

The cambium is the site not only of periclinal divisions but also of anticlinal divisions, the latter being involved in the changes in cell pattern associated with circumferential expansion. For example, the multiplication of fusiform cambial cells is achieved by oblique anticlinal (pseudotransverse) divisions (KLINKEN, 1914; BAILEY, 1923; BANNAN, 1950;