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GENETIC DIVERSITY AND GENE FLOW IN THE MORPHOLOGICALLY VARIABLE, RARE ENDEMICS BEGONIA DREGEI AND BEGONIA HOMONYMA (BEGONIACEAE)

MATOLWENI, LUZUKO ORLYN; BALKWILL, KEVIN; MCLELLAN, TRACY

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Bolandia (Senecioneae, Asteraceae): A new genus endemic to southern Africa

Glynis V. Cron

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa. Glynis@biology.biol.wits.ac.za

Kevin Balkwill

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa. KevinB@biology.biol.wits.ac.za

Eric Knox

Department of Biology, Indiana University, Bloomington, IN 47405, USA. eknox@bio.indiana.edu

ABSTRACT

The genus *Bolandia* (Senecioneae, Asteraceae) comprises two known species, *B. pedunculosa* and *B. argillacea*, previously included in *Cineraria*. Distinguishing features of *Bolandia* include the fusiform shape of the cypselae and strong median rib on the glabrous inner surface of the ray and outer disc cypselae, solitary ecalyculate capitula on long peduncles, and a truncate style apex with a central tuft of sweeping hairs. *Bolandia* occurs in the mountains of the Western Cape with a disjunct population of *B. pedunculosa* in the Witteberg of the Eastern Cape and the nearby Drakensberg mountains in Lesotho. *Bolandia argillacea* is endemic to the mountains near Worcestor in the Western Cape. Two forms of *B. pedunculosa* are informally recognised, a tomentose and a glabrescent form, the latter including plants previously known as *C. albomontana*.

Key words: Asteraceae, Senecioneae, *Bolandia*, *Cineraria*, southern Africa.

The tribe Senecioneae of the Asteraceae is well represented in southern Africa with about 19 genera (mostly senecioid), eight of which contain three or fewer species (Bremer, 1994). Many of these genera and species are found in the Cape and/or montane regions. *Bolandia* G.V.Cron is another such genus comprising two species previously included in *Cineraria* L., namely, *B. pedunculosa* (DC.) Cron and *B. argillacea* (Cron) Cron. Separate and combined molecular and morphological analyses (Cron, Balkwill & Knox, in prep.) have established this pair of species as a sister-group to the monophyletic and morphologically coherent revised genus *Cineraria*.

Compression and shape of the mature cypselae are important characters distinguishing the genus *Cineraria*, along with other features such as palmate venation of the usually auriculate leaves and radiate, calyculate capitula. Although de Candolle (1838) included the type species for *Bolandia*, *B. pedunculosa*, in *Cineraria* (*C. pedunculosa* DC.), he expressed doubt concerning its placement: *"An genus proprium?*" (1838: 305), noting that its fruits were not truly compressed. Harvey (1865), however, placed this species in Section *Cineraria*, noting that the young cypselae were compressed. However, cypselae of many genera of Senecioneae appear compressed when immature and other morphological features also serve to unequivocally distinguish *Bolandia* from *Cineraria*.

Bolandia occurs mainly on the mountains of the Western Cape, in the vicinity of Worcestor and also in the Ceres, Clanwilliam, Laingsburg, and Swellendam divisions (Figure 1). This part of the Western Cape includes an area often referred to amongst the local population as the "boland", an Afrikaans term meaning "highlands" and pertains to a region that includes the original Western Province, namely, the magisterial districts of the Cape, Stellenbosch, Worcestor and Swellendam as they existed at the time of the Cape Colony (Potgieter, 1975). The distribution of *Bolandia* includes mountain ranges in and around this region. A disjunct population of *Bolandia pedunculosa* in the Witteberg of the Eastern Cape and adjacent Lesotho extends the distribution of the genus beyond the Western Cape (Figure 1).

***Bolandia* Cron, gen. nov.** (Asteraceae - Senecioneae)

TYPE: *Bolandia pedunculosa* (DC.) Cron; *Cineraria pedunculosa* DC*., Prodr.* 6: 305 (1838).

Cineraria L. valde affinis, sed involucrum ecalyculatum et apici rami stylorum discorum flosculorum truncata atque cypselae non compressae, fusiforma non obovatae, cypselae exteriorae triangularis, cypselae disci interiorae quadrangularis. Folia pinnatinervia, non palmata, exauriculata.

Perennial or annual herbs, branching mainly from the base or stoloniferous. *Leaves* alternate, simple, entire, lyrate pinnatifid or pinnatisect, ovate to elliptic or obovate in outline, cobwebby or tomentose, glabrescent. *Peduncles* long, bracteate, monocephalous. *Capitula* heterogamous, radiate, ray florets female, disc florets hermaphrodite. *Involucre* ecalyculate, phyllaries uniseriate, with scarious margins, tomentose or cobwebby and glabrescent. *Ray florets* ligulate, with glandular hairs on tube near base of limb; corolla of disc florets tubular below, upper third campanulate with five lobes, with median resin duct, apically papillate. *Anthers* with obtuse, triangular-ovate apical appendages, bases minutely sagittate, filament collar gradually widening towards the base (balusterform), endothecial walls radially thickened. *Styles* of disc florets with discrete stigmatic areas, style apices truncate with a central tuft of acute-tipped sweeping hairs and fringing apex, style base shortly campanulate. *Cypselae* narrowly fusiform to elliptic, dimorphic; ray cypselae and outer disc cypselae with prominent inner median rib, convex outer surface, inner surfaces of ray cypselae glabrous, outer surfaces covered with short white mucilaginous duplex hairs, disc cypselae hairy all over; carpopodium distinct, 4--6 rows of cells. *Pappus* bristles pluriseriate, delicate, scabrid, caducous.

Species 2, South Africa (Western and Eastern Cape), Lesotho.

KEY TO SPECIES OF *BOLANDIA*

Leaves entire and ovate to elliptic to obovate or lyrate pinnatifid ..... *B. pedunculosa*

Leaves pinnatisect ..... *B. argillacea*

Description and distribution of species

Bolandia pedunculosa was first described by De Candolle (1838) in his *Prodromus* and subsequently by Harvey (1865) in *Flora Capensis*. Below is a more detailed description than provided in either reference. A number of specimens that constitute a much more glabrescent form are also considered here to match *B. pedunculosa*. A collection by Esterhuysen [*26629* (BOL)] from the Keeromsberg in the Worcestor Division of the Western Cape has both glabrescent and tomentose forms present. Increased glabrescence is linked to higher altitude and also slightly larger capitula in *B. pedunculosa*. Included in this glabrescent form of *B. pedunculosa* is *Cineraria albomontana* Hilliard from the Witteberg of the Eastern Cape, South Africa and Thaba Ntlenyana in Lesotho. Both tomentose and glabrescent forms have a range of leaf shape, varying in degree of dissection from entire to lyrate-pinnatifid with two to four pairs of lateral pinnae below the terminal lobe.

Bolandia pedunculosa (DC.) Cron, comb. nov.

Basionym: *Cineraria pedunculosa* DC. in *Prodr.* 6: 305 (1838); Harv. in *Fl. Cap*. 3: 308 (1865). TYPE: South Africa, Western Cape, Caledon, Potrivier, Langehoogde, Bontjeskraal, bis am Zwarteberg, 165--660 m [500--2000'], July, *C.F. Ecklon & C.L.P. Zeyher 1519* (holotype, G-DC; isotype, S). Figure 2.

Cineraria albomontana Hilliard in *Notes Roy. Bot. Gard. Edinb*. 45: 185--187 (1989). Syn. nov. TYPE: South Africa, Eastern Cape, Lady Grey, Witteberg, Joubert's Pass, 2465--2530 m [7500--7700'], Jan. 1979, *O.M. Hilliard & B. L. Burtt 12177* (holotype, E; isotypes, K, NU, S).

Perennial herb, up to 30 cm tall, with a vertical woody rootstock. *Stems* woody at the base, branching occasionally from the base, white tomentose, nodes very close together. *Leaves* entire, ovate to elliptic to obovate, or lyrate pinnatifid, deeply to shallowly lobed with terminal lobe ovate to elliptic or obovate in outline, usually with 1 or 2 pairs of lateral pinnae, lamina 11--32 (--73 in glabrescent form) × 8--27 mm, cobwebby above, usually glabrescent, tomentose or cobwebby and glabrescent below; apex rounded; margin dentate to crenate with apiculate tips; base cuneate and decurrent or truncate to slightly cordate; petiole (14--) 23--55 mm (--86 in glabrescent form) long, cobwebby to tomentose; auricles absent, petiole widens somewhat at base to clasp stem. *Capitula* heterogamous, radiate, solitary, axillary; peduncles (30--) 80--240 mm (--330 mm in glabrescent form) long, cobwebby, glabrescent, conspicuously bracteate, bracts (2--) 5--11 mm long. *Involucre* ecalyculate, phyllaries 8--14 (--15), 5--7 mm (--9 mm in glabrescent form), cobwebby to tomentose, glabrescent, margins

scarious. *Ray florets* 8--11, 8·0--9·5 mm long, limb 6--8 mm long (5--12 mm in glabrescent form), 4-veined (mostly 5 or 6-veined in glabrescent form). *Disc florets* (25--) 30--55, corolla 4·5--5·0 mm long (--6·0 mm in glabrescent form). *Cypselae* fusiform, dimorphic; ray cypselae 3-angled with prominent median rib on inner surface, inner surface glabrous, convex outer surface covered with short mucilaginous white hairs, compressed when young, black when mature, ca. 4 mm long; disc cypselae subcylindrical (outer ones with prominent inner median rib), 4-ribbed when mature, black with short white hairs all over, 3--4 mm long. *Pappus* scabrid, three-quarters length of disc floret corolla, caducous.

Phenology. Flowering mainly from September to November (to January in glabrescent form), rarely as early as August.

Distribution. South Africa, Western Cape: In the Witteberg of the Laingsburg Division, the Keeromsberg near Worcester and near Barrydale in the Swellendam districts, the glabrescent form occurs on the summit of Milner's Needle in the Hex River Mountains and on Du Toits peak near Worcester, the Baviaansberg (Ceres Division) and the Cederberg (Clanwilliam Division). The glabrescent form also occurs in the Witteberg near Lady Grey in the Eastern Cape and on Thaba Ntlenyana in Lesotho, these eastern populations being previously treated as *Cineraria albomontana* (Hilliard, 1989).

Habitat. Growing in dense clumps on steep, stony south- or south-east-facing slopes, between grass tussocks, at the base of cliffs, amongst rocks, or on rocky summits, on shale bands, in sand or on basalt, tomentose form mainly at an altitude range of 1000--1500 m; glabrescent form ranging from 1650--2300 m in the Western Cape and at 2450--3450 m in the Eastern Cape and Lesotho.

Conservation status. Localised, not common. Possibly rare.

Other selected specimens examined.

Tomentose form: SOUTH AFRICA. Western Cape. Wuppertal: Duiwelsgat, southern Cederberg (Sneeuwberg area), *Esterhuysen 13104* (BOL); Worcester, Keeromsberg , *Esterhuysen 26629* (BOL); Villiersdorp, Caledon, *Esterhuysen 4870* (BOL); Tweedside, *Keary 4127* (BOL); *Compton 3110* (BM, BOL); *Compton 3111* (BOL); Bantams, Karoo,

Compton 12241 (NBG) Witteberg, south of Bantams, *Esterhuysen 30520* (BOL); Witteberg, Laingsburg, *Compton 2722* (BOL, K); *Compton 21140* (NBG); Fisantekraal, Witteberg, *Compton 21108* (NBG); Witteberg, Whitehill, *Compton 13922* (NBG); *Compton 16263* (NBG); Swellendam district, near Barrydale, *Barker 5398* (NBG); Ladismith Division, Seven Weeks Poort, *Phillips 1468* (SAM); Zwartberg, Caledon, *Zeyher s.n. sub SAM 16975*.

Glabrescent form: LESOTHO. Thaba Ntlenyana, *Guillarmod 2325* (PRE). SOUTH AFRICA. Eastern Cape: Lady Grey, Witteberg, Joubert's Pass, *Hilliard & Burtt 12177* (K, S); *Cron & Goodman 544* (J). Northern Cape: Calvinia, Ekerdam, *Taylor 2686* (BOL); Clanwilliam, Cederberg Mountains, Peak south of Sneeuwkop, *Esterhuysen 7547* (BOL); Cederberg, Sneeuwkop, *Stokoe s.n. sub SAM 57134*; Cederberg, Sneeuwberg, *Esterhuysen 18045* (BOL); Ceres, Bokkeveld, Tafelberg, *Esterhuysen 3918* (BOL). Western Cape: Tulbagh, Great Winterhoek, *Esterhuysen 27004* (BOL); Worcester, Milner's Needle, Hex River Mountains, *Esterhuysen 14880* (BOL); Ceres, Baviaansberg, west of Karoopoort, *Esterhuysen 29858* (BOL); Roodeburg, Hex River Mountains, *Esterhuysen 20924* (BOL); Worcester, Du Toits Peak, *Esterhuysen 8583* (BOL).

Bolandia argillacea (Cron) Cron, comb. nov.

Basionym: *Cineraria argillacea* Cron, *S. African J. Bot*. 63: 402 (1997).

TYPE: South Africa, Western Cape, Worcestor District, on slopes at base of Brandwacht Peak, Nov. 1978, *E. Esterhuysen 35117* (holotype, BOL; isotypes, K, S, UPS).

Annual erect herb (or possibly persisting for more than one season), 30--50 cm tall. *Stems* woody and sometimes branching near the base, finely tomentose, glabrescent towards the base, then reddish in colour. *Leaves* pinnatisect, green, elliptic to ovate or oblanceolate in outline, lamina 18--33 × 14--24 mm, lobes 4--11 × 0·8--3·0 mm, cobwebby above and below, glabrescent with age; apex extremely acute; margins dentate, apex of lobes and teeth tipped reddish-purple; base cuneate and decurrent along petiole; petiole 8--35 mm long, occasionally with lateral pinnae along length, cobwebby; exauriculate, sometimes widening slightly at base to clasp stem. *Capitula* heterogamous, radiate, solitary on terminal peduncles; peduncles 130--175 mm long, cobwebby, glabrescent, bracteate (bracts 2--6 (--13) mm long). Involucre ecalyculate, phyllaries 10--12, 5·5--6·5 mm long, woolly at the base, glabrescent towards the tips, margins membranous. *Ray florets* 6 --9, commonly 8, 8·5--10·5 mm long, limb 6--8 mm long, 5-veined. *Disc florets* 18--32, corolla ca. 4·5 mm long. *Cypselae* narrowly oblong to

fusiform, dimorphic, ray cypselae 3-angled with prominent median rib on inner surface, outer surface of ray cypselae convex, inner surface glabrous outer surface of ray cypselae covered with short white mucilaginous hairs, disc cypselae subcylindrical, hairy on inner and outer surfaces, black when mature, 4·5--5·2 mm long. *Pappus* three quarters length of mature disc floret, caducous.

Phenology. Flowering in October and November.

Distribution. South Africa, in the Western Cape, apparently endemic to the slopes below Brandwacht Peak in the mountains near Worcestor.

Habitat. Bolandia argillacea is reportedly restricted to the clay zones on the mountain, growing in association with *Erica leucanthera*, but not extending into the renosterbos. It grows at 1700--1800 m on the south-eastern and eastern slopes of the mountain.

Conservation status. Very restricted in distribution; occurrence occasional in its particular habitat. Rare, although its habitat is not likely to be threatened.

Other specimens examined. SOUTH AFRICA. Western Cape: Worcestor Division, slopes at base of Brandwacht Peak, along path towards Fonteintjiesberg, *Esterhuysen 36192* (BR, E, K, US); Brandwacht, clay slopes at foot of Chavonnesberg, *Esterhuysen 8195* (BOL).

Discussion

Distinguishing features of *Bolandia* include the shape and surface features of the cypselae, capitula arrangement and style branch apices. The solitary capitula are borne on long peduncles and the involucre is ecalyculate (Figure 2A). The apex of the branches of the style of the disc florets is truncate with a fringe and a central tuft of sweeping hairs (Figures 2D, 3C). The cypselae are fusiform to elliptic in shape and are heteromorphic (Figure 2F, G). Mature ray cypselae have a strong median rib on the inner surface, which is glabrous, the outer surface being convex and covered in short white duplex hairs (Figure 3A, B). The disc cypselae are mostly cylindrical (terete in cross section), although the outermost ones may be markedly curved with a prominent inner median rib as in the ray cypselae, but all disc

cypselae are hairy on inner and outer surfaces. As in Cineraria and many of the Senecioneae, the anthers have ovate apical appendages and balusterform collars (Figure 3D).

In contrast to *Bolandia*, *Cineraria* has obovate, laterally compressed cypselae with distinct margins or wings, a calyculate involucre on capitula that are commonly borne in lax cymes or corymbs of few to many capitula, and an obtuse style apex, that has a fringe of sweeping hairs, as well as a central tuft. In addition, the distinctive palmate venation and lobing of the auriculate leaves of *Cineraria* is not seen in leaves of *Bolandia*, which are pinnately-veined, ovate to elliptic to obovate in outline and exauriculate. In addition, the epicarp cells of cypselae in *Cineraria* are subisodiametric, whereas those of *Bolandia* are more elongate.

Characters shared by *Bolandia* and *Cineraria* include a distinct carpopodium, although it is generally larger in *Cineraria* than *Bolandia*, glandular hairs on the ray florets, and the central tuft of sweeping hairs on the disc styles (present in most species of *Cineraria*). Leaf trichomes in *Bolandia* have two to four narrow basal cells and a multi-celled long apical appendage, attached obliquely to the basal cells. This type of trichome is common in the Senecioneae and is also present in some species of *Cineraria*.

Other species with cypselae apparently morphologically similar to *Bolandia* are species previously known as *Cineraria exilis* DC. and *C. microglossa* DC, now excluded from the genus although their alliances at generic level are unclear. Their growth form is also similar to that of *Bolandia* and they have long peduncles with few capitula (occasionally solitary in *C. exilis*). However they have a calyculate involucre, whereas *Bolandia* is distinctly ecalyculate. Both *C. exilis* and *C. microglossa* are known only from type specimens from the Northern Cape and molecular analyses as well as more detailed examination of their cypselae are required to further investigate their generic affinity and putative relationship to *Bolandia*.

Stilpnogyne DC. is an ecalyculate monotypic genus from the Northern and Western Cape which also has cypselae of the same shape, colour and indumentum as *Bolandia* (i.e. black with all surfaces are covered in short white hairs), but they are not heteromorphic. In addition, it differs from *Bolandia* by its palmately-veined leaves and very small disciform capitula.

Endemism and conservation

The distribution and altitudinal range of *Bolandia* places it in the Cape Floristic Region, the boundaries of which are difficult to define because it extends into neighbouring and other phytochoria and contains enclaves of other floristic regions. Van Wyk and Smith (2001) note that its core area is best defined in geological terms as the outcrops of the Table Mountain and Witteberg Groups of the Cape Supergroup. The average altitude of the mountains is 1000 to 1500 m, with individual peaks over 2000 m. *Bolandia* tends to be associated with mountain fynbos (as opposed to renosterbos) and occurs mainly in fire-free sites at the base of cliffs, overhangs and amongst rocks. The Cape Floristic Region is noted for its high levels of endemism (about 70 %), including 210 endemic or near-endemic genera (Goldblatt & Manning, 2000; Van Wyk & Smith, 2001). *Bolandia* is yet another near-endemic genus, with a connection to the Drakensberg Afro-alpine centre and *Bolandia argillacea* is endemic to the mountains near Worcestor.

Rebelo (1994) notes that up to 90 % of the mountain fynbos in the Cape Floristic Region is protected in nature reserves and mountain catchment areas, or by the "sheer inaccessibility of the terrain". This is in contrast to the lowlands of the Overberg and Worcestor-Robertson Karoo Centre (i.e. below 600 m), where agriculture is a major activity and conservation of remaining natural vegetation is an issue requiring attention (Hilton-Taylor & Le Roux, 1989; Wood 1991; Van Wyk & Smith 2001). As noted previously, *Bolandia* occurs at high altitude (at 1000 m and above), so its continued existence should not be under direct threat from man, although it should be noted that it is never abundant and climate change may have an adverse effect on all such montane vegetation.

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Figures

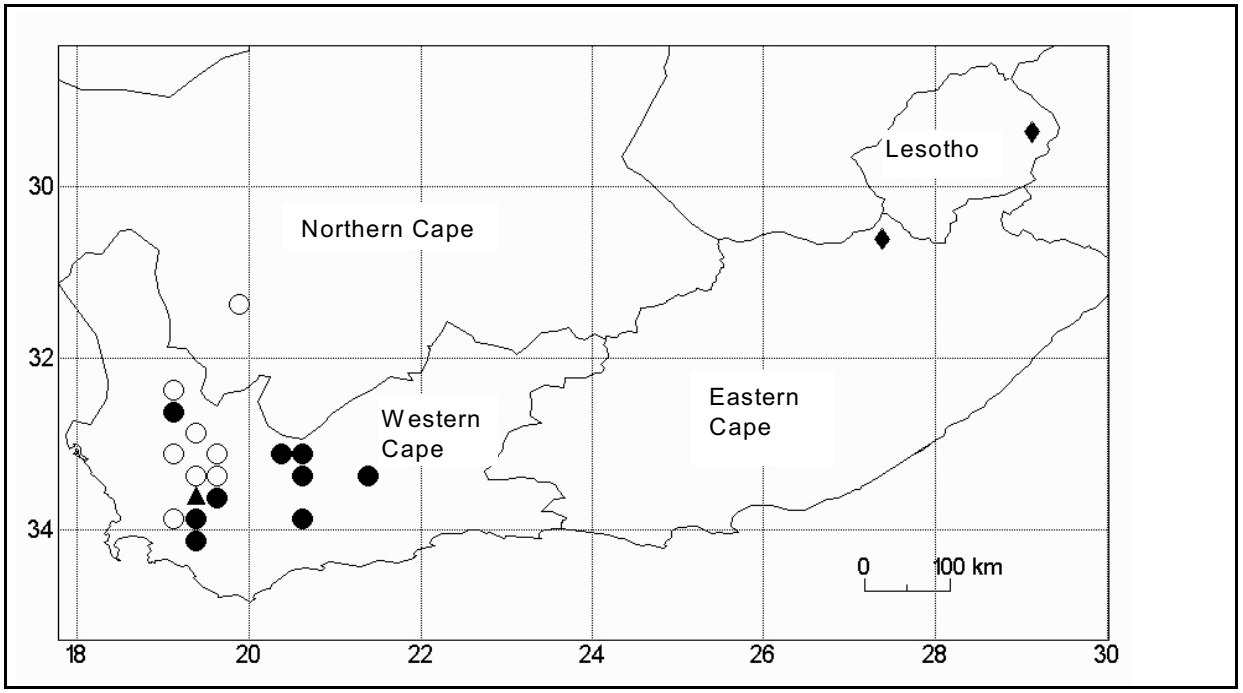


Figure 1. Map of known distribution of *Bolandia. B. pedunculosa*: ● tomentose form, ○ glabrescent form, ◆ glabrescent form with predominantly obovate leaves (previously known as *Cineraria albomontana*); ▲ *B. argillacea*.

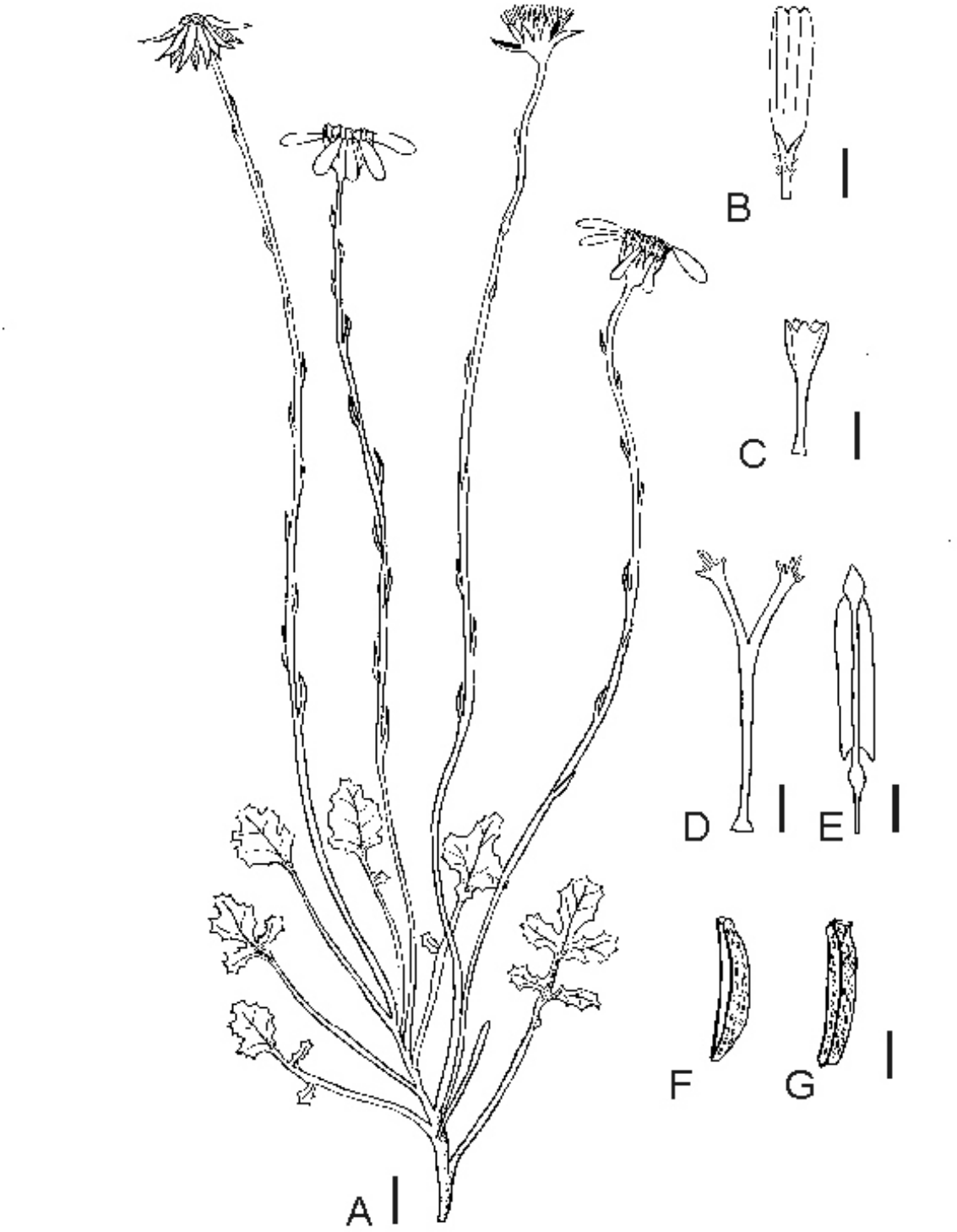


Figure 2. Illustration of *Bolandia pedunculosa* [*Compton 2772* (BOL, K)]. – A. Habit. Scale bar = 13 mm. – B. Ray floret. Scale bar = 2.0 mm. – C. Disc floret. Scale bar = 2.1 mm. – D. Style. Scale bar = 500 μm. – E. Stamen. Scale bar = 500 μm. – F. Ray cypsela. Scale bar = 1.3 mm. – G. Disc cypsela. Scale bar = 1.3 mm.

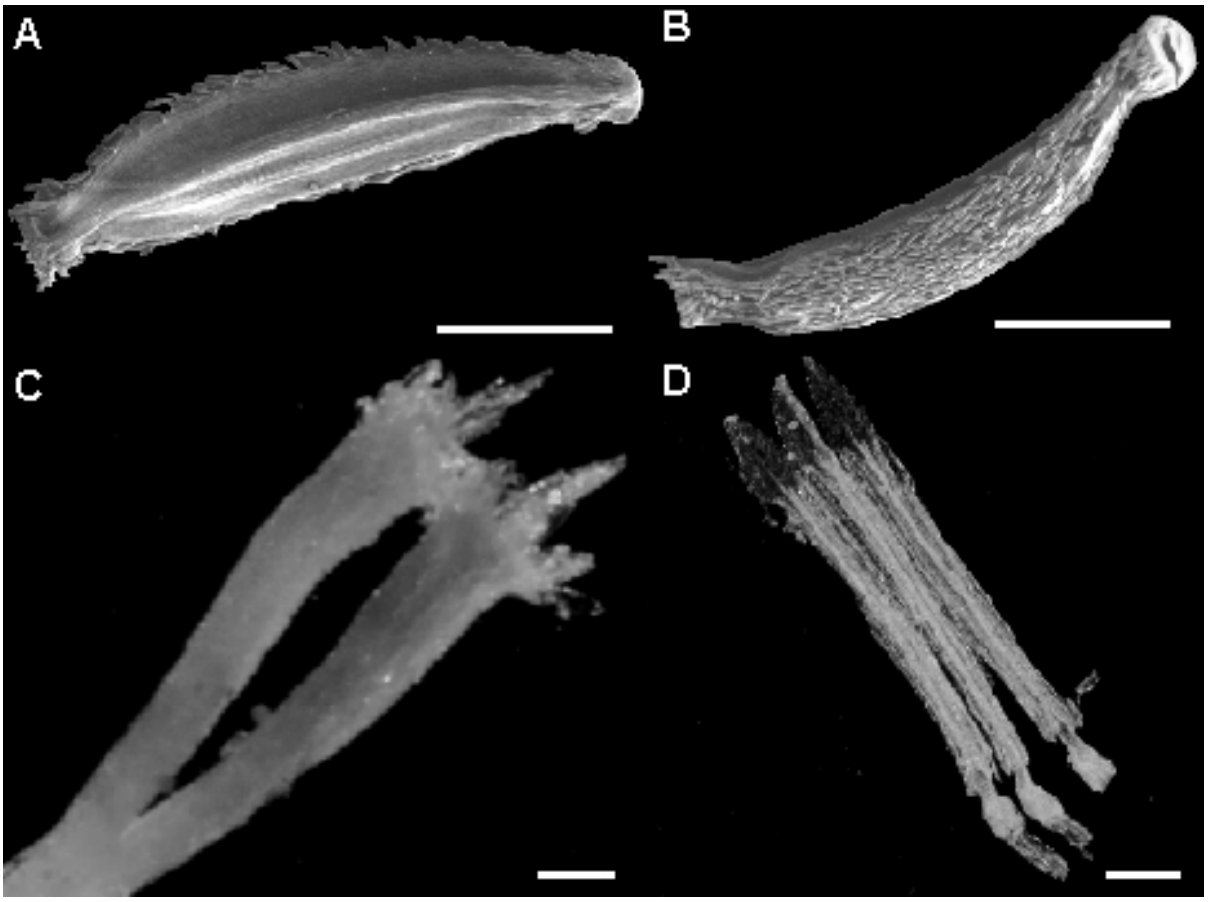


Figure 3. *Bolandia pedunculosa* (A, B) Scanning electron micrograph of ray cypsela with glabrous inner surface and hairy outer surface. Scale bars = 1 mm. (C) Truncate style apices with central tuft of sweeping hairs (papillae). Scale bar = 215 μm. (D) Anthers with ovate apical appendages and balusterform collars. Scale bar = 300 μm.