Codonographia Gorgonum, or the description of a pleiad of bellflowers (Campanula, Campanulaceae) from the Cabo Verde archipelago

Mathieu L. Gardère, Jacques Florence, Serge Muller, Yoland Savriama & Jean-Yves Dubuisson

Abstract

GARDÈRE, M.L., J. FLORENCE, S. MULLER, Y. SAVRIAMA & J.-Y. DUBUISSON (2021). Codonographia Gorgonum, or the description of a pleiad of bellflowers (Campanula, Campanulaceae) from the Cabo Verde archipelago. Candollea 76: 13–40. In English, English and Portuguese abstracts. DOI: http://dx.doi.org/10.15553/c2021v761a2

The previous taxonomic study of Cabo Verdean bellflowers (Campanula L., Campanulaceae) recognized four endemic species. In light of a recently published geometric morphometric study, the reassessment of the Campanula jacobaea complex allows to restrict Campanula jacobaea C. Sm. ex Webb to the island of Santiago. A new lectotype is proposed for this name that conforms to the protologue. Three further new species are described: Campanula monteverdensis Gardère from São Vicente, Campanula fransinea Gardère and Campanula cochleromena from São Nicolau, and Campanula vicinituba Gardère from Santo Antão. Campanula hortelensis Gardère, also from Santo Antão is placed in synonym of Campanula feijoana Gardère. Seven species are recognized in the Cabo Verde archipelago including Campanula bravensis (Bolle) A. Chev., the most widespread bellflower occurring in all southern mountainous islands. A determination key, descriptions, photographs and a distribution map are provided.

Keywords

CAMPANULACEAE – Campanula – Cabo Verde – Macaronesia – Taxonomy – Typification

Addresses of the authors:
MLG, SM, JYD: Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d’Histoire naturelle, CNRS, Sorbonne Université, Université des Antilles, EPHE, CP 39, 57 rue Cuvier, F–75005 Paris, France. E-mail: mathieu.gardere@mnhn.fr
JF: Herbier national, Muséum national d’Histoire naturelle, CP 39, 57 rue Cuvier, F–75005 Paris, France.
YS: Max-Planck-Institute for Evolutionary Biology, Department of Evolutionary Genetics, August-Thienemann-Str. 2, Plön, Germany.
Introduction

The genus *Campanula* L. (Campanulaceae), commonly known as bellflowers, comprises approximately 420 species which are distributed across Arctic and temperate regions of the Northern Hemisphere (Lammers, 2007), with some in tropical continental regions, especially in Africa where it occasionally extends to the Southern Hemisphere (Thulín, 1976, 1977); others are found in insular environments, particularly those of the Cabo Verde archipelago (Gardère, 2020), the focus of the present study. Situated in the mid-Atlantic Ocean c. 570 km off the West African coast and c. 1360 km south from the Canary Islands, the islands of Cabo Verde are the southernmost of Macaronesia (Fig. 1). Confined to the mountainous islands, Cabo Verdean bellflowers [CVB] occur mainly in humid, rupicolous environments (Gardère et al., 2017) and more rarely in shrublands. CVB form very floriferous and lignified subshrubs of remarkable size, which have always fascinated collectors and are of significant horticultural value (Hooker, 1883; Lobin et al., 1993). However, the restricted access to material due to the isolation of the archipelago, and the difficulty of preserving the exact shape of the corolla in herbarium specimens, has long impeded morpho-taxonomic research.

Feijó or the first collections

The first collections of bellflowers in the Cabo Verde archipelago date back to the end of the 18th century and were made by the Portuguese naturalist João da Silva Feijó (1760–1824) during the famous “Philosophical Journeys” (Gardère et al., 2019a). Feijó was assigned by the Portuguese Crown to study the natural history of the archipelago and made numerous collections of plants between 1783 and 1789, including bellflower specimens. In 1788, Feijó wrote a short unpublished manuscript entitled *Plantae Insulanae*, where he described some monospecific genera which he considered as new for science. Among these was the genus “*Fransinea*”, including a single species “*Fransinea insulana*”, since identified as belonging to *Campanula* (Gardère et al., 2019a). At present the only two existing bellflower specimens collected by Feijó are conserved at P. The precise localities where these plant collections were made, unknown until now, have now been determined thanks to examination of the flowers, as discussed below.

Collections from the first half of the 19th century

During the first half of the 19th century, scientific expeditions bound for as-yet unexplored regions of the globe made frequent stopovers, used by botanists to collect plant specimens. In 1816 the Norwegian botanist C. Smith, a member of the expedition of Captain Tuckey, made the second known collection of bellflowers from Santiago during a short visit (Sunding, 1980). Smith later died on the banks of the Congo River during the expedition; his herbarium was brought back by his assistant D. Lockard and his notes were published in the accounts of the expedition (Tuckey, 1818). In his list of specimens, Smith considered the bellflower collected around Pico da Antónia to be new and named it “*Campanula jacobaea*” (Tuckey, 1818: 251), but lacking a description, this name remained a *nomen nudum*. The next collections were made in 1822 by J. Forbes during stopovers in São Nicolau, Santo Antão and Santiago (Owen, 1833). Then in 1832, on the second voyage of the Beagle, C. Darwin made a short visit to Santiago (Vala, 2009), where he collected material around the valley of São Domingo. A few years later, in 1839, J.D. Hooker, heading south with the *Antarctica Expedition* of Captain Ross, also collected material in the same locality and gave a brief description of it in a letter to his father W.J. Hooker: “A most beautiful blue flowered *Campanula* (nº 125) next appeared with corollas 1 ½ inch long quite European in appearance” (Rico et al., 2017: Appendix S1); in addition, he wrote in his journal: “a lovely fern with beautiful soft green foliage growing like our *Cystopteris* [Hypodematum crenatum (Forssk.) Kuhn, Dryopteridaceae] out of the crevices of the rocks; it grew with lots of the *Campanula* and Umbellifer (found on the way up) which so put me in mind of old Scottish forms of plant” (Huxley, 1918: 94). In 1841, the collections made by T. Vogel joined the list: during a stopover of the *Niger Expedition* in São Vicente, he collected some specimens from the summit of Monte Verde (Vogel, 1849).

Taxonomic genesis and successive concepts

In 1848, Webb gathered the collections of Forbes, Darwin, Hooker and Vogel, and, as a prelude to his *Spicilegia Gorgena* (Webb, 1849), made the first description of a species based on these specimens (Webb, 1848). At first, the name “*Campanula daltonii* Webb” was indicated on the specimen labels and included in a list of plants of the Cabo Verde islands prepared by Decaisne (1848) as part of a study by C. Sainte-Claire Deville on the geology of the archipelago. However, Webb ended up adopting Smith’s epithet when he formally described the CVB in *Icones Plantarum*, hence validly publishing the name *C. jacobaea* (C. Sm. ex Webb (Webb, 1848: tab. 762). Later, Bolle (1861) undertook the first study in which infraspecific taxa were proposed, subdividing *C. jacobaea* into four entities: var. “genuina”, an invalid name for the type variety (Santo Antão and São Nicolau), var. *humilis* (São Vicente and São Nicolau), var. *bispida* (Santiago), and var. *brevensis* (Brava). This first taxonomic division was not be entirely upheld, as it was founded on a complex combination of many inconsistent morphological features: ratios of the lengths of the calyx/corolla and different types of indument. Besides this, the supposed geographical ranges of the different varieties were not all confirmed. Chevalier (1935), in his *Flore de l’archipel*, raised...
the var. bravensis to the species level, as C. bravensis (Bolle) A. Chev. (Chevalier, 1935: 889), but most botanists retained a monospecific concept accepting only C. jacobaea (Nogueira, 1976; Sunding, 1982; Lobin, 1982, 1986; Hansen & Sunding, 1985; Rustan & Brochmann, 1993; Figueiredo, 1995). It is only after the taxonomic revision of Leyens & Lobin (1995) that C. bravensis has been re-established as a distinct species. For the first time, a description was provided of its remarkable tubular corolla and the conical pubescent roof of the ovary, characters used to distinguish it from C. jacobaea, a highly polymorphic species with a campanulate corolla in addition to a flat and glabrous roof of the ovary. However, faced with the high level of variability in the floral characters, this taxonomic concept was challenged once again. Alarcón et al. (2013), unable to find reliable identifying characters nor geographic or genetic evidence to support the recognition of two species, retained a single, highly variable species, C. jacobaea, for the entire archipelago. More recently, the bellflowers from Santo Antão, hitherto identified as C. jacobaea, were described as two new species under C. feijoana Gardère and C. borteldensis Gardère (Gardère, 2015). These two species are clearly distinguishable from other CVB species by their infundibuliform corolla, constricted in its median part but distinguish from one another by several floral and foliar characters as the size, shape and position of the lobes and appendages of the calyx, and the shape and texture of the lamina of the rosette leaves.

Campanula jacobaea complex: one or several species?

Although the geographic range of C. jacobaea was reduced in 2015 to the islands of Santiago, São Nicolau, and São Vicente (Gardère, 2015), the species still was considered widespread in the archipelago with a high level of polymorphism. This is particularly pronounced in its floral characters. Field work conducted during numerous expeditions undertaken between 2013 and 2017 made it possible to untangle this enigmatic polymorphism. Campanula jacobaea in the wide sense indeed shows great diversity in the shape of its corolla: from campanulate to infundibuliform, including all the potential intermediate states. Nonetheless, based only on these distinctive shapes, four morphologically and geographically distinct entities can be identified: (1) a first, corresponding to the bellflowers from São Vicente with flared infundibuliform corollas, (2) a second, corresponding to the bellflowers from the western part of São Nicolau (henceforth W São Nicolau) with narrow infundibuliform corollas; and two other different entities with campanulate corollas: (3) one, corresponding to the bellflowers from the eastern part of São Nicolau (henceforth E São Nicolau), and (4) another, corresponding to the bellflowers from Santiago, with a longer corolla that is slightly constricted at the throat. Moreover, on an expedition in November and December 2015, a new entity with a flared, non-constricted infundibuliform corolla was discovered on the far eastern end of Santo Antão, in an isolated mountainous region.

The contribution of geometric morphometrics to distinguishing the species

To distinguish between these previously unsuspected morpho-geographic entities, we recently analysed the corolla shape of all of the CVB using geometric morphometrics (Gardère et al., 2019b). The corolla shapes of 221 photographed flowers were characterized in high detail by placing 2D landmarks and semi-landmarks, and were then subjected to a Generalized Procrustes Analysis to extract shape by removing information on size, location and orientation (Savriama et al., 2012; Gunz & Mitteroecker, 2013; Dryden & Mardia, 2016; Savriama, 2018). The results of this study support the division of C. jacobaea into four morpho-geographic entities and suggest that the concept of C. jacobaea should be restricted to the island of Santiago, i.e. the entity that best fits the original description of the species made by Webb (1848). Moreover, the results confirm the taxonomic re-establishment of C. bravensis proposed by Leyens & Lobin (1995) in which we adhere, as well as the close floral morphological affinities between C. feijoana and C. borteldensis, and the presence of new taxon on Santo Antão. Based on the results of the geometric morphometric analysis and the observation of numerous herbarium specimens, a taxonomic revision of Cabo Verdean species of the genus Campanula is presented here, along with an identification key. The discriminating characteristics are mainly floral (and foliar to a lesser extent), enabling the recognition of seven species (Fig. 1), all endemic to the archipelago, four of which are newly described and illustrated. In this way, C. jacobaea is now characterised as a species restricted to Santiago, and three entities are newly described for populations occurring on the other islands that were once included in its range: C. cocheromena Gardère and C. fransinea Gardère in São Nicolau, and C. monteverdensis Gardère in São Vicente. A new species is described for bellflowers from Santo Antão, C. vicinituba Gardère, whereas C. borteldensis is placed in synonymy under C. feijoana. Finally, given that the lectotype of C. jacobaea designated by Porter (1986) is in serious conflict with the protologue, a new lectotype is designated here.

Material and methods

The taxonomic revision presented below is essentially based on field observations made by the first author (MLG) during several trips to the Cabo Verde archipelago between 2009 and 2017 and specimen collections mainly deposited in the Herbaria of P, LISC and in the Herbarium of Cabo Verde – as yet unreferenced in the Index Herbariorum (Thiers, 2019): CECV Candollea 76, 2021
at the Electron Microscopy technical platform of the MNHN.

Barium specimens and observed using a Hitachi SU-3500 SEM.

Electron Microscopy (SEM), leaves were sampled from herbarium of W. Lobin, initially held in BONN, was transferred to FR in 2016 (W. Lobin, pers. comm.). A large collection of flowers prepared in the field is conserved in alcohol and stored in P. Corolla are described following the terminology of flowers prepared in the field is conserved in alcohol and stored in P. Corolla are described following the terminology proposed by Gardère et al. (2019b: Table 5). For Scanning Electron Microscopy (SEM), leaves were sampled from herbarium specimens and observed using a Hitachi SU-3500 SEM at the Electron Microscopy technical platform of the MNHN.

Key to the Cabo Verdean species of Campanula

1. Corolla campanulate or inflexed in bud; roof of the ovary glabrous and flat .................................................................................. 2
   1a. Corolla tubular (rarely urceolate); roof of the ovary pubescent and conical .............................................................. 2. C. bravenesis

2. Corolla campanulate ................................................................................. 3
   2a. Corolla inflexed .................................................................................. 4

3. Corolla with inflexion point in the upper third, throat slightly constricted; calyx-lobes triangular

   .............................................................................................. 1. C. jacobaea
   3a. Corolla with inflexion point in the middle, throat not constricted; calyx-lobes deltoid ........................................ 7. C. cochleromena

4. Corolla constricted in the median part ...... 3. C. feijoana
   4a. Corolla gradually widening without any visible constriction ......................................................................................... 5

5. Corolla narrowly flared, style included; calyx-lobes triangular, margin not or weakly revolute ........................................ 6
   5a. Corolla widely flared, style exserted; calyx-lobes widely triangular, margin clearly and distinctly revolute .............................................................. 5. C. monteverdensis

6. Corolla-tube ob-tronconical straight, 20–34 mm long; rosette-leaves narrowly obovate to narrowly elliptic, (3–)4–7.5(–10) × (0.8–)1–2.5(–3) cm, surface matt and pubescent with scattered hispidulous trichomes adaxially, with margin obscurely undulate to plane, primary and secondary veins hispidulous to hispid abaxially; margin of calyx-lobes hispidulous to hispid ................. 6. C. fransinea
   6a. Corolla-tube ob-tronconical straight to concave, 16–20 mm long; rosette-leaves narrowly elliptic to obovate, (1.5–)2–3.5(–3.3) × (0.5–)0.7–1(–1.2) cm, surface glossy and glabrescent adaxially, with margin always clearly undulate, primary and secondary veins striate to strigose abaxially; margin of calyx-lobes strigillose to strigose .................................................................................. 4. C. vicinituba

Taxonomic treatment

Campanula L., Sp. Pl.: 163. 1753.

Lectotypus (designated by Hitchcock in Hitchcock & Green, 1929: 131): Campanula latifolia L.

Vernacular names. – Thirteen vernacular names in Cabo Verdean Creole language have been noted from the literature and herbarium labels; new names have been recorded on the field. Historically, the most ancient vernacular name has been reported by Feijó who noted “Campainhas”, a Portuguese vernacular name to designate the bellflowers which is no longer used in the archipelago (Gardère et al., 2019a). Short lists of vernacular names are published by Basto (1988) and Feijão (1960) but without any information about localities. More recently, Gomes et al. (1995b) and Szpera (2015) have grouped all the CVB under “Contra-Bruxas” but this vernacular name is, in fact, peculiar to the bellflowers from Santo Antão (Levens & Lobin, 1995; Figueredo, 1995).

Distribution. – In the archipelago, the genus is found on all islands with elevations above 700 m, i.e. Santo Antão, São Vicente, São Nicolau, Santiago, Fogo, and Brava (Fig. 1).

Phenology. – Flowering and fruiting observed year-round, but flowering peaks after the rainy season between October and December. During the dry season, from April to August, the rosettes of sterile stems contract considerably and the marcescent leaves droop along the stem.

1. C. latifolia

Campanula latifolia C. Sm. ex Webb in Hook., Icon. Pl. 8: tab. 762. 1848 (Fig. 1, 2, 3A, 5C).

Lectotypus (erroneously designated by Porter, 1986: 85; corrected and designated here): Cabo Verde: sine loco, “sp. r. to be figured, Cap Verd”, s.d. [IV.1822], Forbes s.n. (G [G00426961] image!).

Sub-frutex 15–40 cm tall, highly woody in lower part; floriferous stems branched, decumbent to pendulous arising from the base of one or several sterile basal rosettes, glabrous to glabrescent in the woody basal parts with indument hispidulous to hispid toward the extremity, consisting of trichomes 0.2–1 mm long. Leaves: rosette leaves elliptic to narrowly elliptic, (1.5–)2–3.5(–5.5) × (0.5–)0.8–1.5(–2.5) cm, base cuneiform to slightly attenuate, apex ± obtuse to acute; cauleine leaves narrowly ovate to elliptic, (1.5–)2.5–3.5(–5.5) × (0.5–)0.8–1.5(–2.5) cm, base attenuate sometimes asymmetric, apex ± obtuse to acute; margin weakly revolute, crenulate; adaxial side light green in vivo, weakly or densely covered with hispidulous to hispid indument, consisting of trichomes 0.2–0.5 mm long; abaxial side light green in vivo, venation whitish, hispidulous to hispid indument on primary and secondary veins.
consisting of trichomes 0.4–0.6(–0.8) mm long and hispidulous indument on tertiary and ultimate veins consisting of trichomes 0.1–0.3 mm long, lamina glabrescent. Inflorescences in monochasial pauciflorous cyme or rarely in pluriflorous thyrs. Flowers erect rarely pendulous, pedicel 0.5–1.5(–2) cm long, with the same indument as the stem; axillate by one or two bracts subopposite, ovato-triangular or ovate to narrowly ovate, base semi-amplexicaul, apex acute, with the same indument as the leaves. Calyx: calyx-lobes triangular, 10–13 × 4–6 mm, erect, margin weakly revolute; appendages ovate, reflexed, 1.5–2 mm long; calyx-lobes, lobe edges, appendages and median main vein covered with an indument hispidulous to hispid consisting of trichomes 0.3–0.65 mm long. Corolla campanulate with inflexion point in the upper third, purplish-blue sometimes mauve with veins distinctly marked; base wide round c. 8 mm large; tube, 23–30 mm long, gradually widening and reach the maximum diameter of 14–18 mm in the upper third; throat slightly constricted then widening up to 20–26 mm at the mouth; lobes spreading to obliquely erect, 2–4 × 9–12 mm, apex apiculate; primary external veins hispidulous. Stamens
with glabrous filaments; anthers 2–4 mm long. **Ovary** with glabrous to glabrescent roof, flat, topped by a yellowish-with nectary disk. **Style** thick, fleshy, 15–18 mm long, included in the corolla, stigma trifid and papillose.

**Etymology.** – The specific epithet “**jacobaea**”, from the Latin **Jacobus**, refers to Santiago or “Saint James”; the island was given the name because it was discovered on Saint James Day. **Jacobaea** was initially chosen by Smith in 1816 to name the bellflowers from Santiago, which he wanted to describe as new to the Cabo Verde flora.

**Vernacular name.** – GOMES (1994) note “Velho-Teso” but in Brava this name is also use for *Spermacoce verticillata* L. (Rubiaceae) (Barbosa, 1961; DINIZ et al., 2002; MARTINS, 2002) and *Campanula bravensis* (Bolle, 1861).

**Distribution and habitat.** – *Campanula jacobaea*, now circumscribed to Santiago, is a montane chasmophyte that can be found from 600 m to 1100 m in humid rupicolous areas: on cliffs frequently covered in dense fog, with Limonium lobinitii N. Kilian & LEYENS (Plumbaginaceae), Polycarpaea gayi WEBB (Caryophyllaceae), Kickxia elegans (G. Forst.) D.A. SUTTON (Scrophulariaceae), sometimes Hypodematum crenatum (Dryopteridaceae) and abundant lichens, or on seeping rock faces and near to springs (*chupadeiros*) in the depths of valleys, near dense ferns, mainly Adiantum capillus-veneris L. (Pteridaceae), and sometimes Christella dentata (Forssk.) BROWNSEY & JERMY (Thelypteridaceae). *Campanula jacobaea* is confined to the main mountains: Serra do Pico da Antónia and Serra da Malagueta, but also Monte Afonso and Monte Tagarrinho, the last two localities being chorological novelties.

**Notes.** – WEBB (1848: tab. 762) based the description of *C. jacobaea* on collections from different geographical origin and different collectors; only the names of the collectors were indicated. The following year in his *Spicilegia Gorgonea* (WEBB, 1849) added information such as localities, dates and some-
Fig. 2. – *Campanula jacobaea* C. Sm. ex Webb. A. Habit; B. Rosette-leaves; C. Inflorescence; D. Flower in lateral view; E. Flower in face view.

[A–B: Gardère 1620; C: Gardère 1435; D: Gardère 928; E: Gardère 1211] [Photos: M.L. Gardère]
Sub-frutex 20–60 cm tall, highly woody in lower part; floriferous stems branched, erect or decumbent to procumbent arising from the base of one or several sterile basal rosettes, glabrous to glabrescent in the woody basal parts with indument hispidulous to hispid toward the extremity, consisting of trichomes 0.2–0.6 mm long. Leaves: rosette leaves narrowly obovate to narrowly elliptic, (2–)3.5–6(–8) × (0.6–)0.9–1.7 (–2.3) cm, base cuneiform to attenuate, apex obtuse to acute; cauline leaves narrowly obovate to narrowly elliptic, rarely ovate, (1.5–)3–5(–8) × (0.5–)1–1.5(–3) cm, base attenuate sometimes asymmetric, apex acute to ± obuse; margin weakly revolute, crenulate to serrulate; adaxial side light green to pure green in vivo, weakly or densely covered with hispidulous to hispid indument, consisting of trichomes (0.1–)0.2–0.6(–0.75) mm long sometimes with a slight canescent aspect in vivo; abaxial side greenish in vivo, veneration whitish, hispidulous to hispid indument on primary and secondary veins consisting of trichomes 0.4–0.6(–0.8) mm long and hispidulous indument on tertiary and ultimate veins consisting of trichomes 0.1–0.3 mm long, lamina glabrescent. Inflorescences in monochasial pauciflorous cyme or rarely in pluriflorous thyrs. Flowers generally ± pendulous or erect, pedicel 1.5–4 cm long, with the same indument as the stem; axillate by one or two bracts subopposite, ovato-triangular or ovate to narrowly ovate, base semiamplexicaul, apex acute, with the same indument as the leaves. Calyx: calyx-lobes narrowly triangular, 10–15 × 3–5 mm, erect to recurved rarely pressed up against the corolla tube, margin weakly revolute; appendages ovate, reflexed, 1.5–2 mm long; lobe edges, appendages and median main vein covered with an indument hispidulous rarely hispid, consisting of trichomes 0.3–0.45(–0.6) mm long. Corolla tubulate, generally whitish-green (never pure white) with the veins greenish, lobe edges sometime slightly purplish, rarely corolla entirely purplish-blue; base wide round; tube cylindrical, 22–33 × 8–13 mm, sometimes slightly constricted in the lower quarter giving an aspect bounded at the base; throat straight to slightly constricted occasionally highly constricted giving in extreme cases an urceolate shape to the corolla, mouth c. 20 mm; lobes erect to recurved, 2–4 × 7.5–11 mm, apex apiculate; primary external veins micro-hispidulous to hispidulous, 0.1 × 0.15 mm long. Stamens with glabrous filaments; anthers 2–4 mm long. Ovary with pubescent roof, conical, topped by a yellowish–with nectary disk. Style thick, fleshy, 17–22 mm long, included in the corolla, stigma trifid and papillose.

Etymology.—The epithet bravensis refers to the type locality, the island of Brava; brava meaning “wild” in Portuguese.

Vernacular names.—Among the CVB species, C. bravensis holds the most of vernacular names: in Brava, “Ortiga-Branca” and “Velho-Teso” (both according Bolle, 1861); in Fogo, “Fro-Franca” (Chevalier, 1935), “João-Copinho” in Campanas de
Fig. 3. – SEM micrographs of abaxial surface of leaves. A. *Campanula jacobaea* C. Sm. ex Webb; B. *C. bravensis* (Bolle) A. Chev.; C. *C. feijoana* Gardère; D. *C. vicinituba* Gardère; E. *C. monteverdensis* Gardère; F. *C. fransinea* Gardère; G. *C. cochleromena* Gardère. [A: Gardère 1428; B: Gardère 1615; C: Gardère 959; D: Gardère 1035; E: Gardère 612; F: Gardère 1096; G: Gardère 1120]
Fig. 4. – First herbarium sheet from K containing the syntypes of *Campanula jacobaea* C. Sm. ex Webb. A. Darwin’s specimen [K000865902] chosen in 1986 as isotypes of *C. jacobaea* by Porter, determined here as *C. bravensis* (Bolle) A. Chev., black circle showing the small footnote cross; A’. Label of the Darwin’s specimen, black circle showing the small footnote cross; B. Forbes’ specimen [K001134406] determined here as *C. fransinea* Gardère, white circle showing a fragment of *Hypodematiaceae*; C. Specimen attributed to a Forbes’ collect [K000865901] determined here as *C. fransinea*, white circle nº 1 showing a small fragment of *Hypodematiaceae*, white circle nº 2 showing a fragment of *Diplotaxis gracilis* (Brassicaceae); D. Specimen attributed to a Forbes’ collect [K001134405] determined here as *C. fransinea*. © Royal Botanic Gardens, Kew
Fig. 5. – Second herbarium sheet from K containing the syntypes of *Campanula jacobaea* C. Sm. ex Webb. A. Forbes’ specimen [K001134390] determined here as *C. feijoana* Gardère; B. Vogel’s specimen [K001134391] determined here as *C. monteverdensis* Gardère; C. Hooker’s specimen [K001134407] determined here as *C. jacobaea*.  
[© Royal Botanic Gardens, Kew]
Distribution and habitat. – Campanula bravensis has the broadest geographical range: it occurs on the three mountainous southern islands, i.e. Santiago, Fogo and Brava (Hansen & Sunding, 1993; Leyens & Lobin, 1995; Brochmann et al., 1997; Sánchez-Pinto et al., 2005), and is found in the widest range of elevations but in different plant communities according to habitats and islands. In Brava, C. bravensis is found from around 500 m elevation to the highest summits, on rocks regularly submitted to fog with Launaea thalassica N. Kilian et al. (Asteraceae), Tolpis farinulosa Walp. (Asteraceae), Daucus sp. (Apiaceae) and sometimes with Neprolepis undulata J. Sm. (Neprolepidaceae) or Pteris vittata L. (Pteridaceae). In Fogo, it can be found in low-elevation valleys from around 70 m (Brochmann & Rustan CB-916/82) up to the highest point of the island (and the entire archipelago), at around 2850 m (Gardère 1405). In this way, it occupies a diverse range of habitats such as the depths of wet lowland valleys (riberias), grassy slopes around Euphorbia tuckeyana Webb (Euphorbiaceae) shrubland, isolated on volcanic ash slopes, on wet rocks, near springs (chupadeiros), or at the entrance of caves with Adiantum capillus-veneris (Pteridaceae), Pteris vittata L. (Pteridaceae) and sometimes with Asplenium adiantum-nigrum L. (Aspleniacae) for the highest elevation locations. Campanula bravensis is very common across these two islands. On the other hand, in Santiago, it is quite rare and is only known from some field stations in the two main mountain ranges, Serra do Pico da Antónia and Serra da Malagueta, where it generally occurs around wet rocks with Pteris vittata (Pteridaceae) or more rarely along riverbeds, and often in sympatry with C. jacobaea.

Notes. – For Bolle (1861), the concept of his variety bravensis is limited to its type locality, i.e. Brava, because in the protologue he only cited his own collections from this island. Indeed, Bolle made two expeditions to the archipelago in 1851 and 1853 (Salinger & Strehlow, 1991), and collected only in Santo Antão, São Vicente, São Nicolau and Brava (Barbosa, 1962). Later, Andréade (1908) extended the concept of the variety bravensis to Fogo. Then, Chevalier (1935) raised the variety to the rank of species, adopting a broader concept than currently accepted and which included the islands of Brava, Fogo and Santiago. However, some authors have also extended the distribution of C. bravensis (Pettersson, 1960; Sunding, 1973; Eriksson et al., 1974, 1979) to W São Nicolau probably owing to the presence in this island of plants with white narrow infundibuliform corollas (C. fransinea), which slightly resemble C. bravensis.

For C. bravensis, the tubular corolla shape is the most noteworthy and dependable diagnostic feature to distinguish it from the other species. However, this feature is absent from the original description of the basionym. Bolle (1861) described the variety bravensis using features of the calyx-lobes, a calyx/corolla length ratio, and on the indument. That said, he did accurately describe the colour of the corolla: yellowish-white with green veins and with the edge of lamina (i.e. edges of corolla-lobes) slightly purplish. Chevalier (1935) added depth to the description of Bolle (1861) by describing the leaf shape which he used, along with the colour of the flower as a diagnostic feature. However, he did not make any descriptions of the shape of the corolla, even if considered unique in the genus, the character being described much later by Leyens & Lobin (1995).

Selected material seen. – Cabo Verde. Brava: Cruz Nho Basilo, 22.XI.2014, Gardère 899 (P); road between Fajã da Água and V.N. Cintra, 500 m, 3.III.1994, Leyens CV-94–065 (FR); an der Straße oberhalb Fajã da Água, 26.X.1979, Lobin 1144 (COI, FR); entre João de Nole and Cruz Nho Basilo, 850 m, 20.XII.2015, Gardère 1155 (P); Mato Grande, 650 m, 27.X.1984, Cardoso de Matos 5826 (CECV, LISC), N.S. do Monte, 720 m, 23.XI.2014, Gardère 901 (CECV, P); am Fußweg zwischen N.S. do Monte und Cova Rodala, c. 650 m, 19.I.1986, Kilian 1186 (FR); Ribeira Fajã da Água, 580 m, 23.XI.2014, Gardère 906 (P); de Pedra de Água para V.N. Cintra, 10.X.1956, Grandvaux Barbosa 6277 (O); Arco, 400 m, 25.I.1994, Leyens CV-94–1621 (B, FR); sine loco, 1852, Bolle s.n. (C, K pp.: remaining syntype for C. jacobaea var. bravensis); sine loco, 1853, Bolle s.n. (Z: remaining syntype for C. jacobaea var. bravensis); sine loco, “nos sempre flavo albidus”, s.d., Bolle s.n. (COI: remaining syntype for C. jacobaea var. bravensis); sine loco, VI.1873, s.c. “Herb. Dr. Sager” (P). Fogo: Achada Grande, 70 m, 16.II.1882, Brochmann & Rustan CB-916/82 (O); Arco, 400 m, 25.I.1994, Kilian 1368 & Leyens (B, FR); Chã das Caldeiras, 1700 m, 5.II.2014, Audo 21223 (MA); ibid. loco, 2800 m, 7.XI.1983, Cardoso de Matos 5617 (CECV, LISC); ibid. loco, 1800–2000 m, 23–24.VII.1934, Chevalier 44856 (COI); ibid. loco, 1700–1780 m, 14.X.1988, Diniz & Cardoso de Matos 260 (LISC); ibid. loco, 1800 m, 21.XII.2015, Gardère 1164 (CECV, P); ibid. loco, 1740 m, 21.X.2016, Gardère 1407 (CECV, LISC P); ibid. loco, c. 1760 m, 22.III.1994, Kilian 3278 & Leyens (B, FR); ibid. loco, c. 1650–1750 m, 24.I.1994, Kilian & Leyens 3326 (B, FR); ibid. loco, 1700 m, 30.X.1979, Lobin 1261 (FR); ibid. loco, 2.XI.1979, Lobin 1339 (FR); ibid. loco, 5.XII.1979, Lobin 1413 (FR); façade nord du cratère et dans le cratère, 4.XII.1985, Poivre de Fabréuges 4216 (ALF); Chupadeirão, 1350 m, 26.VII.2016, Gardère 1257 (P); Curral Fundo, 1000 m, 7.VII.1934, Leyens CV-94–2246 (O); ribeiras, 2800 m, 21.XII.2015, Gardère 1155 (P); ibid. loco, 1030 m, 3.VIII.2016, Gardère 1291 (CECV, P); Fogo, 1710 m, 22.XII.2017, Gardère 1290 (CECV, P); Figueirinha, 1660 m, 5.XII.1996, Leyens CV-96–662 (FR); Furna Defendida, 900 m, 20.X.2016,
Fig. 6. – *Campanula bravensis* (Bolle) A. Chev. A. Dense rupicolous shrubbery; B. Rosette-leaves; C. Inflorescence; D. Flower in lateral view; E. Flower in front view.

[A: Gardère 1614; B, D: Gardère 1263; C, E: Gardère 1416] [Photos: M.L. Gardère]
Gardère 1401 (P); Espigó, 460 m, 18.X.2016, Gardère 1390 (CECV, P); ibid. loco, 11.I.1956, Grandvous Barbosa 6277 (CECV, LISC), Monte Duarte, c. 1850 m, 23.I.1994, Kilian 3323 & Leyens (B, FR); entre Monte Cruz e Ponta Alto do Sul, 2100 m, 1.XI.1985, Cardoso de Matos 5992 (CECV, LISC); Monte Sodelho, 880 m, 2.VII.2016, Gardère 1282 (P); Monte Velha [or M. Velho], 1650 m, 21.X.1985, Cardoso de Matos 5966 (CECV, LISC); ibid. loco, c. 1500 m, 13.I.1896, Kilian 1117 (B, FR); ibid. loco, c. 1400 m, 28.VII.2016, Gardère 1263 (CECV, P); ibid. loco, 1500 m, 17.VII.2004, Marrero & Almeida s.n. (LPA); ibid. loco, 1200 m, 2.II.1980, Rustan 922 (O); Montinho, c. 1800 m, 23.XII.2017, Gardère 1633 (MARS, P); Nhucó, VIII.1934, Chevalier 45178 (P); ibid. loco, 1000 m, 1.VIII.2016, Gardère 1273 (P); ibid. loco, 24.III.1864, Loué s.n. (P); Penedo Rachado, 1250 m, 20.XI.2016, Gardère 1403 (CECV, P); Pico do Fogo, 2750 m, 21.X.2016, Gardère 1405 (P); Pico Novo, 2600 – 2800 m, 24.I.1994, Kilian & Leyens 3346 (B, FR); entre Fioiro e Monte Cruz, 1540 m, 22.X.2016, Gardère 1416 (CECV, LISC, P); Reva, 360 m, 19.X.2016, Gardère 1266 (CECV, P); Ribeira Campanas, 100 m, 14.X.1991, Martins et al. 492 (LISC); ibid. loco, 490 m, 8.XII.1995, Leyens CP-95-522 (FR); ibid. loco, 5.XI.1979, Lobin 1401 (FR); ibid. loco, 19.X.1982, Lobin 2340 (FR); Ribeira Coço, c. 1200 m, 28.VII.2016, Gardère 1265 (P); Ribeira Jan Reica, 1200 m, 16.II.1995, Leyens CP-95-421 (FR); Ribeira Monte Preto, 1700 m, 17.II.1982, Rustan & Brodsmann ÖHR-2299 (O); ibid. loco, 1005 m, 25.VII.2016, Gardère 1252 (P); Ribeira São Filipe, 950 m, 1.XI.1983, Cardoso de Matos 5532 (CECV, LISC); Ribeira Zóia, 1130 m, 25.VII.2016, Gardère 1253 (CECV, P); Ribeiras im Nordwest-Teil der Insel., c. 250 m, 19.X.1982, Levejeonhavn CV-82-165 (GOET); Suspensorio, 1800 m, 24.XII.2017, Gardère 1614 (P); sine loco, 1500 m, X.1898, Newton s.n. (K). – The species is dedicated to the Portuguese naturalist João da Silva Feijó (Gardère, 2015) who undertook the first scientific expedition entirely dedicated to the study of the natural history of the Cabo Verde islands between 1783 and 1796 during the “Philosophical Journeys” (Gardère et al., 2019a) and who made the first collections of CVB between 1783 and 1789.

**Etymology.** – The species is dedicated to the Portuguese naturalist João da Silva Feijó (Gardère, 2015) who undertook the first scientific expedition entirely dedicated to the study of the natural history of the Cabo Verde islands between 1783 and 1796 during the “Philosophical Journeys” (Gardère et al., 2019a) and who made the first collections of CVB between 1783 and 1789.

**Vernacular names and uses.** – “Guinchino” (Cardoso Júnior, 1905; Chevalier, 1935), “Mataquim” (in Água das Caldeiras, Hiemstra H236; Cardoso Júnior, 1905), “Contra-Bruxas” and “Dedal” (Chevalier, 1935; Barbosa, 1961; Leyens & Lobin, 1995; Figueiredo, 1995); the colour adjectives “branco” (white) and “azul” (blue) are sometimes added to the name; “Hortelâo-da-Rocha” in Moroços areas (Gardère 1560). However, in the archipelago according Chevalier (1935) “Mataquim” can also designate Corchorus trilocularis L. (Malvaceae) and on the
Fig. 7. – *Campanula feijoana* Gardère. Upright form from low-elevation locality: A. Habit; B. Pseudorosette-leaves; C. Inflorescence; D. Flower in lateral view; E. Flower in face view. Form of high-elevation locality in dense rupicolous shrubbery: F. Habit; G. Rosette-leaves.

[A: Gardère 1522; B–E: Gardère 1518; F–G: Gardère 1562] [Photos: M.L. Gardère]
island of Santo Antão, Barbosa (1961) records this name for *Antirrhinum orontium* L. (island of Santo Antão, Barbosa (1961) records this name for 28 –

Adiantum capillus-veneris grows with ferns, notably *feijoana* banks; and up to the highest mountainous areas, on rock rock faces or near to springs [chupadeiros], or rarely on river rocks. It is found from 150 m to 1700 m, in deep and shadowy environments, like *Scrophulariaceae*.[45x430]

Santo Antão, is a rupicolous species confined to steep, moist habitats. – *Campanula feijoana*, endemic to Santo Antão, is a rupicolous species confined to steep, moist rocky areas. It is found from 150 m to 1700 m, in deep and shadowy valleys [ribeiras] (Fig. 7A), surrounding waterfalls, on seeping rock faces or near to springs [chupadeiros], or rarely on river banks; and up to the highest mountainous areas, on rock faces (Fig. 7F) regularly submitted to dense fog. *Campanula feijoana* grows with ferns, notably *Adiantum capitulus-veneris* (*Pteridaceae*) and *Pteris viitata* (*Pteridaceae*) and with other species that are characteristic components of these rupicolous environments, like *Kikxia elegans* (G. Forst.) D.A. Sutton (*Scrophulariaceae*) and *Blumea axillaris* (*Asteraceae*).

Notes. – The bellflowers from Santo Antão have long been identified as *C. jacobaea* (Coutinho, 1914; Chevalier, 1935; Sünding, 1973, 1982; Eriksson et al., 1974, 1979; Nogueira, 1976; Hansen & Sünding, 1985, 1993; Rustan & Brochmann, 1993; Leyens & Lobin, 1995; Figueiredo, 1995; Sánchez-Pinto et al., 2005), moreover material from this island (Forbes s.n. [K001134390]) was chosen by Webb (1848: tab. 762) to be part of the syntypes of this species (see under *C. jacobaea*). In his infraspecific division of *C. jacobaea*, Bolle (1861) considered the bellflowers from Santo Antão and those from the upper humid areas of São Nicolau (see under *C. fransinea*), under the type variety "genuina". Then, Cardoso Júnior (1902) designated the white-flowered bellflowers from Santo Antão under the variety "albiflora". Without description this variety remains a nomen nundum.

More recently, the bellflowers from Santo Antão were described as two new species (Gardère, 2015: (1) *C. feijoana* (Fig. 7A–E) was described with pauciflorous inflorescences, calyx-lobes spread-out to obliquely erect prolonged by reflexed appendages and pseudorosette leaves spatulate with papery lamina, whereas (2) *C. bortelensis* (Fig. 7F, G) was described with pluriflorous inflorescences, calyx-lobes appressed against the corolla tube and prolonged by curved appendages and rosette-leaves elliptical to obovate often falciform with sub-leathery lamina. But the recent discovery of new localities with intermediate forms between *C. feijoana* and *C. bortelensis* (e.g. Gardère 1555) obscures the clean morphological and geographical separation of the two species. *Campanula feijoana* was found mainly in shadowy valleys and *C. bortelensis* in mountainous areas, hence they seem to represent altitudinal ecotypes belonging to a single and unique species. Given that *C. feijoana* is more widespread and representative of bellflowers with infundibuliform constricted corollas on the island, we conserve the name *C. feijoana* and treat *C. bortelensis* as a synonym of *C. feijoana*. In this way, the range of *C. feijoana* now covers almost the entire island of Santo Antão, except for the mountains of the far eastern part (Bordia Perdia) where bellflowers with flared infundibuliform corollas are found (see under *C. vicinituba*).
Fig. 8. – *Campanula vicinituba* Gardère. A. Habit; B. Rosette-leaves; C. Flowers in face view; D. Flower in lateral view. [A–D: Gardère 1563] [Photos: M.L. Gardère]
Campanula vicinituba

4. Campanula vicinituba Gardère, sp. nov. (Fig. 1, 3D, 8).

Holotypus: CABO VERDE. Santo Antão: Borda Perdia, paroi rocheuse sèche surplombant la Ribeira Brava, exposée ESE, 17°05’32”N 25°01’09”W, 1200 m, 30.XI.2017, Gardère 1563 (P [P02442771]!; iso- CECV!).

Plants altimontanis Campanulae feijoanae Gardère affinis, sed folis superne subglabris fulgentibus i n vivo (vs. pilosa ad glabrascentia hebetatique folia), margine crematodentata transverse undulataque (vs. plurumque planam cremato-serrulatum marginem), corolla infundibuliforme sine constrictione (vs. corollam cum constrictione), obtroncica basi corolla (vs. rotundata basi corollam), praeipsue differt.

Sub-frutex 15–20 cm tall, tortuous, highly woody in lower part, rhizome robust producing erect stipitiform stems: sterile stems, 5–10 cm long, topped by an oligophyllous rosette; floriferous stems, 10–20 cm long; glabrous to glabrescent in the woody basal parts, hispidulous to hispid toward the extremity, consisting of trichomes 0.15–0.7(–0.9) mm long. Leaves: rosette-leaves, subcoriaceous, narrow elliptic to obovate, sometimes, (1–)1.5–2.7(–3.3) × (0.5–)0.7–1(–1.2) cm, base attenuate to cuneiform, apex ± obtuse; cauline-leaves narrowly ovate to narrowly elliptic rarely elliptic, (1.5–)2–2.5(–3) × (0.4–)0.7–1(–1.1) cm, base attenuate to cuneiform, apex ± obtuse to acute; margin weakly revolute, undulate, serrulate; adaxial side light green and glossy in vivo, veins distinctly impressed, glabrescent or scattered by strigilllose trichomes, 0.3–0.5 mm long, indument generally more pronounced around the apex, epidermis blistered in sicco; abaxial side greenish in vivo, venation whitish, strigillose to strigose indument on primary and secondary veins consisting of trichomes 0.2–0.5 mm long and micro-hispidulous to hispidulous indument on tertiary and ultimate veins consisting of trichomes c. 0.1 mm long, lamina glabrescent. Inflorescences in monochasial pauciflorous cyme, emerging from lateral ramifications of the previous year inflorescences. Flowers erect, pedicel 1–2.5 cm long, with the same indument as the leaves; axillate by one or two bracts subopposite, narrowly elliptic, base semi-amplexicaul, apex acute, with the same indument as the leaf. Calyx: calyx-lobes triangular, 9–12 × 3–5 mm, erect to pressed up against the corolla, main vein in relief in vivo, margin weakly to distinctly revolute; appendages ovate, curved to reflexed, 1.5–2 mm long; lobe edges and appendages covered with an indument hispidulous to strigose, consisting of trichomes 0.2–0.6 mm long with bulbous base, median main vein glabrescent. Corolla infundibuliform, purple-blue (never white); base straight 7–8 mm large; tube ob-triconal straight to concave 16–20 mm long, widening gradually upwards and reaching 22–25 mm large at the mouth, constrictions absent; throat flared; lobes spreading to obliquely erect, 4 × 10 mm, apex apiculate; primary external veins micro-hispidulous to hispidulous, 0.1–0.12 mm long. Stamens with glabrous filaments; anthers, 2–4 mm long. Ovary with glabrous to glabrescent roof, flat, topped by a yellowish–with nectary disk. Style thick, fleshy, 13–17 mm long, included in the corolla, stigma trident and papillose.

Etymology. – The epithet vicinituba means the “neighboring trumpet” from the Latin vicinus, “close neighbor” and tuba, “trumpet”; the flowers closely resemble those of the bellflowers from São Nicolau which is easily visible from the rocks of Borda Perdia.

Distribution and habitat. – Campanula vicinituba is only known from its type locality: Borda Perdia, an isolated mountainous area on the far eastern part of Santo Antão at around 1200 m elevation and regularly covered by fog. This micro-endemic species is strictly chasmophyte and colonizes dry cliffs exposed ESE above Ribeira Brava along with Aeonium gorgoneum J.A. Schmidt (Crassulaceae), Phagnalon melanoleucum Webb (Asteraceae) and Polycarpacea gayi Webb (Caryophyllaceae).

Notes. – The flower of C. vicinituba is very close to C. fransinea, the corolla shapes of both species are infundibuliform but for C. vicinituba the corolla appears to be slightly more flared and shorter than C. fransinea. However, C. vicinituba can be identified easily by the indument of its primary and secondary venation and those of its margins of calyx-lobes which consist of bulbous and appressed trichomes. Furthermore, C. vicinituba presents a tortuous habit and leaves adaxially glabrescent and glossy, characters unique among CVB species; its flowers are always purple-blue.
Fig. 9. – *Campanula monteverdensis* Gardère. A. Habit; B. Rosette-leaves; C. Inflorescence; D. Flower in lateral view; E. Flower in face view. [A–C, E: Gardère 1092; D: Gardère 1506] [Photos: M.L. Gardère]
Additional specimens examined. – CABO VERDE. Santo Antão: Borda Perdida, 1200 m, 1.XII.2015, Gardère 1035–1037 (P); sine loco, “in rupestribus ins. S. Antonii”, III.1851, Schmidt s.n., (HBG p.p.).

5. **Campanula monteverdensis** Gardère, sp. nov. (Fig. 1, 3E, 5B, 9).

**Holotypus:** CABO VERDE. São Vicente: Monte Verde, 16°52′08″N 24°56′04″W, 740 m, 10.XII.2015, Gardère 1092 (P [P02442690]); iso-: CECV!.

= *Campanula jacobaea* var. *humilis* Bolle in Bonplandia 9: 50. 1861. **Lectotypus** (designated by Leyens & Lobin, 1995: 216): CABO VERDE. São Vicente: Monte Verde, 1852, Bolle s.n. (K [K001134400]).

**Campanulae jacobaeae** C. Sm. *ex* Webb affinis, *sed* foliis supra leviter bullatis *in vivo*, corolla late infundibuliforme *sine* constrictione (*vs.* *campanulatum* fauce paulo constricta), obovata *in vivo*, *exserta* a corollae, stigma *trifida* et *papillosa*.

**Sub-frutex** 5–20 cm tall, highly woody in lower part; floriferous stems branched, procumbent to decumbent arising from the base of one or several sterile basal rosettes, glabrous to glabrescent in the woody basal parts with indument hispidulous to hispid toward the extremity, consisting of trichomes 0.1–0.2 mm long. **Leaves:** rosette-leaves elliptic to ovate to narrowly ovate, base semi-amplexicaul, apex acute to obtuse, margin weakly revolute, crenulate; adaxial side light green *in vivo*, weakly bullate *in vivo*, glabrescent or scattered of strigose trichomes, 0.15–0.4 mm long, indument generally more pronounced around the apex; abaxial side light green *in vivo*, venation whitish, hispidulous–strigillose indument on primary and secondary veins consisting of trichomes 0.15–0.4 mm long, indument generally more pronounced around the apex; adaxial side light green *in vivo*, venation whitish, hispidulous–strigillose indument on primary and secondary veins consisting of trichomes 0.4–0.6(–0.7) mm long and hispidulous indument on tertiary and ultimate veins consisting of trichomes 0.1–0.3 mm long, lamina glabrescent. **Inflorescences** in monochasial pauciflorous cyme with continuous growth. **Flowers** erect, pedicel 0.5–1.5(–2) cm long, with the same indument as the leaves; axillate by one or two bracts subopposite, ovato-triangular or ovate to narrowly ovate, base semi-amplexicaul, apex acute, with the same indument as the stem. **Calyx:** calyx-lobes triangular, 10–13 × 4–6 mm, always pressed up against the corolla, margin distinctly revolute; appendages ovate, reflexed, c. 2 mm long; lobe edges, appendage and median main vein covered with an indument strigillose or hispidulous to hispid, consisting of trichomes 0.15–0.7 mm long. **Corolla** infundibuliform, dark purple (never white); base straight 7–8 mm long; tube ob-tronconical concave 13–18 mm long, widening gradually upwards and reaching 21–25 mm at the mouth, constrictions absent; throat widely flared; lobes spreading to obliquely erect, 4–8 × 2–4 mm, apex apiculate; external lamina entirely covered with indument microhispidulous c. 0.1 mm long, except the primary veins micro-hispidulous to hispidous, 0.15–0.2 mm long. ** Stamens** with glabrous filaments; anthers, 2–4 mm long. **Ovary** with glabrous to glabrescent roof, flat, topped by a yellowish–with nectary disk. **Style** thick, fleshy, 12–18 mm long, exserted from the corolla, stigma trifid and papillose.

**Etymology.** – The epithet *monteverdensis* for the bellflower “from Monte Verde” and refers to the name of the type locality; Monte Verde, meaning “Green Mountain”.

**Distribution and habitat.** – *Campanula monteverdensis* is confined to the summit of Monte Verde, the highest summit of São Vicente, reaching 720 m, frequently battered by the trade winds and covered by fog. This microendemic species grows between rocks in shrubland made up principally of *Daucus insularis* (Parl.) Spalik et al. (*Apiaceae*), *Echium stenosiphon* Webb (*Boraginaceae*) and *Euphorbia tuckeyana* (*Euphorbiaceae*).

**Notes.** – The first collection from São Vicente was made by Vogel in 1839 (*Vogel* 73 [K001134391]), which he linked to *Campanula dulcis* Decne. (*Vogel*, 1849: 27), a species endemic to the mountains of the southern Sinai (Decaisne, 1834). This specimen was chosen by Webb (1848: tab. 762) as one of syntypes of *C. jacobaea* (see under *C. jacobaea*). Then, Schmidt (1852: 208) noticed few differences in the habitus and the indument of the bellflowers of São Vicente and those of Santo Antão that he judged insufficient to warrant taxonomic separation. However, Bolle (1861) included both the bellflowers from São Vicente and the rupicolous forms from the “xeric” areas from São Nicolau (see under *C. fransinea*) when he made the description of the variety *humilis*. Those from São Vicente, identified until now as *C. jacobaea* (Krause, 1892; Chevalier, 1935; Sunding, 1973, 1982; Eriksson et al., 1974, 1979; Hansen & Sunding, 1985, 1993; Lobin, 1986; Figuereido, 1995; Leyens & Lobin, 1995; Brochmann et al., 1997; Sánchez-Pinto et al., 2005), are described as new under *C. monteverdensis*, a species easily identifiable by: a widely flared infundibuliform corolla, never white, dark purple colour (“gentian blue” according to Bolle, 1861: 50); an exserted style; triangular sepals with distinctly revolute margins; and elliptic to obovate leaves with a surface slightly bullate *in vivo*.

The succinct description of Bolle (1861) was built on inconsistent diagnostic characters (notably related to indument) and on a mixed collection (presence on Bolle s.n. [K001134400] of one *C. fransinea* flower in the fragment packet). We therefore prefer to describe a new species with an unambiguous recently collected original material than making a nomen novum on Bolle’s variety.

Additional specimens examined. – CABO VERDE. São Vicente: Monte Verde, III.1853, Bolle s.n. (MPU: remaining syntype for *C. jacobaea* var.
Fig. 10. – Campanula fransinea Gardère. Dumicolous form from humid locality: A. Habit, erect flowers; B. Rosette-leaves; C. Flower in lateral view; D. Flower in face view; E. Inflorescence with pendulous flowers; F. Habit, rupicolous form from xeric locality. [A–B, D: Gardère 1566; C: Gardère 1572; E: Gardère 1100; F: Gardère 1577] [Photos: M.L. Gardère]
6. **Campanula fransinea** Gardère, sp. nov. (Fig. 1, 3F, 4B–D, 10).

**Holotypus:** Cabo Verde. W São Nicolau: Massif du Monte Gordo, Monte Vermelho, 16°37’02”N 24°20’22”W, 905 m, 18.XI.2014, Gardère 822 (P [P02442651]!; iso-: CECV!).

*Campanulae jacobaeae C. Sm. ex Webb affinis, sed foliis semi-amplexicaulis.*

*Campanula fransinea* Gardère, sp. nov.

**Etymology.** – To pay tribute to Feijó’s work on CVB, the epithet *fransinea* (devoid of taxonomic significance) is adopted to name the bellflowers from W São Nicolau. Feijó dedicated the genus to the Italian mathematician Miguel Franzini (c. 1730–1810), one of his professors at the University of Coimbra (Gardère et al., 2019a).

*Vernacular name. –* “Dedal” (Cardoso Júnior, 1905; Henriques, 1896; Barbosa, 1961; Leyens & Lobin, 1995; Figueiredo, 1995) a Portuguese word meaning “thimble”, the colour adjectives “branco” (white) or “azul” (blue) is sometimes added to the name.

**Distribution and habitat.** – *Campanula fransinea* is endemic to W São Nicolau and can be found from 600 m to 1200 m. The species occurs in diverse habitats: wet areas, in high-elevation shrubland with *Euphorbia tuckeyana* (*Euphorbiaceae*), *Asteriscus smithii* (Webb) Walp. (*Asteraceae*) and *Daucus insularis* (Apiaceae) on the flanks of Monte Gordo, and up to the most “xeric” rupicolous areas, on rocks with *Aeonium tomentosum* (*Crassulaceae*), *Polycarpaea gayi* (*Caryophyllaceae*), *Kickxia elegans* (*Scrophulariaceae*). The lowest locality is at c. 400 m, in Ribeira Tucuda (Gardère 880), and corresponds to the single known occurrence in a spring, where *Campanula fransinea* grows together with *Adiantum capillus-veneris* (*Pteridaceae*) and *Pteris viitata* (*Pteridaceae*).

**Notes.** – Until now, the populations from W São Nicolau were traditionally identified as *C. jacobaea* (COUTINHO, 1914; CHEVALIER, 1935; SUNDING, 1973, 1982; ERIKKSON et al. 1974, 1979; NOGUEIRA, 1976; HANSEN & SUNDING, 1985, 1993; RUSTAN & BROCHMANN, 1993; GOMES et al., 1995a; LEYENS & LOBIN, 1995; FIGUEIREDO, 1995; SÁNCHEZ-PINTO et al., 2005) but some authors have also recognized the presence of *C. bravensis* in this region (see under *C. bravensis*).

Three Forbes’ specimens collected in 1822 in W São Nicolau ([K000865901, K001134405, K001134390]) were chosen by Webb (1848: tab. 762) to be part of the syntypes.
of *C. jacobaea* (see under *C. jacobaea*). Later, in his taxonomic treatment, Bolle (1861) grouped the bellflowers of high-elevation humid areas from W São Nicolau with those from Santo Antão in the type variety "genuina" (see under *C. feijoa*), and the bellflowers of the more “xeric” areas from W São Nicolau and those from São Vicente in the variety humilis (see under *C. montevedensis*).

All the populations from W São Nicolau are described here as new under *C. fransinea*. This species differs from other CVB species by its narrow infundibuliform corolla of 20–34 mm long (Fig. 10C). However, it remains quite close to *C. vicinituba* which has a corolla also narrow infundibuliform but shorter (20 mm) and more flared (Fig. 8D); and differs from the characters indicated in the key. According to its habitats, *C. fransinea* shows different forms with upright forms in high-elevation shrubland (Fig. 10A), and tufted forms in drier rupicolous areas (Fig. 10F).

Additional specimens examined. – **Cabo Verde. W São Nicolau:** Água das Patas, 675–700 m, 20.VII.2004, Marrero & Almeida s.n. (LPA); “ad rupes loco dicto Caçaço”, X.1851, Bolle s.n. (Z; remaining syntype for *C. jacobaea var. humilis*), Cachaço, 750 m, 17.I.1992, Cardoso de Matos & Gomes 693 (LISC); ibid. loco, 590 m, 30.I.1982, Rustan & Brochmann ØHR-1901 (O); betw. Cachaço and Monte Gordo, 900 m, 23.XI.1976, Sunding 3773 (O); Caminho da Caldeira, 22.II.1864, Lowe s.n. (BM, K); Cachao, 21.IV.1956, Grandvaux Barbosa 7257 (CECV, LISC); Monte Caramuito, 720 m, 20.XII.2017, Gardère 1566.5 (CECV, LISC, P); Monte Desertó, 715 m, 8.XII.2017, Gardère 1577 (CECV, P); ibid. loco, 700 m, 25.I.X.1976, Sunding 3859 (O); Monte Gordo, 1270 m, 29.I.1982, Brochmann & Rustan CB-541/82 (O); ibid. loco, 1030 m, 3.III.1992, Cardoso de Matos & Gomes 7039 (LISC); ibid. loco, X.1891, Cardoso Júnior 68 (COI); ibid. loco, 24.X.1891, Cardoso Júnior s.n. (Z); ibid. loco, XII.1893, Cardoso Júnior s.n. (LISU); ibid. loco, Monte Vermelho, 990 m, 18.XII.2014, Gardère 818 (P); ibid. loco, Hortelând, 865 m, 18.XII.2014, Gardère 819 (CECV, P); ibid. loco, sentier menant à Assomada de R. Calhau, 1005 m, 19.XII.2014, Gardère 856 (P); ibid. loco, 980 m, 12.XII.2015, Gardère 1096 (P); 1100 (CECV, LISC, K, P); ibid. loco, 950 m, 4.XII.2017, Gardère 1566.1–4 (P); ibid. loco, 950 m, 4.XII.2017, Gardère 1566.5 (MARS); ibid. loco, 1030 m, 6.XII.2017, Gardère 1572 (CECV, P); ibid. loco, c. 1000 m, 1.I.1986, Kilián & Leyens 3136 (B, FR); ibid. loco, c. 950–1050 m, 13.I.1994, Kilián & Leyens 3136 (B, FR); ibid. loco, c. 950 m, 28.XI.1980, Levesqueau CB-80-261 (GOET); ibid. loco, 15.X.1953, Lindberg 20 (H); ibid. loco, 28.XII.1978, Lobis CB-231 (FR); ibid. loco, 1270 m, 17.I.1994, Rustan & Brochmann ØHR-1849 (O); ibid. loco, 1000 m, 23.XI.1976, Sunding 3778 (O); Monte Janto, X.1891, Cardoso Júnior 10 (COI); Ribeira Calhau, 955 m, 6.XII.2017, Gardère 1574 (P); Ribeira Camarões, c. 300 m, 17.I.1994, Kilián & Leyens 3218 (B, FR); Ribeira da Prata, 1893, Cardoso Júnior 12269 (LISC); ibid. loco, 1893, Cardoso Júnior s.n. (COI); Ribeira Tucuda, 400 m, 20.XI.2017, Gardère 813 (CECV, LISC, P); on weg van Tarrafal vanaf Ribeira Brava, 500–800 m, 19.XII.2002, Peul homme van Reis s.n. (L); sine loco, “CANCAP-VI Expedition”, c. 1000 m, 14.VI.1982, Boekschoten PH60 (L); sine loco, 1851, Bolle s.n. (C, MPU; remaining syntype for *C. jacobaea var. humilis*); sine loco, “in ripetibus”, X.1851, Bolle s.n. (K pp: remaining syntype for *C. jacobaea var. humilis*); sine loco, s.d., Bolle s.n. (COI; remaining syntype for *C. jacobaea var. humilis*); sine loco, s.d. [27.III.1822], Forbes s.n. [35] (K pp: remaining syntype for *C. jacobaea*); sine loco, 22.II.1864, Lowe s.n. (LISU).

**Sine loco:** 1895, Cardoso Júnior III (K); 1783–1789, Feijó V-V’-1 (P).

7. **Campanula cochleromena** Gardère, sp. nov. (Fig. 1, 3G, 11).

**Holotypus:** CABO VERDE. E São Nicolau: Alto das Cabaças, végétation rupicole au bord des falaises sommitales, 16°35’57”N 24°06’20”W, c. 650 m, 14.XII.2015, Gardère 1120 (P [P02091100]); iso.: CECV!, LISC!.

**Campanulae jacobaeae** C. Sm. ex Webb affinis, sed calycis deltatis lobis (vs. triangulares lobos), corolla campanula sine contristione (vs. campanulatam corollam fauce paulo constricta), stylo corollae subexerto (vs. stylo corollae inclusum), pracite differt.

**Sub-frutex** 5–20 cm tall, prostrate in dense clump, highly woody in lower part; floriferous stems branched, procumbent to decumbent arising from the base of one or several sterile basal rosettes, glabrous to glabrescent in the woody basal parts with indument hispid toward the extremity, consisting of trichomes ± 0.5 mm long. **Leaves:** rosette-leaves elliptic to narrowly elliptic (1.5–)2.5–3.5(–4) × (0.7–)1–1.5(–2) cm, base cuneiform to attenuate, apex ± obtuse to acute; cauline-leaves elliptic to narrowly elliptic, (1.5–)3.5–4(–5) × (0.7–)1–1.3(–1.5) cm, base cuneiform to attenuate, apex ± obtuse; margin weakly revolute, crenate to slightly denticulate; adaxial side medium green in vivo, glabrescent or scattered by hispidulous to hispid of trichomes 0.2–0.5 mm long, indument generally more pronounced around the apex; abaxial side light green in vivo, venation whitish, hispidulous to hispid indument on primary and secondary veins consisting of trichomes 0.2–0.5 mm long and glabrescent on tertiary and ultimate veins, lamina glabrous. **Inflorescence** in monochasial pauciflorous cyme. **Flowers** erect, pedicel 0.5–1.5(–2) cm long, with the same indument as the stem; axillate by one or two bracts subopposite, ovato-triangular or ovate to narrowly ovate, base semi-amplexicaul, apex acute, with the same indument as the leaf. **Calyx** calyx-lobes deltoid, 5–8 × 4–6 mm, pressed up against the corolla, margin distinctly revolute; appendages ovate, reflexed, 1.5–1.5 mm long; lobe edges, appendage and median main vein hispid, 0.5–0.75 mm long, lamina glabrous to weakly hispidulous, 0.35–0.5 mm long. **Corolla** campanulate with inflexion point in the middle, purplish-blue; base wide round c. 6–8 mm large; tube, 20–22 mm long, gradually widening and reach the maximum diameter of 11–13 mm in the middle then widening up to 22–28 mm large at the mouth, constrictions absent; throat straight; lobes spreading to obliquely erect, 2–4 × 8–10 mm, apex apiculate; external lamina entirely covered with indument micro-hispidulous c. 0.1 mm long, except the primary veins micro-hispidulous to hispidulous, 0.1–0.2 mm long. **Stamens** with glabrous filaments; anthers, 2–4 mm long. **Ovary** of the ovary glabrous to glabrescent, flat, topped by a yellowish-nectary disk. **Style** thick, fleshy, 16–20 mm long, slightly exserted from the corolla, stigma trifid and papilllose.
**Etymology.** – The species epithet **cochleromena** meaning “loved by snails”, is a compound of two words of ancient Greek: **cochlos**, “snail” and **eremos**, “loved, desired by”. Indeed, a rare phenomenon of pollination by snails was recently observed in the species (Gardère, 2018).

**Vernacular name.** – “Flor-de-caracol” literally “snail flower”, the name is not very widespread and only known by a few shepherds working on the summits of Alto das Cabaças (Gardère, 2018).

**Distribution and habitat.** – *Campanula cochleromena* is endemic to E São Nicolau, between 550 and 650 m. The species is mainly confined to the edges of cliffs, on summit ridges of Alto Joaquina and Alto Cabaças, facing completely north, windblown and regularly covered by the fog. *Campanula cochleromena* is part of rupicolous vegetation principally made up of microendemic species such as *Coryza schlechtendalii* Bolle (Asteraceae), *Helichrysum* nicolai N. Kilian et al. (Asteraceae), *Diplotaxis sundingii* Rustan (Brassicaceae) and *Limonium sundingii* Leyens et al. (Plumbaginaceae) with other more broadly ranging Cabo Verdean endemic species like *Daucus* sp. (Apiaceae), *Verhassum capitis-viridis* Hub.-Mor. (Scrophulariaceae) and some *Euphorbia* tuckeyana (Euphorbiaceae). One locality is an exception, as being located in a stabilized landslide in Tope Simon around 500 m elevation, where the floristic community is poorer and composed of *Daucus* sp. (Apiaceae) and *Echium* stenosiphon (Boraginaceae).

**Notes.** – The populations from E São Nicolau, identified until now as *C. jacobaea* (Erikkson et al., 1979; Hansen & Sunding, 1985, 1993; Sunding, 1982; Rustan & Brochmann, 1993; Leyens & Lobin, 1995; Gardère, 2018), are described here as new under *C. cochleromena*. The discovery of this bellflowers is relatively recent, the first collect dates back to 1976. The discovery of this *C. cochleromena* here as new under *C. jacobaea* Sunding, 1985, 1993; Sunding, 1982; Rustan & Brochmann, 1993. \(\text{Kilian} 1063, 600 \text{m}, 6.\text{I.} 1986, \text{Schmidt CV/FR}; \text{Tope Jalunga}, 29.\text{XI.} 1996, \text{Schmidt CV/KS-1996-22 (FR)}; \text{Tope Simon, 550 m, 17.XII.2017, Gardère 1127 (CECV, P).}

**Nomen dubium**

*C. jacobaea* var. *hipida* Bolle in Bonplandia 9: 51. 1861.

**Typus:** CABO VERDE. Santiago: “loco natali specialiore ignoto”, s.d., Bocandé s.n. (not found).

**Notes.** – We transcribe here the note of Bolle (1861: 51) on the variety *hipida*: “Hab. in insula Santiago, loco natali specialiore ignoto. Inter reliquias B. Bocandé invenit a pessimis exemplis imperfecte tantum novimus. Fieri potest, banc propriam esse speciem; eximia setositate florumque exiguitate habitu saltam a stirpe Webbiana, quae probabiliter et Smithiana, magnopere recedit; tamen ab hac eam separare non ausi sumus”; and we give here-after this loose translation: “Grows on the island of Santiago, the exact locality is unknown. We only know it [var. *hipida*] imperfectly from poor specimens of B. Bocandé. It may be a particular species. By the extreme hairiness of the flower and the weakness of the habit, it differentiates itself strongly from that of Webb and is probably that of Smith; however, we dare not separate it from that (*C. jacobaea*).

*Bolle* (1861) described the var. *hipida* for the island of Santiago based on the Bocandé’s collection, currently untraceable. The specimens from B used by Bolle for the description of his varieties were destroyed in the fire of Berlin in 1943 (Hiępko, 1987) and probably alongside those of Bocandé. Leyens & Lobin (1995) treated the variety as a synonym of *C. jacobaea* but the same authors saw and identified a specimen of Bocandé conserved at “D” as *C. bravensis*. However, “D” does not correspond any indexed herbarium (Thiers, 2019) and it is probably a typing error (W. Lobin, pers. comm.).

The only known European Herbaria to hold Bocandé’s collections are B, FI-W and S (M.L. Gardère, unpubl. data) but S is temporarily closed for renovation. We were unable to check this specimen and to confirm or not the identification of Leyens & Lobin (1995). The description of Bolle is insufficient to place the variety *hipida* among the CVB species. Given that Santiago harbors both *C. jacobaea* and *C. bravensis*, we prefer a precautionary approach and rather consider it to be a *nomen dubium*.

**Discussion**

In the flora of the Cabo Verde archipelago, the genus *Campanula* is now represented by seven species and appears to be one of the most diversified genera of vascular plants in the archipelago, after the eight species of the genus *Diplotaxis* DC. (Brassicaceae) (Rustan, 1996).

Except *C. bravensis*, which occurs in all southern mountainous islands, the other species are each confined to a single island or even to a specific region of an island. The geographical origin of collections for which the locality data are unknown can therefore be determined by an accurate morphological examination of the flowers. This is the case with Feijó's
Fig. 11. – *Campanula cochleromena* Gardère. A. Habit; B. Rosette-leaves; C. Flower in lateral view; D. Flower in bottom view with a focus on the deltoid calyx-lobes; E. Flower in face view.
[A, C: Gardère 1120; B, D–E: Gardère 1119] [Photos: M.L. Gardère]
specimens, date and locality of which are unknown. Despite the poor state of conservation of the Feijó’s specimens, some crumpled flowers have been rehydrated, thus restoring the roof of the ovary and corolla shapes. These restored characters revealed that Feijó collected at least two different species: (1) *C. bravensis* (Feijó V–V–2), most probably from Fogo where he identified a collection under “Franquina” in his plant list of Fogo between April 1786 and April 1787 (Gardère et al., 2019a); and (2) *C. fransinea* (Feijó V–V–1), probably from São Nicolau where he collected 24 specimens around 1784 but no detailed list was able to be found (Gardère et al., 2019a).

Only one taxon, *C. jacobea* var. *bravensis*, remains from the first revision of CVB by Bolle (1861), of which we retain the combination and the enlarged concept proposed by Chevalier (1935). On the other hand, no morphological, or even geographical group could be considered for the three other Bollean varieties (“genuina”, *humilis* and *bispida*). Among the diagnostic features used to separate these varieties, Bolle (1861) attached great importance to the indument of stems and leaves but in Bolle’s work the interpretation of this feature seems to be strongly related to the microclimatic environmental conditions. Indeed, for the northern taxa, Bolle described the prostrate xero-mesophytic forms from São Vicente and São Nicolau under the variety *humilis* whereas the erect hygrophytic forms from Santo Antão and São Nicolau are described under the variety *genuina*. The same bold true for the southern taxa where the bellflowers from Brava are described under the variety *bispida* and the prostrate and strongly hispidulous ones from Santiago under the variety *bispida* (Bolle, 1861).

As emphasized by Leyens & Lobin (1995), the variations of the indument density observed in the CVB are correlated to the microclimatic conditions of the habitat. The bellflowers that grow on cliffs or ridges exposed to the wind and clouds are often prostrate with a dense indument. On the contrary, those found in deep humid valleys or close to springs and shielded from the wind have an erect habitus and a thinly scattered indument.

**Acknowledgments**

The authors are grateful to J.F. Dejouannet (UMS 2700 2AD) of the Atelier d’Iconographie Scientifique of the MNHN, who carefully prepared the illustrations, to Dr. W. Lobin (ex-BONN) and to Dr. M.C. Duarte (LISC) of the University of Lisbon for their precious information about their herbarium collections, to C. McReynolds and J. Farinhãno for help with translation, to Pr. M. Egetmeyer (UMR 8167 “Orient et Méditerranée”) of the Paris-Sorbonne University for advice in ancient Greek, to the Direção Geral do Ambiente in Cabo Verde for the collecting permit, to G. Toutirais (UMR 7245 MCAM) of the Electron Microscopy technical platform (MNHN) for his assistance with the SEM, to Dr. P.P. Lowry II (UMR 7205 ISYEB) of the Missouri Botanical Garden for his useful comments on the original manuscript, and to herbarium curators of ALF, B, BM, C, COI, FI, FR, G, GDOR, GOET, H, HBG, K, LISU, LPA, MA, MPU, O, ORT , TFC and Z.

**References**

Alarcón, M., C. Roquet, A. García-Fernández, P. Vargas & J.J. Aldasoro (2013). Phylogenetic and phylogeographic evidence for a Pleistocene disjunction between Campanula jacobaea (Cape Verde Islands) and C. balfourii (Socotra). *Molec. Phylogen. Evol.* 69: 828–836.

Andrade, A.C.A. (1908). Notícia da flora das ilhas de Cabo Verde. I – Fogo e Brava. *Revista Oficial da Missão Agronomica* 4: 1–44.

Barrosa, L.A.G. (1961). Subsídios para um dicionário utilitário e glossário dos nomes vernáculos das plantas do arquipélago de Cabo Verde. *Garcia de Orta* 9: 37–91.

Barrosa, L.A.G. (1962). Les Botanistes dans l’Archipel du Cap-Vert. *Inv: Fernandes, A. (ed.), Comptes rendus de la IVe réunion plénière de l’AEFAT, Lisbonne & Coimbre, Portugal, 16–23 septembre 1960: 77–94.

Basto, M.F.P. (1988). Plantas vascular endémicas do arquipélago de Cabo Verde. *Garcia de Orta, Sér. Bot.* 3: 11–15.

Bolle, C. (1861). Addenda ad floram Atlantidis, praecipue insularum Canariensium Gorgadumque V. *Bonplandia* 9: 50–55.

Brochmann, C., Ø.H. Rustan, W. Lobin & N. Killian (1997). The endemic vascular plants of the Cape Verde Islands, W Africa. *Sommersfélta* 24.

Cardoso Júnior, J.A. (1902). *Subsídios para a matéria médica e therapeutica das possessões ultramarinas portuguezas 1.* Typographia da Academia Real das Ciencias, Lisboa.

Cardoso Júnior, J.A. (1905). *Subsídios para a matéria Médica e therapeutica das possessões ultramarinas portuguezas 2.* Typographia da Academia Real das Ciencias, Lisboa.

Chevalier, A. (1935). *Les îles du Cap Vert: géographie, biogéographie, agriculture. Flore de l’archipel. Rev. Bot. Appl. Agric. Trop.* 15: 733–1090.

Coutinho, A.X.P. (1914) Herbarii Gorgonei Universitatis Olisiponensis Catalogus. *Arq. Univ. Lisboa* 1: 268–334.

Decaisne, J. (1854). Flora de Fogo suivi d’une statistique abrégée des îles du Cap-Vert et d’une notice bibliographique: 232–234. Gide et Cie, Paris.
Porter, D.M. (1986). Charles Darwin’s plant specimens from the voyage of HMS Beagle. *Bot. J. Linn. Soc.* 93: 1–172.

Rico, L., M.C. Duarte, M.M. Romeiras, A. Santos-Guerra, C. Nepi & J. Francisco-Ortega (2017). Joseph D. Hooker’s 1839 Cabo Verde collections. *Bot. Mag.* 34: 146–168.

Rustan, Ø.H. (1996). Revision of the genus *Diplotaxis* (Brassicaceae) in the Cape Verde Islands, W Africa. *Nordic J. Bot.* 16: 19–50.

Rustan, Ø.H. & C. Brochmann (1993). Additions to the vascular flora of Cabo Verde – III. *Garcia de Orta, Sér. Bot.* 11: 31–62.

Salinger, S. & H. Streihlow (1991). The travels of Carl Bolle to the Cape Verde and the Canary Islands. *Arch. Nat. Hist.* 18: 251–254.

Sánchez-Pinto, L., M.L. Rodríguez, S. Rodríguez, K. Martín, A. Cabrera & M. Carmen Marrero (2005). Pteridophyta, Spermatophyta. In: Arechavalea, M. et al. (ed.), *Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales terrestres): 38–57*. Consejería de Medio Ambiente e Ordenación Territorial, Gobierno de Canarias.

Savriama, Y. (2018). A step-by-step guide for geometric morphometrics of floral symmetry. *Front. Plant Sci.* 9: 1433.

Savriama, Y., J.M. Gómez, F. Perfectti & C.P. Klingenberg (2012). Geometric morphometrics of corolla shape: dissecting components of symmetric and asymmetric variation in *Erysimum mediohispanicum* (Brassicaceae). *New Phytol.* 196: 945–954.

Schmidt, J.A. (1852). *Beiträge zur Flora der Cap Verdischen Inseln*. Akademische Buchhandlung von Ernst Mohr, Heidelberg.

Sunding, P. (1973). *Check-list of the vascular plants of the Cape Verde Islands*. Botanical Garden, University of Oslo, Oslo.

Sunding, P. (1980). Christen Smith as pioneer botanist in the Cape Verde Islands. *Blyttia* 38: 181–188.

Sunding, P. (1982). Additions to the flora of Cape Verde Islands – III. *Garcia de Orta, Sér. Bot.* 5: 125–138.

Szpera, A. (2015) *Encyclopédie nature de l’archipel du Cap Vert*. Ed. 2. ArtOpera, Ponta do Sol.

Thiers, B. (2019). *Index Herbariorum: A global directory of public herbaria and associated staff*. [http://sweetgum.nybg.org/science/ih]

Thulin, M. (1976). Campanulaceae. In: Polhill, R.M. (ed.), *Fl. Trop. E. Africa*. Balkema, Rotterdam.

Thulin, M. (1977). Campanulaceae. In: Bamps, P. (ed.), *Fl. Afrique centrale (Zaire, Rwanda, Burundi)*. Spermatophyte. Jardin Botanique National de Belgique, Meise.

Tuckey, J.K. (1818). *Narrative of an expedition to explore the River Zaire, usually called the Congo, in South Africa, in 1816, under the direction of Captain J.K. Tuckey*. R.N. to which is added the journal of Professor Smith. John Murray, London.

Turland, N.J., J.H. Wiersema, F.R. Barrie, W. Greuter, D.L. Hawksworth, P.S. Herendeen, S. Knapp, W.-H. Kubert, D.-Z. Li, K. Marhold, T.W. May, J. McNeill, A.M. Monro, J. Prado, M.J. Price & G.F. Smith (2018). International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017. *Regnum Veg.* 159.

Vala, F. (2009). *Darwin em Cabo Verde*. Fundação Calouste Gulbenkian, Lisbon.

Vogel, T. (1849). Journal of the voyage to the Niger. In: Hooker, W.J. (ed.), *Niger Flora*: 21–72. Hippolyte Bailliére, London.

Webb, P.B. (1848). *Campanula jacobaea*. In: Hooker, W.J. (ed.), *Icon. Pl.* 8: tab. 762.

Webb, P.B. (1849). *Spicilegia Gorgonea; or a catalogue of all the plants as yet discovered in the Cape Verde Islands. From the collections of J.D. Hooker, Esq. M.D.R.N., Dr. T. Vogel, and other travellers*. In: Hooker, W.J. (ed.), *Niger Flora*: 89–197. Hippolyte Bailliére, London.