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SOME MORPHOLOGICAL ASPECTS OF THE ADAPTIVE RADIATION OF CANARY ISLANDS *ECHIUM* SPECIES

by

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This paper is dedicated to Prof. S. Rivas Goday on his 70th birthday.

THE CONCEPT OF ADAPTIVE RADIATION

Since 1947 when David Lack presented the case for the adaptive evolution of Darwin's Finches in the Galapagos Islands, the term *adaptive radiation* has become almost synonymous with island biology. The example of Darwin's finches was first studied in detail by LACK (1947), and there have since been a number of attempts to define adaptive radiation on an insular scale (CARLQUIST 1965, 1974; MCARTHUR & WILSON, 1967; BRAMWELL, 1972 etc...).

A number of biologists have, however, appreciated the parallel between the island situation exemplified by the Geospizoid finches of the Galapagos Islands, ie. the evolution of groups of related organisms on a relatively small scale, and the fundamental evolution of large groups of organisms on a major scale (HUXLEY 1954; STEBBINS 1972; VERNE GRANT, 1963). STEBBINS (1972) uses this parallel in relation to major angiosperm evolution, and MAYR (1954), for example, when discussing the evolution of Hawaian Honey-creepers by means of adaptive radiation states that he visualizes all major evolutionary novelties to arise in a similar manner. VERNE GRANT (1963) considers that the component taxa of a genus, tribe, family etc... usually show a diversity of forms correlated with a range of ecological niches or habitats within their territory and that these different phylogenetic lines within the natural groups are adapted for different ways of life. This diversification of a group of organisms is, he suggests, in relation to the ways of surviving and successfully reproducing, a product of an adaptive radiation during the evolutionary history of the group.

The general acceptance that evolution proceeds by way of adaptive radiation means, as STEBBINS (1972) implies when considering the hypothesis of genetic uniformitarianism, that the detailed study of such phenomena on a relatively small scale such as in island ecosystems, can by comparison provide invaluable information on the processes and patterns of evolution at all levels from the major higher categories downwards.

ADAPTIVE RADIATION ON ISLANDS

It is at a local level where most of the «classical» examples of adaptive radiation have been studied and where the so-called island laboratory plays an important role. Most definitions of the phenomenon have been proposed by island biologists such as CARLQUIST (1974) who presents adaptive radiation as the entry of a group into a variety of habitats in a reasonably discrete geographical area.

MCARTHUR & WILSON (1967) in their excellent treatise on the theoretical background to island biology, consider that towards the periphery of the dispersal range of a taxon speciation and exchange of newly — formed autochthonous species within an archipelago can take place more rapidly than the immigration from sources outside the archipelago and this leads to the accumulation of local species on single islands. Despite their common origin such species tend to be adaptively quite different from each other, and the result is adaptive radiation in the strict sense.

The basis of this definition, changes at the margin of the range of a taxon, parallels closely the concept of quantum speciation which GRANT (1971) describes as the budding off of a new, different daughter species from a semi-isolated peripheral population of the ancestral species in a cross-fertilizing organism. He considers this process to be rapid and radical in both its phenotypic and genotypic effects. This type of speciation seems very appropriate to the situation on volcanic islands such as the Canary Islands where frequent volcanic activity and rapid erosion lead to near extinction of populations leaving only small isolated ones and also produce a constant series of habitat changes. Small populations isolated in this way can then act as founder populations responding to the sudden ecological shifts by genetic reorganization and rebuilding of genetic variability which allows rapid evolutionary changes and this, as MAYR (1954) suggests, offers otherwise unavailable opportunity for drastic ecological change of a somewhat unbalanced genetic system. Such populations have passed through what Mayr describes as a «bottleneck of reduced variability» thus providing the possibility for origin of numerous evolutionary novelties.

Biotic communities disturbed by natural agencies open up new habitats and, importantly, reduce potential competition. In many island situations, *Sonchus*, *Aeonium*, *Argyranthemum* etc. in the Canary Islands, *Cyanea*, *Bidens* in Hawaii and *Hebe* and *Coprosma* in New Zealand, this has had far-reaching effects on plant speciation and has resulted in what is generally considered to be adaptive radiation.

THE GENUS *Echium* IN THE CANARY ISLANDS

Several examples of adaptive radiation in the Canary Islands have already been described, notably in *Aeonium* (LEMS, 1960) and *Sonchus* (BRAMWELL, 1972a). The genus *Echium (Boraginaceae)* also shows a considerable degree of morphological diversity within the islands. The Canarian *Echium* species are considered to be much closer to the ancestral stock of the genus than their nearest relatives in Europe and North Africa (BRAMWELL, 1973). It is apparent that the islands were originally colonized by a much smaller number of species than exists there at the present time where the genus now has a remarkable range of forms and habitats.

In response to the enormous diversity of climate/vegetation zones, habitat types and the complexity of base geology the number of species has expanded from the few original colonizers to some 22 species occupying every major zone (Table 2) from sea-level to the upper limit of plant life at over 2300 m. Most Canarian *Echium* species are pachycaul or rosette shrubs though there are also three endemic herbaceous species. The pachycaul habit is considered, in the most recent studies, to be a relatively primitive one (MABBERLEY, 1974) and it is probably amongst this group that we might find the *archetype* of the genus *Echium*.

Taxonomy

The taxonomy of the Macaronesian group of *Echium* species has recently been revised (BRAMWELL, 1972) and the shrubby species placed in seven sections (Table 1) on the basis of their floral morphology and inflorescence types. This division into sections is supported by results obtained from studies of leaf-flavonoids (BRAMWELL, 1973).

Two of these sections are relatively large, Section *Virescentia* with 10 species and Section *Gigantea* with six. The Section *Virescentia* contains most of the laurel forest species of the Canaries and Madeira but also has both pine forest and lowland species. The Section *Gigantea*, on the other hand, has, with Section *Decaisnea*, most of the dry montane and coastal region species of the Canaries and Cape Verde Islands; within these sections species have radiated into different habitats in each major vegetation zone.

The Section *Simplicia*, consisting of three unbranched monocarpic species, is found only in the Canary Islands. The three species, *E. simplex*, *E. pininana* and *E. wildpretii* are closely related (BRAMWELL, 1973) but each occupies a distinct habitat in a different vegetation zone, *E. simplex* on cliffs near the coast, *E. pininana* in forest regions and *E. wildpretii* in the subalpine region.

The most widespread Canarian *Echium* species is *E. strictum* which along with the Cape Verde Islands *E. stenosiphon*, form the Section *Stricta*. *E. strictum* is very polymorphic and has the widest ecological amplitude of any of the Canarian species. It is found in habitats ranging from sea-cliffs on the north coast of Tenerife where it is a small, rough-leaved, blue-flowered shrub to the lower montane zone where it is pink-flowered with a lax habit and rather spiny leaves, and in the laurel forest zone where the flowers may be blue or pink and the leaves usually relatively broad and somewhat silky.

Sections *Auberana* and *Gentianoidea* are both monotypic. *E. auberianum* is a subalpine semi-desert species found in volcanic pumice and fine cinder. *E. gentianoides* occurs only on pine forest cliffs in the highest regions of the northern part of La Palma in the Western Canaries.

TABLE I

Distribution of the endemic sections of Echium *in Macaronesia*

Species	Archipelago	Islands
Sect. Gigantea:		
1 *E. giganteum* L. Fil.	Canaries.	Tenerife.
2. *E. aculeatum* Poir.	Canaries.	Tenerife, Hierro, Gomera, Gran Canaria.
3. *E. leucophaeum* Webb.	Canaries.	Tenerife.
4. *E. brevirame* Spr. & Hutch.	Canaries.	La Palma.
5. *E. triste* Svent.	Canaries.	Gran Canaria, Gomera, Tenerife.
6. *E. vulcanorum* A. Chev.	Cape Verde I.	Fogo.
Sect. Simplicia:		
7. *E. simplex* DC.	Canaries.	Tenerife.
8. *E. pininana* W. & B.	Canaries.	La Palma.
9. *E. wildpretii* Pearson	Canaries.	Tenerife, La Palma.
Sect. Virescentia:		
10. *E. virescens* DC.	Canaries.	Tenerife.
11. *E. sventenii* Bramwell	Canaries.	Tenerife.
12. *E. webbii* Coincy	Canaries.	La Palma.
14 *E. acanthocarpum* Svent....	Canaries.	Gomera.
15. *E. hierrense* Webb. ex Bolle.	Canaries.	Hierro.
16. *E. candicans* L. Fil.	Madeira.	Madeira, Porto Santo.
17. *E. nervosum* Ait.	Madeira.	Madeira, Porto Santo.
18. *E. onosmifolium* W. & B.	Canaries.	Gran Canaria.
19. *E. callithyrsum* Webb. ex Bolle. ...	Canaries.	Gran Canaria.
20. *E. handiense* Svent.	Canaries.	Fuerteventura.
Sect. Stricta:		
21. *E. strictum* L. Fil.	Canaries.	Tenerife, G. Canaria, Gomera, La Palma, Hierro.
22. *E. stenosiphon* Webb.	Cape Verde I.	San Vicente, S. Antao.
Sect. Auberana:		
23. *E. auberianum* W. & B.	Canaries.	Tenerife.
Sect. Decaisnea:		
24. *E. decaisnei* W. & B.	Canaries.	Gran Canaria, Lanzarote, Fuerteventura.
25. *E. hypertropicum* Webb.	Cape Verde I.	San Tiago, Fogo, Brava.
Sect. Gentianoidea:		
26. *E. gentianoides* Webb. ex Coincy...	Canaries.	La Palma.

TABLE II

Principal Climate & Vegetation zones in Canary Islands

Vegetation	Altitude	Climate
Subalpine scrub................	2.000 m. & above	Sub-continental, cold winters, hot dry summers,
Pine Savanna..................	800 – 1.900 m.	Dry Mediterranean
Evergreen Forest..............	400 – 1.300 m.	Wet Mediterranean
Transition zone...............	300 – 800 m.	Mediterranean
Semi-desert and lower-montane...	0 – 700 m. to 1.500 m on G. Canaria	Hot dry Mediterranean

Morphological Radiation and Ecology

Macaronesia is a major centre of evolution of the Mediterranean genus *Echium*. The frutescent species found in the Canaries, Madeira and the Cape Verde Islands are very different from the other members of the genus from outside Macaronesia. These are almost all herbaceous perennials, biennials or annuals with major centres of distribution in the Iberian Peninsula and North Africa and within the insular group there has obviously been a considerable amount of independent local evolution.

Evolution in Habit

The principal growth-forms in the Canarian species of *Echium* in relation to their habitat and ecology are summarized in Figure 1. These range from the herbaceous annual/biennial forms found in dry semi-desert lowlands or as short-lived weeds, to the tall shrubs of the dry montane and forest regions and the perennial dense rosette species of the subalpine zone. The main morphological differences in the frutescent group are paralleled by the monocarpic species, with the «shrubbiest» species *E. pininana* occurring in forest regions and a dense, almost sessile rosette species *E. wildpretii* in the subalpine zone.

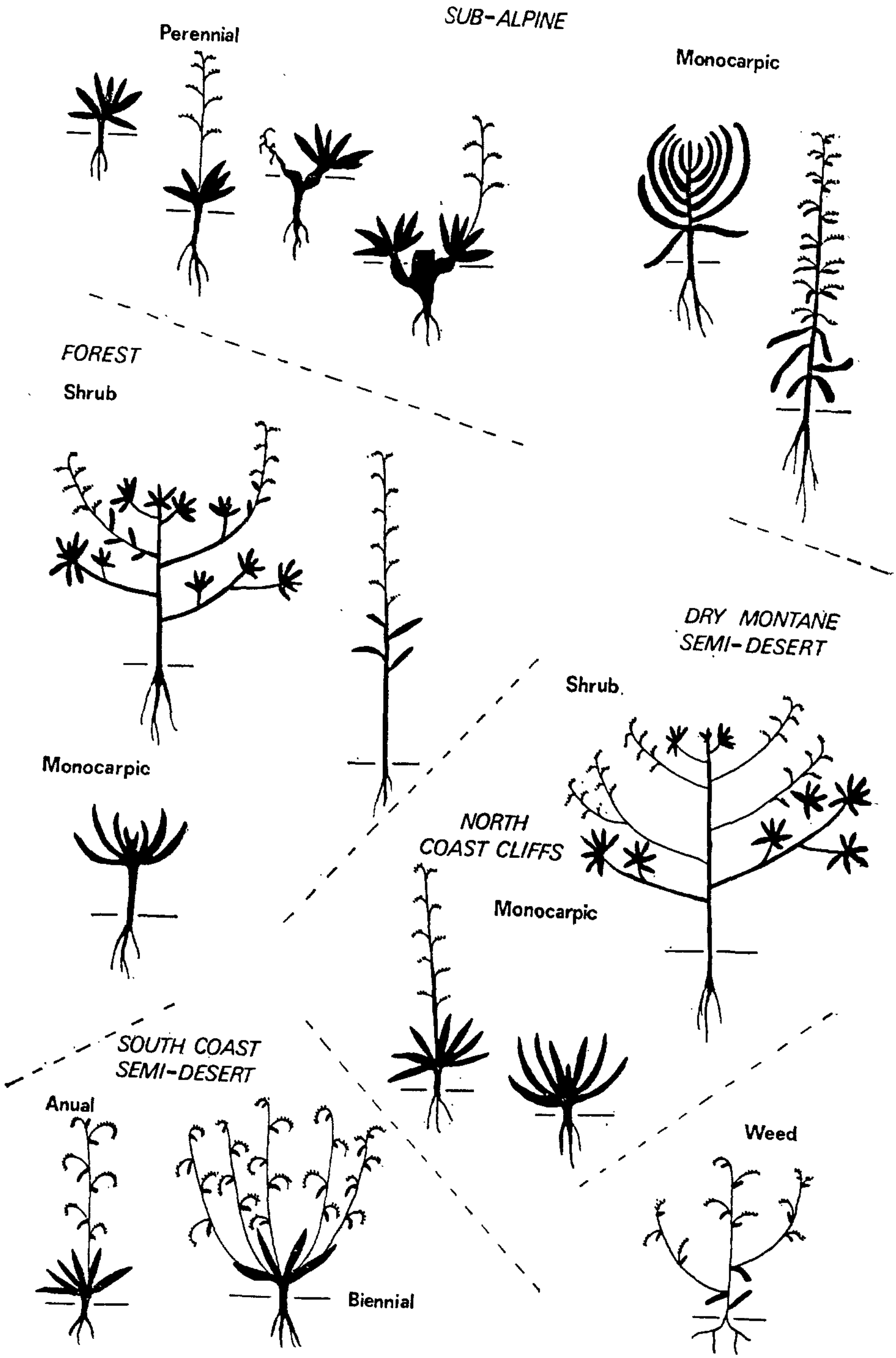

Fig. 1.—The growth-form of Canarian *Echium* species in relation to principal habitats.

The «candelabra» shrubs of the sections *Gigantea* and *Virescentia* differ in that those of the former section produce their first inflorescence on the main stem while those of the latter section flower first on lateral branches. The forest species generally have a lax, open habit with long branches whereas the lowland and dry-montane species are normally very dense shrubs, dome-shaped and with short, compact branches.

Leaf Types

The most remarkable morphological radiation in Canary Islands *Echium* species has taken place in leaf characters and indumentum types. The different forms of hairs and spines on *Echium* leaves have been extensively studied by LEMS & HOLZAPFEL (1968) and BRAMWELL (1972) and Table 3 is a summary of the distribution of the major indumentum types found in species from the island of Tenerife in relation to the major ecological zones of the island.

There is also very close correlation between leaf-shape in *Echium* species and ecological zone occupied throughout the Canary Islands and Madeira (Figure 2). The very dry semi-desert/coastal species *E. strictum* which occupies the driest, hottest habitats of any of the Canarian species, has small, narrow, very tough leaves with large spines on the margins and midrib. In more montane regions of the dry zone there are species such as *E. aculeatum* and *E. brevirame* on the Western Canaries and *E. onosmifolium* and *E. decaisnei* on the eastern group. All these species also have relatively tough, narrow leaves with thick, fleshy midribs and very spiny margins. *E. aculeatum* and *E. brevirame* have a dense covering of apressed white reflecting hairs on the upper surface whilst the other two species have a thick, leathery cuticle.

The upper region of the dry zone grades into a forest region on all but the two eastern islands of Lanzarote and Fuerteventura where the close proximity of the dessicating influence of the Sahara and the absence of land over 700 m. have combined to prevent forest development.

In the transition zone between semi-desert and forest there is an area of scrub vegetation with leguminous shrubs, *Erica* heath and several of the more xerophilous forest elements. In this zone three *Echium* species, *E. leucophaeum* on Tenerife, *E. hierrense* on Hierro and

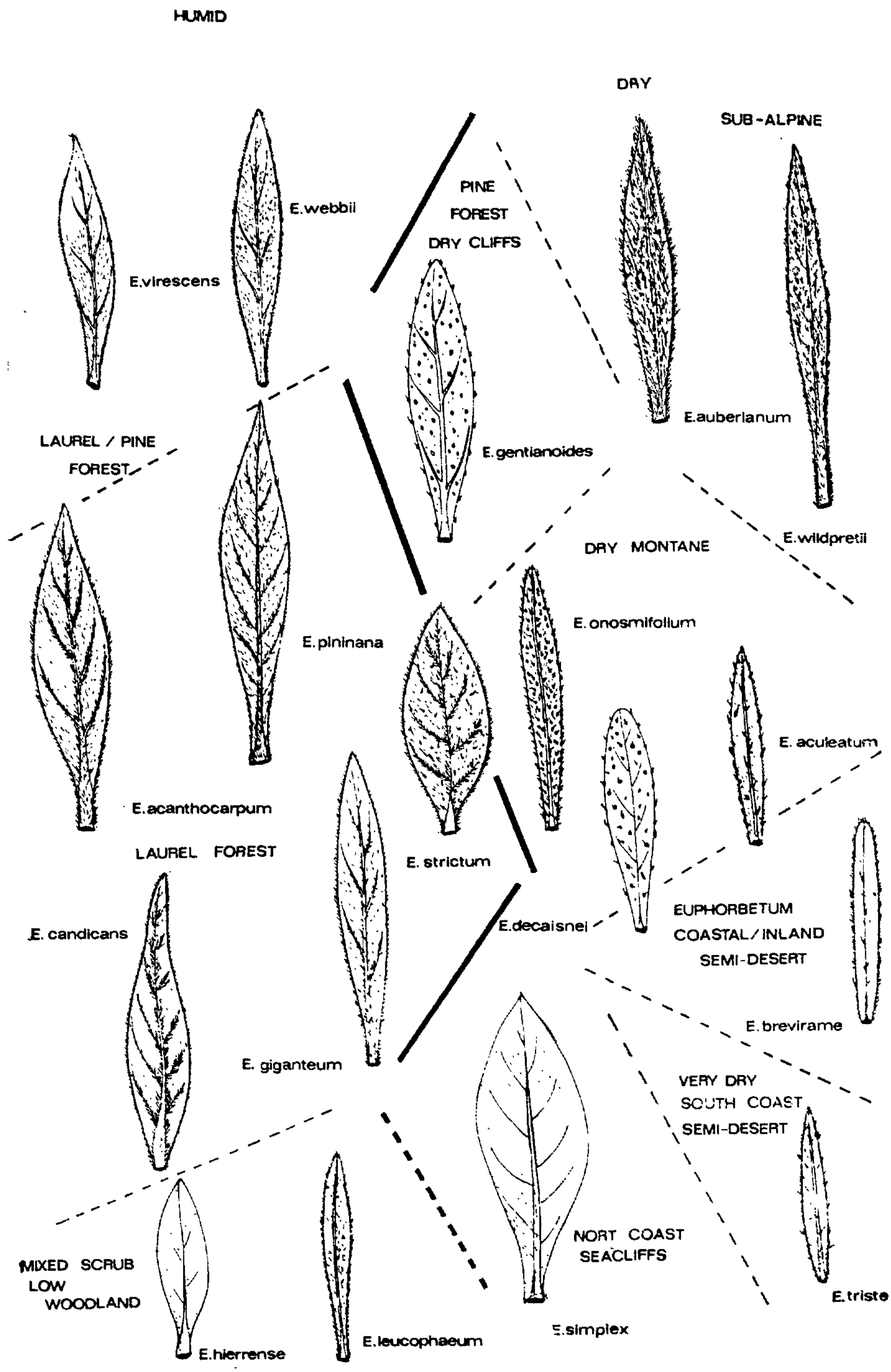

Fig. 2.—The adaptive radiation of leaf-types in Macaronesian *Echium* species in relation to the principal habitats found in the islands.

E. strictum can usually be found, though *E. webbii* and *E. brevirame* (La Palma), *E. giganteum* (Tenerife) and *E. decaisnei* (Gran Canaria) also sometimes occur especially when the scrub vegetation is a degradation stage caused by felling of laurel forest. The species of the transition zone tend to have larger leaves than those of the dry zone and the indumentum is rather more silky than spiny.

TABLE III

Distribution of Echium *species in the vegetation zones of Tenerife*

Species / Vegetation Zone	E. triste ●	E. leucophaeum +	E. sventenii +	E. wildpretii ¡	E. auberianum ¡	E. strictum + to ●	E. virescens +	E. giganteum + to ●	E. aculeatum ●	E. simplex +
Subalpine 2000 3000 m	—	—	—	+	+	—	—	—	—	—
Pine forest 1000—2000 m	—	—	—	+	—	—	+	—	—	—
Laurel forest 1000–1500 m	—	—	—	—	—	+	+	+	—	—
Forest transition zone ca. 500 900 m	—	+	+	—	—	+	+	+	—	—
Upper xerophytic zone 500–900 m	—	+	+	—	—	+	+	+	+	—
Lower xerophytic zone 0–500 m	+	—	—	—	—	+	—	—	+	+

● Leaves spiny; + leaves silky with appressed hairs; ¡ leaves with very long, dense indumentum.

Within the true forest zone there is a large increase in surface area of leaves in response to shade conditions. The silky covering is less dense than in the transition zone and spines are very rare. The typical forest leaf in *Echium* has deeply set veins and midrib on the upper surface *(E. pininana, E. acanthocarpum)* and pronounced dripping points at the apex *(E. candicans, E. acanthocarpum)* to allow rapid run-off of excess water. Several forest species are found in drier areas of the laurel forest and in the *Pinus canariensis* forest at higher altitudes. In these species *(E. virescens, E. webbii)* the leaves again tend to be of the transition zone type with a dense silky covering to resist insolation and a few marginal spines. The most unusual species is *E. gentianoides* found only on pine forest cliffs at high altitudes on La Palma. The leaves of this plant closely resemble those of *E. decaisnei* from the dry lowland and lower montane regions of Gran Canaria, Lanzarote and Fuerteventura. *E. gentianoides* seems to occupy a habitat with relatively high insolation and low rainfall and thus its leaves parallel those of other species in similar micro-ecological conditions in other zones.

The subalpine zone occurs only on the two highest islands, Tenerife and La Palma. Two *Echium* species, *E. wildpretii* and *E. auberianum*, are restricted to this zone. These two species have remarkably similar long, narrow leaves with a characteristic covering of very long, dense stiff hairs. These hairs seem likely to trap a layer of air which helps to resist the very large diurnal temperature range in the region.

Physiological Radiation

Carlquist (1974) suggests that there has been some adaptive physiological evolution in Canarian *Echium* species citing some rather circumstantial data obtained as a result of the effect of frost damage on *Echium* plants during a severe Californian winter. The high mountain species have evolved some degree of frost resistance. *E. wildpretii* has a dense rosette which protects the apical growing point from damage and *E. auberianum* can be grown out of doors in England if kept relatively dry in winter. Other species such as *E. aculeatum* and *E. onosmifolium* are able to survive long periods of drought, usually shedding most of their leaves and young branches in the process. The forest species are, however, much more sensitive to dessication and die very quickly in periods of prolonged dryness.

There is also some association between ecology and time and duration of the flowering period. The subalpine species flower relatively late in the summer and have a short flowering period of a few months. The forest species tend to flower in late spring or early summer and finish before the summer drought but the more robust species of the dry zone such as *E. aculeatum* and *E. decaisnei* can be found with some individuals in flower at almost any time of the year and nearly always have a second period, besides their main spring flowering, in the early autumn especially if there are autumn rains.

CONCLUSIONS

Evolution of *Echium* in the Canary Islands has proceeded to such an extent that there are now 22 recognisable endemic species in a relatively small group of islands. These species appear to have developed in response to the strong selection pressures of the wide range of ecological conditions available for colonization.

The characters used for taxonomic delimitation of species within each section, habit, leaf-shape, indumentum types etc. are strongly correlated with habitat, whereas those such as floral morphology, inflorescence types etc. used to delimit sections within the endemic group are more independent of local ecological conditions. It seems most probable that the basic models for each of the larger sections arose early in the evolution of the Macaronesian group, the basic model of sections *Virescentia* and *Simplicia* in mesic forest and that of section *Gigantea* in drier conditions. From the ancestral models all three sections have radiated into a wide range of differing and often parallel ecologically adapted species in response to the spectrum of habitats available. This has resulted in adaptive radiation in the classical insular sense.

RESUMEN

Se discute brevemente el concepto de la radiación adaptativa y su significación general en relación a la evolución de las plantas en islas volcánicas. La radiación adaptativa se considera extremadamente importante en la especiación vegetal de varios y extensos grupos de plantas de Macaronesia, concretamente en las especies macaronésicas del género *Echium* (*Boraginaceae*). En este ejemplo se hace referencia particular a la evolución de formas de crecimiento y diversos tipos de hoja e indumento, en respuesta a la extensa variedad climática y ecológica encontrada especialmente en las Islas Canarias. La radiación de *Echium* ha llevado a la formación de 26 especies en Macaronesia (22 en las Islas Canarias) en siete secciones distintas.

Summary

The concept of adaptive radiation is briefly reviewed and its general significance in relation to the evolution of plants on volcanic islands discussed. Adaptive radiation is considered to be very important in plant speciation in several large groups of Macaronesian plants and an example in the Macaronesian species of the genus *Echium* (*Boraginaceae*) is presented. In this example particular reference is made to the evolutions of growth forms and diverse leaf and indumentum types in response to the wide range of Climate/Ecological conditions found especially in the Canary Islands. The radiation of *Echium* has resulted in the formation of 26 Macaronesian species (22 in the Canary Islands) in seven distinct sections.

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