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Evolution in the Canary Islands II. Revision of the annual and biennial species of *Echium* (Boraginaceae)

Kornelius Lems and Christina M. Holzapfel
Goucher College, Baltimore, Maryland

LEMS, K., and C. M. HOLZAPFEL (Goucher College, Baltimore, Maryland) Evolution in the Canary Islands. II. Revision of the annual and biennial species of *Echium* (Boraginaceae). Bull. Torrey Bot. Club 95: 37–57. 1968.—Detailed comparison of the blue-flowered annual and biennial *Echium* from the Canary Islands shows that there are several fairly distinctive taxa: *E. plantagineum* L., *E. bonnettii* Coincy, with a variety, var. **pachycaulon** nov. var., **E. fuerteventurae** nov. sp., and **E. lancerottense** nov. sp. with a var. **macrantha** nov. var. These taxa are described and illustrated. It is proposed that reports of *Echium arenarium* Guss., *E. creticum* L., *E. maritimum* Willd., and *E. stenosiphon* Webb be deleted from the flora of the Canary Islands, since the specimens were incorrectly identified. The geographic distribution of the Canarian species is defined. It appears that most local endemism in annual *Echium* occurs in the dry regions, especially on the eastern islands Fuerteventura and Lanzarote.

Among the Atlantic Islands designated as Macaronesia (Good, 1953), the Canary Islands are the richest in endemic plant species. The high degree of endemism, estimated at about 35% (Lems, 1960a), is in part due to the survival of Tertiary relict species now extinct in the Mediterranean region (e.g. *Ocotea foetens, Dracaena draco*), but most species have undergone local evolution in response to a variety of climates and substrates (e.g. *Aeonium* (Lems, 1960b), *Sonchus, Euphorbia, Limonium, Echium*). The growth forms of these endemic groups of species are of interest because there is a much higher degree of endemism among the shrubby and semi-woody perennials than among the biennial, annual, and herbaceous perennial species (Lems, 1961).

The present study is part of an investigation of the genus *Echium* in the Canary Islands (Lems and Holzapfel, 1968). This genus is represented by more than 15 species of branched shrubs and subshrubs, four monocarpic perennials, one herbaceous perennial, and a number of biennial and annual herbs. The woody and perennial species are endemic to the Atlantic Islands, but the affinities of the annual and biennial plants have never been critically established. It is the purpose of this study to determine exactly how many annual and biennial species there are, how they are distributed, and how they are related to one another. It will be shown that a good deal of insular evolution has taken place in the annual *Echium* population, resulting in several well defined species, a number of populations that may represent locally adapted ecotypes of these species, and some populations ex-

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hibiting intermediate characteristics. It appears that local evolution of these annuals has centered chiefly on the dry eastern islands of Fuerteventura and Lanzarote.

Echium triste Sventenius (1960) of Gomera, Tenerife and Gran Canaria, although annual, is not included in this study. Its floral and trichome characteristics indicate that it is related to the endemic shrubby species e.g. *Echium onosmaefolium* (Lems and Holzapfel, 1968).

Materials and methods. Table 1 lists the materials of annual and biennial *Echium* examined. Most of the plants were collected by the authors; additional material was studied in the following herbaria: Faculdad de Farmacia, Universidad de Madrid; Musée d'Histoire Naturelle, Paris; Royal Botanic Garden, Kew; Rijksherbarium, Leiden; U.S. National Herbarium, Washington, D.C.; New York Botanical Garden; Missouri Botanical Garden, St. Louis; and Dudley Herbarium of Stanford University, California.

The procedure used in the comparison of specimens and populations was made as objective as possible. It consisted of scoring each population or collection number with respect to 19 different characteristics, ranging from vegetative development to floral features, all of them receiving equal weight regardless of their supposed importance in distinguishing between species. Each collection was then compared with all others, and its similarities calculated.

The characteristics which were employed in the comparison of *Echium* specimens, and the categories established in each of these characteristics are as follows:

Height (3–10 cm, 11–25 cm, 26–50 cm, 51–more)
Number of basal branches (none, 1–2, 3–4, 5 or more)
Number of inflorescence branches (none, 1–3, 4–7, 8 or more)
Number of cauline leaves below inflorescence (none, 1–6, 7–14, 15 or more)
Basal leaf length to width ratio (1.5–3.0, 3.1–4.5, 4.6–6.0, 6.1 or more)
% of upper leaf surface covered by pubescence (less than 23%, 23–38%, 38–53%, over 53%)
% of lower leaf surface covered by pubescence (less than 13%, 13–28%, 28–43%, over 43%)
Length of leaf trichomes (0.2–0.5 mm, 0.6–1.0 mm, 1.1–1.8 mm, 1.9 mm or more)
% of stem covered by pubescence (10–25%, 26–40%, 41–55%, more than 55%)
Length of stem trichomes (0.5–0.8 mm, 0.9–1.3 mm, 1.4–2.0 mm, more than 2.0 mm)
Presence of short appressed hairs on stem (present, absent)
Calyx length (3–5 mm, 6–8 mm, 9–12 mm, 13 mm or more)
Color of calyx lobes (green, dark blue)
Length of corolla, base to margin of upper lobes (less than 13 mm, 13–17 mm, 18–22 mm, more than 22 mm)
Zygomorphy of corolla (length to upper lobes/length to lower lobe 0.99–1.07, 1.08–1.16, 1.17–1.25, 1.25 or more)
Annulus type (10 lobes, smooth ring, 5-lobed ring, 2-lobed ring)
Branching position of corolla veins (below annulus, at annulus, above annulus)
Attachment of upper stamen (toothed membrane, inconspicuous membrane)
Pubescence of corolla (glabrous to very sparsely pilose, with thin but well developed pubescence, densely pubescent)

The corolla in most annual *Echium* plants is rose when young, turning blue at maturity. When fully developed, the upper lobes are longer than the lower median and lateral lobes, and degree of zygomorphy may be calculated as the quotient of upper and lower lobes. In materials from Lanzarote this often approaches 1, while in *E. plantagineum* and *bonnetii* the upper lobes are as much as 25% longer than the lower. Variability in this feature may be due to immaturity of the flowers.

The five stamens are adnate to the corolla tube (Fig. 1), the lower pair about midway, the lateral pair below the middle, the upper stamen nearest

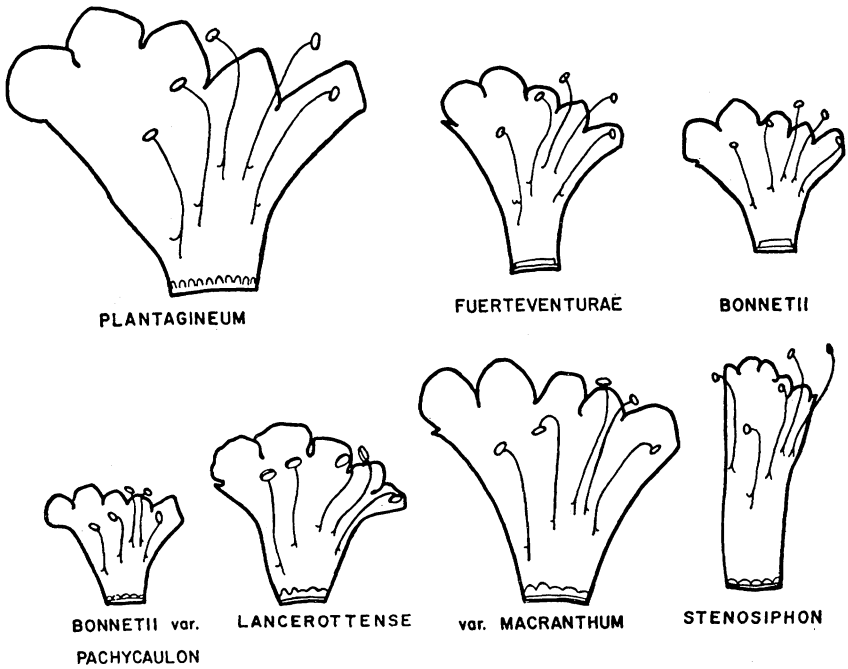

Fig. 1—Tracings of corollas of seven taxa of *Echium*, cut between the upper and lateral lobes, the upper lobes to the left. The annulus outlined near the base of each corolla. 1.6x natural size.

the base. Only the lower stamens protrude from the corolla in most of these annuals. In some of them, the anthers open before anthesis, so that self pollination is very probable. One striking characteristic is the presence of a prominent tooth on the membrane which connects the upper stamen with the corolla. This is found in several common Mediterranean plants, but in the Canary Islands it was encountered only in one *Echium* population on Fuerteventura.

Near the base of the corolla there is a ring of tissue called the annulus (Fig. 1). De Coincy (1900, 1902, 1903) used this structure as the principal

criterion to divide the genus *Echium* into the sections Eleutherolepis (annulus of 10 separate lobes), Gamolepis (with continuous ring) and Pachylepis (annulus a heavy, fleshy ring). This single character approach may lead to oversimplification of the real relationships, but it does emphasize the importance of dissecting the corolla and determining the annulus type. In our study, we encountered several conditions: all plants assigned to *E. plantagineum* have 10 separate lobes; the remainder of the species are more variable, and transitions are often encountered: a continuous ring in *E. bonnetii,* a five-lobed ring in material from Fuerteventura and Lanzarote, some from the latter island with more prominent lobes at the base of the upper corolla lobes.

The calyx of *Echium* is more uniform than the corolla, differing only in size in most of the species. It enlarges during the maturation of the fruit, and may have a function in dispersal. In most species the calyx is asymmetrical, upper lobe being the longest, while the lower lateral lobe on the side of the inflorescence axis is shortest. All populations from Lanzarote differ from the others by having obtuse, rather than acute lobes, ordinarily with dark blue tips.

Pubescence of the leaves and stems in annual species of *Echium* is much less diverse than in the shrubby plants (Lems and Holzapfel, 1968). Generally, the leaves are thinly covered by erect hairs 0.3 to 1.5 mm long, which are "pustular" or "boraginaceous," i.e. the base of the trichome is surrounded by one to three rows of calcified epidermal cells. The only differences noted were in the density of the trichomes, and in the presence or absence of very short appressed hairs on the stem, especially along the inflorescence branches. The greatest variability in pubescence appears on the outside of the corolla, which is densely hairy in some of the Lanzarote populations, and practically glabrous in *E. plantagineum* from the western islands.

The largest leaves occur at the base of the stem, and are generally petiolate. Successive nodes of the stem produce progressively smaller leaves, grading into sessile, linear bracts in the inflorescence. In *E. plantagineum* the upper cauline leaves and bracts are typically broad based and truncate. Length-width ratios indicate that *Echium bonnetii* has the narrowest leaf shape.

Growth form is one of the most variable characteristics. Nevertheless, there is genetic determination of the production of basal branches, the size of the rosette, and the size of the inflorescence. This was determined by growing seeds from biennial and annual populations of *E. bonnetii* and *E. plantagineum* under uniform greenhouse conditions. The annual *E. bonnetii* flowered and died within four months, having formed a small rosette and

several branches from the base and the lower portion of the stem. In *E. plantagineum* the biennial plants formed a vegetative rosette which flowered after six months with up to 13 basal branches in addition to the main axis; the annual plants of *E. plantagineum* flowered without forming a distinct rosette and basal branches. These experiments showed that although greenhouse-grown specimens become larger, and develop more rapidly than those in the field, the basic pattern of rosette and branch formation is preserved, as well as the relative rates of development.

Similarity index and speciation. Each collection of *Echium* was compared with all others, with respect to the 19 characteristics listed above. For example, Collection No. 6760 was compared with No. 5806, and found to agree in 6 of the 19 criteria, for which 6 points were awarded; in addition, 3 points were awarded for partial similarity in 6 other criteria, because the ranges of these measurements overlapped; no points were awarded for the remaining 7 criteria because the two plants were completely different in these 7 respects. The similarity index is the percentage of points out of a total of 19; in the example this comes to 9 in 19, or 47%. Table 1 lists all possible comparisons with their similarity indices. In this table, the collections are arranged roughly from East to West.

In interpreting such a table, it should be remembered that the probability that any two collections will agree by pure chance in all of their characteristics is very small indeed. The probability of agreement in a given characteristic is approximately 0.33.[1] Hence, perfect agreement in 19 criteria has a probability of 0.000,000,000,7, and it can be calculated that agreement in 53% or more of the criteria carries a probability P = 0.05 of being due to chance, while an agreement of at least 61% has a P = 0.01. In Table 1, several significant (P between 0.05 and 0.01) and highly significant (P less than 0.01) similarities are noted.

There are at least three groups of collections with high similarity indices within the group, and low similarities with other groups. One of these corresponds to *Echium plantagineum,* all collections of which are highly significant in their similarity to one another. A second group corresponds to *Echium bonnetii,* and a third to an as yet undescribed set of populations from Lanzarote, hereafter to be named *Echium lancerottense* nov. sp.

The collections from Fuerteventura remain somewhat problematical, having both high and low rates of similarity with several of these well-defined species. The collections from La Oliva (KL7061) are so unique (lack of rosette, tooth on upper stamen membrane, long slender branches), that it may be regarded as a separate taxon; had more collections been avail-

[1] Since there is a variety of probabilities of similarity in individual criteria ranging from 0.25 to 0.53, "average" probability was calculated as $P = (P_1 \times P_2 \times \ldots . P_{19})^{\frac{1}{19}}$

Table. 1. Percentage of similarity among 18 collections of *Echium*, calculated from 19 characteristics. *Italics:* significant similarities, **bold face:** highly significant similarities.

ISLAND	LOCALITY	ELEV. (M)	COLL.	NO.	NUMBER PLANTS	TAXON	% SIMILARITY WITH NO. 5806	6894	6855	6330	6465	6531	6530	519B	6982	630	7002	7061	706	6597	6654	6676	264
Lanzarote	Mirador Rio	400	Lems	6760	2	*lancerottense* var. *macrantha*	47	45	42	37	42	34	39	25	40	47	47	34	26	*55*	47	50	37
Lanzarote	Famara	500	Pitard	264	10	*lancerottense*	37	29	29	34	40	40	42	42	47	37	42	37	*60*	52	*56*	**66**	—
Lanzarote	Peñas Chaché	650	Lems	6676	16	*lancerottense*	37	26	34	34	47	26	31	36	34	37	47	*58*	47	*55*	*56*	—	
Lanzarote	Ermita Nieves	600	Lems	6654	5	*lancerottense*	31	25	28	28	37	37	28	47	44	31	50	34	**68**	59	—		
Lanzarote	Teguise	425	Lems	6597	6	*lancerottense*	40	34	37	32	40	29	36	31	42	50	**63**	37	47	—			
Lanzarote	Arrecife	—	Knoche	706	1	*lancerottense*	29	19	19	24	34	34	33	50	37	37	47	29	—				
Fuertevent.	La Oliva	300	Lems	7061	5	*fuerteventurae*	34	29	34	37	40	34	25	31	42	42	*55*	—					
Fuertevent.	Mal Nombre	5	Lems	7002	9	*bonnetii var. pachycaulon*	34	26	26	32	45	32	25	44	42	*55*	—						
Fuertevent.	Pto. Rosario	—	Knoche	630	1	cf. *bonnetii*	40	32	37	34	52	32	25	33	50	—							
Fuertevent.	Antigua	250	Lems	6982	3	*bonnetii*	*55*	42	42	40	**76**	**63**	**61**	*56*	—								
Gr. Canaria	Aguimes	—	Knoche	519B	1	*bonnetii*	28	27	26	31	*60*	*58*	52	—									
Tenerife	Güimar	50	Lems	6530	1	*bonnetii*	40	44	42	44	62	75	—										
Tenerife	Güimar	50	Lems	6531	34	*bonnetii*	26	32	29	37	**68**	—											
Tenerife	Adeje	150	Lems	6465	30	*bonnetii*	40	37	34	40	—												
Tenerife	Punta Hidalgo	90	Lems	6330	19	*plantagineum*	**66**	**74**	**76**	—													
Tenerife	Las Mercedes	700	Lems	6855	8	*plantagineum*	**63**	**82**	—														
Tenerife	Aguamansa	1000	Lems	6894	3	*plantagineum*	**66**	—															
La Palma	Caldera	800	Lems	5806	3	*plantagineum*	—																

able from northern Fuerteventura, we probably would have had a good "cluster" of similar populations, as we did for Lanzarote. The material from southern Fuerteventura (KL7002) is also unique; its small size, and floral characteristics suggest an affinity to *E. bonnetii,* but its leaves and growth form set it apart as an unrecognized taxon.

Taxonomic conclusions. The literature on the flora of the Canary Islands is unclear on the species of *Echium*. The annuals have been assigned to various continental species, e.g. *E. plantagineum* L., *E. creticum* L., *E. maritimum* Willd., *E. arenarium* Guss., and if these determinations were correct, our earlier hypothesis that herbaceous plants in the Canaries tend to be non-endemic, would be confirmed. The only endemic annual *Echium* on record is *E. bonnetii* Coincy, reported from Tenerife.

We have examined Moroccan and Mediterranean material of the continental species mentioned above, and find that none of them resemble the Canarian annuals, with the exception of *Echium plantagineum*. Hence we must reject reports of *E. creticum, E. arenarium, E. maritimum,* and propose two new species, **E. fuerteventurae** and **E. lancerottense,** the latter with a large flowered variety, var. **macranthum.** In addition we recognize the peculiar small plant of southern Fuerteventura as a distinctive variety: *E. bonnetii* var. **pachycaulon.**

It should be noted that all of these species are closely related, and that they are described on morphological basis. Experimentation would have to show whether sterility barriers exist between them, before we can regard these as biological species. As a first step we present the following key and descriptions of the entities as we see them.

Key to the annual and biennial species of *Echium* in the Canary Islands.

1. Corolla 22–30 mm long; upper cauline leaves and bracts sessile with broad bases; annulus of 10 separate lobes; annual or biennial ..... *Echium plantagineum*
1. Corolla 9–22 mm; upper cauline leaves and bracts narrowed to the base; annulus an even or 5-lobed ring; annual
   2. Upper stamen attached to corolla by conspicuous toothed membrane; plants erect, over 25 cm tall, the leaves not clearly in a rosette, basal branches lacking ..... *Echium fuerteventurae*
   2. Upper stamen attached by an inconspicuous, straight membrane; plants usually lower, with a basal rosette
      3. Calyx lobes obtuse, often blue at tips ..... *Echium lancerottense*
         4. Corolla less than 18 mm long, densely pubescent; leaves more or less acute; calyx lobes with dark blue tips ..... *var. lancerottense*
         4. Corolla about 20 mm long, sparsely pubescent; leaves, or some of them, obtuse; calyx lobes mostly green ..... *var. macrantha*
      3. Calyx lobes acute, green ..... *Echium bonnetii*
         5. Basal leaves lanceolate, more than 4 times as long as wide, acute; branches slender ..... *var. bonnetii*
         5. Basal leaves ovate; less than 3 times as long as wide, obtuse; branched from the base with thick, short branches ..... *var. pachycaulon*

DESCRIPTION OF THE SPECIES.

Echium plantagineum L. (Fig. 2, 3)—Annual and biennial, the annuals simple, 10–80 cm tall, with a loose basal rosette of long-petiolate, oblanceolate, obtuse leaves 12–16 cm long; the biennial form with up to 13 basal branches and a dense rosette of ovate leaves. Cauline leaves below the inflorescence petiolate, oblanceolate, reduced upwards to sessile bracts, with broad, truncate bases. Stems with two kinds of trichomes: stiff erect hairs 0.5–3 mm long, and short appressed hairs 0.1–0.3 mm long. Calyx 11–16 mm long at anthesis, with acute lobes, the lower lobes 1–2 mm shorter than the upper, hispid. Corolla purplish blue, 22–30 mm long, flared, the upper lobes longer than the lower ones, glabrous except along the veins and with occasional hairs on the distal portion. Annulus of the corolla of 10 distinct lobes. Lower pair of stamens slightly protruding from the corolla, the upper 3 shorter than the lower ones.

DISTRIBUTION. Mediterranean weed found also on Madeira, Gran Canaria, Tenerife, Gomera, Palma and Hierro. Reports from Lanzarote and Fuerteventura refer to other species. ECOLOGY. In meadows and roadsides from near sea level to 2000 m, the populations below 500 m predominantly annual, above 800 m usually of the biennial form. Experiments show that the growth form is in part genetically controlled, seeds from biennial plants giving rise to large branched rosette forms, seeds from annuals producing simple forms that flower more rapidly.

Echium bonnetii Coincy var. *bonnetii* (Fig. 4)—Annual averaging 6 cm high, occasionally to 20 cm, simple or with 1–3 branches from the rosette or lower nodes, the inflorescences simple or with 1–2 branches. Stems hispid with erect hairs .5–2 mm long. Basal rosette of 3–5, occasionally 10 oblanceolate leaves, 4–9 cm long, gradually narrowed to the base, the tip acute, the hairs .5–1.5 mm long, covering about 30% of the leaf surface. Cauline leaves reduced upward to linear–lanceolate bracts. Flowers distinctly pedicelled. Calyx 3.5–5 mm long at anthesis, enlarged to 10 mm in fruit, the upper lobe 1–2 mm longer than the lower ones, linear, acute, hispid pubescent, the hairs to 2 mm long. Corolla blue, 8–15 mm long, with a narrow tube and flaring limb, the upper lobes slightly longer than the lower, the distal portion of the corolla finely hairy with short, even pubescence. Annulus of the corolla a continuous ring of even or slightly undulating width. Lower 2 stamens slightly surpassing the lower corolla lobes, the upper 3 stamens shorter than the lower ones.

DISTRIBUTION. Endemic to Tenerife (Teno, Adeje, Escobonal, Güimar), Gran Canaria (Aguimes), Fuerteventura (Antigua). ECOLOGY. Below 500 m on level or slightly sloping loamy soil, associated with small annuals and grasses (*Pennisetum ciliare, Eragrostis poaeoides*). SYNONYMS. *E. arenarium* Perraudierre, Webb & Berthelot, non Guss.

Echium bonnetii Coincy var. **pachycaulon** nov. var. (Fig. 5)—*Planta annua humilis ramis brevibus, carnosis, pilis brevibus appressis atque longioribus erectis vestitis; foliis rosulatis, petiolatis, obtusis, caulinibus lanceolatis, subpetiolatis; floribus caeruleis calyce acute lobata, corolla ad 17 mm longa, extus pubescenti, annulo 5-lobato. Typus in solo petroso litorali prope "Boca del Mal Nombre" insulae Fuerteventurae.*

Fig. 2—*Echium plantagineum* L. annual growth form, from Las Mercedes, Tenerife. Habit scale 10 cm, flower scale 5 mm.

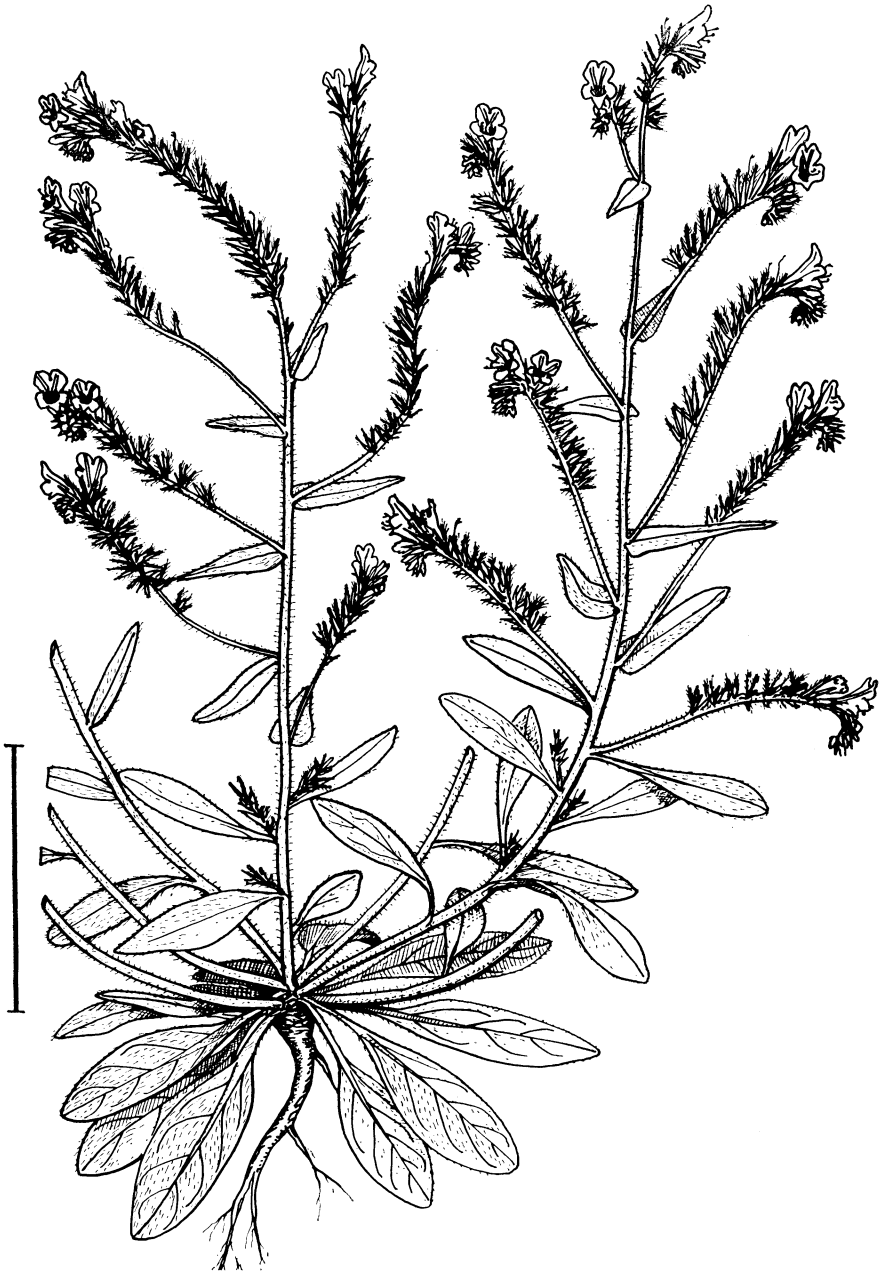

Fig. 3—*Echium plantagineum* L. biennial growth form, from Aguamansa, Tenerife. Scale 10 cm.

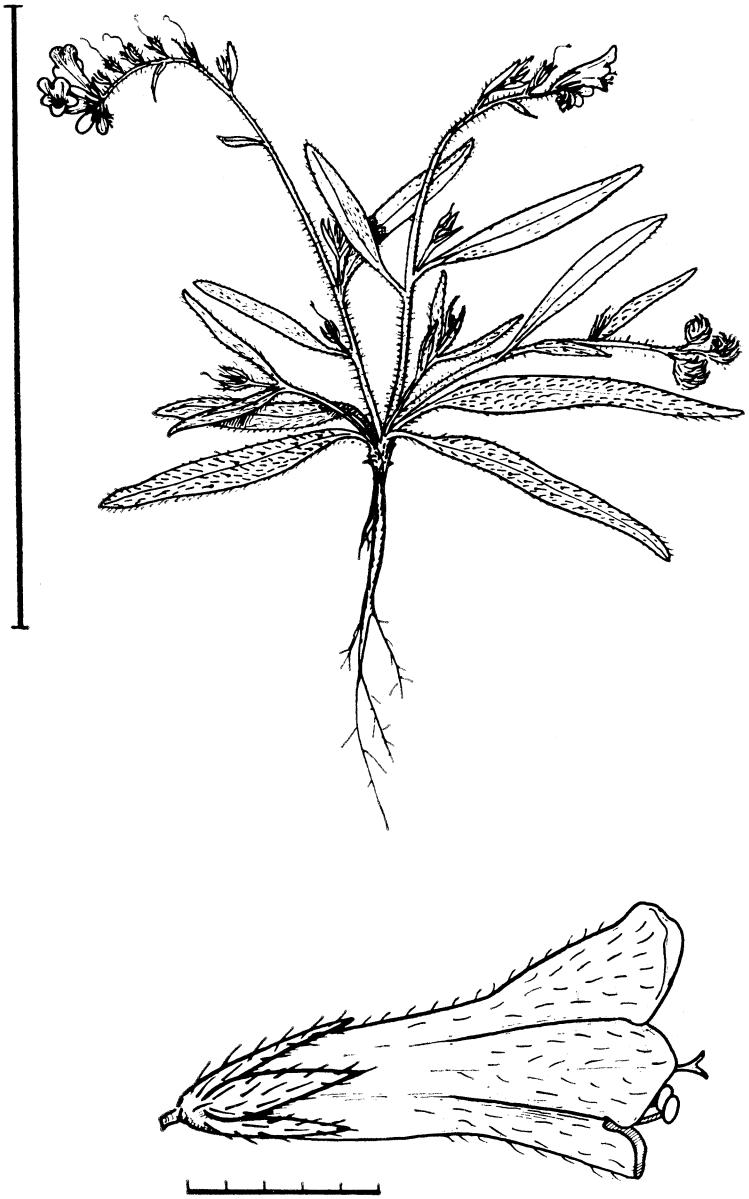

Fig. 4—*Echium bonnetii* Coincy var. bonnetii from Güimar, Tenerife. Habit scale 10 cm, flower scale 5 mm.

Annual less than 5 cm tall, with 3–5 fleshy basal branches, and a succulent root; stems somewhat branched, densely pubescent with two kinds of trichomes: erect hairs 0.5–2 mm long, and short appressed hairs 0.1–0.5 mm long. Basal rosette of 5–10 ovate, petiolate leaves 5–8 cm long, with obtuse tips and cuneate bases; the pubescence of ascending pustular hairs 0.5–1.5 mm long, covering 25% of the upper, 10% of the lower leaf surface. Cauline leaves reduced upward in size, lanceolate. Calyx hispid 2.5–4 mm long at anthesis, not enlarging much in fruit, the calyx lobes acute. Corolla blue, 9–17 mm long with abundant hairs on the outer surface. Annulus a 5-lobed ring. Lower pair of stamens protruding from the corolla, the other 3 included.

Fig. 5—*Echium bonnetii* Coincy var. *pachycaulon* nov. var. (Lems No. 7002) from Boca del Mal Nombre, Fuerteventura. Habit scale 10 cm, flower scale 5 mm.

DISTRIBUTION. Endemic to the coastal regions of Fuerteventura, common on the Jandia peninsula. ECOLOGY. Very dry stony soil with *Aizoon canariense, Chenolea canariensis, Heliotropium erosum, Lycium afrum.* Related to *Echium lancerottense* of Lanzarote. TYPE SPECIMEN. K. Lems, No. 7002, Boca del Mal Nombre, Fuerteventura, deposited in U.S. National Herbarium, duplicates at Kew (Royal Botanic Gardens) and Paris (Musée d'Histoire Naturelle).

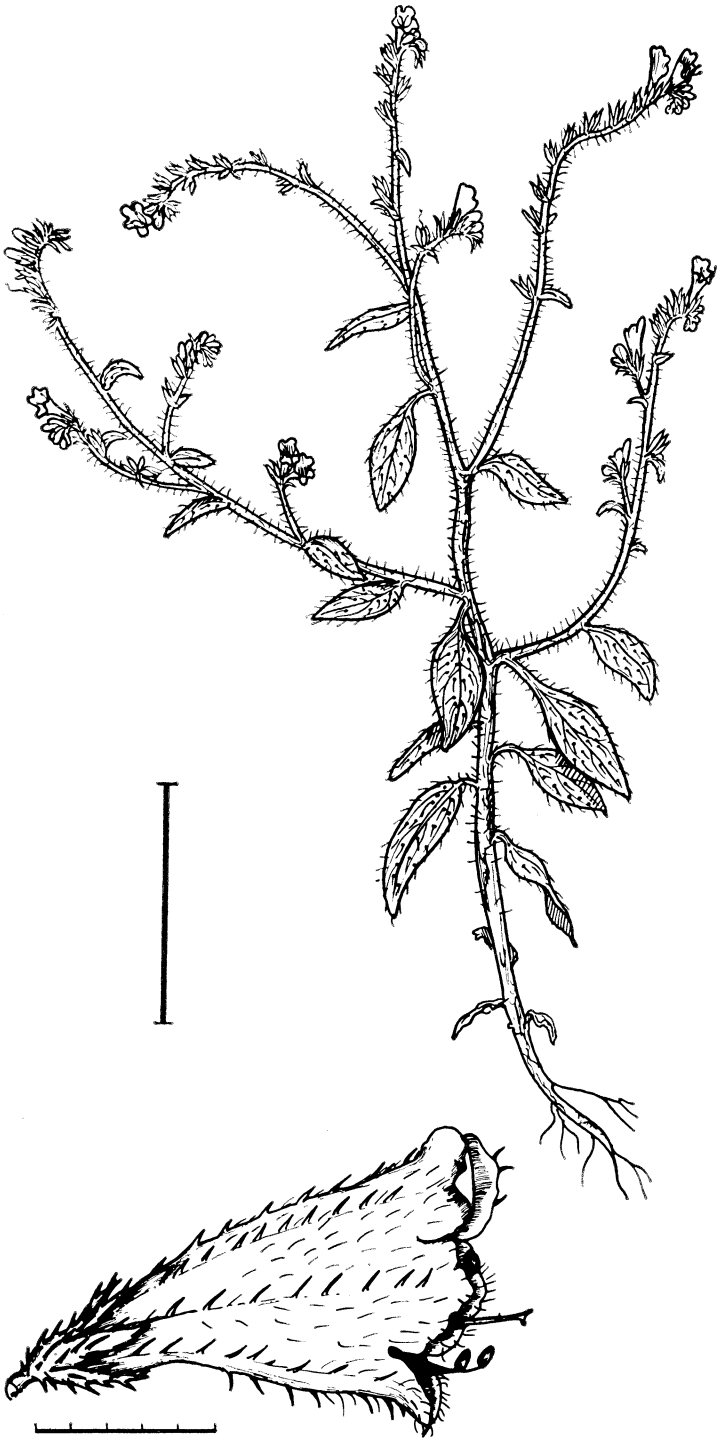

Fig. 6—*Echium fuerteventurae* nov. sp. (Lems No. 7061) from La Oliva, Fuerteventura. Habit scale 10 cm, flower scale 5 mm.

Echium **fuerteventurae** nov. sp. (Fig. 6)—*Planta annua 30–50 cm alta, simplex; foliis alternis non rosulatis, ovatis, petiolatis; floribus in inflorescentia ramosa, caeruleis, corolla extus valde pubescenti, annulo latitudinis aequalis vel paululum lobato; stamine superiori ad basim tubi adnato membrano dentato.*

Typus in rupibus volcanicis loci "Malpais del Volcán" prope La Oliva, insulae Fuerteventurae.

Annual to 50 cm high, without evident basal rosette, and not branched from the base, but bearing 4–12 long inflorescence branches. Stems with erect hairs 0.5–3 mm long. Cauline leaves below the inflorescence narrowly ovate, the petiole about 15 mm long, the blade 4–10 cm long, with acute tip and base, pubescent with hairs .5–1.5 mm long, covering 25% of the upper, 10% of the lower leaf surface. Calyx length 3.5–5.0 mm at anthesis, 5 to 7 mm in fruit, the lobes acute, densely hispid. Corolla blue, 12–17 mm long, with abundant pubescence on the distal, flared portion, the lobes ciliate. Annulus of the corolla a continuous ring, densely pubescent. Upper stamen attached to the corolla by a membrane bearing a distinct tooth; lower pair of stamens slightly exceeding the corolla lobes, the others included.

DISTRIBUTION. Endemic to Fuerteventura, on the Volcán N. of La Oliva. ECOLOGY. Growing at 300 m elevation in small soil pockets of coarse lava, dominated by *Kleinia neriifolia, Asparagus albus, Lycium afrum,* and other low xerophytic shrubs. TYPE SPECIMEN. K. Lems No. 7061, deposited in the U.S. National Herbarium, Washington, D.C., with duplicates at Kew (Royal Botanic Garden) and Paris (Musée d'Histoire Naturelle).

Echium **lancerottense** nov. sp. (Fig. 7)—*Planta annua simplex vel sparsim ramosa, foliis rosulatis, petiolatis, ovatis, pilis erectis vel aliquando appressis; floribus caeruleis, dense pilosis, calyce lobis obtusis, apice purpuracentibus. Typus olim a cl. Pitard lectus in rupibus "Famara" dictis insulae Lancerottae, et sub nomine "Echium stenosiphon" (civis insularum caboverdensium) editus.*

Annual of variable height, ranging from 1 cm to about 25 cm, the stem simple, or with up to 2 basal branches and up to 6 inflorescence branches originating from the main stem; stems densely covered with long erect hairs, 0.5 to 3 mm long, and shorter appressed hairs. Basal leaves petiolate, ovate, blade 4–6 cm long, very densely covered by pubescence .5–2 mm long, the coverage up to 60%. Cauline leaves like the basal leaves, reduced upward in size. Calyx 4–7 mm long at anthesis the lobes obtuse, with dark blue tips, hispid. Corolla 10–13 mm long, the upper lobes about equalling the lower, often remaining closed even after pollen discharge; corolla densely pubescent outside. Annulus a 5 lobed ring, the upper two lobes longer than the lower three. Stamens included, or the lower two slightly exceeding the corolla.

DISTRIBUTION. Abundant on the northern part of Lanzarote, from Teguise to Haria. ECOLOGY. Chiefly above 300 m, up to 670 m, abundant in meadows with *Euphorbia obtusifolia* and *Odontospermum sericeum,* on flat soil with annual plants and on ledges of cliffs. TYPE. We designate as the type a collection made by J. Pitard at Famara, Lanzarote (Pitard 264), and deposited in the herbarium of the Missouri Botanical Garden, St. Louis. This collection has many duplicates in the herbaria of Europe, which may

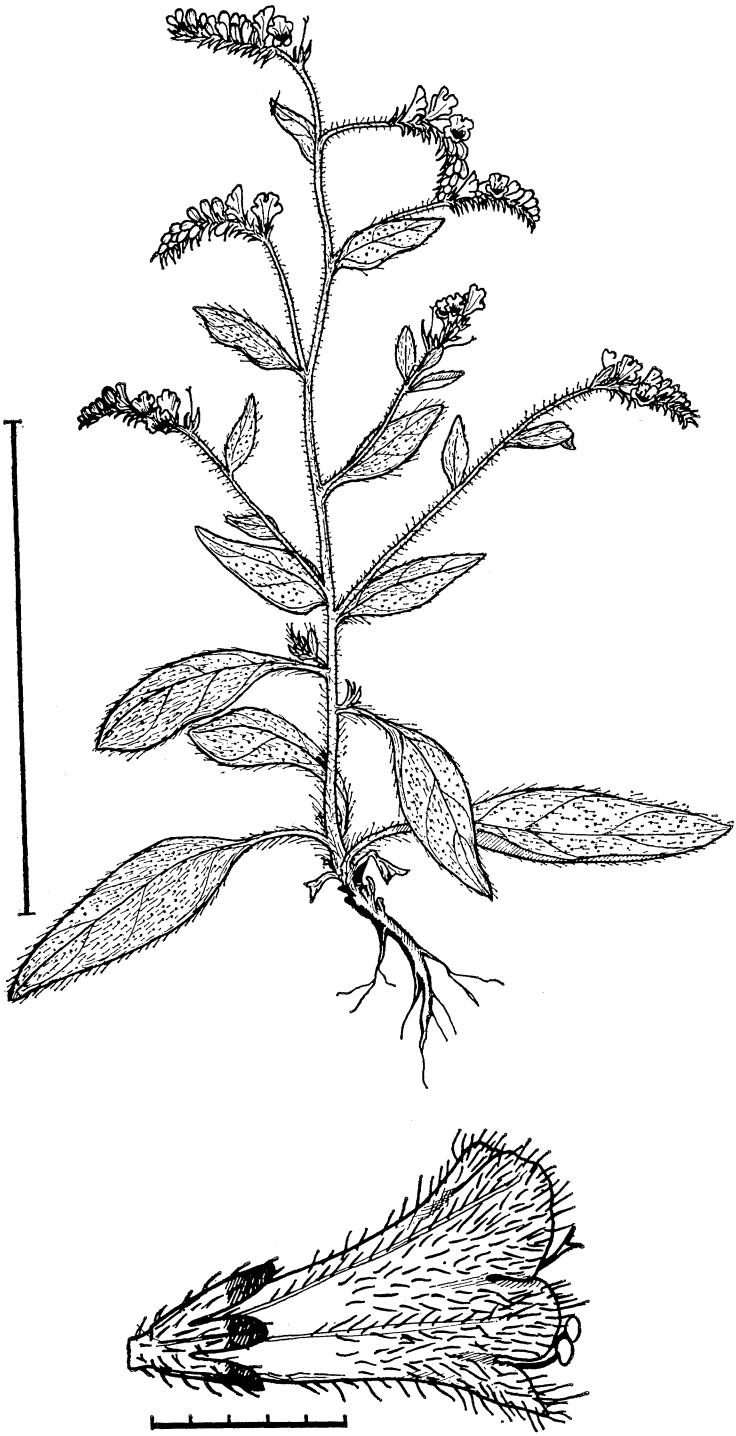

Fig. 7—*Echium lancerottense* nov. sp. (Pitard No. 264) from Famara, Lanzarote. Habit scale 10 cm, flower scale 5 mm.

be regarded as isotypes. Other materials of *E. lancerottense* are Lems No. 6597, 6654, 6676. Pitard No. 264 was the basis for the erroneous report (Pitard and Proust, 1908) of *E. stenosiphon* in the Canary Islands. This species, otherwise limited to the Cape Verde Islands, appears to be a half-shrub with branched woody stem, and tubular corollas with an annulus of five separate lobes (Fig. 1), while the Pitard collection is a branched annual with flared corollas and a ring-shaped lobed annulus. Differences in the trichome complement further confirm that Pitard was in error when he reported *E. stenosiphon* from the Canaries, and we propose that that species be deleted from the flora.

Echium **lancerottense** nov. sp. var. **macrantha** nov. var. (Fig. 8)—*Planta annua radice lignosa, caulibus herbaceis, pubescentibus pilis erectis; foliis rosulatis petiolatis subobtusis; floribus in inflorescentiis brevibus, speciosis coeruleis, usque 2 cm longis, calyce obtuse lobata, corolla sparsim pilosa, annulo inaequaliter 5-lobato. A typo differt habitu robustiori, floribus speciosis. Typus in solo arido loci "Mirador del Rio" dicti, prope pagum "Yé" insulae Lancerottae septentrionalis.*

Annual averaging 17 cm high, somewhat woody below the basal rosette, with several branches arising from the base and from the stems. Stems with erect hairs 0.5–2 mm long and some appressed ones. Leaves petiolate, ovate, up to 8 cm long with an obtuse or acutish tip, softly pubescent with pustular hairs 0.5–1.2 mm long covering 25% of the upper surface, denser below. Calyx 5–7 mm long at anthesis, to 9 mm in fruit, hispid, with obtuse lobes. Corolla blue, about 20 mm long, with sparse robust hairs above the flare, the lobes short-ciliate. Annulus of the corolla a continuous, lobed ring, the upper lobes prominent. Lower stamens exceeding the corolla, the upper 3 included.

DISTRIBUTION. Endemic to the northern tip of Lanzarote, on cliffs NW of Yé. ECOLOGY. On loamy soil at 500 m, with *Lotus lancerottensis, Limonium papillatum, L. pectinatum, Ononis hebecarpa.* Differs from the typical variety by its more robust habit, obtuse leaves, and showy corolla. TYPE. K. Lems No. 6760, from the cliffs of Mirador del Rio, near the village of Yé, northern Lanzarote, deposited in the U.S. National Herbarium, Washington, D.C.

Phytogeographic implications. Figures 9–12 illustrate the distribution patterns of the annual and biennial *Echium* species. Each of the species is associated with one of the major vegetation zones of the Canary Islands. These zones, discussed by many authors (Ceballos and Ortuño, 1951; Lems, 1958; Schmid, 1954, Oberdorfer, 1965; Dansereau, 1966) may be characterized by their dominant climax species as follows: Zone 1: *Launaea spinosa* desert, Zone 2: *Euphorbia regis-jubae* scrub, Zone 3: *Laurus canariensis* forest, Zone 4: *Pinus canariensis* woodland, Zone 5: *Spartocytisus nubigenus* scrub.

Launaea spinosa desert extends over much of Lanzarote and Fuerte-

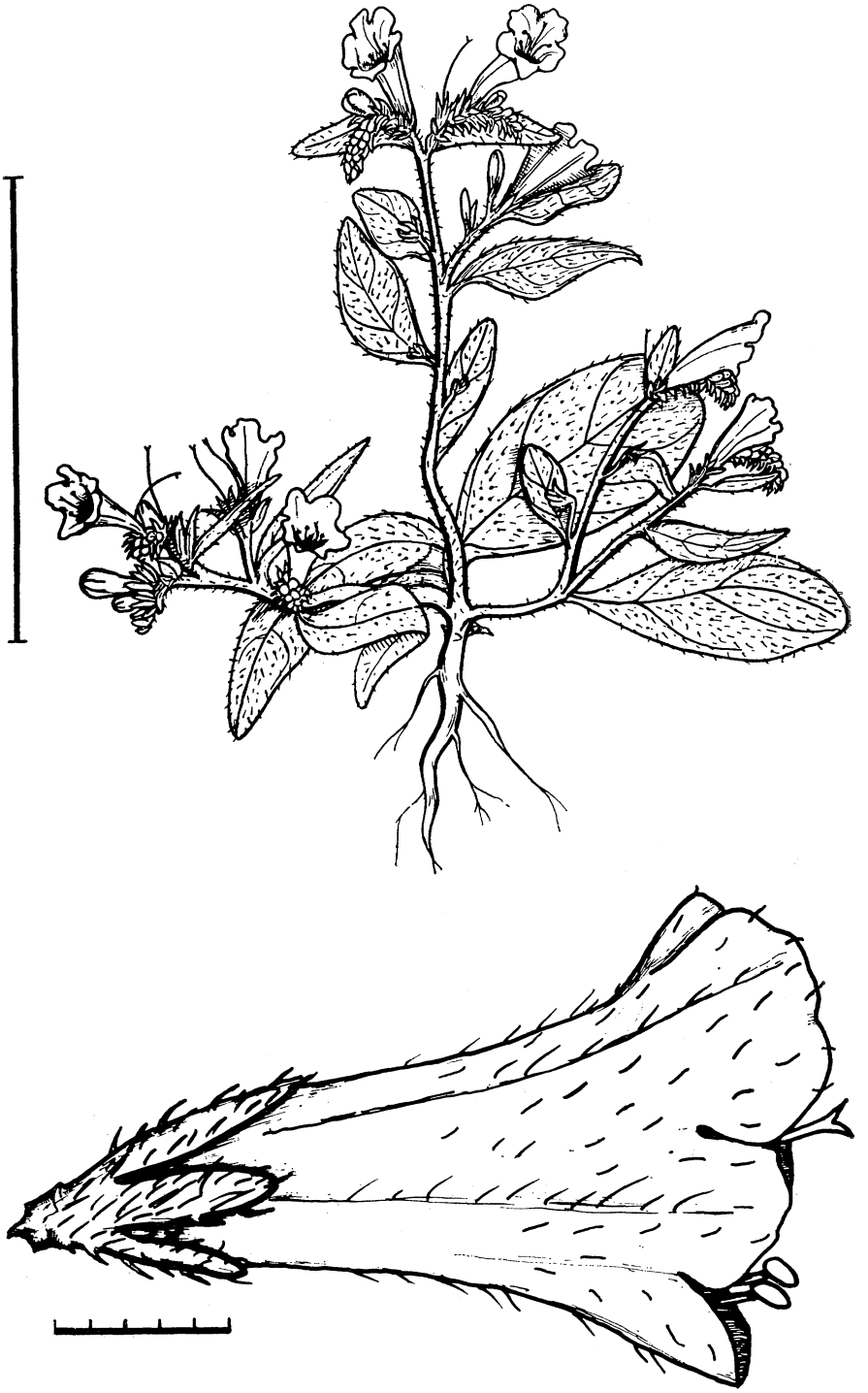

Fig. 8—*Echium lancerottense* nov. sp. var. *macrantha* nov. var. (Lems No. 6760) from Mirador del Rio, Lanzarote. Habit scale 10 cm, flower scale 5 mm.

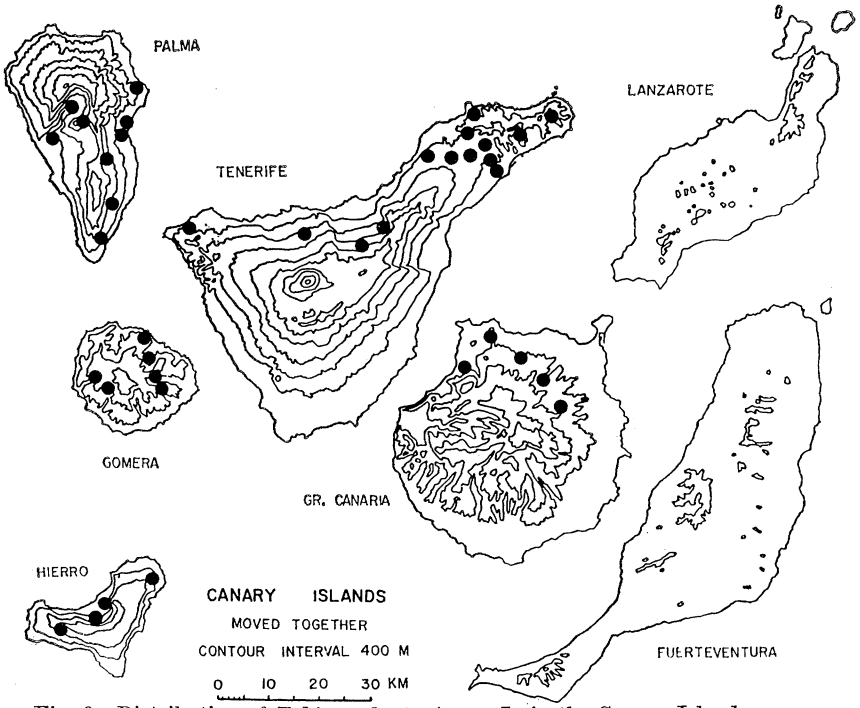

Fig. 9—Distribution of *Echium plantagineum* L. in the Canary Islands.

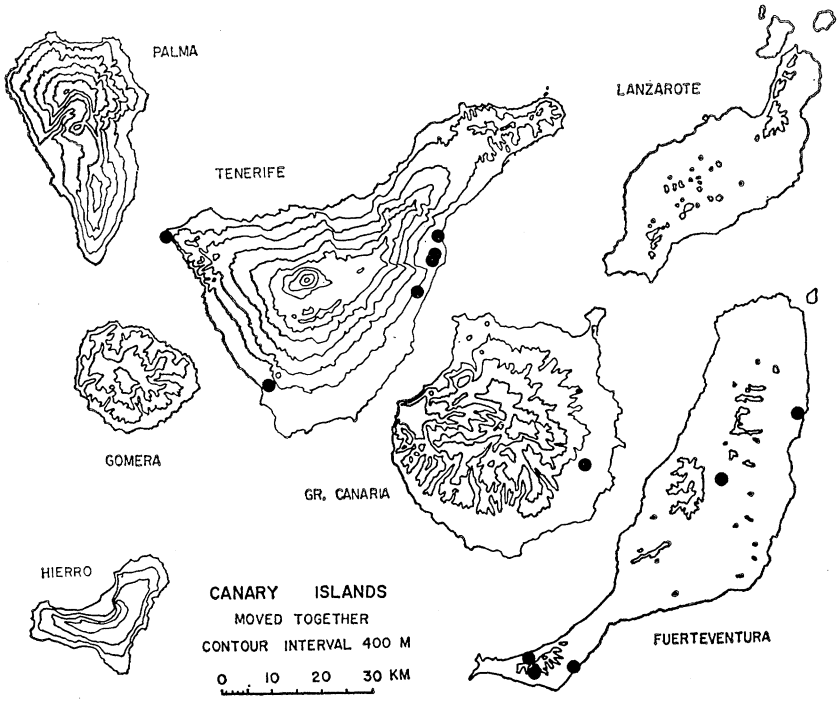

Fig. 10—Distribution of *Echium bonnetii* Coincy.

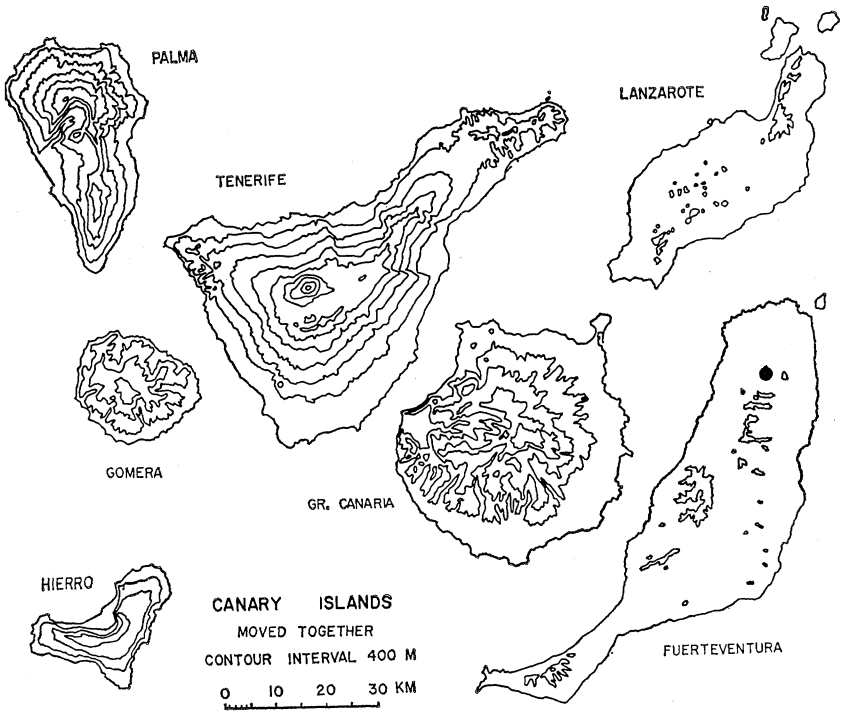

Fig. 11—Distribution of *Echium fuerteventurae* nov. sp.

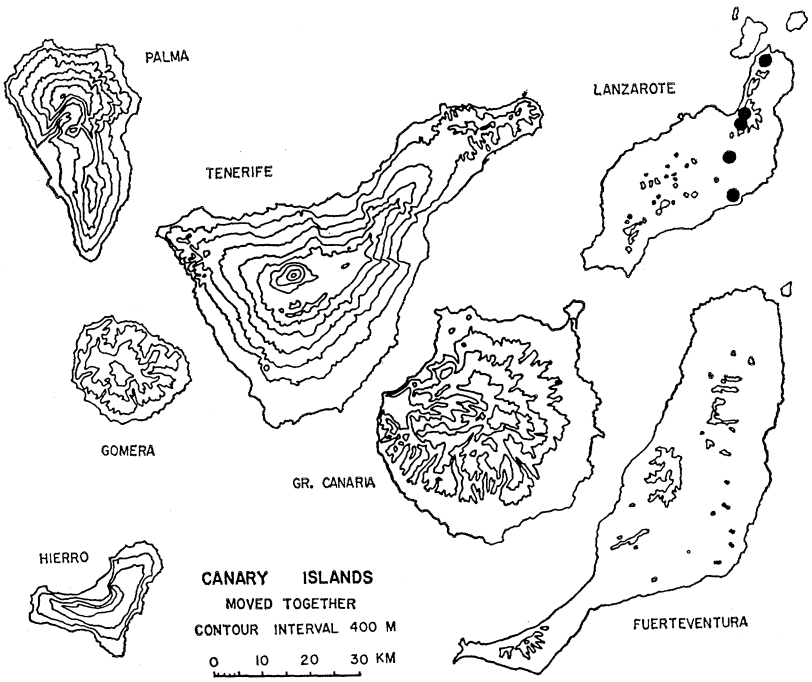

Fig. 12—Distribution of *Echium lancerottense* nov. sp.

ventura, the dry islands to the East, and occurs also near sea level on southern Gran Canaria and Tenerife (Oberdorfer, 1965). *Echium bonnetii* is found in communities of this belt (Fig. 10).

The *Euphorbia* zone is present on all of the Canary Islands, and is highly differentiated into local communities (Oberdorfer, 1965; Rivas Goday and Esteve Chueca, 1964). On Fuerteventura, *Echium fuerteventurae* occurs in a community of *Euphorbia regis-jubae, Kleinia neriifolia, Caralluma burchardii* and *Asparagus albus* (Fig. 11). On Lanzarote, *Echium lancerottense* is most common in a community of *Euphorbia obtusifolia* and *Odontospermum sericeum* (Fig. 12).

Echium plantagineum is found in the forested zones at mid-elevation, especially on the windward (N and E) sides of the islands (Fig. 9). In the *Laurus canariensis* zone very little of the original forest is left, and various degradation stages with *Myrica faya* and *Erica arborea* have replaced the climax vegetation. Pine woodland is more common, but degradation stages of *Cytisus proliferus, Cistus monspeliensis* and *Pteridium aquilinum* are not unusual. Open grassy spots in these zones are the habitat of *Echium plantagineum.* The forest zones do not extend to the eastern islands.

Two hypotheses may be advanced to explain the distribution of the several taxa of annual *Echium* on the Canary Islands. First, it may be supposed that the endemic species were derived from one original invader, the non-endemic *Echium plantagineum,* by adaptation to dry habitats. To explain the endemics on Lanzarote and Fuerteventura, one could assume that *E. plantagineum* was originally present on these islands. Berthelot (1836) reports stumps and other relicts of laurel forest, and suggests that the eastern islands were once forested along the highest crests. Since the dissappearance of the forest belt, the *Echium* population has adapted to the drier climates of the *Euphorbia* scrub zone and the *Launaea spinosa* desert zone. One argument against this explanation is that *E. plantagineum* is not a member of the natural vegetation, but rather a weedy plant found along roadsides, in open meadows, and other early stages of secondary succession. This means that it is probably a recent invader, and does not allow sufficient time for the evolution of several insular endemics.

A second explanation is that several invasions took place, *Echium plantagineum* taking hold in the western islands, and the ancestors of the other annual species on the eastern islands. The Lanzarote population evolved on the mountainous plateau in the North (Fig. 12) and gave rise to *E. lancerottense*; the Fuerteventura plants are more diverse, at higher elevations in the *Euphorbia* zone forming tall, slender growth forms (*E. fuerteventurae,* Fig. 11), those of the coastal lowlands in the *Launaea* zone much reduced in size of leaves, stems and inflorescences (*E. bonnetii*). Subsequently, *Echium bonnetii* invaded the driest, lowest parts of Gran Ca-

naria and Tenerife (Fig. 10), where the *Launaea* zone has a few outposts. It seems to us that the latter hypothesis, assuming at least two original invaders, is the most satisfactory.

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