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

Authors: White, Oliver W., Reyes-Betancort, J. Alfredo, Chapman, Mark A., and Carine, Mark A.

Source: Willdenowia, 51(1) : 129-139

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.51.51111
OLIVER W. WHITE1,2,3*, J. ALFREDO REYES-BETANCORT4, MARK A. CHAPMAN2 & MARK A. CARINE1

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

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.

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

Citation: White O. W., Reyes-Betancort J. A., Chapman M. A. & Carine M. A. 2021: Recircumscription of the Canary Island endemics Argyranthemum broussonetii and A. callichrysum (Asteraceae: Anthemideae) based on evolutionary relationships and morphology. – Willdenowia 51: 129–139. doi: https://doi.org/10.3372/wi.51.51111

1 Algae, Fungi and Plants Division, Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.
2 Biological Sciences, University of Southampton, Southampton, SO17 1BJ, U.K.
3 Present address: Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, U.K.; *e-mail: o.william.white@gmail.com (author for correspondence).
4 Jardín de Aclimatación de La Orotava (Instituto Canario de Investigaciones Agrarias – ICIA), C/ Retama 2, 38400 Puerto de la Cruz, Tenerife, Spain.
1996). However, the sister relationships of *A. broussonetii* 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. broussonetii* are distinct evolutionary lineages. Specifically, *A. broussonetii* subsp. *broussonetii* is sister to the multi-island endemic *A. frutescens* (L.) Sch. Bip., whereas *A. broussonetii* 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. broussonetii* subsp. *broussonetii* and *A. callichrysum*, ruling out the possibility that *A. broussonetii* subsp. *gomerensis* is the result of historical hybridization between *A. broussonetii* and *A. callichrysum*.

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

**Material and methods**

We identified ten characters that differed between the two subspecies of *Argyranthemum broussonetii* 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 identified 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. broussonetii* subsp. *broussonetii*, 14 *A. broussonetii* 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).
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), primary 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.
The PCA of both continuous and discrete variable showed a clear separation on the x axis, with *Argyranthemum broussonetii* subs. *gomerensis* and *A. callichrysum* clustering together and *A. broussonetii* subs. *broussonetii* forming a distinct group (Fig. 7). There was a slight separation between *A. broussonetii* subs. *gomerensis* and *A. callichrysum* in the PCA plot. However, mclust identified only two clusters: the first corresponding to *A. broussonetii* subs. *gomerensis* and *A. callichrysum*, the second composed of *A. broussonetii* subs. *broussonetii* (Fig. 7).

**Discussion**

From a morphological perspective, we found that *Argyranthemum broussonetii* subs. *broussonetii* and subs. *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* subs. *broussonetii* and subs. *gomerensis* can be distinguished based on leaf attachment, capitula width and cypselae characteristics. Indeed, *A. broussonetii* subs. *gomerensis* shows greater similarity to *A. callichrysum* based on these characters, which is in agreement with their phylogenetic relationships (White & al. 2020; Fig. 3) and the hypothesis proposed by Francisco-Ortega & al. (1996). While our ordination analysis shows some overlap between *A. broussonetii* subs. *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* subs. *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* subs. *gomerensis* should be recognized as a subspecies of *A. callichrysum*. While *A. broussonetii* subs. *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

---

**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         | Leaf lobes defined as paired or obovate or ovate limbs; consensus taken across specimen |
|                               | 1. petiolate (≥ 1.5 cm)                                                |                                                                            |
|                               | 2. shortly petiolate ± sessile (0.5–1.5 cm)                            |                                                                            |
|                               | 3. sessile (≤ 0.5 cm)                                                  |                                                                            |
| 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                                                  | Used extra cypselae in packet if available or dissection of specimen       |
|                               | 2. chestnut brown                                                     |                                                                            |
|                               | 3. brown-purple                                                       |                                                                            |
|                               | 4. black                                                               |                                                                            |
| Ray cypselae arrangement       | 1. solitary                                                            | Used same cypselae as above                                               |
|                               | 2. coalesced                                                           | solitary: single cypselae                                                  |
|                               | 3. both                                                                | coalesced: 2–6 coalesced cypselae                                          |
| Ray cypselae wings             | 1. absent                                                              | Used same cypselae as above                                               |
| presence or absence            | 2. present                                                             |                                                                            |
| Disc cypselae wing number      | 1. no wings                                                            | Used same cypselae as above                                               |
|                               | 2. one wing                                                            |                                                                            |
|                               | 3. two wings                                                           |                                                                            |
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 broussonetii* 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. broussonetii* 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. broussonetii* 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 cypsela 1-winged; ray cypsela either coalesced or solitary.  
   - Leaves sessile with teeth and/or primary lobes to leaf base; capitulum 1.4–2.0 cm wide; disc cypsela 2-winged; ray cypsela typically solitary. ...  
     \[\text{Primary lobe dissection typical of this taxon, but the width of the primary lobes is more similar to that found in subsp. *gomerensis*. This may suggest potential hybrid ancestry of this individual.}\]  

2. Leaves bipinnatifid, primary lobes obovate, 0.75–1.5 cm wide.  
   - Leaves bipinnatisect, primary lobes linear-lanceolate, 0.2–0.75 cm wide.  
     \[\text{Primary lobe width} \quad \text{Primary lobe length} \quad \text{Lamina width} \quad \text{Leaf width} \]

![Fig. 4. Leaf measurements used in the morphological analysis.](https://bioone.org/journals/Willdenowia)

Leaves sessile, bipinnatifid; primary lobes ovate. Disc cypsela 2-winged; ray cypsela 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, Broussonet 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]); Fico Inglés in laurel forest, 2 Dec 1968, *D. Bramwell* 421 (RNG!); Icod el alto, laurel forest above road to Realejo, 13 Apr 1969, *D. Bramwell* 1257 (RNG!); Vueltas de Taganana, 21 May 1969, *D. Bramwell* 1534 (RNG!); ridge between Las Animas and Azaro, 9 Apr 1971, *D. Bramwell* & *C. J. Humphries* 3364 (BM! [BM013846023], RNG!); Roque de las Pasas, 9 Apr 1971, *D. Bramwell* & *C. J. Humphries* 3382 (BM! [BM013846026], RNG!); Roque de las Pasas, 9 Apr 1971, *D. Bramwell* & *C. J. Humphries* 3378 (RNG!); Punta de Anaga, Roque del Agua, 9 Apr 1971, *D. Bramwell* & *C. J. Humphries* 3382 (BM! [BM013846026], RNG!); 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 Chincobre, 3 May 1977, Jarvis & D. Bramwell 544 (BM! [BM013846022], RNG [image!]); Monte de las Mercedes, Mirador 4 km W of Pico del Inglês, 22 Apr 1997, Jarvis 467 (BM! [BM013846019], RNG [image!]); La Cumbriella, Anaga, 6 May 2015, O. White & al. 69 (BM! [BM000828683], ORT!); La Cumbriella, Anaga, 6 May 2015, O. White & al. 70 (BM! [BM000828682], ORT!); La Cumbriella, 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. ≡ *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 Palmita and Agulo on the NW coast (Fig. 1).
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! [ORT260199]); 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]); Aguajilva, Apr 1976, M. Fernández Galván 26459 (ORT! [ORT26459]); 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.
Notes — Chrysanthemum callichrysum, the supposed basionym 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 ‘Igualero’ dictum, versus 1.000 m. supra mare” [near to the village called Igualero, toward 1000 m above the sea]) or in the protologue by Humphries (“Igualero [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 Igualero. 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]); Feie. Tamadauche, 3 Mar 1946, E. R. Sventenius 4827 (ORT! [ORT4827]); Fuente Tamadauche, 14 May 1946, E. R. Sventenius 4838 (ORT! [ORT4838]); planta orig. del Igualero. 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]); Ardenes 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]); Jerdúche, 6 May 1970, E. R. Sventenius 4849 (ORT! [ORT4849]); Taculucue, 11 Jun 1970, E. R. Sventenius 4862 (ORT! [ORT4862]); Igualeiro, 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 Alajera 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]).

Acknowledgements
The authors would like to acknowledge the Cabildos of Tenerife (permit number 18297), and La Gomera (3102) for permission to undertake fieldwork. In addition, we would like to thank Arnoldo Santos-Guerra for advice and assistance with fieldwork, Kevin Webb of the Natural History Museum (London) photographic unit for cypexae images and Mike Cotton (University of Southampton) for maintenance of greenhouse plants. Finally, we thank Christoph Oberprieler (Universität Regensburg) and Inés Álvarez Fernández (Real Jardín Botánico de Madrid, CSIC) for their reviews of an earlier version of this paper.

References
Borgen L. 1976: Analysis of a hybrid swarm between Argyranthemum adauctum and A. filifolium in the Canary Islands. – Norw. J. Bot. 23: 121–137.
Bramwell D. 2019: The typification of species names published by Eric Sventenius. – Vieraea 46: 1–10.
Brochmann C. 1984: Hybridization and distribution of Argyranthemum coronopifolium (Asteraceae, Anthemideae) in the Canary Islands. – Nordic J. Bot. 4: 729–736.
Brochmann C., Borgen L. & Stabbetorp O. E. 2000: Multiple diploid hybrid speciation of the Canary Island endemic Argyranthemum sundingii (Asteraceae). – Pl. Syst. Evol. 220: 77–92.
Chavent M., Kuentz-Simonet V., Labenne A. & Saracco J. 2017: Multivariate analysis of mixed data: the R package PCAMixdata. – Published at https://arxiv.org/abs/1411.4911.
Chavent M., Kuentz-Simonet V. & Saracco J. 2012: Orthogonal rotation in PCAMIX. – Advances Data Analysis Classific. 6: 131–146.
Francisco-Ortega J., Jansen R. K. & Santos-Guerra A. 1996: Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora. – Proc. Natl. Acad. Sci. U.S.A. 93: 4085–4090.
Humphries C. J. 1976: A revision of the Macaronesian genus Argyranthemum Webb ex Schultz Bip. (Compositae–Anthemideae). – Bull. Brit. Mus. (Nat. Hist.), Bot. 5: 145–240.
R Core Team 2018: R: a language and environment for statistical computing. – Vienna: R Foundation for Statistical Computing. – Published at https://www.r-project.org/
Scrucca L., Fop M., Murphy T. B. & Raftery A. E. 2016: mclust 5: clustering, classification and density estimation using gaussian finite mixture models. – J. R Stat. Soc. B 8: 289–317.
Sventenius E. R. 1960: Additamentum ad floram canariensem I. – Matriti: Agronomiarum Investigationem Nationale Hispanicum Institutum.
Turland N. J., Wiersema J. H., Hawksworth D. L., Herendeen P. S., Knapp S., Kusber W.-H., Li D.-Z., Marhold K., May T. W., McNeill J., Monro A. M., Prado J., Price M. J. & Smith G. F. (ed.) 2018: International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. – Glashütten: Koeltz Botanical Books [= Regnum Veg. 159].
White O. W., Reyes-Betancort J. A., Chapman M. A. & Carine M. A. 2020: Geographical isolation, habitat shifts and hybridisation in the diversification of the Macaronesian endemic genus Argyranthemum (Asteraceae). – New Phytol. 228: 1953–1971.
Yu G.-C., Smith D. K., Zhu H.-C., Guan Y. & Lam T. T.-Y. 2016: ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. – Meth. Ecol. Evol. 8: 28–36.

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.