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INFRASPECIFIC VARIATION IN ARGYRANTHEMUM PINNATIFIDUM (ASTERACEAE — ANTHEMIDEAE) IN MADEIRA.

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With 9 figures and 2 tables

Abstract

The infraspecific variation in *Argyranthemum pinnatifidum* (L. f.) Lowe (Asteraceae), endemic to Madeira, is studied by numerical analysis. The phenetic variation is correlated with distribution patterns and ecological factors. Three eco-geographical subspescies are recognized, ssp. *pinnatifidum*, ssp. *succulentum* (Lowe) C. J. Humphries, and ssp. *montanum* Rustan, ssp. nov.

1. Introduction

Argyranthemum Webb ex Schultz Bip. contains 22 woody perennials restricted to the Canary Islands, the Salvage Islands and the Madeira Islands. The genus is divided into five sections on the basis of cypsela morphology (Humphries 1976 a). Sect. *Stigmatotheca* (Schultz Bip.) C. J. Humphries contains one polymorphic species, *A. pinnatifidum* (L. f.) Lowe, endemic to Madeira. This species is distinguished from its nearest relatives of sect. *Sphenismelia* (Schultz Bip.) C. J. Humphries by the vestigial wings, lack of pappus and irregular ribbing of both ray and disc cypselas (Humphries 1976 a). The species occurs at all altitudes and in different vegetation zones in Madeira, and has been divided into two varieties (Lowe 1868) or subspecies (Humphries 1976 a). The aim of this study has been to examine the infraspecific

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phenetic variation in *A. pinnatifidum*. To fulfil this purpose, numerical methods were used. Subsequently, the phenetic variation was correlated with distribution patterns and ecological factors.

Table I. Populations and specimens used in the numerical analyses. The capital letters and numbers refer to those used in the text.

Populations	Specimens
A. Ribeiro Frio, NW-slope of Rocha da Moitada. Alt. 850 m. UTM grid ref. CB 2123.	1. (ØHR 1007), 2. (ØHR 1009), 3. (ØHR 1010), 4. (ØHR 1011), 5. (ØHR 1012), 6. (ØHR 1013), 7. (ØHR 1014), 8. (ØHR 222).
B. Encumeada. Alt. 1000 m. UTM grid ref. CB 1125.	9. (ØHR 1040), 10. (ØHR 1041).
C. Between Poiso and Pico Arieiro.Casa do Arieiro. Alt. 1575 m. UTM grid ref. CB 2022.	13. (ØHR 979).
D. Pico das Torres, SW-slope. Alt. 1650 m. UTM grid ref. CB 1824.	14. (ØHR 989), 15. (ØHR 996).
E. Pico da Cagada. Alt. 1620 m. UTM grid ref. CB. 1825.	16. (ØHR 998), 17. (ØHR 999).
F. Curral das Freiras, near Montado. Alt. 900 m. UTM grid ref. CB 1725.	18. (ØHR 1003).
G. Between São Vicente and Seixal, near Ribeira da Pedra. Alt. 100 m. UTM grid ref. CB 0631.	19. (ØHR 1038), 20. (ØHR 1039). 21. (ØHR 196).
H. Pedro Rijo. Alt. 1725. UTM grid ref. CB 1923.	22. (ØHR 736).
K. Along the Levada from Encumeada to Folhadal, Rocha do Folhadal. Alt. 1030 m. UTM grid ref. CB 0826.	12. (ØHR 494).
M. Between Ribeira de São Jorge and Ponta de São Jorge, Pontinha. Alt. 50 m. UTM grid ref. CB 2234.	23. (ØHR (621).
N. W of Encumeada, along the path below Rocha Negra. Alt. 1075 m. UTM grid ref. CB 1025.	11. (ØHR 287)

2. Material and methods

2.1. Material

This study is based on 23 specimens belonging to 11 populations. Some of the populations are represented by one specimen only. Data about the localities are given in Tab. I. The field work was carried out during 1978 and 1980. Herbarium vouchers are deposited in O.

2.2. Data-gathering methods

The numerical analyses are based on characters found to be variable within the species. Characters varying on the specimens were omitted. Among the 26 characters evaluated, 10 characters were selected and used in the numerical analyses (Tab. II). These characters include those used by previous authors (Lowe 1868, Humphries 1976 a) as diagnostic on the infraspecific level in *A. pinnatifidum*. The characters were recorded on the best developed parts of the specimen. Each character value is the mean of three to five measurements. The descriptive terminology follows Radford et al. (1974).

Table II. Characters and character states used in the numerical analyses.

Character	Character type	Character states
1. Plant size (cm)	2	Continuous
2. Leaf length (mm)	2	Continuous
3. Leaf length: leaf width	2	Continuous
4. Leaf lobe shape	3	A. Elliptic, B. Ovate, C. Triangular
5. Leaf lobe margin	1	A. Open serate, B. Closed serrate
6. Leaf texture	1	A. Succulent, B Papery
7. Leaf lobe length (mm)	2	Continuous
8. Leaf lobe length: length from lobe tip to midvein	2	Continuous
9. Capitula number	2	Discrete
10. Involucre diameter (mm)	2	Continuous

1) Two-state character
2) Quantitative multistate character
3) Qualitative multistate character

2.2.1. Leaves

The leaves are alternate and slightly differentiated into lamina and petiole. The lamina is sub-entire to pinnatilobed and differences in size, texture, and dissection are taxonomically significant. A considerable part of the variation in the dissection of the leaves in *A. pinnatifidum* is related to habitat and climate. The differences are maintained in cultivation and are rarely, if ever, due to environmentally induced plasticity (Humphries 1976 a). The leaf characters used are shown in Fig. 1.

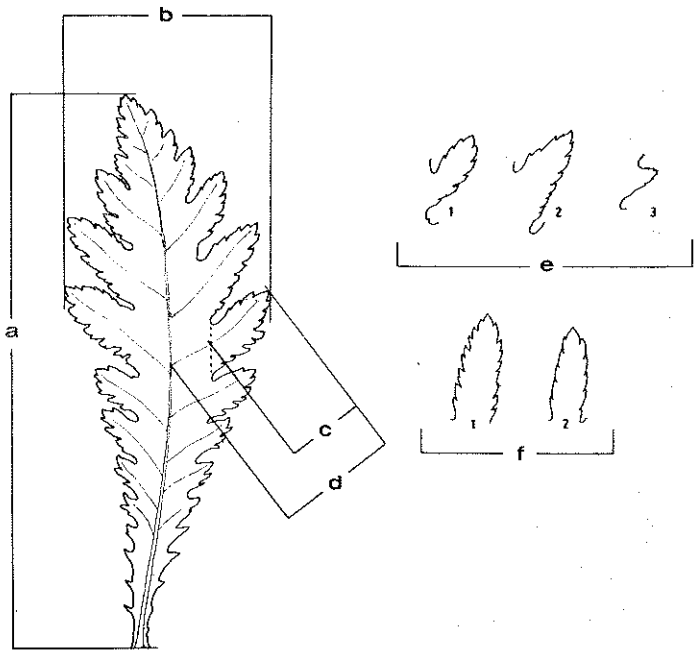


Fig. 1. — Leaf characters used in the numerical analyses. a. Leaf length; b. Leaf width; c. Leaf lobe length; d. Length from lobe tip to midvein; e. Leaf lobe shapes, e 1. Elliptic, e 2. Ovate, e 3. Triangular; f. Leaf lobe margins, f 1. Open serrate, f 2. Closed serrate.

2.2.2. Inflorescence

The number of capitula in an inflorescence varies from one to 30. A terminal capitulum develops in the early stages of the inflorescence formation, followed by irregular, alternate branching from lower bracts. The number of capitula in a mature inflorescence (Fig. 2) is a taxonomically important character, which seems to be related to ecological factors.

2.2.3. Capitulum

The shape of the capitulum is broadly to narrowly hemispherical and its size (Fig. 2) is extremely variable due to the wide ecological tolerance of *A. pinnatifidum*. The size is normally quite uniform within one population, while it frequently differs among completely separated populations. This suggests that it is controlled genetically, and that the differences are maintained by the lack of outcrossing between isolated populations (Humphries 1976a).

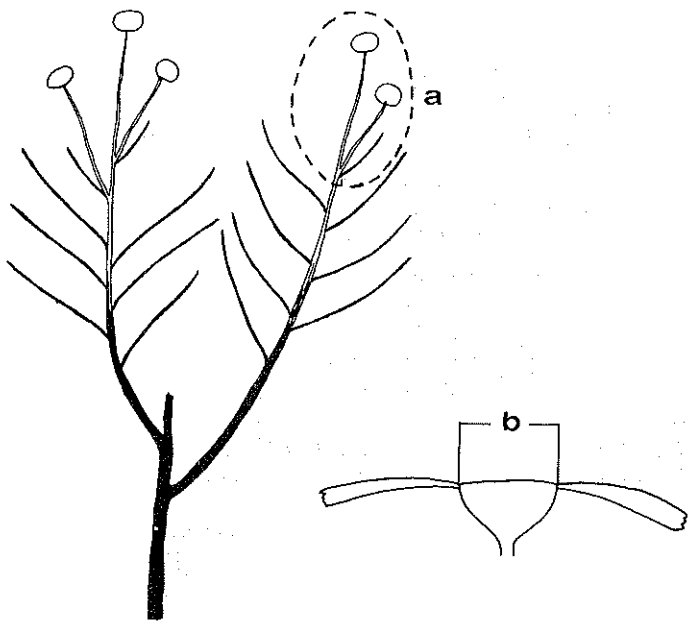


Fig. 2. — Inflorescence and involucre characters used in the numerical analyses. a. Circumscription of an inflorescence; b. Involucre diameter.

2.3. Data-analysis methods

The numerical methods were chosen for circumscribing groups of specimens and populations by estimating phenetic resemblance. The numerical analyses are carried out as follows.

To produce a similarity matrix between OTU's similarity values for each pair of OTU's were computed according to the coefficient $S\ (i, j) = \frac{\sum_{k=1}^{n} S_k\ (i, j)}{n}$, where $S\ (i, j)$ is the

similarity value for any two OTU's *i* and *j*; S_k *(i, j)* is the similarity value for any character *k*, for which data are available for two OTU's *i* and *j*; and *n* is the total number of characters used in the study for which data are available for both OTU's *i* and *j*.

For each character the degree of similarity varies between 0 and 1 for each pair of states. If two OTU's *i* and *j* are the same for character *k* then S_k (i, j) = 1. If two OTU's are different for character *k*, one of three rules may be chosen to calculate S_k (i, j):

1. S_k (i, j) = 0 (two-state characters).
2. S_k (i, j) = $1 - |X_{ki} - X_{kj}|$ (continuous and discrete quantitative characters). The similarity coefficient is the *city-block metric* (Sneath & Sokal 1973) where X_{ki} and X_{kj} are the values of character *k* in OTU *i* and *j* respectively after standardization by *ranging* (Gower 1971).
3. S_k (i, j) = arbitrary values assigned in advance by providing a matrix of values between 0 and 1 (qualitative multistate characters). The type of character defined by each rule as used in this study is given in Table II.

The similarity matrix so obtained was used as the input data for clustering OTU's. A *cluster* is defined as a group of OTU's for which there exists at least one continuous pathway of connections joining the specimens. A *connection* is the joining of two specimens, populations or clusters that are at least as similar as a specified similarity level (C).

Two clustering methods were used; the unweighted pair-group method using arithmetical averages (UPGMA) (Sokal & Michener 1958) and a modified single linkage clustering (MSLC). The single linkage clustering was modified to reduce chaining (Sneath & Sokal 1973), setting two links as necessary for each new OTU that is to be connected to an already existing cluster. Three phenograms were then produced as a result of the two clustering procedures, UPGMA with specimens and populations as OTU's and MSLC with specimens as OTU's. For each phenogram the cophenetic correlation coefficient *rcs* (Sneath & Sokal 1973) was calculated by comparing the cophenetic values generated in making the phenograms by the original similarity matrix. This correlation coefficient indicates the amount of distortion produced in constructing the phenograms. The closer the correlation value is to 1.0, the less is the distortion (Sneath & Sokal 1973).

The structure and distinctness of the clusters formed were then examined and interpreted to derive a classification for the OTU's being clustered.

3. Results

The results of the UPGMA and MSLC clustering procedures are summarized in Figs. 3 - 5. In the following, clusters are referred to by the prefix «CS-» when specimens are OTU's and «CP-» when populations are OTU's, with a reference to the first OTU (Tab. I) as postfix. All OTU's not connected to other OTU's at a given similarity level are termed single-member clusters (SMC).

3.1. Specimen analysis

During the UPGMA analysis of specimens (Fig. 3), all the peak zone specimens join to form CS-13 by a similarity value C=0.84. The north coast specimens join and form the distinct CS-19 by a similarity value C=0.81. The third cluster CS-1 is composed of

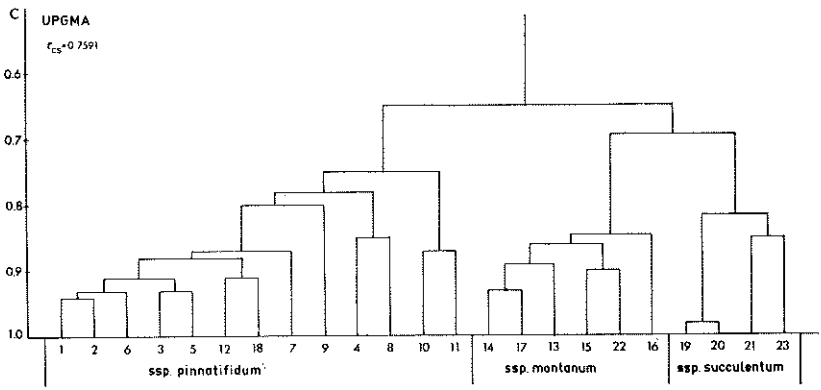


Fig. 3. — UPGMA clustering using specimens as OTU's. OTU numbers refer to those used in Tab. I. The level values shown are the similarity values at which OTU's cluster together.

specimens from the cloud zone and is completed by a similarity value C=0.75. The C-1 cluster shows that considerable variability exists among the cloud zone populations. Specimens from different populations cluster together at high similarity levels, while specimens from the same population join at low similarity levels. The first clusters to join are CS-13 and CS-19 by a similarity value C=0.69. These will again be connected to CS-1 by a similarity value C=0.64, indicating a closer relationship between CS-13 and CS-19, than with CS-1. The cophenetic correlation coefficient for the cluster procedure is rsc = 0.7591.

The results of the MSLC analysis are shown in Fig. 4. The similarity graphs show the similarity within and among the clusters at different levels in the clustering procedure. In order to simplify representation, clusters comprising more than three members are graphically presented as circles. The connectedness

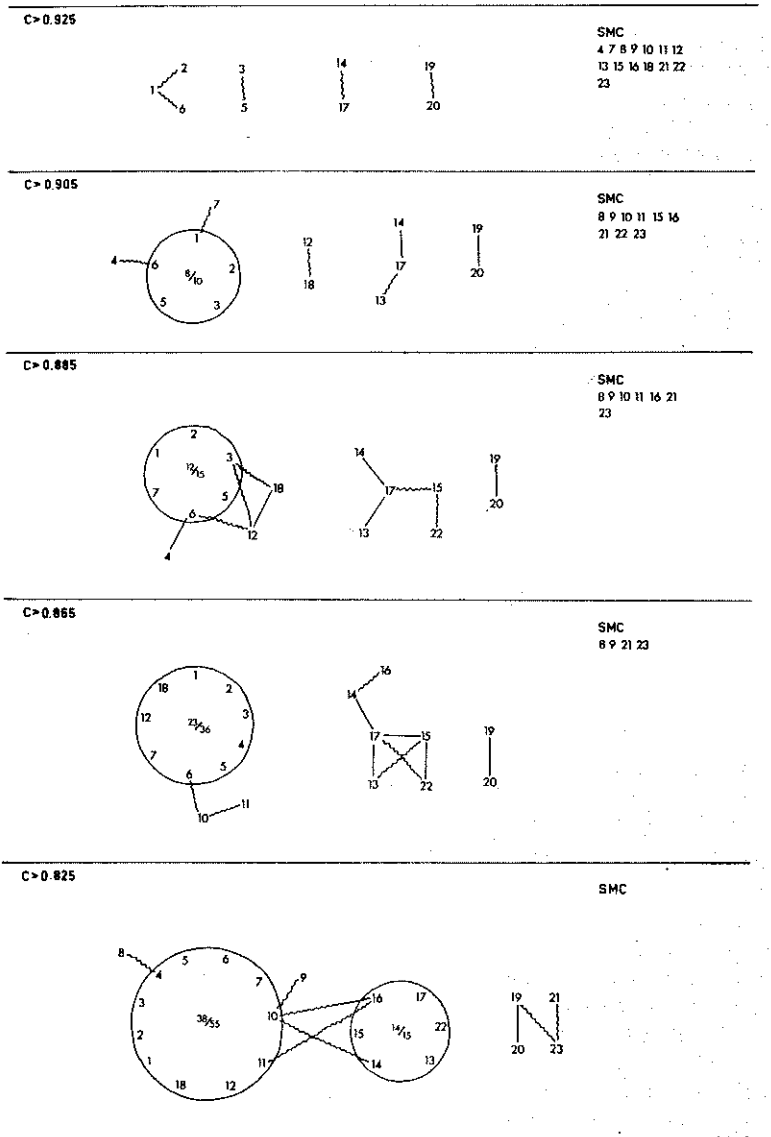
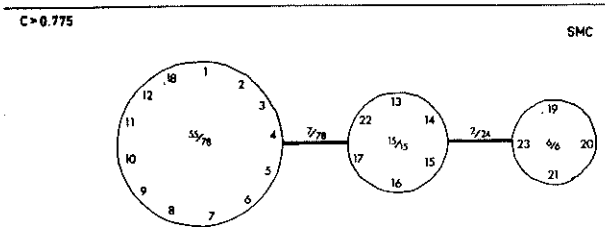
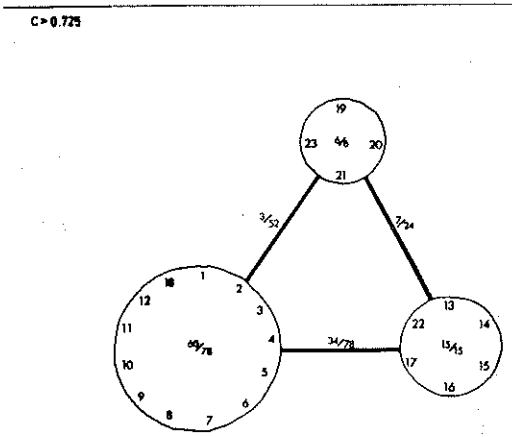
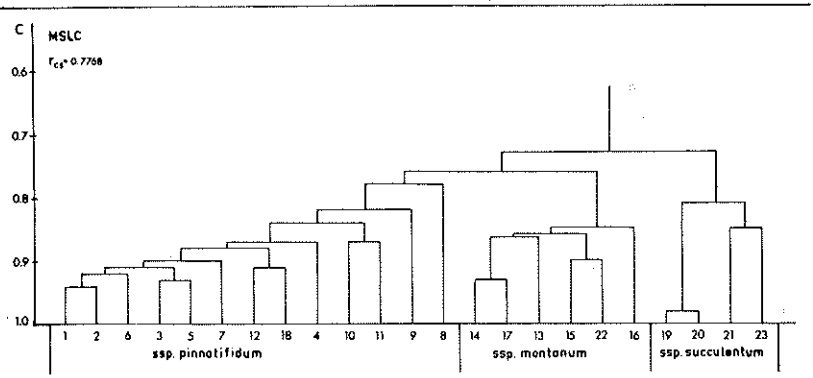


Fig. 4. — MSCL using specimens as OTU's. OTU numbers refer to of the clustering procedure at different similarity levels. The







those used in Tab. I. The similarity graphs show the result final phenogram summarizes the clustering procedure.

of the clusters is represented by a fraction, the numerator representing the number of actual connections and the denominator the number of possible connections. Connections formed during the similarity levels summarized are represented by wavy lines, connections formed during previous similarity levels by straight lines. The final phenogram summarizes the clustering procedure.

During the MSLC analysis, all the peak zone specimens and all the north coast specimens form the distinct clusters CS-13 and CS-19 by the similarity values C=0.85 and C=0.81, respectively. The cloud zone specimens form CS-1 by a similarity value C=0.78. While the internal structure of CS-13 and CS-19 remain unchanged compared with the UPGMA analysis, some minor changes have been made in the structure of CS-1. The most important difference compared with the UPGMA analysis is that the first clusters to join are CS-1 and CS-13, by a similarity value C=0.76. This indicates slightly greater phenetic similarity among the cloud zone and peak zone specimens than among the specimens of the two groups and the north coast specimens. The north coast specimens in CS-19 are connected to CS-1 and CS-13 by a similarity value C=0.73. The rcs = 0.7768 for the MSLC analysis.

3.2. Population analysis

The UPGMA analysis produced three clusters CP-A, CP-C and CP-G (Fig. 5). CP-C is completed by a similarity value C=0.85 and consists of the peak zone populations. The north coast populations compose CP-G which is completed by a similarity value C=0.83. The

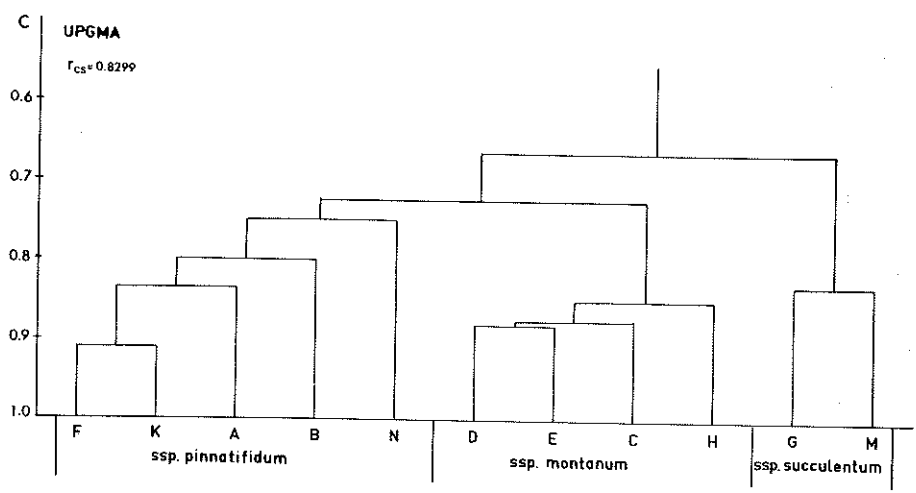


Fig. 5. — UPGMA clustering using populations as OTU's. OTU's refer to those in Tab. I. The level values shown are the similarity values at which OTU's cluster together.

cloud zone populations are variable *inter se* and CP-A is completed by a similarity value as low as C=0.75. Within CP-A the two Encumeada populations (population B and N1) show lowest resemblance with the other populations. The peak zone populations in CP-C and the cloud zone populations in CP-A are connected by a similarity value C=0.72. This indicates greater phenetic resemblance between these two groups than between them and CP-G which connects at a similarity value C=0.66. The analysis has rcs = 0.8299.

4. Discussion

4.1. Phenetic relationship

The analyses by UPGMA and MSLC (Fig. 3-5) clearly show three groups of specimens and populations to be present in the examined material of *A. pinnatifidum*. CS-1 is composed of specimens and CP-A of populations from the cloud zone which constitute the variable ssp. *pinnatifidum* s. str., characterized by a well developed woody stem, large papery leaves, and branched inflorescences with many, small capitula. The variability observed in ssp. *pinnatifidum* is probably due to its wide distribution in the cloud zone with geographically isolated populations and lack of outcrossing. CS-13 and CP-C comprises ssp. *montanum*, here described as a new subspecies. This subspecies is found in the peak zone and is characterized by a less woody stem, small and succulent leaves, and inflorescences with few, moderately large capitula. It has formerly been included in ssp. *pinnatifidum*. CS-19 consists of specimens and CP-G of populations from the north coast. These belong to ssp. *succulentum*, characterized by a less woody stem, succulent leaves with triangular leaf lobes, and inflorescences with few, large capitula.

The specimens and populations of ssp. *pinnatifidum* in the Encumeada area show phenetic resemblance with ssp. *montanum* and transitional forms are likely to occur. A similar condition has been observed between ssp. *pinnatifidum* and ssp. *succulentum* by Lowe (1868), who states that the extreme forms of ssp. *succulentum* passes by imperceptible gradiations on seacliffs in the north into ssp. *pinnatifidum*.

The phenetic similarity among the three subspecies is interpreted in different ways depending on the clustering method and the type of OTU's. UPGMA with specimens as OTU's gives closest relationship between ssp. *montanum* and ssp. *succulentum*. A different result is obtained with MSLC and specimens as OTU's and with UPGMA and populations as OTU's. In these analyses ssp. *pinnatifidum* and ssp. *montanum* seem most closely related. Owing to these deviating results, it is difficult to draw conclusions about the relationship among the three subspecies.

4.2. Distribution and ecology

A. pinnatifidum is a highly variable species that covers a broad altitudinal span and forms three distinctive ecotypes in the various zones. The three ecotypes are here given formal recognition as subspecies and their distribution is shown in Fig. 6. The three subspecies all represent adaptations to different habitats. This adaptation is most probably due to evolution by a process of allopatric divergence in response to the different habitats (Humphries 1976 b).

The large leaved ssp. *pinnatifidum* is a common plant, which has its main distribution in the cloud zone where it is found in all the principal ravines. The cloud zone (between 700-1200 m

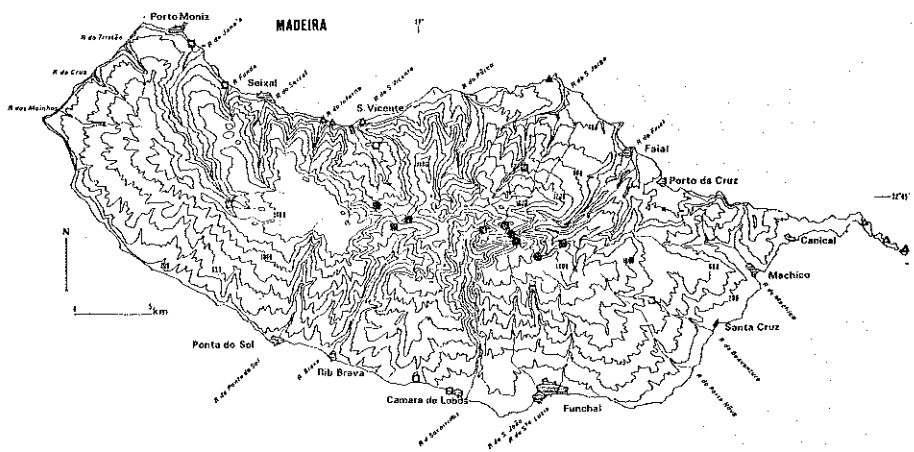


Fig. 6. — Distribution of *Argyranthemum pinnatifidum* in Madeira. Ssp. *pinnatifidum*, ■ own collections, □ literature references; ssp. *montanum*, ● own collections; ssp. *succulentum*, ▲ own collections, △ literature references.

a.s.l. on the south side and between 300-1300 m a.s.l. on the north side of Madeira) is characterized by a relative humidity (rh) which is generally about 90% and an annual precipitation > 1700 mm (Sjögren 1974). The dominating plant community is laurel-shrub forest *(Clethro-Laurion,* Sjögren 1972). The subspecies is usually found on rocks and open clearings of wet ravines, especially near cascades or water trickles. It therefore seems to be hygrophilous, the increased size, the branched inflorescenes with many capitula and the large, papery leaves representing an adaptation to the moist conditions in the cloud zone. The subspecies is also found at lower altitudes in the ravines above Funchal on the south coast and above São Vicente on the north coast where the climatic conditions are favourable for this subspecies.

The ssp. *montanum* is relatively rare on rocks in the central mountains between Pico Arieiro and Pico Ruivo at altitudes above 1500 m. The peak zone (alt. 1200-1800 m) has an rh which is generally about 70%, but desert winds from the African continent bring periods with rh about 30%, especially to altitudes above 1300 m (Sjögren 1974). The precipitation is generally the same as in the cloud zone. Unfavourable frost occurs occasionally above 1300-1500 m (Sjögren 1974). The vegetation *(Ericetum cinerae,* Sjögren 1972) is therefore subjected to periods of severe water deficit and drought, and occasional frost. The reduced size, the reduced inflorescences, and the small and succulent leaves of ssp. *montanum* are most likely to be an adaptation to the dry conditions occurring in the peak zone.

The third subspecies, ssp. *succulentum,* is a rare plant on the north coast were it grows between Seixal and Ponta de São Jorge and reaches its most extreme form on Ponta de São Lourenço, Ilhéu dos Embarcadores and Ilhéu de Fora (Lowe 1868). It grows on sea-cliffs, and the reduced size, the reduced inflorescences and the succulent leaves represent adaptations to this habitat. The leaf succulence increases with salinity and is most significantly pronounced on individuals which grow permanently in the spray zone along the coast.

5. Taxonomy

Argyranthemum pinnatifidum (L. f.) Lowe, Lowe 1868: 460 (sect. *Stigmatotheca* (Schultz Bip.) C. J. Humphries). Basionym: *Chrysanthemum pinnatifidum* L. f., Linnaeus fil. 1781: 377.

Citation of synonyms and detailed descriptions are given by Lowe (1868) and Humphries (1976 a).

Key to the subspecies:

1. Leaves papery, leaf lobe length (10-)20-60 mm, (3-)10-30 capitula ..... ssp. *pinnatifidum*
1. Leaves succulent, leaf lobe length 6-16 mm, 1-3(-5) capitula 2
2. Leaves pinnatilobed, leaf lobes ovate to elliptical, involucre diameter 10-14 mm ..... ssp. *montanum*
2. Leaves slightly pinnatilobed to ± entire, leaf lobes triangular, involucre diameter 14-17 mm. ..... ssp. *succulentum*

ssp. *pinnatifidum* (Fig. 7).

Argyranthemum pinnatifidum (L. f.) Lowe [var.] *α flaccida* Lowe, Lowe 1868: 461, *nom. illeg.,* pro parte.
Argyranthemum pinnatifidum (L. f.) Lowe ssp. *pinnatifidum,* Humphries 1976 a: 223, pro parte.

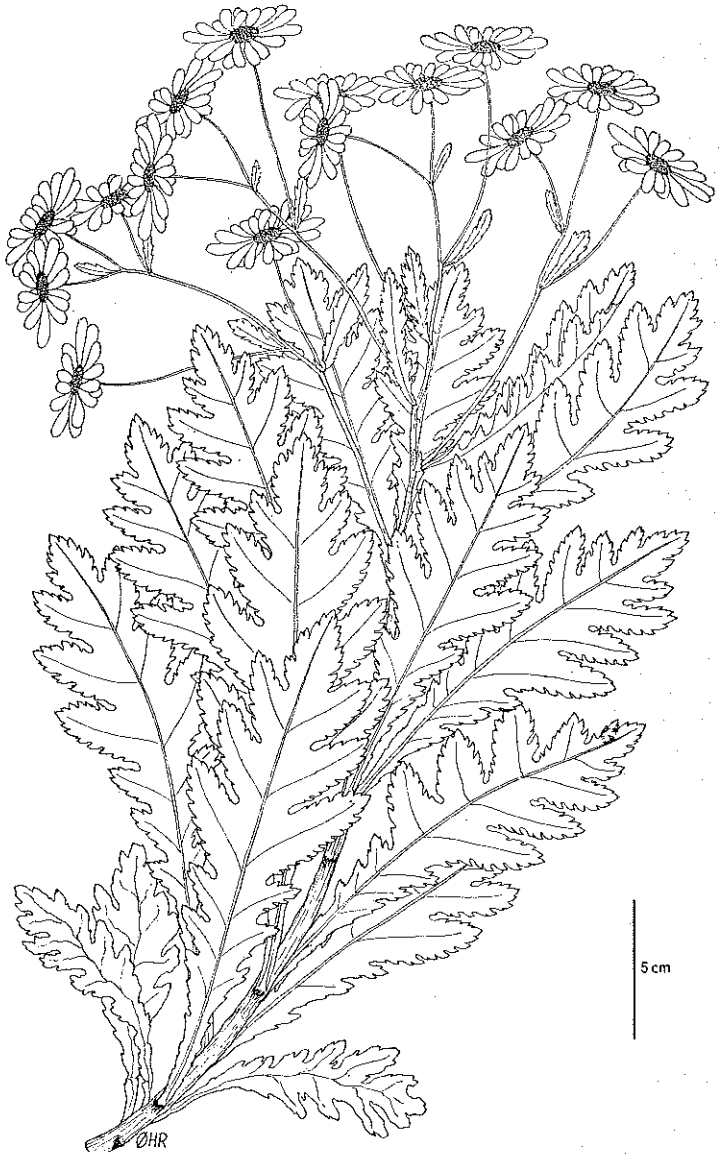


Fig. 7. — *Argyranthemum pinnatifidum* ssp. *pinnatifidum*, portion of the plant. Drawn from herbarium specimens.

Leaves 7-22 × 2.5-10 cm, pinnatilobed, papery; primary lobes (10-)20-60 mm, ovate to elliptic. *Inflorescence* with (3-)10-30 capitula. *Involucre* 6-12 mm in diameter.
Type: Masson, in herb. L. f. 1332 14 apud herb. Smith (LINN, holotypus; C, microfiche!).
Flowering period: April-July.
Endemic to Madeira, introduced in São Miguel in the Azores. Common in the principal ravines in the cloud zone at altitudes between 300-1300 m.

ssp. *montanum* Rustan, ssp. nov. (Fig. 8).

> *Argyranthemum pinnatifidum* (L. f.) Lowe [var.] *α flaccida* Lowe, Lowe 1868: 461, *nom. illeg.*, pro parte.
> *Argyranthemum pinnatifidum* (L. f.) Lowe ssp. *pinnatifidum*, Humphries 1976 a: 223, pro parte.

Folia 4-8 × 1.5-3 cm, pinnatilobata, succulenta; lobi primarii 6-12 mm, ovati vel elliptici. *Inflorescentia* 1-2(-5) capitulata. *Involucrum* 10-14 mm diametro.
Leaves 4-8 × 1.5-3 cm, pinnatilobed, succulent; primary lobes 6-12 mm, ovate to elliptic. *Inflorescence* with 1-2(-5) capitula. *Involucre* 10-14 mm in diameter.
Type: Madeira: Pico da Cagada, alt. 1620 m. UTM grid ref. CB 1825. 13.06.1980. Rustan 999 (O, holotypus), Rustan 998 (BM, isotypus).
Flowering period: April - July.
Endemic to Madeira. Rare in the peak zone between Pico do Arieiro and Pico Ruivo at altitudes above 1500 m.

ssp. *succulentum* (Lowe) C. J. Humphries, Humphries 1976 a: 225 (Fig. 9).

> *Argyranthemum pinnatifidum* (L. f.) Lowe [var.] *β succulenta* Lowe 1868: 462.
> *Chrysanthemum mandonianum* Cosson, Cosson 1868: 100, *nom. nud.*

Leaves 4-10 × 1-3 cm, slightly pinnatilobed to ± entire, succulent; primary lobes 7-16 mm, triangular. *Inflorescence* with 1-3(-5) capitula. *Involucre* 14-17 mm in diameter.
Type: Madeira: Punta do San Lorenzo, Lowe 225 (BM; K, holotypus).
Flowering period: March - June.
Endemic to Madeira. Rare on sea-cliffs along the north coast between Seixal and Ponta de São Jorge, Ponta de São Lourenço, Ilhéu dos Embarcadores and Ilhéu de Fora.

Fig. 8. — *Argyranthemum pinnatifidum* ssp. *montanum*, portion of the plant. Drawn from herbarium specimens.

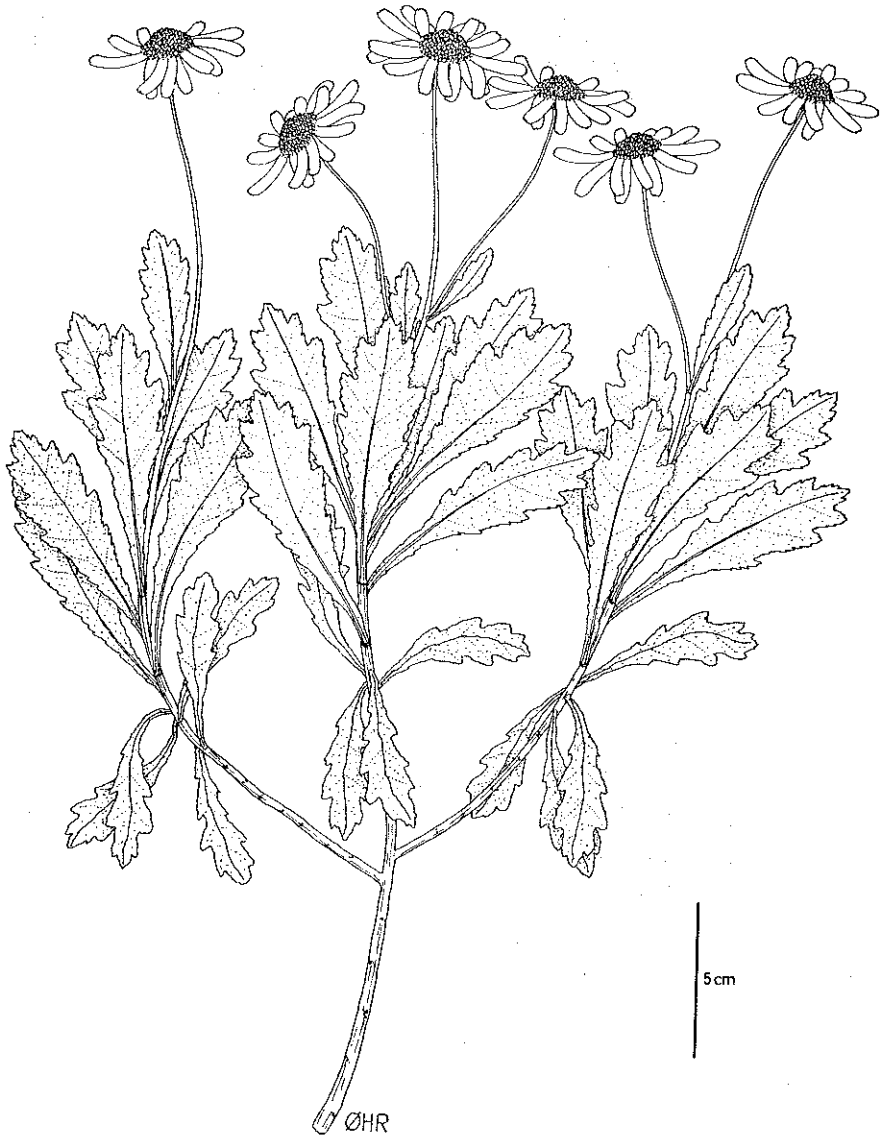


Fig. 9. — *Argyranthemum pinnatifidum* ssp. *succulentum*, portion of the plant. Drawn from herbarium specimens.

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REFERENCES

Cosson, M. E. :
1868. Catalogue des plantes recueillies par G. Mandon, en 1865 et 1866, dans les iles de Madère et Porto Santo. *Bull. Soc. bot. Fr. 15:* 94-103.

Gower, J. C. :
1971. A general coefficient of similarity and some of its properties. *Biometrics 27:* 857-871.

Humphries, C. J. :
1976 a. A revision of the Macaronesian genus Argyranthemum Webb ex Schultz Bip. (Compositae-Anthemideae). *Bull. Br. Mus. nat. Hist. (Bot.) 5(4):* 145-240.
1976 b. Evolution and endemism in Argyranthemum. *Bot. Macaronesica 1:* 25-50.

Linnaeus, C. filius. :
1781. *Supplementum Plantarum.* Braunschweig.

Lowe, R. T. :
1868. *A manual flora of Madeira and the adjacent islands of Porto Santo and the Desertas 1.* London.

Radford, A. E., Dickison, W. C., Massey, J. R. & Bell, C. R. :
1974. *Vascular plant systematics.* New York.

Sjögren, E. :
1972. Vascular plant communities of Madeira. *Bol. Mus. Mun. Funchal 26(114):* 45-125.
1974. Local climatic conditions and zonation of vegetation on Madeira. *Agronomia lusit. 36(2):* 95-139.

Sneath, P. H. A. & Sokal, R. R. :
1973. *Numerical taxonomy.* San Francisco.

Sokal, R. R. & Michener, C. D. :
1958. A statistical method for evaluating systematic relationships. *Univ. Kanas Sci. Bull. 38:* 1409-1438.