

## EVOLUTION AND ENDEMISM IN ARGYRANTHEMUM Webb ex Schultz Bip. (Compositae: Anthemideae).

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### RESUMEN

C. J. Humphries: Evolución y Endemismo en *Argyranthemum* Webb ex Schultz Bip. (Compositae: Anthemideae).

1. El género *Argyranthemum* (Compositae: Anthemideae) está centralizado en las Islas Canarias, en donde 18 de las 22 especies se encuentran en 4 de las 5 zonas principales de vegetación. Otras 3 especies se presentan en el archipiélago de Madeira y una endémica en Las Islas Salvajes.

2. El género, es probablemente de origen Terciario, presentando un ejemplo de radiación adaptativa monofilética. Con respecto a la morfología los caracteres más adaptativos incluido leñosidad, hábito, forma y anatomía de la hoja y tamaño de la flor. En un extremo se encuentran con forma densa, arbustos muy lignificados perennes con amplia superficie de hojas y un largo capítulo, mientras que en el otro extremo se encuentran especies ligeras, poco ramificadas con ciclo de vida reducido, ligeramente leñosas y hojas muy divididas. El género puede ser dividido en 5 secciones discretas basándose en la morfología de la cipsela.

3. La distribución de las 5 secciones se correlacionan estrechamente con las zonas principales de vegetación y son así consideradas como representantes de viejas divergencias. Especies de las secciones *Sphenismelia* y *Stigmatotheca* probablemente poseen más atributos morfológicos antiguos que las especies de las otras secciones ecogeográficas y paleogeográficas.

4. Cada especie se compone de poblaciones aisladas morfológicamente pequeñas pero genéticamente amplias procurando una distribución «Rassenkreislehre».

5. La evolución ha sido un proceso gradual (todas las especies son diploides) por una vigorosa selección natural de los genotipos adaptables en gradientes ecológicos escalonados.

El aislamiento entre las diferentes especies ha sido enteramente influenciado por factores extrínsecos ecológicos y posiblemente geográficos. El aislamiento genético se ha originado sólo por la acumulación de genes disarmónicos y han retardado una amplia vía re-basando una divergencia morfológica y fisiológica.

6. Cada población tiene una clara ventaja selectiva en los habitats en que se encuentra. Los híbridos se han formado sólo en las áreas de alteración masiva a pesar de la evidencia de que existe una considerable transferencia de genes entre las poblaciones adyacentes.

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## INTRODUCTION

Of the 2500 species of flowering plants, which occur in the Macaronesian Islands, the Azores, Madeira, the Salvage Islands, the Canary Islands and the Cape Verde Islands some 600 species constitute the dominant endemic element (Bramwell, 1972; Sunding 1973). As pointed out by Bramwell (1972) the Canary Island endemics, and indeed the Macaronesian endemics as a whole fall into three main categories; the relicts or palaeoendemics, which are taxa surviving in a remnant of their former territory and have no easily identifiable relatives elsewhere, the neoendemics which have arisen by evolution in the Macaronesian Islands from various easily identifiable continental elements and the active epibiotics which are neoendemics derived from a palaeoendemic stock. Active epibiotics are morphologically and ecologically diverse, with representative taxa occurring in most principal habitats in a large number of the islands. *Argyranthemum* Webb ex Sch. Bip. is one such genus, consisting of twenty - two species distributed in 4 of the 5 major vegetation zones of the Canary Islands, the Salvage Islands and the islands of the Madeiran archipelago (Humphries 1973; 1975 (a)). In this paper an attempt has been made to examine why so many species of *Argyranthemum* occur in such a small total surface area and to give some idea of their evolutionary history in relation to ecology, geography and palaeogeography.

## ADAPTIVE RADIATION IN THE MACARONESIAN ISLANDS

The evolution of active epibiotics from the palaeoendemic flora has proceeded mainly by a process of adaptive allopatric divergence in response to the wide range of habitats and the isolated island condition characteristic of the Macaronesian region. Lems, (1960) and Bramwell (1972 (a) and (b)) have demonstrated various morphological trends associated with adaptive radiation in different endemic sections of Macaronesian genera such as *Aeonium* Webb & Berth. (Crassulaceae), *Sonchus* L. (Compositae) and *Echium* L. (Boraginaceae), suggesting that 'diversification of form in response to [selection] pressures, is a positive process where genetical response to the stimulus of the environment is the main factor'. Also, as an explanation for apparently random morphological variation in vicariant species of different localities, but in similar ecological habitats, Bramwell (1972) invokes genetic drift and weak selection as an explanation for divergence.

Evidence accumulated from ecological, morphological, cytological and hybridisation studies in *Argyranthemum* suggests that powerful differential selection in

steep ecological gradients with extremely narrow ecotones, i. e. external isolating mechanisms, has created an allopatric speciation pattern which accounts equally for divergence in widely different species as well as closely related vicariants. Comparison of distributions with palaeogeographical data suggests also that adaptive phenotypes can be directly equated with known geological events and provides partial dated evidence for the phylogenetic history of the genus.

#### THE TAXONOMIC POSITION OF *Argyranthemum*

Within the Anthemideae, *Argyranthemum* is one of the most distinctive Old World genera of the *Chrysanthemum* L. complex, closely allied to the Mediterranean sister group annuals of *Chrysanthemum* L. sensu stricto and *Heteranthemis* Schott. Morphologically these three genera can be distinguished from all others in the *Chrysanthemum* complex on the basis of their heteromorphic v. homomorphic cypselas and unmodified pericarp anatomy (Humphries, 1973). In turn all species of *Argyranthemum* can be distinguished from *Chrysanthemum* and *Heteranthemis* by their perennial habit, their unique bi - sporic embryo sac development (Harling, 1951; Borgen, 1972), and their flavonoid profile (Greger, 1969; Humphries, 1973).

The most closely related species of the sister group is *Chrysanthemum carinatum* Schousb., a distinctive North African endemic from the south Atlantic coast of Morocco. With *Heteranthemis viscidohirta* Schott, *C. carinatum* shares a similar cypselas morphology to the distinctive Canary Island laurel forest species *Argyranthemum broussonetii* (Pers.) Humphries, but is easily characterised by its annual habit, the tricoloured ray florets (yellow, white and maroon) the deep red corolla lobes of the disc florets, and the tetra - sporic embryo sac development. *A. broussonetii* has, together with the generic characters already mentioned, white ligules and yellow corolla lobes on the disc florets. The red pigmentation of the ligules and disc corolla lobes in *C. carinatum* is found also in another species of *Argyranthemum* section *Sphenismelia*; the Madeiran coastal endemic, *A. haemotomma* (Lowe) Lowe. It seems, therefore, that *Argyranthemum* has a morphological and phytogeographical link with the Mediterranean annual species of *Chrysanthemum*, this link being between the predominantly laurel forest and halophyte species of Macaronesia and a coastal species from the African continent.

This is interesting since Schmid (1955), considers *Argyranthemum* to have had its origins in the Mediterranean flora and possibly associated with the Miocene Laurel forest elements of Europe. These have been extinct since the Pliocene and now only exist as relictual fragments in the Western Canary Islands and Madeira.

#### GEOGRAPHY OF THE MACARONESIAN ISLANDS

The Canarian archipelago consists of seven major islands and five minor islets (Fig. 1) lying to the west of the Spanish Sahara and bordering the oval Atlantic depression known as the Canary Abyssal Plain (Heezen *et al.*, 1959). The Madeiran archipelago consists of the large island, Madeira itself, and a number of small volcanic islands, Chao, Deserta Grande and Bugio. About 50 km N. E. of Madeira lies Porto Santo and the islets of Ilheo de Fonte, Feno, Baixo, Limo and Pescardo. These islands

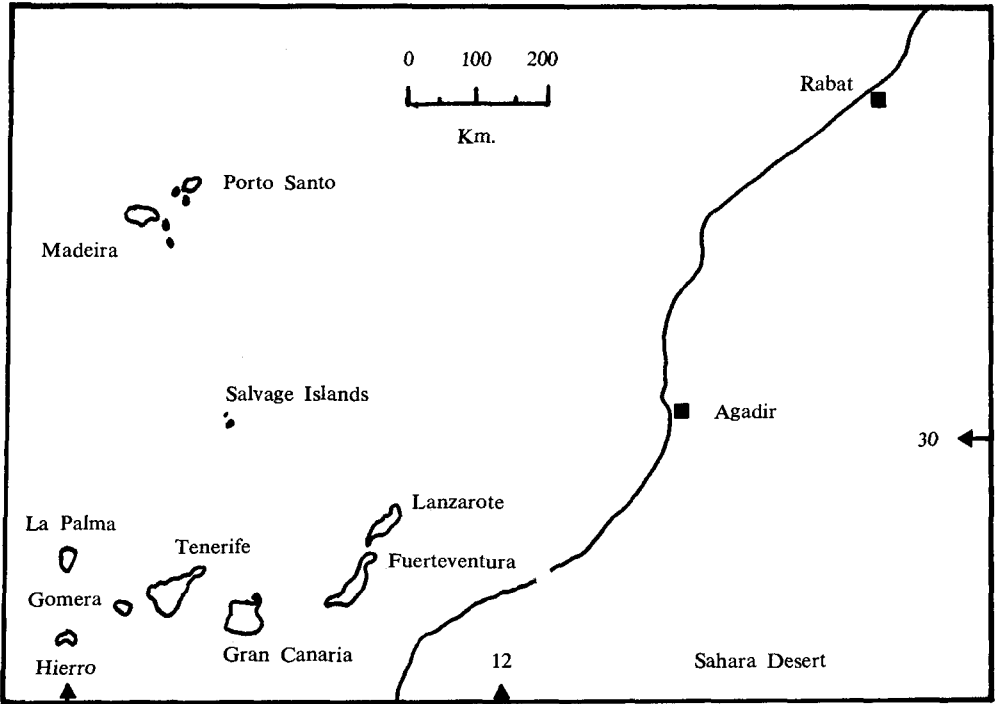


Fig. 1. Sketch Map showing the location of the north-east Atlantic Archipelagoes in relation to the African mainland.

are much more isolated than the Canaries group and border the huge Madeiran Abyssal plain 100 km west of Morocco and 500 km north of the Western Canary Islands. The Salvage Islands are situated between these two principal island groups lying about 200 km north of Tenerife.

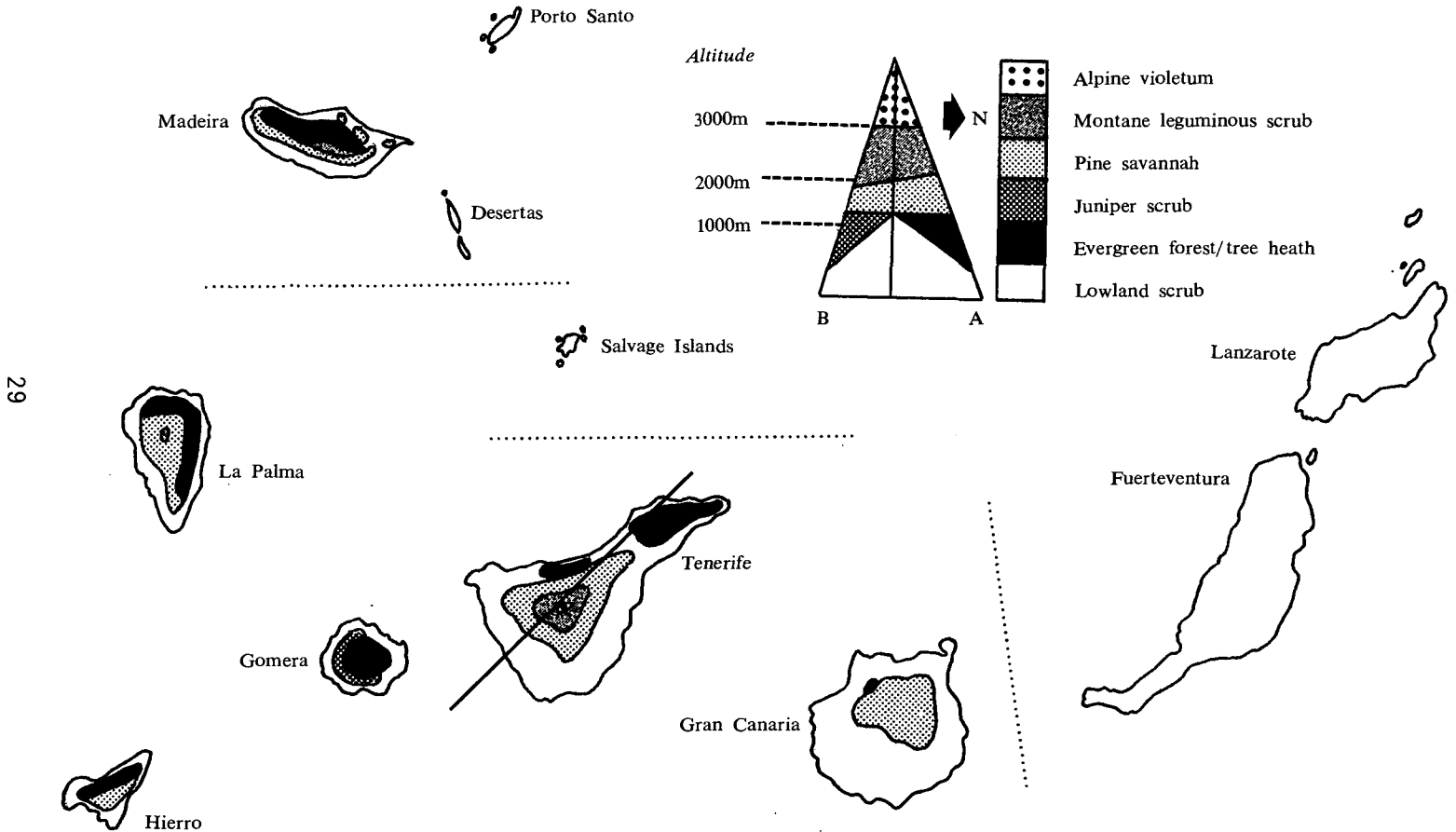
Details of the Azores and the Cape Verde archipelagos are omitted since they are not inhabited by any species of *Argyranthemum*.

#### ECOLOGICAL DIVERSITY IN THE MACARONESIAN ISLANDS

Details of the climatic and floristic elements, and the limits of the principal vegetation zones in the Macaronesian Islands and indeed the Canary Islands in particular have been discussed extensively by various authors (Webb and Berthelot, 1836 - 1850; Christ, 1885; Schenk, 1907; Ceballos and Ortuño, 1951; Lems, 1960; Cifferi, 1962; Oberdorfer, 1965; Bramwell, 1971, 1972 (a); Bramwell & Bramwell, 1974) and so are only briefly summarised here. The distribution of the vegetation zones is given in fig. 2 and Table 1 gives a summary of their characteristics.

The Canary Islands can be subdivided into two major phytogeographical regions. The eastern islands of Lanzarote, Fuerteventura, Lobos and Graciosa which constitute one region differ from the remainder of the archipelago in a number of ways. They all have a low elevation (max. altitude of 650m) and a low rainfall, consequently being very arid for much of the year. Being close to the African mainland, they tend

Fig. 2. Distribution of the main vegetation zones in the Canary Islands, the Salvage Islands and Madeira\*



\*Based on Ceballos & Ortuño, 1951 and Tibeiro, 1949

Table 1: Principal Vegetation Zones

Vegetation Zone	Altitude	Distribution	Habit
I. Macaro - alpine <i>Violetum</i>	2700 - 3500	Tenerife	Monotypic perennial herb, <i>Viola cheiranthifolia</i>
II. Sub - alpine leguminous scrub	1900 - 2700	Tenerife, Gran Canaria and La Palma	Small leaved shrubs including <i>Spartocytisus supranubis</i> , <i>Echium wildpretii</i> and <i>Argyranthemum tenerifae</i> .
III. Pine - savannah	800 - 1900	La Palma, Tenerife Hierro, Gran Canaria and Madeira	Dominated by <i>Pinus canariensis</i> in the Canaries but often broken down into sub - climax communities of <i>Chamaecytisus proliferus</i> and <i>Adenocarpus foliolosus</i> .
IV. Juniper scrub	S. slopes 400 - 600	La Palma, Tenerife Hierro and Gran Canaria	Small leaved shrubs dominated by <i>Juniperus phoenicea</i> .
V. Tree heath and Evergreen forest	400 - 1300	Hierro, La Palma, Gomera, Tenerife and Madeira	Predominately N. facing but on southern slopes in climatically favourable conditions. Broad leaved, evergreen trees and tree heaths.
VI. Lowland xerophytic scrub	0 - 600 ( - 800)	All Macaronesian islands	Important species in this very variable zone include stem and leaf succulents of the Euphorbiaceae and Crassulaceae. Other prominent families include Compositae, Caryophyllaceae and Liliaceae.

to be influenced by the Saharan climatic conditions. The western islands, however, are situated between 200 and 360 km from the continental coast. They are much less influenced by the Saharan conditions and have an equable oceanic climate. Their comparatively higher elevations (almost to 4000 m on Tenerife) together with prevailing northerly winds allows the development of a wide range of habitats in several distinct vegetation zones.

On northern aspects the climate is fairly warm and wet throughout the year as indicated by the presence of wet laurel forests on the mountain slopes and rich halophyte communities along the coastal cliffs. The southern aspects tend to be much less influenced by the prevailing north winds and are consequently arid throughout the summer months. Here, the lowland xerophytic zone extends to greater altitudes and intergrades directly with the pine (*Pinus canariensis* Chr. Smith) savannah zone.

The distinct vegetation zonation is best seen on Tenerife (fig. 2), the largest and highest of the Canaries archipelago, which is approximately 80 km in length, 50 kms wide at the widest point and rises to almost 4000 m. Localities above 1900 m are snow - covered for about 5 months of the year between November and April. The predominant vegetation of this zone consists of microphyllous shrubs, which eventually extends into a monospecific *Viola cheiranthifolia* H. B. and K., pseudo - alpine vegetation zone about 2700 m. The remaining vegetation zones of the islands can be subdivided into discrete montane and lowland zones. Much of the montane area consists of endemic Pine savannah (*Pinus canariensis*) but there are many other sub - climax communities, such as *Adenocarpus foliolosus* (Ait.) DC., *Erica arborea* L. and *Juniperus phoenicea* L. scrub. The lowland xerophytic zone is extremely variable in relation to local topographic and climatic conditions. At one extreme are the steep, sheltered inland cliffs (laderas) principally dominated by leaf and stem - succulent plants of the Crassulaceae and Liliaceae. At the other extreme are the *Polycarpea - Lotetum* communities on the 'coastal flats' of the east coasts of Tenerife and Gran Canaria. Between these two extremes many other communities exist but for the most part, the dominant vegetation of the lowland xerophytic zone consists of several endemic stem - and leaf - succulent perennials of the Euphorbiaceae (*Euphorbia* L.), the Compositae (*Kleinia* L.) candelabra shrubs of the Boraginaceae (*Echium*) and many therophytes.

Madeira, like the western Canary Islands is very much influenced by the northern prevailing winds. However, it does not have discrete vegetation zones but has gradual transitions from the upland evergreen forest and subclimax *Erica arborea* heath down to the wet, coastal halophyte communities and lowland xerophytic scrub. The island is fairly warm and wet all year round but the south facing slopes tend to be hotter than the north facing slopes in the summer months when the streams dry up.

The vegetated Salvage Islands of Great and Little Piton are little more than sand banks in comparison to Madeira and the Canaries, with various parts sometimes becoming completely covered by the sea at high tides. The halophyte communities which are to be found on the rocky Great Salvage are very exposed and have a similar climate to the lowland north - facing xerophytic zone communities of the western Canary Islands.

TABLE 2:

Synopsis of classification of *Argyranthemum* according to Humphries (1975a), together with geographical distribution and summary of ecology [Figures refer to number of each vegetation zone given in Table 1]

Genera/Species	*Island Distribution	Vegetation Zone (Sec Table 1)	Ecology
<p><i>Argyranthemum</i> Webb ex Schultz Bip.                      Section <i>Argyranthemum</i>  <i>A. frutescens</i> (L.) Webb ex Schultz Bip.                          subsp. <i>frutescens</i>                          subsp. <i>succulentum</i> C. J. Humphries                          subsp. <i>gracilescens</i> (Christ) C. J. Humphries                          subsp. <i>parviflorum</i> C. J. Humphries                          subsp. <i>foeniculaceum</i> (Pitard) C. J. Humphries                          subsp. <i>canariae</i> (Christ) C. J. Humphries                          subsp. <i>pumilum</i> C. J. Humphries  <i>A. lemsii</i> C. J. Humphries  <i>A. haouarytheum</i> C. J. Humphries &amp; D. Bramwell  <i>A. foeniculaceum</i> Webb ex Schultz Bip.  <i>A. gracile</i> Webb ex Schultz Bip.  <i>A. tenerifae</i> C. J. Humphries  <i>A. maderense</i> D. Don  <i>A. winteri</i> (Svent.) C. J. Humphries  <i>A. lidii</i> C. J. Humphries  <i>A. sventenii</i> C. J. Humphries &amp; A. Aldridge  <i>A. dissectum</i> (Lowe) Lowe  <i>A. thalassophilum</i> (Svent.) C. J. Humphries  <i>A. callichrysum</i> (Svent) C. J. Humphries                      Section <i>Sphenismelia</i>  <i>A. coronopifolium</i> (Willd.) Webb ex Schultz Bip.</p>	<p>T, GC, LP                      T                      T                      T, GO                      GO                      GC                      GC                      T                      LP                      T                      T                      T                      L                      F                      GC                      H                      M                      SI                      GO                      T</p>	<p>VI                      VI                      VI                      VI                      VI                      VI                      VI                      VI - V                      III - VI                      VI                      VI                      II                      VI                      VI                      VI                      VI                      VI                      VI                      VI                      VI</p>	<p>open coast                      coastal halophyte                        distributed in coastal habitats                      coastal halophyte                      coastal cliffs                      open clearing                      Pine forest to coast                      cliff chasmophyte                      coast                        coastal cliffs, sand dunes                      mountains of Handia                      west coast cliffs                      dry south slopes                      coastal                      coastal halophyte                      montane scrub                        coastal cliff halophyte</p>



TABLE 2: cont.

Genera/ Species	*Island Distribution	Vegetation Zone (See Table 1)	Ecology
<i>A. broussonettii</i> (Pers.) C. J. Humphries subsp. <i>broussonetti</i> subsp. <i>gomerensis</i> C. J. Humphries <i>A. hierrense</i> C. J. Humphries <i>A. webbii</i> Schultz Bip. <i>A. haemotomma</i> (Lowe) Lowe	T GO H LP M	V V V - VI V V	open clearings coastal cliffs laurel forest coastal cliffs
Section <i>Stigmatotheca</i> <i>A. pinnatifidum</i> (L. fil.) Webb ex Schultz Bip. subsp. <i>pinnatifidum</i> subsp. <i>succulentum</i> (Lowe) C. J. Humphries	M M	V - VI VI	widespread in lowland and forest zones
Section <i>Monoptera</i> <i>A. filifoliums</i> (Schultz Bip.) C. J. Humphries <i>A. escarrei</i> (Svent.) C. J. Humphries	GC GC	VI III	dry scrub montane scrub
Section <i>Preauxia</i> <i>A. adauctum</i> (Link) C. J. Humphries subsp. <i>canariense</i> (Schultz Bip.) C. J. Humphries subsp. <i>gracile</i> (Schultz Bip.) C. J. Humphries subsp. <i>jacobaefolium</i> (Webb ex Schultz Bip.) C. J. Humphries subsp. <i>dugourii</i> (Bolle) C. J. Humphries subsp. <i>adauctum</i> subsp. <i>erythrocarpon</i> (Svent.) C. J. Humphries	GC GC GC T T H	III - VI III - VI III III III III	pine forest to open scrub montane scrub pine forest pine forest

\* Key to Islands: T - Tenerife, Go - Gomera, H - Hierro, M - Madeira, GC - Gran Canaria, F - Fuerteventura, SI - Salvage Islands, LP - La Palma, L - Lanzarote.

## TAXONOMY AND ADAPTIVE MORPHOLOGICAL TRENDS IN ARGYRANTHEMUM

The taxonomy follows that of Humphries, 1975 and so will not be discussed in detail here. Table 2 gives a synopsis of the sections and recognised species together with a brief summary of their ecology and distribution in the Macaronesian Islands. Fig. 3 gives the distribution of the four Canary Islands sections and section *Stigmatotheca* in Madeira. As can be seen they have a distinct correlation with the principal vegetation zones. The degree of variation in morphology, distribution and ecology differs widely from section to section. Section *Argyranthemum* is the most widespread, with thirteen species distributed throughout the Canary Islands, Madeira and the Salvage Islands. Most species occur in the lowland xerophytic zone but a few, e.g. *A. haouarytheum* and *A. callichrysum* occur in montane areas and *A. tenerifae* can be found in the subalpine leguminous scrub of Tenerife (table 2). Section *Sphenismelia* is restricted to north facing montane areas and lowland cliffs on all of the western Canary Islands, except for *A. haemotomma* which can be found on Madeira. Most localities are situated in open laurel forest or on coastal cliffs in areas of considerable geological antiquity. The monotypic section *Preauxia* is found primarily in pine forests of Gran Canaria, Tenerife and the broad leaved evergreen forest on Hierro, but also extends to lowland xeric areas in the south of Gran Canaria. Section *Monoptera* is the most restricted of the genus and is confined to xerophytic scrub communities on S. W. slopes of Gran Canaria.

Phenotypic variation of infra-sectional taxa in such characters as degree of woodiness, habit, leaf shape and capitulum diameter can readily be explained in terms of adaptive trends associated with ecological conditions. Support for natural selection of highly adaptive populations is provided by examples of convergent morphologies in species of the same and different sections which grow in habitats of similar ecological amplitude. To explain regional responses to natural selection a scheme is presented in Fig. 4, wherein the overall adaptive trends are derived from a basic type.

In the Canary Islands *A. broussonetii* has close associations with Miocene basalt rocks and relict laurel forest habits (see fig. 5) and is thought to have the least derived morphological attributes (see p. 47). The lignified stem is shared by all taxa of the genus but not at all by close continental relatives of the *Chrysanthemum* complex and is thus considered to be a relictual character state now only suited to the island condition. Similar conclusions for other general have been reached by Meusel (1952), Lems (1960) and Bramwell (1972 (a)). The most woody species of the genus is *A. broussonetii*, presumably since it is a species of the laurel forest, which allows growth more or less continually through the year. Consequently, the characteristic shrubby habit of *Argyranthemum* is most developed in this species. Some plants of *A. broussonetii* from the Anaga peninsula on Tenerife grow up to 6 m in diameter and up to 2 m in height. The bipinnatifid petiole or sessile ovate leaves are of a very unreduced type being perhaps only one step removed from the large ovate, more or less entire or slightly toothed leaves to be found in the most taxonomically isolated species of the genus, *A. pinnatifidum* from Madeira.

From this relatively unmodified form in *A. broussonetii* it is possible to derive a number of independent, adaptive morphological trends. In lowland arid environments reduction in lignification, habit, capitulum size and leaf area produces forms of the B and C type (fig. 4), such as *A. frutescens* subsp. *gracilescens* and *A. gracile*

Fig. 3. The distribution of sections and species density in *Argyranthemum*

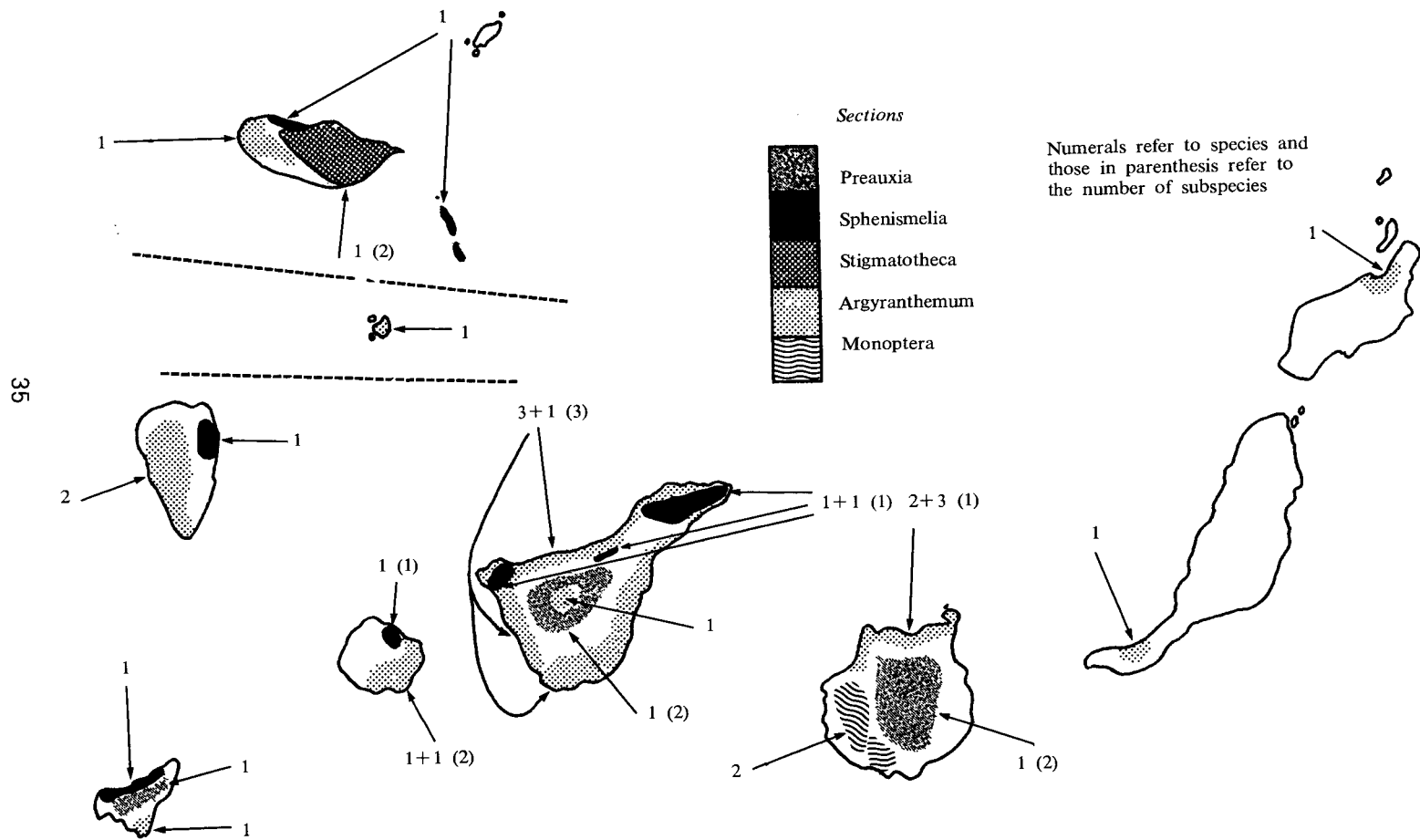


Fig. 4 Adaptive trends in Leaf shape, Habit and Capitulum Diameter in *Argyranthemum*.

<i>Species</i>	<i>Ecology</i>
A <i>A. broussonetii</i>	
A1 <i>A. adactum</i> subsp. <i>jacobaeifolium</i>	sheltered, warm wet forest.
A2 <i>A. pinnatifidum</i>	
B <i>A. frutescens</i> subsp. <i>frutescens</i>	xerophytic zone
C1 <i>A. folifolium</i>	
C2 <i>A. frutescens</i> subsp. <i>gracilescens</i>	arid, south facing slopes of
C3 <i>A. gracile</i>	xerophytic zone
D <i>A. tenerifae</i>	sub - macaro - alpine zone
E1 <i>A. pinnatifidum</i> subsp. <i>succulentum</i>	
E2 <i>A. coronopifolium</i>	halophytic coastal cliffs of the north
E3 <i>A. maderense</i>	facing slopes of the xerophytic zone
E4 <i>A. frutescens</i> subsp. <i>succulentum</i>	
F <i>A. adactum</i> subsp. <i>adactum</i>	arid, high montane regions
G <i>A. foeniculaceum</i>	low montane (xerophytic zone) in sheltered ladera.

EVOLUTION AND ENDEMISM IN ARGYRANTHEMUM

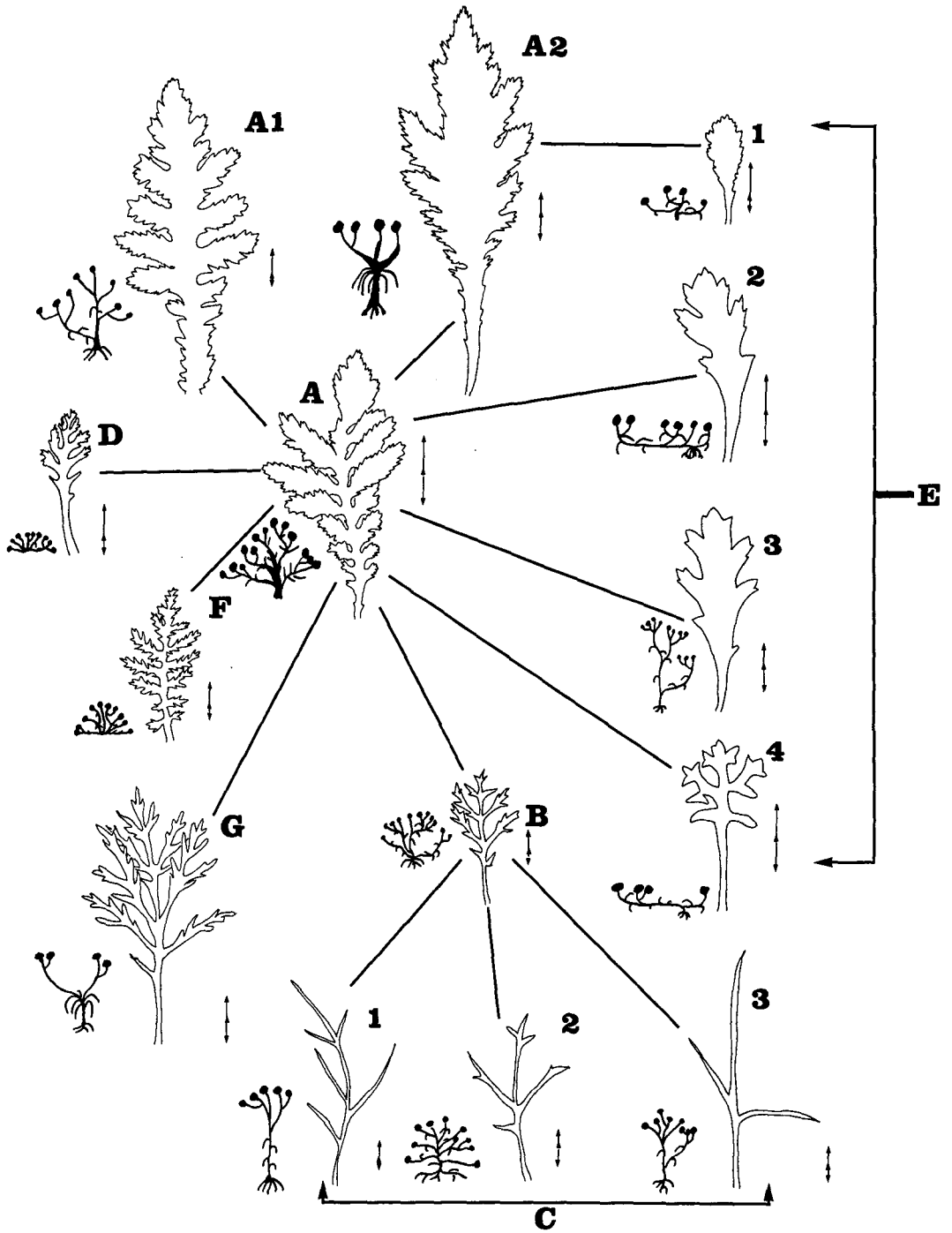
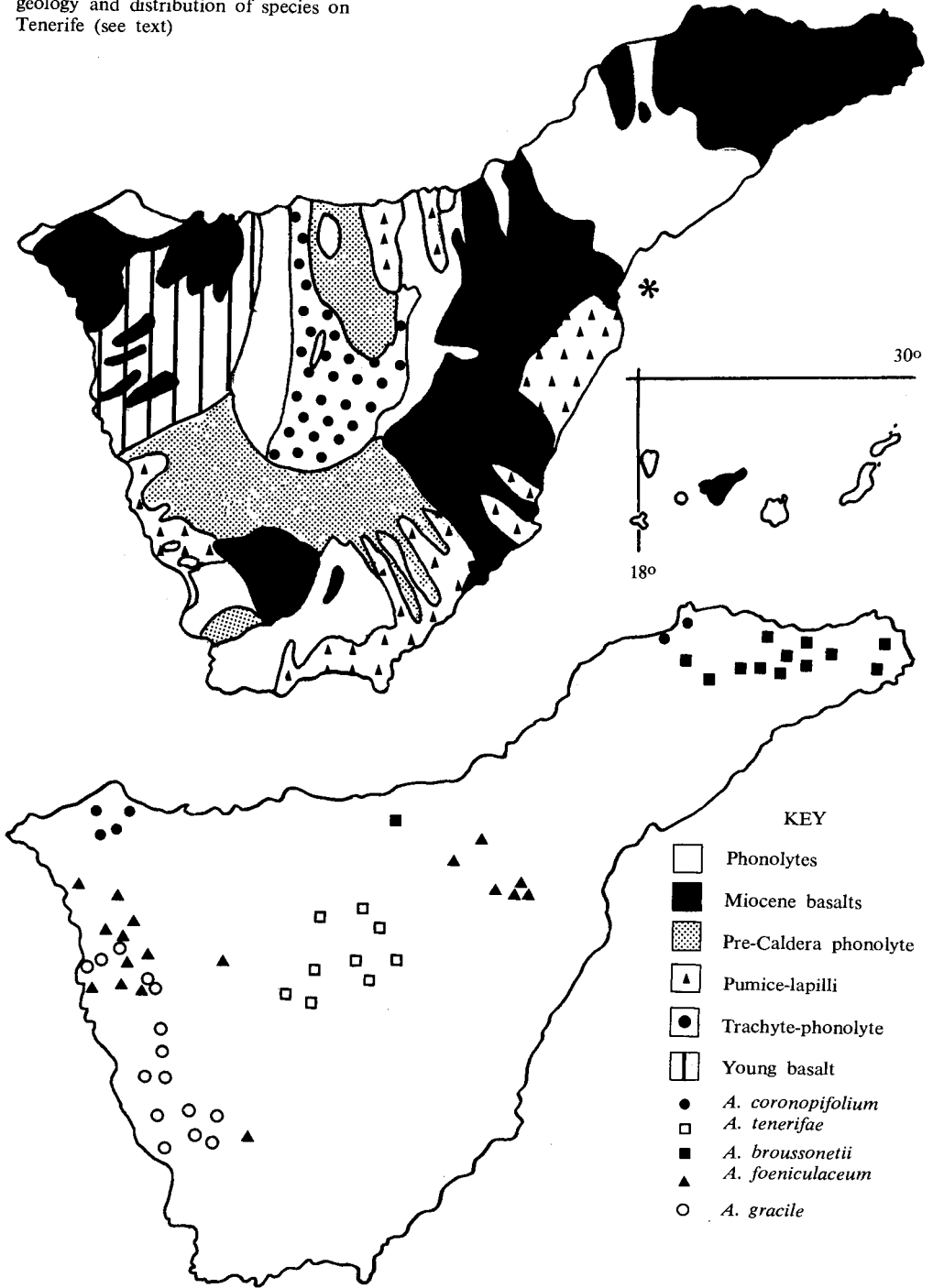


Fig. 5. The Relationship between volcanic geology and distribution of species on Tenerife (see text)



\* After Hausen, 1955

on Tenerife, *A. frutescens* subsp. *parviflorum*, *A. adauctum* subsp. *gracile* on Gran Canaria and *A. sventenii* on Hierro. Plants of very xeric conditions discontinue growth after shedding seed at the end of spring and remain fairly inactive during the hot summer months. They tend to be short lived and only become lignified at the base of the stems. The extreme condition can be found in *A. filifolium* (type C), a species often consisting of a single, slender unbranched stem up to about 1 cm in height, with trifid, pinnatisect, filiform leaves and extremely small flowers.

A reduction trend also occurs in taxa of subalpine and high montane environments (type D). Here, *A. tenerifae* and *A. adauctum* subsp. *dugourii* are unable to grow for up to 5 months of the year owing to persistent snow cover in the Cañadas region of Tenerife. Old shoots die down after flowering at the end of the year and new ones are produced each year from low lying stems which are only woody at their bases. The leaves of these species are both again highly dissected and tend to have increased hairiness at the higher altitudes. The flowers are moderately small and the plants set seed in a matter of four or five months.

In exposed north coastal areas of the Canary Islands plants of type E (fig. 4) with a reduced habit, pinnatifid or pinnatifid leaves and increased succulence, large capitula, and reduced inflorescences can be found. Characteristic species of this type include *A. coronopifolium*, *A. frutescens* subsps. *canariae* and *succulentum* and *A. maderense*. In very exposed places the stems can be very short or procumbent and adpressed to the substrate. It can be seen in figs. 3 and 4 that taxa from similar environments in different localities on one or more islands develop similar morphological adaptations. For example, the spectacular *A. broussonetii* of the laurel forests of Tenerife and Gomera is replaced in the laurel forest of La Palma by its most closely related but nevertheless quite distinct species *A. webbii*. Similarly, *A. adauctum* (type A1, fig. 4) is the dominant species of montane habitats of Gran Canaria, Tenerife and Hierro. Despite its great variability in form it is replaced in similar habitats on La Palma by *A. haouarytheum* and on Gomera by the montane endemic *A. callichrysum*.

Species of *Argyranthemum* sect. *Monoptera* are very distinct from all other sections of the genus but it is quite clear that *A. filifolium* from the lowland xeric *Euphorbia* scrub of Gran Canaria has a convergent morphology with *A. frutescens* subsp. *gracilescens* and *A. gracile* from comparable arid environment on Tenerife. Similarly, south slope upland ecotype specimens of *A. adauctum* subsp. *dugourii* from Tenerife have frequently been named as the sub - alpine *A. tenerifae* on the basis of convergent vegetative morphology when in fact both species are quite distinct when flowering and fruiting material is available.

Other convergent pairs include the Grand Salvage coastal species *A. thalassophilum* which is superficially very similar to *A. frutescens* subsp. *frutescens* on Tenerife and Gran Canaria, and *A. winteri* from the Handia mountains of Fuerteventura, which closely resembles *A. lidii* from the west facing cliffs of the Tamadaba Massif on Gran Canaria.

#### MACARONESIAN PALAEOGEOGRAPHY

Extensive geological studies on the Canary Islands have recently been summarized by Hausen (1955, 1958, 1959, 1962, 1965 and 1971) and also by Bourcart (1946).

The Canary Islands combine volcanic and tectonic origins since the two major eastern islands of Fuerteventura and Lanzarote and the islets Graciosa and Lobos are considered to have originated from the Ifni Gap on the African mainland and the western group to be a line of islands resulting from Eocene (or Cretaceous) to Pliocene (and later) volcanism after continental seafloor spreading of the major continents. Volcanic rocks overlie the eastern islands (Watkins *et al.*, 1966; Engel *et al.*, 1955) and totally comprise the western islands of Gran Canaria, Tenerife, Gomera, La Palma and Hierro. The oldest volcanic rocks have been reported from La Gomera (Hausen, 1962) where possible Cretaceous 'basement complexes' have been exposed in a number of localities. The youngest volcanic rocks derived from recent lava flows have been dated most accurately from known historical eruptions. The Las Cañadas, for example, dominating the central volcanic region of Tenerife, is a remnant of a vast Quaternary complex resting on a basement Tertiary or Cretaceous complex. The central cone (Pico de Teyde) has produced radial flows as recently as 1704, 1798, and 1909 (Macfarlane and Ridley, 1968).

Recent geological records for Madeira and the Salvage islands are much more scanty. But, like the western Canary Islands they are of truly oceanic volcanic origin and date back to the early Tertiary or late Cretaceous periods. In the same way they have also been covered by more recent overlays of Pliocene and later volcanic rock (Bourcart, 1946).

#### PALAEOGEOGRAPHY AND DISTRIBUTION IN ARGYRANTHEMUM

In a limited way Macaronesian palaeogeography helps to determine the distribution of particular taxa and in some cases provides crude evidence for dating the origin of some species. Thus, distinctive taxonomically isolated phenotypes occurring on old rocks possibly resemble some of the earliest divergences within the genus. Species such as *A. pinnatifidum*, *A. maderense*, *A. broussonetii* and *A. foeniculaceum* are all found in habitats composed of basal rocks of relative antiquity. For example, populations of *A. broussonetii* are confined entirely to the laurel forests overlying the Miocene basalt formations of Tenerife (fig. 5) and La Gomera. Also, the present day disjunct distribution of the cliff chasmophyte *A. foeniculaceum* (fig. 5) correlates exactly with the present day distribution of Miocene basalt rocks. Between the disjunction lies a more recent covering of Pliocene basalt and volcanic lava from the Quaternary epoch. *A. foeniculaceum* was presumably once distributed throughout the region between the two population groups but has been prevented from re-invading the intermediate regions simply by the drastically changed ecological conditions and possibly by competition from species better adapted to the more recent habitats. It is interesting that the two population groups are more or less identical and cannot be subdivided into separate taxa. For this reason alone the outlined hypothesis of events is favoured rather than one involving a more adaptive species inhabiting areas of ecological preference since all other taxa of obligate ecology show different morphological trends in geographically distinct population groups.

*A. tenerifae* is one of the most distinctive species of *Argyranthemum* separated easily from all other species by its loose fitting triangular involucre bracts, wide petioles and cushion habit. Its habitat in the sub-alpine reaches of Tenerife is composed entirely of extremely young rocks produced by volcanic activity of the



Quaternary period to present day historical eruptions. *A. tenerifae* therefore, represents either a relatively recent adaptation to the Cañadas region or an adaptive immigrant now extinct in its source localities (fig. 5).

Another interesting example on Tenerife is that of *A. gracile*. Pliocene lava from the eruptions of Teide has run down the mountain side to form an overlying coastal shield on the south western platform of the island. *A. gracile* is almost entirely restricted to habitats associated with this characteristic substratum whilst being absent from the older rocks that flank it on either side.

#### CYTOLOGY

All of the 16 species of *Argyranthemum* so far examined cytologically have the same chromosome number,  $2n=18$ , and similar karyotype morphology (Humphries, 1973, 1975 (b)). The same diploid number and karyotype symmetry is common to many other related genera within the Anthemideae and thus provides no obvious clue to the origin or coherence of the species within the genus.

Studies of pairing behaviour of chromosomes at meiosis are much more useful in *Argyranthemum* since they indicate that there is some genetic and cytological control of population variability (Humphries, 1975 (b)). It has been shown that significant differences in chiasma frequencies (and hence adjustments in the degree of recombination) occur between individuals and populations and are the principal regulating devices for control of variability. Pioneer populations of widespread species and isolated populations of narrow endemics such as *A. filifolium* and *A. lidii* tend to have a high chiasma frequency and hence increased chances of recombination. Large populations of variable species, for example *A. adauctum* and *A. frutescens*, on the other hand, were observed to have a much lower chiasma frequency and in some cases up to 25% of the dividing pollen mother cells exhibited a single reciprocal translocation between non-homologous chromosomes.

The high chiasma frequency of the pioneer or specialised endemic is interpreted to be a compensatory device for increasing flexibility in plants with depleted variability, i. e. those which are relatively homozygous, and inversely as a conservation mechanism for well adapted genotypes in the more variable taxa with low chiasma frequencies and structural heterozygosity. It seems that such fluctuations in chiasma frequency provide a very effective genetic control of variability in natural populations and hence adaptability in a diploid genus with species of the same genomic constitution.

#### ARTIFICIAL HYBRIDS AND CROSSING RELATIONSHIPS

There are no previous reports of hybridisation experiments within the Anthemideae involving species of *Argyranthemum*. However, accounts of artificial crosses within other genera of the *Chrysanthemum* complex have indicated that many species of quite diverse origin are fairly easy to hybridise (Shimotomai, 1933; Villard, 1970). Wide crosses in the *Matricaria* L. group of the Anthemideae (Mitsuoka and Ehrendorfer, 1972) have shown that geographically and morphologically remote genera are quite closely related. All attempts to cross Canary Island species of *Argyranthemum* with related continental genera, including *Chrysanthemum* L. sensu stricto, *Coleos-tephus* Cass., and *Tanacetum* L. have failed.

Table 3 F<sub>1</sub> Crossing Relationships between Canary Island Species of *Argyranthemum*

A. frutescens subsp. canariae	1																	
" " "	2	+																
" " parviflorum	3	+	+															
" " frutescens	4	+	+	+														
" " gracilescens	5	+	+	+	+													
" " foeniculaceum	6	+	+	+	X	X												
" " "	7	+	+	+	X	o	o											
" " frutescens	8	+	o	+	+	o	+	o										
A. gracile	9	+	o	+	o	+	+	+	X									
A. haouarythemum	10	+	+	X	o	o	o	X	X	o								
A. maderense	11	+	+	+	+	+	+	o	o	+	o							
A. callichrysum	12	+	o	+	+	+	+	o	o	+	+	-						
A. foeniculaceum	13	+	X	X	+	+	o	+	X	+	X	+	X					
A. filifolium	14	+	+	+	+	+	+	•	+	+	+	-	•	-				
A. broussonetii	15	-	-	o	-	-	X	-	-	-	X	X	-	-	-			
A. adauctum	16	-	-	-	o	-	-	-	-	X	-	X	-	-	-			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16

+ Normal Fertile Hybrids (F<sub>1</sub>)  
 • Abnormal weak plants  
 o Normal fruit, inviable seed  
 - Wrinkled fruit, abortive embryos  
 X pollination failures, unattempted crossed

Infra-generic crosses, on the other hand produced many fertile hybrids and results from 900 attempts of artificial hybridisations on 16 diverse populations are summarized in Table 3. Detailed accounts of the methods and analysis of the data are given in Humphries (1973).

The results can be briefly considered in four ways i) Crossability expressed in terms of fruit set; ii) morphology and vitality of hybrids; iii) pollen fertility in hybrids; iv) meiosis in pollen mother cells of hybrids.

i) *Crossability expressed in terms of fruit set*: Normal cypselas containing viable embryos are not usually produced in the crosses between *A. broussonetii* of sect. *Sphenismelia* (pop. 15) and *A. adauctum* of sect. *Preauxia* (pop. 16) nor with species belonging to sects. *Argyranthemum* (pops. 1 - 13) and *Monoptera* (pop. 14). These inter-sectional crosses usually produced abortive, wrinkled fruit, but two apparently good crosses involving female plants of *A. frutescens* subsp. *frutescens* and pollen from *A. broussonetii* and *A. adauctum* (Table 3) had a few normal cypselas but these later failed to germinate.

Other crosses involving intra- and interspecific hybridisations in sect. *Argyranthemum* and intersectional crosses between species of sect. *Argyranthemum*, *A. coronopifolium* of sect. *Sphenismelia* (see p. 46) and *A. filifolium* of sect. *Monoptera* showed little evidence of barriers to gene exchange. The apparently random failures which did occur and the overall general reduction of cypselas production were considered to be the result of unsuccessful pollinations rather than the result of disharmonious interactions.

ii) *Hybrid morphology and vitality*: In nearly all cases of successful crosses the hybrids developed as normal plants of intermediate morphology between the parents. However, in some F<sup>1</sup> crosses e. g. *A. frutescens* subsp. *foeniculaceum* *A. filifolium* and *A. filifolium* x *A. callichrysum* chlorotic and dwarf individuals were produced. Similar individuals were obtained in F<sup>2</sup> generations obtained by selfing F<sup>1</sup> hybrids of the crosses *A. ochroleucum* x *foeniculaceum* and *A. frutescens* subsp. *frutescens* x *foeniculaceum*. One F<sup>1</sup> plant raised from the cross *A. frutescens* subsp. *frutescens* x *callichrysum* produced abnormal capitula without any florets. The involucre bracts and receptacle appeared to be fairly normally developed but were dwarfed in comparison to other capitula having well developed florets. Plants from the reciprocal cross when *A. callichrysum* was the maternal parent were completely normal with high pollen fertility.

iii) *Pollen fertility in the hybrids*: The pollen fertility of the parental plants as determined by stainability in 0.3% cotton blue in lactophenol was extremely high producing figures for good pollen between 98% and 100%. In the vigorous hybrids of intrasectional crosses of sect. *Argyranthemum* pollen fertility was similarly very high producing good pollen results in the range of 88 - 100%. Such results indicate considerable genetic affinity. The lowest figure recorded from all of the hybrids produced, even in F<sub>2</sub> and later generation hybrids of intersectional crosses such as *A. frutescens* x *A. coronopifolium* was still around 60%.

iv) *Meiosis in F<sub>1</sub> and F<sub>2</sub> hybrids*: As with parental populations nine bivalents were invariably found in all fertile hybrids. The only measurable variation seen to occur was a slight depression of overall chiasma frequency. This suggests either that minor 'cryptic' cytological differences exist between different populations, or more likely that there is increased heterozygosity and varying degrees of genic imbalance between parental genomes causing some overall effect on meiotic pairing.

Table 4

Meiotic configurations in aneuploid and triploid plants of the natural hybrid *A. frutescens* X *A. coronopifolium*

Chromosome Number - 2n	Configurations	Frequency	Number of cells examined
19	9 II+ 1 I	30	18
	1 III+8 II	70	
27	9 III	16.6	6
	7 III+2 II+2 I	16.6	
	6 III+3 II+3 I	16.6	

NATURAL HYBRIDISATION BETWEEN *A. frutescens* AND *A. coronopifolium* ON TENERIFE

There are no other examples besides that between *A. frutescens* and *A. coronopifolium* of natural hybrids occurring between neighbouring populations of different taxa in *Argyranthemum*. In this isolated, intersectional cross, hybrids have only developed since the formation of scree slopes from material produced by tunnelling

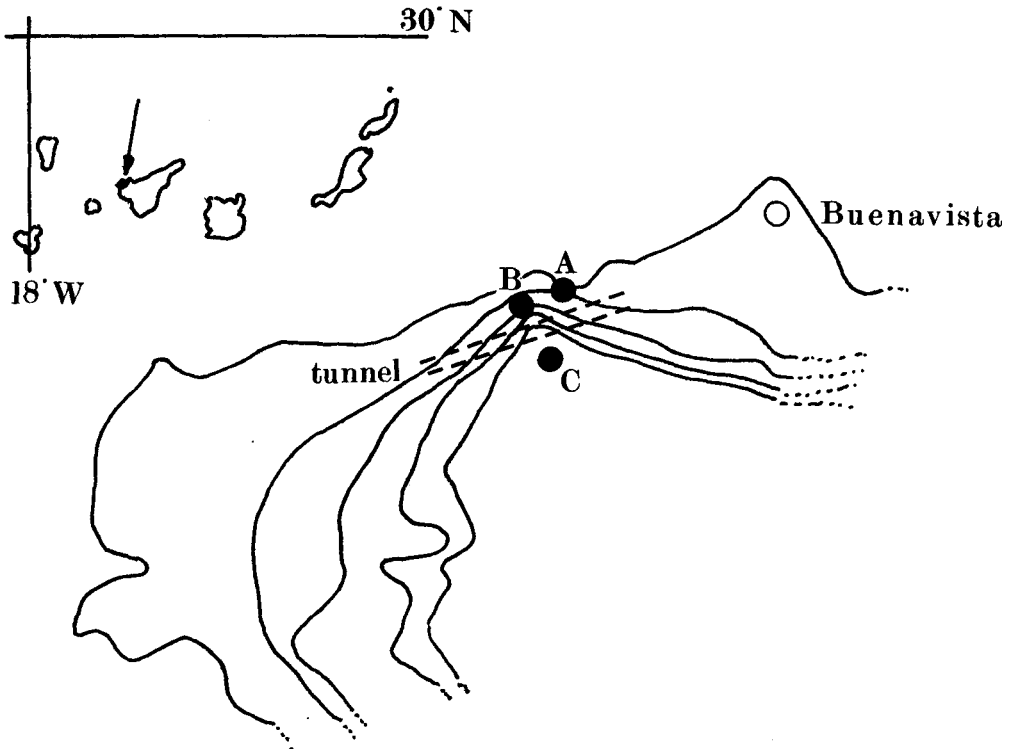


Fig. 6. Sketch map of the Teno region Tenerife, showing the collection sites for *Argyranthemum frutescens* (A), *A. coronopifolium* (C) and their hybrids (B).

EVOLUTION AND ENDEMISM IN ARGYRANTHEMUM

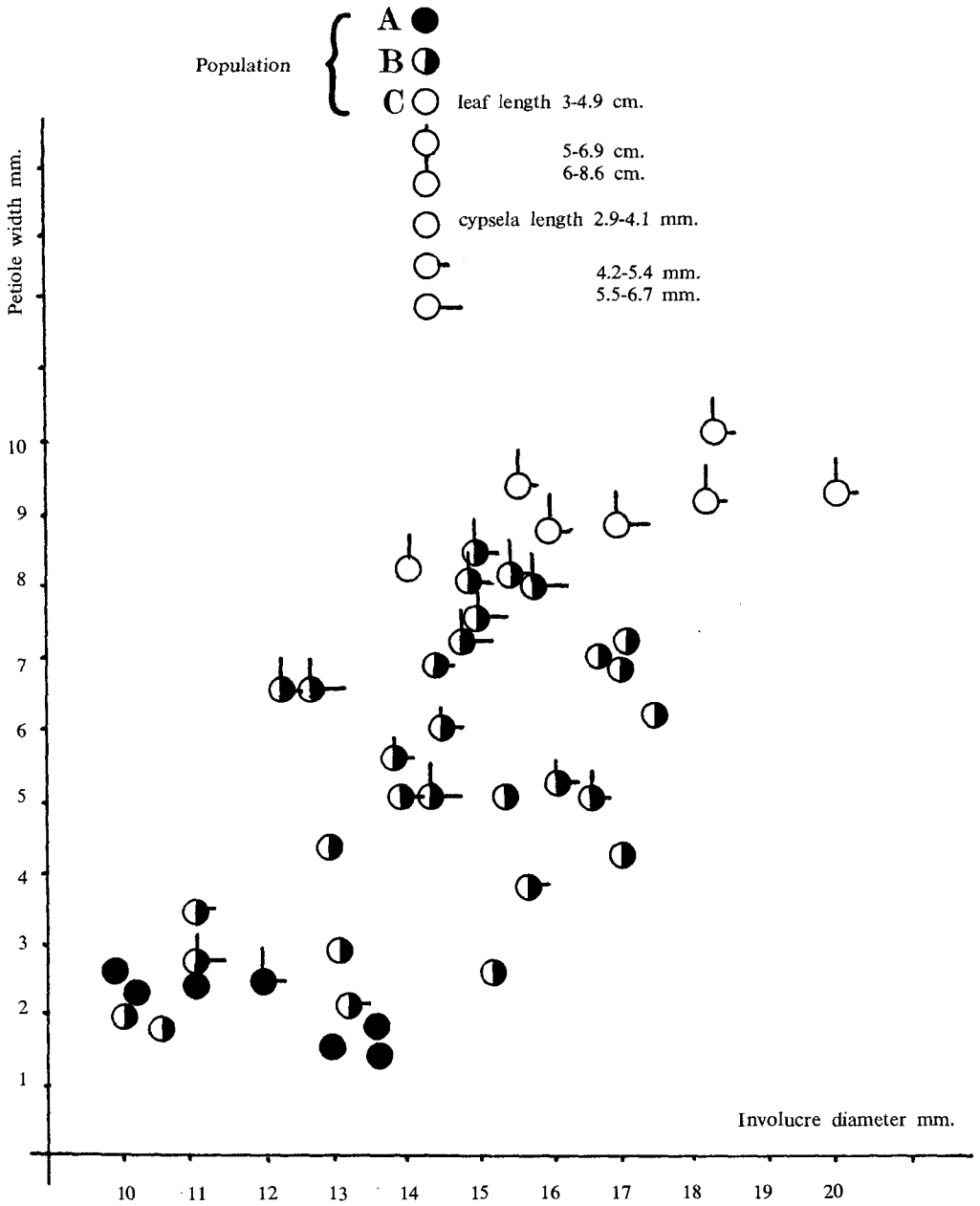


Fig. 7. Variability in natural populations of *Argyranthemum frutescens* and their hybrids

activities on Tenerife, through the Teno cliffs connecting the Teno promontory with the Buenavista region (fig. 6). The hybrid population has developed since the construction of the tunnel in 1965 (and it is significant that no pre 1965 collections of the hybrid seem to exist) and is restricted entirely to the disturbed scree slope which is found

directly between the two parental populations — the cliff populations of *A. coronopifolium* and the coastal populations of *A. frutescens*. To show the intermediacy of the hybrid population, pictorial representation of variation in four characters *i. e.* petiole width, leaf length, involucre diameter and cypselas length is given in fig. 7. The long, wide, pinnatifid leaves, with characteristic cuneiform petioles, wide capitula and large ray cypselas provide reliable data for separating *A. coronopifolium* from *A. frutescens*, which has comparatively much dissected leaves, narrower petioles, smaller capitula and generally shorter ray cypselas.

Examination of chromosomes in pollen mother cells from buds collected in the field show that all naturally occurring hybrids are diploid ( $2n=18$ ) with normal pairing of 9 bivalents at meiosis. However, in root tips from cultivated plants raised from wild hybrid cypselas, the range of somatic mitotic chromosome numbers varied between  $2n=18$  and  $2n=36$  (Humphries, 1975 (b)). Pairing at meiosis in pollen mother cells of triploid individuals showed a large number of trivalents, several bivalents and only one or two univalents suggesting considerable genome homology between the parents (table 4). The absence of aneuploids in natural populations suggest that even in disturbed habitats, selection pressures are still very strong and sufficient to eliminate such plants. This was also reflected in the observations that many cypselas cultivated in the greenhouse failed to germinate and several chlorotic seedlings which did emerge died within a few days.

#### DISCUSSION: PATTERNS OF EVOLUTION

On the basis of the evidence just presented, the species of *Argyranthemum* are a monophyletic assemblage of active epibiotics of warm temperate, Old World, possibly Mediterranean derivation. The exact relationship of *Argyranthemum* with *Chrysanthemum* L. s. s. and other genera is difficult to ascertain since all attempts to produce intergeneric hybrids with their nearest relatives have so far failed. Similarly, the evolutionary relationships of sections and species in the genus are no less difficult to demonstrate, but there is little reason to doubt that most diversification has taken place in the Macaronesian Islands. Perhaps the most intriguing question concerning the origin of *Argyranthemum* is which of the contemporary forms most resembles the immediate ancestors. Other well documented examples of adaptive radiation have been based on shizo- or patroendemic groups, e. g. *Aeonium* (Lems, 1960), *Sonchus* and *Echium* (Bramwell, 1971, 1972 (a)) where it is possible to arrange species groups into putative phylogenies on the basis of life - form sequences. For example in *Aeonium*, Lems (1960) has considered the ancestral (or least derived) species to be tall, woody, slow growing sparsely branched perennials with large inflorescences. The direction of evolutionary trends is assessed by relating variation in growth form with non - endemic members of the genus. Those species or sections which are endemic to the Macaronesian islands and are clearly different from non - endemic taxa are believed to be derivative groups. Thus, in *Aeonium* divergent growth forms have resulted from a number of different lines towards low - growing, herbaceous annuals, large - leaved monocarpic biennials, compact bushes and sprawling, hanging cliff plants with small inflorescences.

As *Argyranthemum* is endemic to the Macaronesian islands and cannot be considered to be directly derived from *Chrysanthemum* or any other genera of the

Anthemideae it is impossible to determine directions of evolutionary trends by comparison to continental taxa. The most fruitful systematic evidence for speculation of the evolutionary situation in *Argyranthemum* comes from the relationship between morphology, ecology and palaeogeography. For this approach it is assumed that ancestral taxa came to the Macaronesian islands associated with other (now relict) migrants. Therefore, species of section *Sphenismelia* restricted to relict habitats and associated with laurel forest and halophyte relicts together with the monotypic section *Stigmatotheca* (*A. pinnatifidum*) of Madeira occurring in similar habitats, probably possess the highest number of ancestral character states for the genus. Features these two sections have in common include thick woody stems, large, glabrous, sessile or shortly petiolate leaves, large capitula with conspicuous white ray florets and winged disc cypselas.

It is possible then to suggest that one derived evolutionary line has given rise to *A. adauctum* (sect. *Preauxia*) with pubescent, sessile pinnatisect leaves, small capitula and wingless cypselas. This species has a predominantly montane distribution in habitats of relatively recent origin. Other lines have given rise to species of sections *Argyranthemum* and *Monoptera*. Section *Argyranthemum* is the most diverse of the genus with 13 species distributed through a whole range of habitats and developed in response to relatively arid environments and varied geological conditions. Principal morphological features of this section as distinct from sect. *Sphenismelia* include glabrous pinnatilobed to pinnatisect leaves, smaller capitula and reduced habit. Section *Monoptera* represents a very specialised group of two species adapted to arid conditions on Gran Canaria. Its obvious adaptive features include a much reduced life cycle, reduced lignification, highly dissected more or less filiform leaves and extremely small capitulas.

From the crossing data it would appear evident that more than one coenospecies is present within the genus. It is also abundantly clear however, that despite a wide range of variation in morphology and eco-geographic localisation, the ability to exchange genes in very divergent taxa still remains.

Cytological studies on the pairing behaviour of chromosomes in parental and hybrid populations suggest that population differences within and between taxa result from genic changes rather than by major chromosomal reorganisation. Should there have been even minor structural chromosome differences between species such as inversions or translocations one would have expected at least to find a considerable decrease in pollen fertility. The high fertility values in *Argyranthemum* in all hybrids endorses the possibility of high chromosomal homology between different taxa. The formation of gametangial defects preventing pollen formation in some natural  $F_{2-6}$  hybrids of *A. frutescens* x *coronopifolium* and floretless individuals of the synthesised hybrid *A. frutescens* x *callichrysum* maintains the idea that differentiation has proceeded at the genic rather than the chromosomal level.

The behaviour of chromosomes at meiosis in  $F_2$  aneuploids of the intersectional *A. frutescens* x *coronopifolium* hybrids is similar to species of autopolyploid origin. This fact, together with regular bivalent pairing at meiosis in all other fertile synthesised hybrids, is in keeping with the interpretation that divergence is a result of adaptation by natural selection of variants derived from a common genomic stock. Many taxa are thus potentially interfertile and internal (post-zygotic) isolating factors play little, if any, rôle in keeping species apart. This is shown plainly by the fact aht natural hybrids are produced only when the natural habitat is severely disturbed near

the zone of contact of populations of different taxa; in such circumstances hybrid swarms are readily produced indicating that pollen flow is common even though gene flow is rare. External (pre - zygotic) isolating mechanisms in *Argyranthemum* are entirely the result, it seems, of ecological differentiation and despite the archipelagic situation there is little direct evidence to show that geographical isolation has played a critical rôle in speciation. That such a wide range of adaptive forms can exist within the Macaronesian islands depends not only on the diversity of the habitat but also on steep ecological gradients with very narrow ecotones between habitats which have remained stable over long periods of time. Evidence for stability is shown by the survival of relict palaeoendemics in the Canary Islands such as *Dracaena draco* L., *Bencomia* Webb and Berth. and *Marcetella* Svent. and the patroendemics *Laurus* L. and *Adenocarpus* DC. Evidence for steep ecological gradients comes from a general absence of hybrids between widespread active epibiotics such as *Argyranthemum*, *Aeonium*, *Echium* and *Sideritis* L. In all these cases hybrids only occur readily in localities of considerable disturbance.

## SUMMARY

1) The genus *Argyranthemum* (Compositae: Anthemideae) is centred in the Canary Islands, where 18 of the 22 species are found in 4 of the 5 principal vegetation zones. 3 other species are found in the Madeiran archipelago and one is endemic to the Salvage Islands.

2) The genus, of probable early Tertiary origin, presents an example of monophyletic adaptive radiation. With respect to morphology the most adaptive characters include woodiness, habit, leaf shape and dissection, and flower size. At one extreme species form dense, very lignified long - lived shrubs with large leaf area and large capitula, whilst at the other extreme slender single - stemmed species with reduced life cycle, slight woodiness and very dissected leaves are found. The genus can be divided up into 5 discrete sections on the basis of cypselas morphology.

3) The distribution of the 5 sections closely correlates with the principal vegetation zones and they are therefore considered to represent old divergences. Species of sections *Sphenismelia* and *Stigmatotheca* probably possess more ancestral morphological attributes than species of sections *Argyranthemum*, *Monoptera* or *Preauxia*, an assumption based on the ecogeographical and palaeogeographical associations.

4) Each species consists of morphologically discrete but genetically related, isolated populations forming a 'Rassenkreislehre' distribution.

5) Evolution has been a gradual process (all species are diploid) by strong natural selection of adaptable genotypes in steep ecological gradients. Isolation between different species has been influenced entirely by extrinsic ecological and possible geographical factors. Genetic isolation has proceeded only by accumulation of disharmonious genes and has lagged a long way behind morphological and physiological divergence.

6) Each population has a clear selective advantage in the habitats in which it occurs. Hybrids are formed only in areas of massive disturbance despite the evidence that considerable gene transfer exists between adjacent populations.



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