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Recircumscription of the Canary Island endemics *Argyranthemum broussonetii* and *A. callichrysum* (Asteraceae: Anthemideae) based on evolutionary relationships and morphology

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Abstract: Phylogenetic analysis has revealed that *Argyranthemum broussonetii* is polyphyletic, with subsp. *broussonetii* (Tenerife) and subsp. *gomerensis* (La Gomera) resolved in separate clades within the Macaronesian endemic genus *Argyranthemum*. We show that *A. broussonetii* subsp. *broussonetii* and subsp. *gomerensis* are similar in leaf traits, likely a consequence of adaptation to similar habitats, but that the two can readily be distinguished based on capitula and cypselae characteristics. Indeed, *A. broussonetii* subsp. *gomerensis* was found to share greater affinity with *A. callichrysum*, also from La Gomera based on capitula and cypselae characters, in agreement with its phylogenetic placement. Therefore, we propose that *A. broussonetii* subsp. *gomerensis* should be recognized as a subspecies of *A. callichrysum*, specifically *A. callichrysum* subsp. *gomerensis*. A key to differentiate *A. broussonetii*, *A. callichrysum* subsp. *callichrysum* and subsp. *gomerensis* is provided.

Key words: *Anthemideae*, *Argyranthemum*, *Asteraceae*, Macaronesia, phylogenetics, taxonomy

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Introduction

Argyranthemum Webb is the largest endemic flowering plant genus of the Macaronesian region. It comprises 24 species (39 terminal taxa when subspecies are considered; Humphries 1976) and is distributed across the archipelagos of Madeira, the Selvagens and the Canary Islands.

Argyranthemum broussonetii (Pers.) Humphries is endemic to the Canary Islands where it is restricted to laurel forest clearings on Tenerife and La Gomera. It is distinguished from other members of the genus by its large bipinnatifid leaves, its often wingless ray cypselae,

typically two-winged disc cypselae, and large capitula and ray florets. Humphries (1976) recognized two subspecies, namely *A. broussonetii* subsp. *broussonetii* endemic to Tenerife and subsp. *gomerensis* Humphries endemic to La Gomera (Fig. 1; Fig. 2). He differentiated the two largely by size, with subsp. *broussonetii* larger than subsp. *gomerensis* in stature, leaf size, involucre width and ray cypselae dimensions.

A phylogenetic analysis of *Argyranthemum* based on chloroplast restriction site markers found that *A. broussonetii* is not monophyletic, because the two subspecies were resolved in different clades (Francisco-Ortega & al.

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1996). However, the sister relationships of *A. broussetii* remained unresolved. More recently, a phylogenetic study of *Argyranthemum* that employed a Next Generation Sequencing (NGS) approach (White & al. 2020) provided improved resolution of species relationships and confirmed that the two subspecies of *A. broussetii* are distinct evolutionary lineages. Specifically, *A. broussetii* subsp. *broussetii* is sister to the multi-island endemic *A. frutescens* (L.) Sch. Bip., whereas *A. broussetii* subsp. *gomerensis* is sister to *A. callichrysum* (Svent.) Humphries, which is also endemic to La Gomera (Fig. 2; Fig. 3). D-statistics computed to test for evidence of hybridization provided no evidence of introgression between *A. broussetii* subsp. *broussetii* and *A. callichrysum*, ruling out the possibility that *A. broussetii* subsp. *gomerensis* is the result of historical hybridization between *A. broussetii* and *A. callichrysum*.

Francisco-Ortega & al. (1996) suggested that the subspecies of *Argyranthemum broussetii* are morphologically distinct and that each should be considered a unique species; however, no subsequent taxonomic work on *A. broussetii* has been published. In this study, we reassess the taxonomy of *A. broussetii* in the light of recent phylogenetic analyses. The morphological distinctiveness of the two subspecies of *A. broussetii* is demonstrated, with subsp. *gomerensis* found to be more similar to *A. callichrysum*. We propose that *A. broussetii* subsp. *gomerensis* should be recognized as a subspecies of *A. callichrysum* and provide a key with which to differentiate *A. broussetii* and the subspecies of *A. callichrysum*.

Material and methods

We identified ten characters that differed between the two subspecies of *Argyranthemum broussetii* and *A. callichrysum* based on Humphries (1976). These were: leaf attachment (petiolate, shortly petiolate or sessile); leaf dissection (bipinnatisect or bipinnatifid); primary lobe length (cm); primary lobe width (cm); primary lobe shape (linear-lanceolate or obovate); capitulum width (cm); ray cypselae colouration (yellow-brown, chestnut-brown, brown-purple or black); ray cypselae arrangement (solitary, coalesced in groups of 2–6 or both identi-

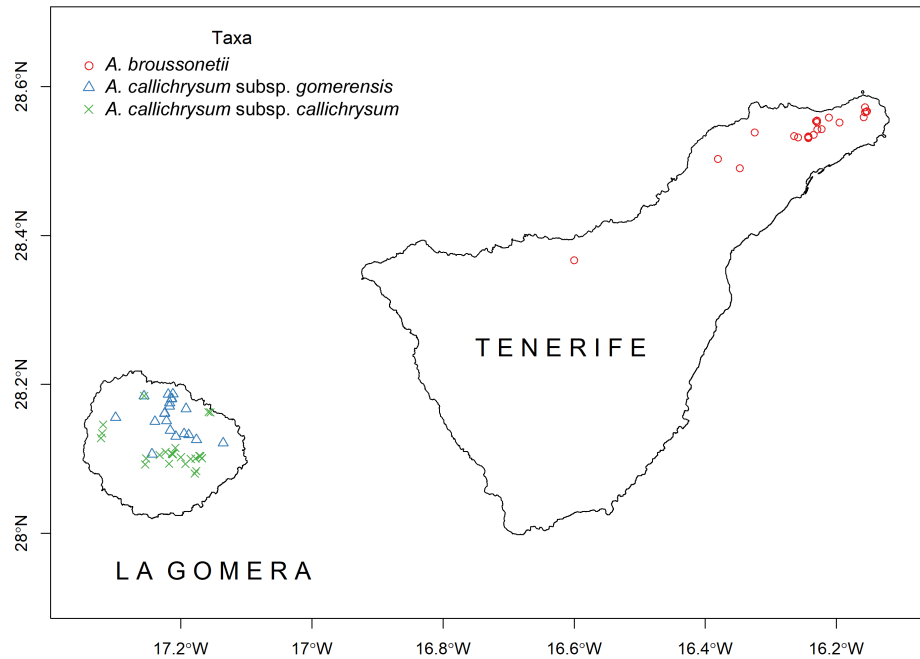


Fig. 1. Distribution map of *Argyranthemum broussetii*, *A. callichrysum* subsp. *gomerensis* and *A. callichrysum* subsp. *callichrysum* (names as accepted in this study). Point localities are based on vouchers used in the morphological analysis. Specimens lacking latitude and longitude were georeferenced based on the locality description provided using Google maps and IDECanarias (<https://visor.grafcan.es/visorweb/>).

fied in the same capitulum); ray cypselae wings (present or absent); and disc cypselae wing number (zero, one or two wings). Leaf dissection was estimated using a ratio of leaf width and lamina width (Fig. 4). For an estimate of lobe shape, a ratio of lobe length and width was calculated. Descriptions of the characters and definitions are provided in Table 1 and Fig. 4. A total of 27 recent collections of *Argyranthemum* made between July and August 2015 were examined and scored for these traits together with ten further collections accessioned at the Natural History Museum, London (BM). The 37 voucher specimens examined for the morphometric analysis comprised 16 *A. broussetii* subsp. *broussetii*, 14 *A. broussetii* subsp. *gomerensis* and seven *A. callichrysum*.

For continuous characters, we checked for normality using histograms, Q-Q norm plots and a Shapiro-Wilk test. Characters with a non-normal distribution were transformed and we tested for significant differences between taxa using ANOVA followed by *post hoc* Tukey's honest significant difference test. For discrete variables, we used chi-square tests of independence to identify significant associations between character frequencies and taxa. To further investigate the morphological relationships, we employed the R package PCAmixdata (Chavent & al. 2012, 2017) which implements principal components analysis (PCA) using both continuous and discrete variables. For the PCA analysis, we excluded the ratio of lobe length and width to avoid the inclusion of strongly correlated variables. The number of clusters identified by the PCA was determined using the R package mclust (Scrucca & al. 2016; R Core team 2020).

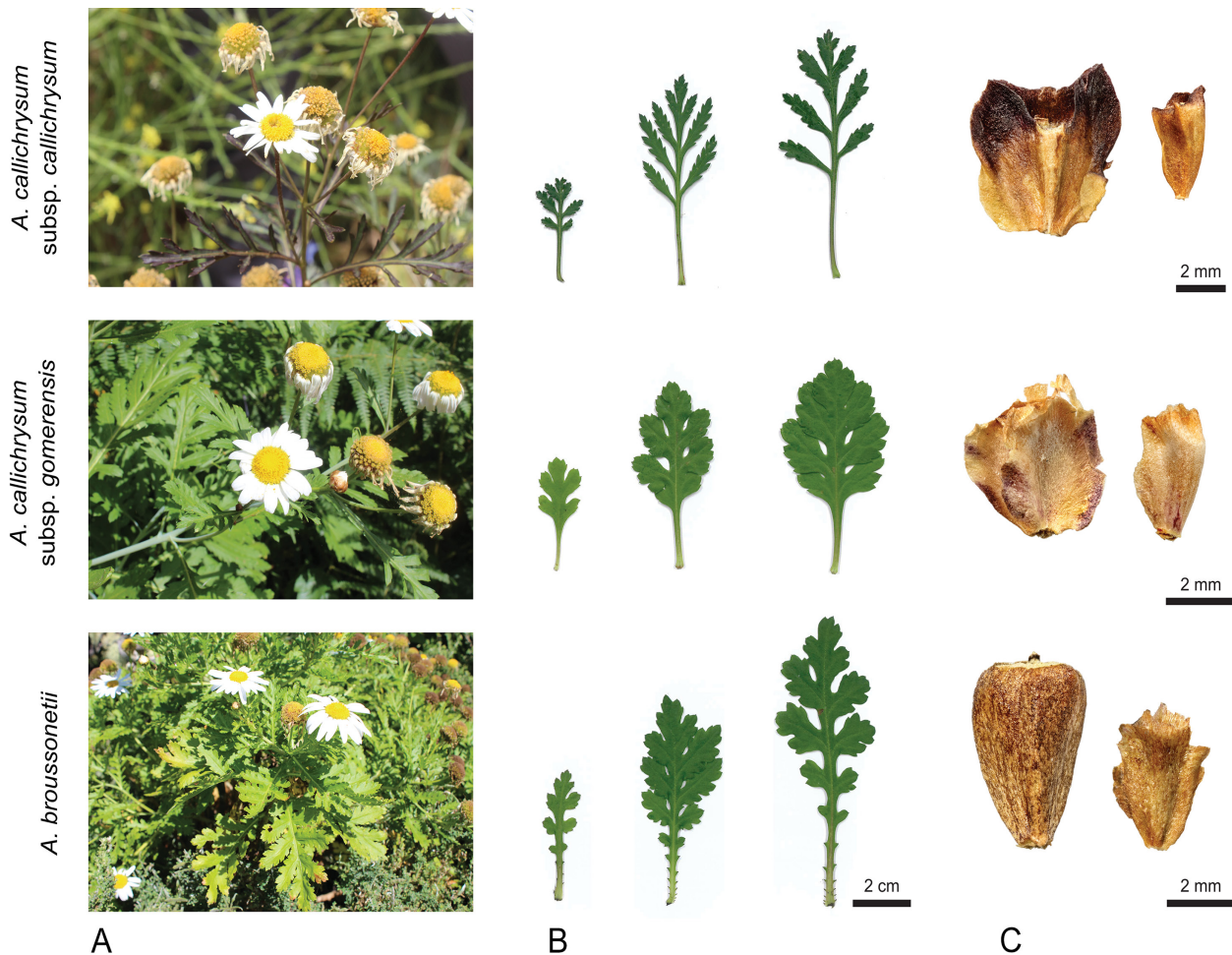


Fig. 2. Morphology of *Argyranthemum callichrysum* subsp. *callichrysum*, *A. callichrysum* subsp. *gomerensis* and *A. broussonetii* (names as accepted in this study). – A: plants in situ; B: leaves from glasshouse-grown plants; C: ray cypselae (left) and disc cypselae (right) from plants collected in the field. – Photos: A and B taken by Oliver White; C taken by Kevin Webb, photographic unit, Natural History Museum, London.

Further specimens at BM, ORT and RNG were examined to further test the taxon circumscriptions proposed in light of the morphometric analysis.

Results

Ten of the 37 samples included in the morphometric analysis had missing characters scores, including three of *Argyranthemum broussonetii* subsp. *broussonetii* and seven of subsp. *gomerensis*. Input data can be found in Supplementary Table S1. All continuous variables were normally distributed except for leaf:lamina width ratio, which required a log transformation (Shapiro-Wilk test; primary lobe length, $P = 0.194$; primary lobe width, $P = 0.054$; primary lobe length:width ratio, $P = 0.099$; log leaf:lamina width ratio, $P = 0.909$; capitulum width, $P = 0.173$). One-way ANOVA found no significant difference in primary lobe length between taxa ($F = 0.098$, $P = 0.906$; Fig. 5A). In contrast, significant differences were identified based on primary lobe width ($F = 10.580$, $P < 0.001$; Fig. 5B), pri-

mary lobe length:width ratio ($F = 38.580$, $P < 0.001$; Fig. 5C), log-transformed leaf:lamina width ratio ($F = 10.080$, $P < 0.001$; Fig. 5D) and capitulum width ($F = 16.050$, $P < 0.001$; Fig. 5E). For primary lobe width, *A. broussonetii* subsp. *broussonetii* had significantly wider lobes than *A. broussonetii* subsp. *gomerensis* and *A. callichrysum* (Fig. 5B). Primary lobe length:width ratio was significantly different across all taxa (Fig. 5C). Subspecies of *A. broussonetii* shared a similar leaf:lamina width ratio and were significantly different to *A. callichrysum* (Fig. 5D). *Argyranthemum broussonetii* subsp. *broussonetii* had significantly wider capitula with respect to *A. broussonetii* subsp. *gomerensis* and *A. callichrysum* (Fig. 5E).

Chi-squared tests identified no association between ray cypselae colour ($\chi^2 = 4.9887$, $P = 0.545$; Fig. 6B) or ray cypselae wings ($\chi^2 = 1.909$, $P = 0.385$; Fig. 6D) and taxa. However, there were significant associations between leaf attachment ($\chi^2 = 37.000$, $P < 0.001$; Fig. 6A), ray cypselae arrangement ($\chi^2 = 30.159$, $P < 0.001$; Fig. 6C) and disc cypselae wing number ($\chi^2 = 27.000$, $P < 0.001$; Fig. 6E) and taxa.

Table 1. Characters used in our morphological analysis with information on how it was scored and definitions for repeatability.

Character	Scoring	Definitions
Leaf attachment	Based on distance from leaf base to first primary lobe or tooth 1. petiolate (≥ 1.5 cm) 2. shortly petiolate \pm sessile (0.5–1.5 cm) 3. sessile (≤ 0.5 cm)	Leaf lobes defined as paired or obovate or ovate limbs; consensus taken across specimen
Leaf dissection	Ratio of leaf width and lamina width	See Fig. 4
Primary lobe length	cm	Selected third leaf below lowest peduncle and longest lobe; if third leaf could not easily be measured, next leaf down was used
Primary lobe width	cm	Same lobe as above
Primary lobe shape	Ratio of lobe length and width	Same lobe as above
Capitulum width	cm	Selected uppermost capitulum
Ray cypselae colour	1. yellow-light brown 2. chestnut brown 3. brown-purple 4. black	Used extra cypselae in packet if available or dissection of specimen
Ray cypselae arrangement	1. solitary 2. coalesced 3. both	Used same cypselae as above solitary: single cypselae coalesced: 2–6 coalesced cypselae both: both solitary and coalesced cypselae identified
Ray cypselae wings presence or absence	1. absent 2. present	Used same cypselae as above
Disc cypselae wing number	1. no wings 2. one wing 3. two wings	Used same cypselae as above; wings defined as extensions of cypselae surface ≥ 1 mm long

The PCA of both continuous and discrete variable showed a clear separation on the x axis, with *Argyranthemum broussonetii* subsp. *gomerensis* and *A. callichrysum* clustering together and *A. broussonetii* subsp. *broussonetii* forming a distinct group (Fig. 7). There was a slight separation between *A. broussonetii* subsp. *gomerensis* and *A. callichrysum* in the PCA plot. However, mclust identified only two clusters: the first corresponding to *A. broussonetii* subsp. *gomerensis* and *A. callichrysum*, the second composed of *A. broussonetii* subsp. *broussonetii* (Fig. 7).

Discussion

From a morphological perspective, we found that *Argyranthemum broussonetii* subsp. *broussonetii* and subsp. *gomerensis* are similar in leaf traits including primary lobe length and leaf dissection (leaf:lamina width ratio), which supports their current taxonomic treatment. However, *A. broussonetii* subsp. *broussonetii* and subsp. *gomerensis* can be distinguished based on leaf attachment, capitula width and cypselae characteristics. Indeed, *A. broussonetii* subsp. *gomerensis* shows greater similarity to *A. callichrysum* based on these characters, which is in agreement with their phylogenetic rela-

tionships (White & al. 2020; Fig. 3) and the hypothesis proposed by Francisco-Ortega & al. (1996). While our ordination analysis shows some overlap between *A. broussonetii* subsp. *gomerensis* and *A. callichrysum* (Fig. 7), the two can be differentiated using primary lobe shape (length:width ratio; Fig. 5C) and leaf dissection (leaf:lamina width ratio; Fig. 5D). The differences in leaf morphology between *A. broussonetii* subsp. *gomerensis* and *A. callichrysum* are also apparent in plants grown under common glasshouse conditions (Fig. 2B), ruling out the possibility that the observed differences in wild-collected material were simply due to environmentally induced plasticity. In light of the morphological findings that are congruent with the molecular phylogenetic data, we propose that *A. broussonetii* subsp. *gomerensis* should be recognized as a subspecies of *A. callichrysum*. While *A. broussonetii* subsp. *gomerensis* could arguably be recognized as a distinct species, we propose recognition as a subspecies of *A. callichrysum* given the sister group relationships and overlap in morphology in some instances (see below). The necessary new combination is provided below together with a key to the three taxa considered here.

Morphological traits that are advantageous in a particular habitat may be susceptible to morphological convergence. The two independently derived lineages

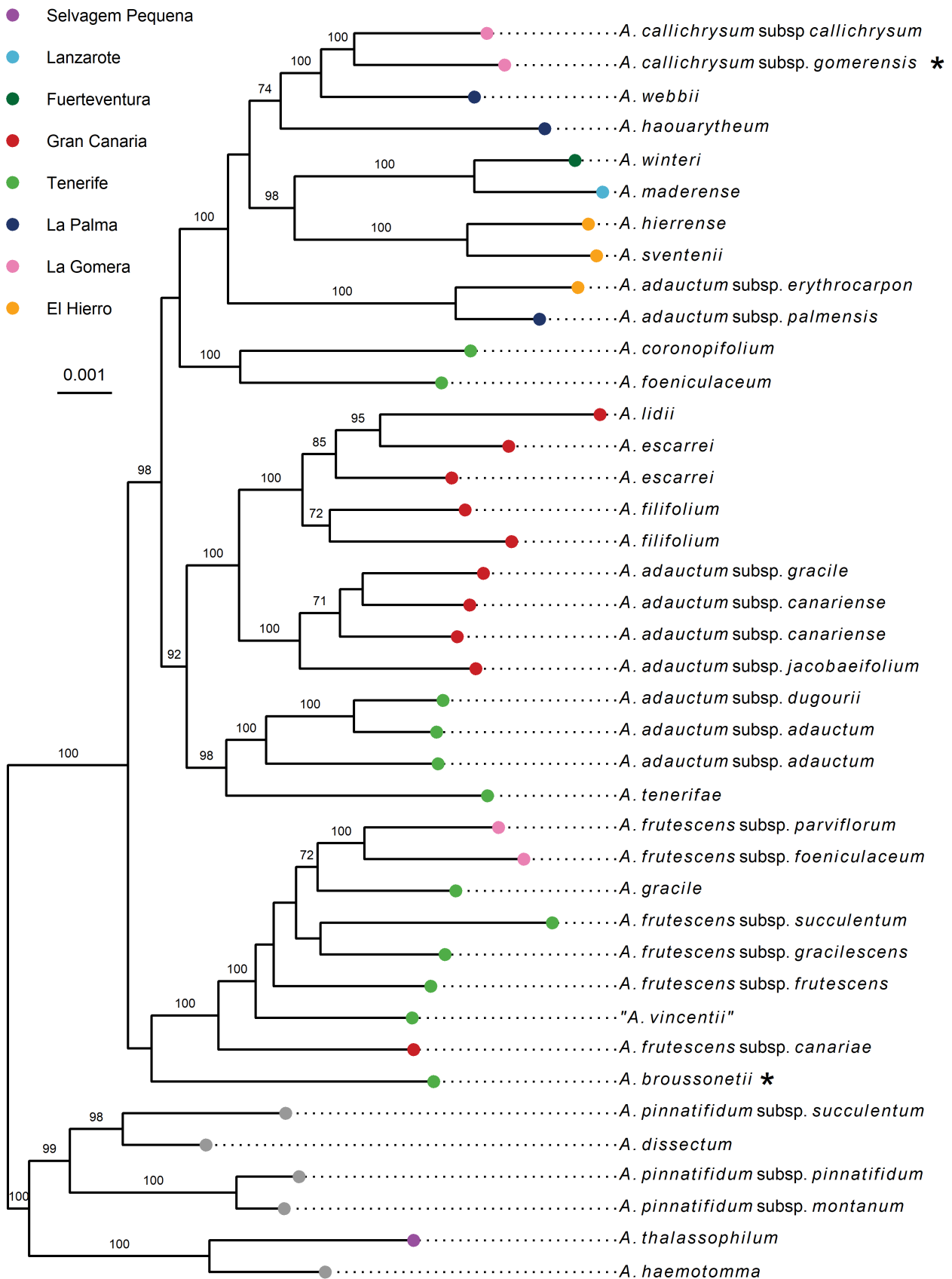


Fig. 3. Maximum likelihood tree of *Argyranthemum* adapted from White & al. (2020) and visualized using ggtree in R (Yu & al. 2016; R Core team 2020), where the tips are coloured by island and branches show bootstrap support values ≥ 70 . The positions of *A. callichrysum* subsp. *gomerensis* and *A. broussonetii* (names as accepted in this study) are highlighted with an asterisk (*).

that comprised *Argyranthemum broussoletii* as circumscribed by Humphries (1976) occupy humid laurel forests of Tenerife and La Gomera, where they can be found in forest clearings. The similarity in leaf shape exhibited by these two lineages would appear to be a convergence in response to similarities in habitat. Based on our collections and georeferenced samples, the distributions of *A. broussoletii* subsp. *gomerensis* and *A. callichrysum* are largely non-overlapping (Fig. 1). They do co-occur at “El Cano” (*M. Fernández Galván*, ORT26020; Supplementary Table S2) and “Laderas del Roque Cano” (*M. Fernández Galván*, ORT26022), although here *A. broussoletii* subsp. *gomerensis* is typically distributed on N-facing slopes, whereas *A. callichrysum* is generally found on SW-facing slopes. Two specimens of *A. callichrysum* from “Taguluche Norte” (*E. R. Sventenius*, ORT4843 and ORT4846; Supplementary Table S2) are also outliers for this species. In *Argyranthemum*, hybrids may occur where taxa come into close proximity, given weak barriers to gene flow (Borgen 1976; Brochmann 1984; Brochmann & al. 2000). In the case of *A. callichrysum* as circumscribed here, one specimen (*A. E. Aldridge s.n.*, BM013846033; Supplementary Table S2) that we refer to *A. callichrysum* subsp. *callichrysum* has the primary lobe dissection typical of this taxon, but the width of the primary lobes is more similar to that found in subsp. *gomerensis*. This may suggest potential hybrid ancestry of this individual.

Taxonomy

Note — in the list of specimens seen, those used in the morphometric analysis are indicated in boldface.

Key to taxa

1. Leaves petiolate, lacking teeth or primary lobes at leaf base; capitulum 0.75–1.5 cm wide; disc cypselae 1-winged; ray cypselae either coalesced or solitary ***Argyranthemum broussoletii***
- Leaves sessile with teeth and/or primary lobes to leaf base; capitulum 1.4–2.0 cm wide; disc cypselae 2-winged; ray cypselae typically solitary ***Argyranthemum callichrysum*** subsp. *gomerensis*
- Leaves bipinnatisect, primary lobes linear-lanceolate, 0.2–0.75 cm wide ***Argyranthemum callichrysum*** subsp. *callichrysum*

Argyranthemum broussoletii (Balb. ex Pers.) Humphries in Bull. Brit. Mus. (Nat. Hist.), Bot. 5: 214. 1976 ≡ *Chrysanthemum broussoletii* Balb. ex Pers., Syn. Pl. 2: 461. 1807. – Holotype: cultivated?, s.d., *Persoon*, s.n. (L0012057 [image!]).

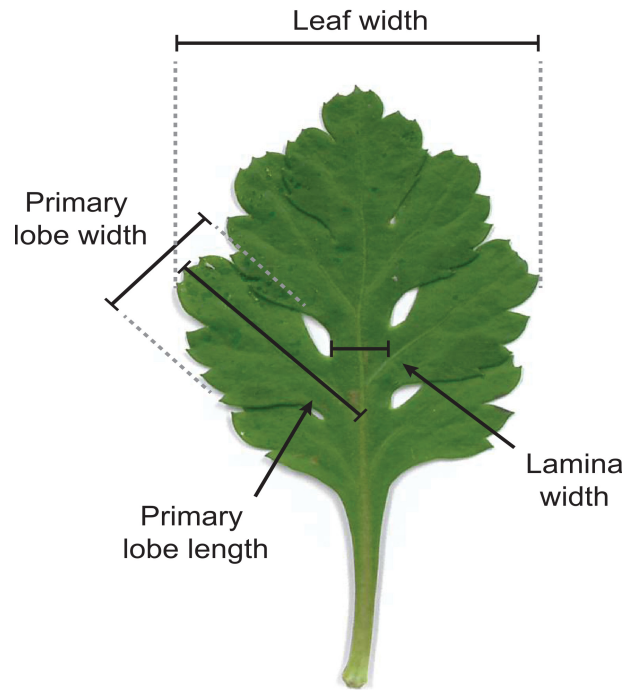


Fig. 4. Leaf measurements used in the morphological analysis.

Leaves sessile, bipinnatifid; primary lobes ovate. Disc cypselae 2-winged; ray cypselae typically solitary.

Distribution — Tenerife: locally common in the Anaga peninsula of Tenerife; small populations also reported in the Orotava valley between Icod el Alto and Realejo.

Habitat — Along roadsides and open clearings of *Laurus novocanariensis* Rivas-Mart. & al. forest between 550 and 1000 m.

Additional specimens examined — SPAIN, Canary Islands, Tenerife: s.loc., 1801, *Broussolet s.n.* (BM! [BM000810845]); s.loc., 1877, *R. J. Shuttleworth s.n.* (BM! [BM013846021]); Anaga, 19 May 1890, *R. P. Murray s.n.* (BM! [BM013846015]); Pico Inglés in laurel forest, 2 Dec 1968, *D. Bramwell 421* (RNG [image!]); Icod el alto, laurel forest above road to Realejo, 13 Apr 1969, *D. Bramwell 1257* (RNG [image!]); Vueltas de Taganana, 21 May 1969, *D. Bramwell 1534* (RNG [image!]); ridge between Las Animas and Azaro, 9 Apr 1971, *D. Bramwell & C. J. Humphries 3364* (BM! [BM013846023], RNG [image!]); Roque de las Pasas, 9 Apr 1971, *D. Bramwell & C. J. Humphries 3378* (RNG [image!]); Punta de Anaga, Roque del Agua, 9 Apr 1971, *D. Bramwell & C. J. Humphries 3382* (BM! [BM013846026], RNG [image!]); Roque de las Pasas, 9 Apr 1971, *D. Bramwell & C. J. Humphries s.n.* (BM! [BM013846027]); Anaga, near to Cumbrilla, road to Taganana, 28 Jan 1973, *A. E. Aldridge 558* (BM! [BM013846025], RNG [image!]); near aeropuerto, by side of autopista, W of La Laguna, 29 Jan 1973, *A. E. Aldridge 625A* (BM! [BM013846024], RNG [image!]); road from Valle de Guerra to Cruz Chiquita, 1 Apr 1975, *J. F. M., M.*

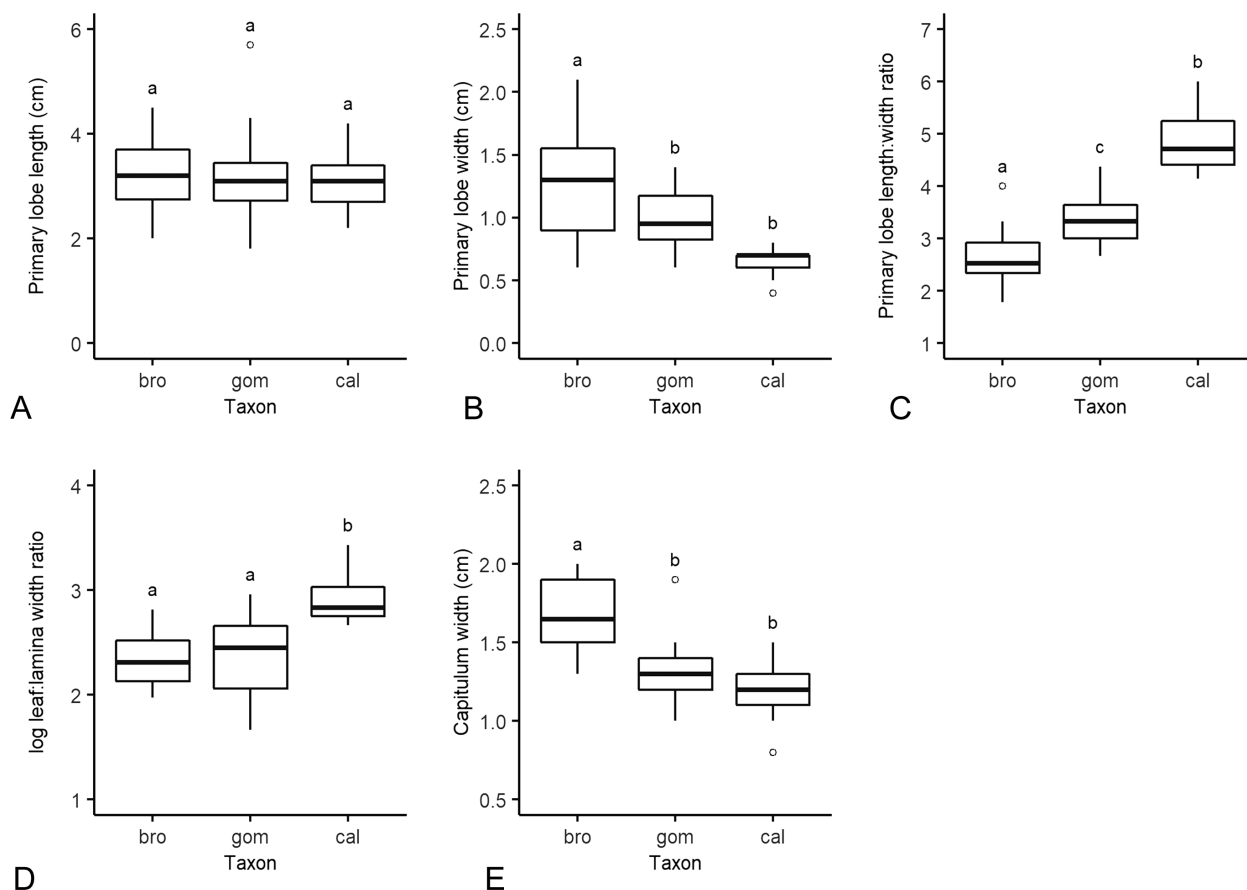


Fig. 5. Boxplots of continuous characters with letters above each box referring to the groups identified by Tukey tests. – Taxon abbreviations: bro = *Argyranthemum broussonetii*; gom = *A. callichrysum* subsp. *gomerensis*; cal = *A. callichrysum* subsp. *callichrysum* (names as accepted in this study).

J. & P. F. Cannon 4426 (BM! [BM013846016]); WSW of Tegueste, on the road TF 5118, El Boqueron, 6 Jul 1976, *R. & M. Dittrich s.n.* (BM! [BM013846018]); Sierra Anaga, 4 km W of Chinobre, 3 May 1977, *Jarvis & D. Bramwell 544* (BM! [BM013846022], RNG [image!]); Monte de las Mercedes, Mirador 4 km W of Pico del Inglés, 22 Apr 1997, *Jarvis 467* (BM! [BM013846019], RNG [image!]); La Cumbrilla, Anaga, 6 May 2015, *O. White & al. 69* (BM! [BM000828683], ORT!); La Cumbrilla, Anaga, 6 May 2015, *O. White & al. 70* (BM! [BM000828682], ORT!); La Cumbrilla, Anaga, 6 May 2015, *O. White & al. 71* (BM! [BM000828681], ORT!); path to Mesa del Sabinal, Anaga, 6 May 2015, *O. White & al. 79* (BM! [BM000828673], ORT!); Barranco de Valle Crispin, 13 May 2015, *O. White & al. 84* (BM! [BM000828668], ORT!); Barranco de Valle Crispin, 13 May 2015, *O. White & al. 85* (BM! [BM000828667], ORT!); Barranco de Valle Crispin, 13 May 2015, *O. White & al. 87* (BM! [BM000828665]); Barranco de Valle Crispin, 13 May 2015, *O. White & al. 88* (BM! [BM000828664]); Barranco de Valle Crispin, 13 May 2015, *O. White & al. 89* (BM! [BM000828663]); Barranco de Valle Crispin, 13 May 2015, *O. White & al. 90* (BM! [BM000828662]); Roques del Fraile, 25 May 2015, *O. White & al. 155* (BM! [BM000828600]); Roques del Fraile, 25 May 2015, *O.*

White & al. 156 (BM! [BM000828599]); Roques del Fraile, 25 May 2015, *O. White & al. 157* (BM! [BM000828598]); Chamorga, Anaga, 20 Jun 2015, *O. White & al. 679* (BM! [BM000828483]); Chamorga, Anaga, 20 Jun 2015, *O. White & al. 683* (BM! [BM000828482]); Chamorga, Anaga, 20 Jun 2015, *O. White & al. 686* (BM! [BM000828481]); Chamorga, Anaga, 20 Jun 2015, *O. White & al. 688* (BM! [BM000828480]); Las Casas de la Cumbre, Anaga, 21 Jun 2015, *O. White & al. 726* (BM! [BM000828476], ORT!).

Argyranthemum callichrysum* subsp. *gomerensis (Humphries) O. W. White, **comb. nov.** \equiv *Argyranthemum broussonetii* subsp. *gomerensis* Humphries in Bull. Brit. Mus. (Nat. Hist.), Bot. 5: 216. 1976. – Holotype: Spain, Canary Islands, La Gomera: amongst woodland and open hillside between Agulo and Las Rosas, 6 Apr 1971, *D. Bramwell & C. J. Humphries 3355* (BM! [BM000810844]).

Leaves petiolate, bipinnatifid; primary lobes ovate. Disc cypselae 1-winged; ray cypselae often coalesced.

Distribution — La Gomera: scattered populations on steep slopes of La Gomera between Las Rosas, La Palmitta and Agulo on the NW coast (Fig. 1).

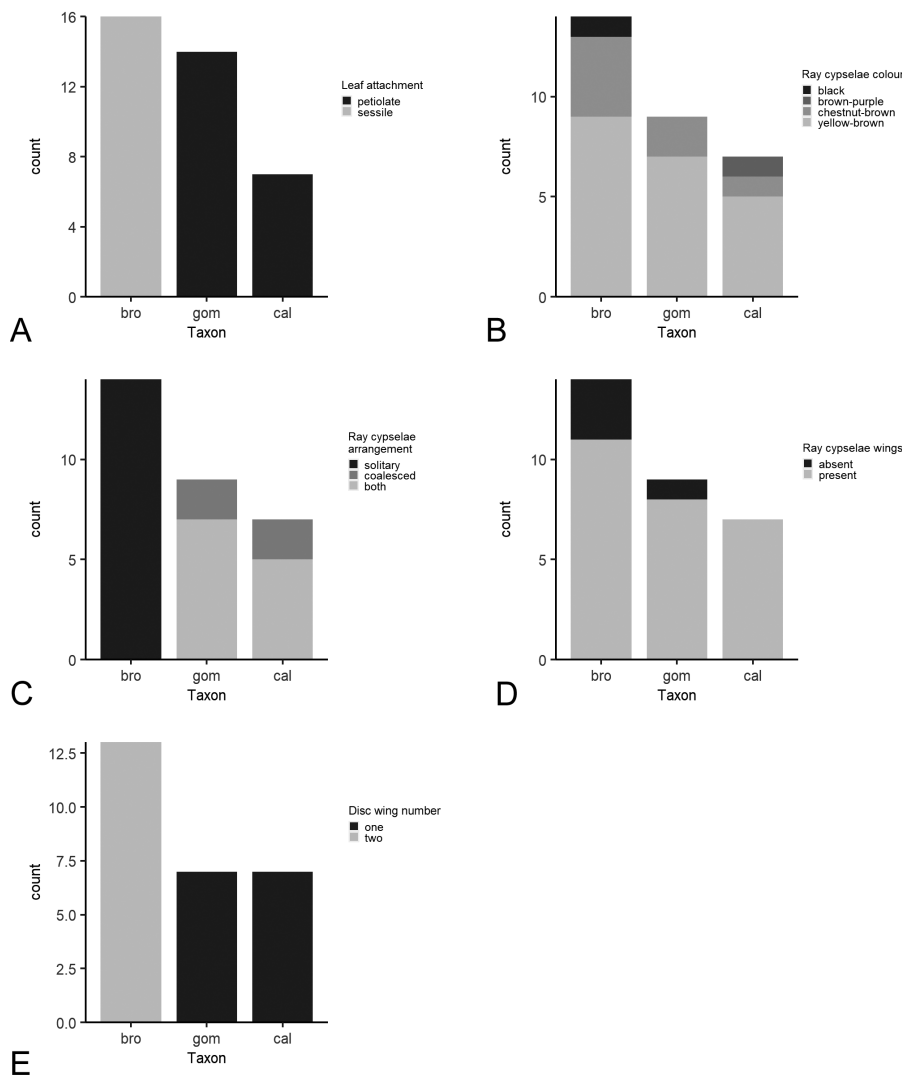


Fig. 6. Stacked bar plots with frequency counts for each discrete character. – Taxon abbreviations: bro = *Argyranthemum broussonetii*; gom = *A. callichrysum* subsp. *gomerensis*; cal = *A. callichrysum* subsp. *callichrysum* (names as accepted in this study).

Habitat — Along roadsides and open clearings of *Laurus novocanariensis* forest between 550 and 1000 m.

Additional specimens examined — SPAIN, Canary Islands, La Gomera: Degollada de San Sebastian, 1845, *E. Bourgeau* 247 (BM! [BM013846021]); Bco. de Liria, 15 May 1945, *E. R. Sventenius* (ORT! [ORT4825]); Hermigua, 7 Jul 1960, *E. R. Sventenius* (ORT! [ORT4833]); Hermigua, 18 Apr 1961, *R. T. Lowe* 133 (BM! [BM000083898]); Pico Aragán, 19 May 1965, *E. R. Sventenius* (ORT! [ORT4848]); El Cano, 1973, *M. Fernández Galván* 26022 (ORT! [ORT26022]); La Meseta, 20 Apr 1975, *M. Fernández Galván* 26019 (ORT! [ORT26019]); La Meseta, 20 Apr 1975, *M. Fernández Galván* 26024 (ORT! [ORT26024]); Las Casas del Cedro, 16 Jul 1975, *M. Fernández Galván* s.n. (ORT!); Aguajilva, Mar 1976, *M. Fernández Galván* 26338 (ORT! [ORT26338]); Meriga, límite inf. del monte, Apr 1976, *M. Fernández Galván* 26344 (ORT! [ORT26344]); Aguajilva, Apr

1976, *M. Fernández Galván* 26469 (ORT! [ORT26469]); top of Barranco del Hermigua, 8 May 1977, *Jarvis* 603 (BM! [BM013846029]); borde superior del monte del Cedro, 27 Jul 1977, *M. Fernández Galván* 26661 (ORT! [ORT26661]); alongside CV-17 above Igualero, 16 May 2015, *O. White & al.* 100 (BM! [BM000828652], ORT!); alongside CV-6 S of Epina, 17 May 2015, *O. White & al.* 104 (BM! [BM000828648], ORT!); Las Rosas, 17 May 2015, *O. White & al.* 108 (BM! [BM000828644], ORT!); Las Rosas, 17 May 2015, *O. White & al.* 109 (BM! [BM000828643], ORT!); between Las Rosas and La Palmita, 17 May 2015, *O. White & al.* 110 (BM! [BM000828642], ORT!); between Las Rosas and La Palmita, 17 May 2015, *O. White & al.* 111 (BM! [BM000828641], ORT!); S of La Palmita, 17 May 2015, *O. White & al.* 112 (BM! [BM000828640], ORT!); S of La Palmita, 17 May 2015, *O. White & al.* 113 (BM! [BM000828639], ORT!); S of La Palmita, 17 May 2015, *O. White & al.* 114 (BM! [BM000828638], ORT!); N of La Palmita, 17 May 2015, *O. White & al.* 115 (BM! [BM000828637], ORT!).

Argyranthemum callichrysum Humphries in Bull. Brit. Mus. (Nat. Hist.), Bot. 5: 210. 1976 subsp. *callichrysum*. – Holotype: Spain, Canary Islands, La Gomera, Fuente de la Yegua, 18 May 1945, *E. R. Sventenius* (ORT! [ORT4828]).

Leaves petiolate, bipinnatisect; primary lobes linear-lanceolate. Disc cypselae 1-winged; ray cypselae often coalesced.

Distribution — La Gomera: distributed from Barranco de Argaga on the SW coast to the central mountains of Igualero, Agando and Tagamiche, where it is found on S-facing slopes (Fig. 1).

Habitat — Associated with xerophytic scrub on rocky slopes or disturbed vegetation.

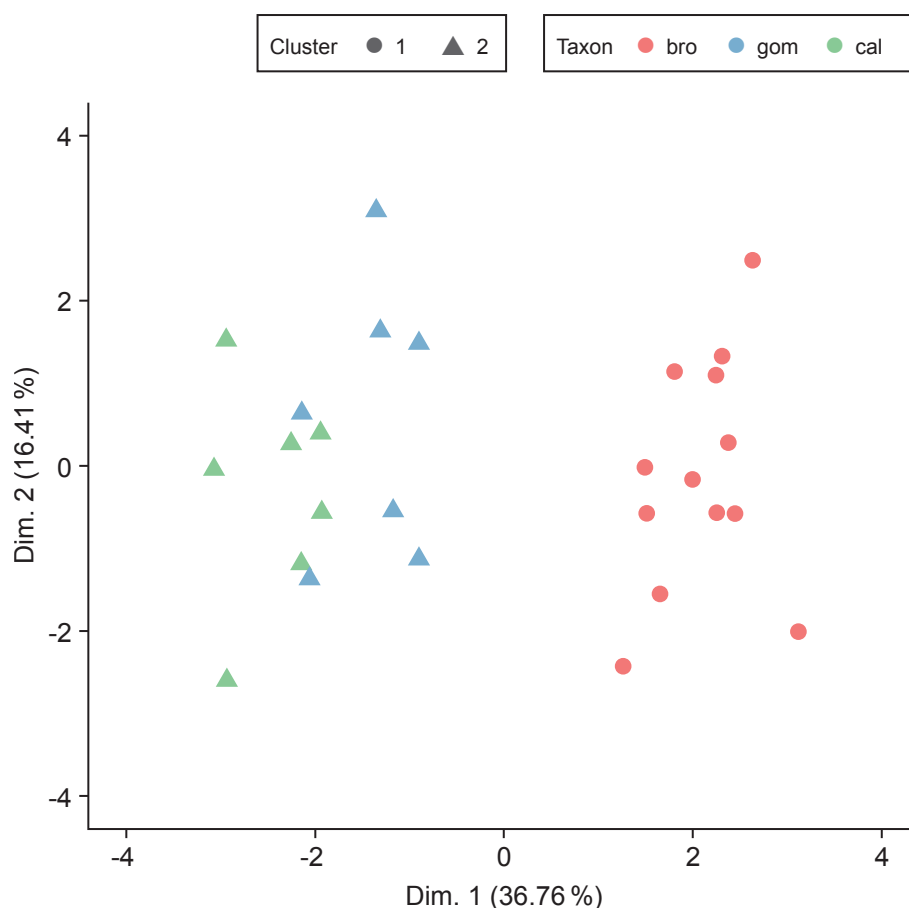


Fig. 7. PCA based on continuous and discrete characters. Point colour indicates the taxon recognized in this study, whereas shape indicates the cluster defined using mclust. The proportion of variation explained on each dimension is shown in parentheses. – Taxon abbreviations: bro = *Argyranthemum broussonetii*; gom = *A. callichrysum* subsp. *gomerensis*; cal = *A. callichrysum* subsp. *callichrysum* (names as accepted in this study).

Notes — *Chrysanthemum callichrysum*, the supposed synonym of *Argyranthemum callichrysum*, was published by Sventenius (1960). The validity of names published in this work has been called into question, but Bramwell (2019) has argued convincingly that they are validly published. In the case of the *Argyranthemum* names described by Sventenius, the types were examined by Humphries, who visited ORT in 1971 and cited them in his monograph (Humphries 1976).

Unfortunately, in the case of *Chrysanthemum callichrysum*, the name was not validly published because Sventenius cited two gatherings, “Legit cum flore die 18 Maio 1945 et cum fructu die 12 Augusto 1952”, without indicating either one of them as the type. If he had cited only one gathering, the name would have been validly published, even though he did not explicitly designate a type (Turland & al. 2018: Art. 40.2, 40.3). Humphries (1976) explicitly cited a single specimen (or gathering) as the holotype and provided a full and direct reference to the Latin description previously published by Sventenius, thereby validly publishing *Argyranthemum callichrysum* as the name of a new taxon, not a new combination.

During the course of this study, we were unable to find a specimen with a locality that matched exactly that given in the original description of *Chrysanthemum callichrysum* by Sventenius (“circa pagum ‘Igualeiro’ dictum, versus 1.000 m. supra mare” [near to the village called Igualeiro, toward 1000 m above the sea]) or in the protologue by Humphries (“Igualeiro [sic], 1000 m, 18 May 1946”, presumably in error for 1945). Nevertheless, there is a specimen at ORT collected by Sventenius (ORT4828) on the same date (18 May 1945) as that cited in his original publication, from “Fuente de la Yegua”, a locality less than 1 km from Igualeiro. We therefore propose that this specimen is one of those to which Sventenius was referring as well as the holotype cited by Humphries.

Additional specimens examined — SPAIN, Canary Islands, La Gomera: Las Carboneras, s.d., *M. Fernández Galván* 26340 (ORT! [ORT26340]); Roque de

Agando, 20 May 1945, *E. R. Sventenius* 4832 (ORT! [ORT4832]); Fte. Tamadauche, 3 Mar 1946, *E. R. Sventenius* 4827 (ORT! [ORT4827]); Fuente Tamadauche, 14 May 1946, *E. R. Sventenius* 4838 (ORT! [ORT4838]); planta orig. del Igualeiro. Cult. en Tafira, 7 Mar 1954, *E. R. Sventenius* 23872 (ORT! [ORT23872]); Seima, Risco Serradero, 19 May 1958, *E. R. Sventenius* 4829 (ORT! [ORT4829]); Seima, Risco Serradero, 19 May 1958, *E. R. Sventenius* 4830 (ORT! [ORT4830]); Ojila, 29 Mar 1959, *E. R. Sventenius* 4831 (ORT! [ORT4831]); Taguluche, 13 May 1959, *E. R. Sventenius* 4863 (ORT! [ORT4863]); Bco. de la Laja, Roque Grande, 22 May 1965, *E. R. Sventenius* 4853 (ORT! [ORT4853]); Pico Gomero, 19 Apr 1966, *E. R. Sventenius* 4851 (ORT! [ORT4851]); Degollada Blanca, Pico Gomero, 19 Apr 1966, *E. R. Sventenius* 4852 (ORT! [ORT4852]); Andenes sobre Benchijigua, 23 Apr 1966, *E. R. Sventenius* 4834 (ORT! [ORT4834]); Andenes sobre Benchijigua, 23 Apr 1966, *E. R. Sventenius* 4835 (ORT! [ORT4835]); Andenes de Tagasmiche, 5 May 1968, *E. R. Sventenius* 4854 (ORT! [ORT4854]); Andenes de Tagasmiche, 5

May 1968, *E. R. Sventenius 4855* (ORT! [ORT4855]); Ardenes de Benchijigua, 8 May 1968, *E. R. Sventenius 4860* (ORT! [ORT4860]); Andenes de Benchijigua, 8 May 1968, *E. R. Sventenius 4861* (ORT! [ORT4861]); Taguluche Norte, 12 Jul 1968, *E. R. Sventenius 4846* (ORT! [ORT4846]); Taguluche Norte “Las Puertas”, 14 Jul 1968, *E. R. Sventenius 4843* (ORT! [ORT4843]); sobre los Andenes de Benchijigua, 23 May 1969, *E. R. Sventenius 4859* (ORT! [ORT4859]); s.loc., May 1969, *E. R. Sventenius 4858* (ORT! [ORT4858]); Roque de Agando, 27 Jun 1969, *D. Bramwell 1999* (RNG [image!]); Jerduñe, 6 May 1970, *E. R. Sventenius 4849* (ORT! [ORT4849]); Tacaluco, 11 Jun 1970, *E. R. Sventenius 4862* (ORT! [ORT4862]); Igualero, 30 Mar 1971, *D. Bramwell & C. J. Humphries 3174* (BM! [BM013846031]); near Arure, 7 Mar 1973, *A. E. Aldridge 1081* (BM! [BM013846032]); Laderas del Rq. Cano, May 1973, *M. Fernández Galván 26020* (ORT! [ORT26020]); Dgda. de Peraza, 17 May 1975, *M. Fernández Galván 26025* (ORT! [ORT26025]); Orillas de Izque, 1 May 1976, *M. Fernández Galván 26422* (ORT! [ORT26422]); Arure, 16 Apr 1978, *M. Fernández Galván 27921* (ORT! [ORT27921]); sobre Dgda. Peraza, 8 Mar 1997, *A. Santos 34.327* (ORT! [ORT34327]); Dgda. Peraza, 8 Mar 1997, *A. Santos 34.328* (ORT! [ORT34328]); Bajada, 9 Mar 1997, *A. Santos 34.329* (ORT! [ORT34329]); Las Nieves, 10 Mar 1997, *A. Santos 34.324* (ORT! [ORT34324]); Lomo de Carretón between Alojera and Taguluche, 10 Jan 1998, *M. Nydegger 25188* (RNG [image!]); Barranco de la Guancha, 16 May 2015, *O. White & al. 94* (BM! [BM000828658], ORT!); Barranco de la Guancha, 16 May 2015, *O. White & al. 95* (BM! [BM000828657], ORT!); Barranco de la Guancha, 16 May 2015, *O. White & al. 96* (BM! [BM000828656]); Roque de Agando, 16 May 2015, *O. White & al. 97* (BM! [BM000828655], ORT!); Roque de Agando, 16 May 2015, *O. White & al. 98* (BM! [BM000828654], ORT!); alongside TF-713 W of Roque de Agando, 16 May 2015, *O. White & al. 99* (BM! [BM000828653], ORT!); Vallehermosa, s.d., *A. E. Aldridge s.n.* (BM! [BM013846033]).

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Supplemental content online

See <https://doi.org/10.3372/wi.51.51111>

Supplementary Table S1. Input data used for morphological analyses.

Supplementary Table S2. Full list of vouchers analysed and seen as part of this study with locality descriptions.

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