The monotypic Andean genus Fulcaldea (Compositae, Barnadesioideae) gains a new species from northeastern Brazil

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Abstract The family Compositae has ca. 25,000 species and is estimated to have diverged approximately 45 Ma. Within the family, the small subfamily Barnadesioideae (91 spp.) is the sister group of the rest of Compositae. Four of its nine genera have only one species; one of these, Fulcaldea, is restricted to northern Peru and Ecuador as is its sister group, Arnaldoa (3 spp.). A new species, Fulcaldea stuessyi, is described from the Chapada Diamantina of Bahia, Brazil, a remarkable 4000 km disjunction. The new species is clearly a member of Fulcaldea sharing a number of important characters with the type, F. laurifolia, including a single-flowered capitulum, “plumose” pappus, shrubby habit, and style with a unique swelling. It is distinguished from that species by its red corolla and pappus, greater number of series of phyllaries, and much greater length of the corolla, style, and pappus. The location of the new taxon may be the result of vicariance or long-distance dispersal; it is named in honor of Professor Tod Stuessy.

Keywords Arnaldoa; Asteraceae; Bahia; Barnadesioideae; Chapada Diamantina; Dasyphyllum; Mutisieae

INTRODUCTION

The subfamily Barnadesioideae (Bremer & Jansen, 1992) contains 91 species in nine genera and is entirely restricted to South America (Stuessy & Urtubey, 2007); most species are found south of the Equator. In addition to the lack of two DNA inversions found in the chloroplast genome of all other Compositae (Jansen & Palmer, 1987; Kim & al., 2005; Panero & Funk, 2008), Barnadesioideae are clearly distinguished from other daisies by the possession of axillary spines, a unique type of pubescence (unbranched three-celled hairs) called “barnadesioid trichomes”, peculiar types of testa-epidermis, and various pollen features (Stuessy & Urtubey, 2007; Stuessy & al., 2009).

Of the nine genera, four are considered monotypic (Duse-nilka K. Schum., Fulcaldea Poir., Huarpea Cabrera, and Schlechtendalia Less.), all endemic to narrow areas in Argentina, Peru, Ecuador, and Uruguay and adjacent Brazil (Stuessy & al., 2009). None of the monotypic genera are in a sister group relationship with any of the other monotypic genera. In fact, Fulcaldea is the sister group of another genus, Arnaldoa (3 species; Stähl & al., 1999; Stuessy & Sagastegui, 1993) also from northern Peru and Ecuador (Gruensteudl & al., 2009; Stuessy & al., 2009). The sister group to this pair of genera is the much larger genus Dasyphyllum Kunth which breaks into two clades that do not form a monophyletic group (Figs. 1–3; Gustafsson & al., 2001; Gruensteudl & al., 2009).

According to Ferreyra (1995), Fulcaldea laurifolia (Bonpl.) Poir. possesses a habit quite similar to some Barnadesia Mutis species. However, it differs from Barnadesia in having a single floret per capitulum, a distinctly swollen style below the branching point, and spinulous pollen while Barnadesia has more than one floret per capitulum, lacks the swollen style, and has lophate pollen. An examination of Figs. 1 and 3 shows them to be in separate clades.

A recent collection (I. Abreu 123) from the Chapada Diamantina in Bahia, Brazil, clearly belongs to the genus Fulcaldea because of its single-flowered capitulum, “plumose” pappus, shrubby habit, and unique swollen style. However, it is distinct from the type of Fulcaldea by virtue of its red corolla and pappus bristles, greater number of series of phyllaries, and much longer corolla, style, and pappus.

The Chapada Diamantina has spectacular scenery and is often called the “Lost World of Brazil” because of the similar appearance of these Brazilian mountains to those of the Guiana Shield. The Chapada Diamantina dates back to the Precambrian and occupies an area of 50,610 km²; its elevation varies from ca. 300 to 2000 m with most of the formation being located between 800 and 1200 m (Parrini & al., 1999). The relief is very irregular, with rocky peaks, steep slopes, and narrow, deep valleys. Because of the special altitudinal conditions the climate is mesothermic with two main seasons. The numerous microclimates and habitats in this area are responsible for maintaining a high diversity of plant communities and an elevated number of endemic species (Giulietti & Pirani, 1988).

According to Harley (1995) the Chapada Diamantina extends into the semi-arid zone of Northeast Brazil where the winter drought is more severe and of longer duration. Within in this community type you find the floresta estacional which is a seasonally deciduous forest. There are various types of savanna...
or savanna woodland, known as *cerrado* that occur in the intermediate zone. In the upper altitudinal zone (above 900–1000 m), you find the *campo rupestre* that occupies a mosaic of rocky, sandy flats and bogs which dominate the landscape. From the lower zone of the mountains upwards one finds mixed or evergreen forests, including gallery forest and even “montane forest” where conditions are favorable. At higher altitudes, within the *campo rupestres* zone, cloud forest can also occur.

The “montane forests” of the semi-arid portion of northeastern Brazil (*floresta estacional*) represent fragmented remnants of a formerly continuous vegetation that stretched throughout northern and eastern Brazil. Under paleoclimate conditions during more humid periods there was a biological corridor linking the Atlantic rainforest and the Amazon rainforest including this area (Andrade-Lima, 1982). However, these forests are now isolated because of the arid climate and as a result its biota is extremely vulnerable. Currently these forests occur only in small areas, having been reduced by human activity (diamond mining, fires, logging, etc.).

Harley (1995) states that of all the “montane habitat” in the Chapada Diamantina, the forest is perhaps the most threatened, the least well understood and the most interesting in terms of phytogeographic links and past vegetational history of the region and of eastern South America. New taxa are found frequently and it is not surprising to discover yet another new species.

In the present paper, we describe the new species *Fulcaldea stuessyi* and discuss the main biogeographic implications based on the distribution of the related taxa.

Fig. 1. Cladogram of Barnadesioideae with the branches color coded for extant distributions (modified from Stuessy & al., 2009). Note that *Schlechtendalia* is in two positions with one based on molecular data and the other on morphological data. Color code: red = southern South America; orange = central and northern Andes; purple = Brazil.

Fig. 2. Distribution maps: left, *Fulcaldea* and its sister taxon *Arnaldoa*; right, *Dasyphyllum*. Note the disjunct distributions in *Fulcaldea* and *Dasyphyllum*. A = *Dasyphyllum* subg. *Archidasyphyllum*; D = *Dasyphyllum* subg. *Dasyphyllum*; maps drawn with information from Cabrera, 1959; Ståhl & al., 1999; Stuessy & al., 2009.
MATERIALS AND METHODS

Chloroplast DNA sequence data from the trnL-F and psbA-trnH regions were obtained from leaf material taken from the isotype and recently collected material of the other newly sequenced taxa. The material was processed in the Laboratory of Molecular Systematics at the National Museum of Natural History (for details see Funk & Chan, 2008). For comparison purposes the trnL-F and psbA-trnH data originally published by Gruenstaeudl & al. (2009) were downloaded from GenBank for Barnadesioideae and the sister group of Compositae (Calyceraceae). We added our own sequences of the new species, three additional outgroup species (all from Stifftia Mikan), and Duseniella (O. Hoffm.) K. Schum. (the sequence of this last taxon was incomplete in GenBank) for a total of five new taxa (10 new gene regions). The GenBank accession numbers and voucher information are listed in Table 1. All of the remaining GenBank numbers can be found in Gruenstaeudl & al (2009). The database had 1684 characters, 169 of which were parsimony-informative. The analyses were run using the parsimony bootstrap option in PAUP* v.4.0a114 (1000 reps; Swofford, 2011). The branch swapping option was selected.

The pollen grains were removed from two different sets of anthers taken from the isotype (US) and dropped in 95% alcohol onto two SEM stubs. They were sputter-coated with carbon and examined using a Leica Stereoscan 440 with LaB6 electron source. The study was done in the SEM lab at the National Museum of Natural History, Smithsonian Institution.
Results and Discussion

Molecular implications. — To confirm the placement of *Fulcaldea stuessyi*, sequence data were obtained from the trnL-F and psbA-trnH regions of the chloroplast gene. The strict consensus tree as well as the bootstrap consensus tree (Fig. 3) placed the new species in an unresolved clade with *F. laurifolia*, *Arnoldoa*, and the two southern Andean species of *Dasyphyllum* (Fig. 3, see Fulcaldea clade). At the “groups of genera” level, the overall structure of the tree is mostly in agreement with Gruenstaeudl & al. (2009) except for the placement of *Schlechtendalia* (which is on a very long branch and whose placement has been problematic in the past; Stuessy & al., 2009) and the placement of the typical subgenus of *Dasyphyllum* (Fig. 2, *Dasyphyllum*-D; Figs. 1, 3). However, not surprisingly, given that we used only trnL-F and psbA-trnH, there is little resolution among the species within the small clades. The parsimony analysis resulted in 21 equally parsimonious trees (number of parsimony informative characters = 169; length = 371; consistency index = 0.836; retention index = 0.923) and the strict consensus tree was identical to the bootstrap majority-rule consensus tree shown in Fig. 3.

In summary, the molecular data show that the new species belongs in a small clade (along with *F. laurifolia*, *Arnoldoa*, and the two southern Andean *Dasyphyllum* species; Fig 2, *Dasyphyllum*-A) and the morphological data place it as the sister taxon of *F. laurifolia*.

Biogeography. — Figure 1 is the phylogeny modified from Stuessy & al. (2009); it is color coded to show generic level distributions. It seems clear that the current members of the tribe had their origins in southern South America (including southern most Brazil) with repeated incursions into the central and northern Andes and northern Brazil. The clade that contains *Fulcaldea* (Fig. 1, arrow 1) shows Arnoldoa as its sister group; both genera were previously restricted to Ecuador and northern Peru but the new species of *Fulcaldea* has extended the range of that genus by 4000 km (Fig. 2). The sister group to these two genera is *Dasyphyllum*, a large and complex genus with much morphological variability and a much wider distribution from northeastern Brazil to southern Brazil, west to the Andes and north to Colombia and Venezuela, and with two disjunct areas, one on the west side of the southern Andes, and a second in the northern Andes (Cabrera, 1959) (Fig. 2). Gruenstaeudl & al. (2009) sampled the two species of *Dasyphyllum* subg. *Archidasyphyllum* Cabrera (Fig. 2, *Dasyphyllum*-A) and six species of the typical subgenus (Fig. 2, *Dasyphyllum*-D). The subgeneric separations coincided with their geographic disjunction on the western (Fig. 2, *Dasyphyllum*-A) and eastern (Fig. 2, *Dasyphyllum*-D) sides of the Andes. However, as the genus has 39 species, additional sampling is necessary before description of a new genus for the species west of the Andes may be considered. Based on the close proximity of *Fulcaldea stuessyi* to some members of *Dasyphyllum* subg. *Dasyphyllum* (Fig. 2, *Dasyphyllum*-D) one might be tempted to consider the new species as a member of that clade. However, both cladograms (Figs. 1, 3) place it in a separate clade with *Dasyphyllum* subg. *Archidasyphyllum* and *Arnoldoa*.

How can the disjunct distribution of *Fulcaldea* be explained? Interestingly, all three major clades (Fig. 1) in Barnadesiaeae have a similar pattern with one larger more widespread genus for which the clade is named (*Chuquiraga* luss. in the *Chuquiraga* Clade; *Barnadesia* in the *Barnadesia* Clade, and *Dasyphyllum*), and 2 to 3 smaller genera that have more restricted distributions (Fig. 1). Perhaps it is common in this tribe to have widespread taxa that have small, isolated genera where they have speciated in new habitats. But *Fulcaldea* has a well-developed pappus so it could have wafted or hitchhiked its way to new territory.

Taxonomic Treatment

Key to *Fulcaldea* and related genera (sensu Stuessy & al., 2009)

1. Capitula with 1 floret; style with distinctive swelling immediately below branches; involucr 12–17 × 3–4 mm; receptacle epauleaceous, glabrous............. *Fulcaldea*

2. Phyllaries green, brownish at apex and margins; florets bisexual or unisexual; corollas white to yellowish; anther apical appendages bifid to emarginate........ *Dasyphyllum*

2. Phyllaries pink, rose, red, or orange; florets bisexual; corollas cream-white, light orange to orange or purple; anther apical appendages entire ................................... *Arnoldoa*

*Fulcaldea* Poir. (amended from Harling, 1991; Ferreyra, 1995)

*Shrubs* or small *trees* to 8 m in height; trunks to 25 cm, usually with long paired axillary spines. *Leaves* alternate,
subsessile to petiolate, glabrous; blades ovate or elliptic, 3-veined, margins entire. Inflorescences of corymbose or paniculate cymes, terminal and axillary. Capitula small, sessile or subsessile, 1-flowered; involucres cylindrical or narrowly cylindrical; phyllaries 5–13-seriate. Florets hermaphrodite, actinomorphic, 5-merous, corolla tubular, lavender, pale pink or red, 5-lobed, densely villous; anthers ecadaule; styles exerted, apically minutely bifid, distal portion swollen, nearly smooth, with rounded or slightly bulging cells, apex acute or rounded, glabrous. Achenes narrowly cylindrical, densely villous, carpodopium anuliform with several rows of thick-walled cells; pappus of “plumose” bristles, appearing pink or red, 1-seriate.

Fulcaldea, like other members of Barnadesioideae, has the characteristic hairs that help define the tribe: unicellular and attached to a more or less swollen basal cell (Bremer, 1987; Hansen, 1991). In addition, these unique hairs help make up the “plumose” pappus often found in the tribe. In fact, the “plumose” pappus in Barnadesioideae is made of villose bristles (bristles with “barnadesioid hairs”) rather than the typical plumose pappus (bristles with elongated pappus cells) found in various places in the rest of the family (Bremer, 1987).

Key to species of Fulcaldea

1. Phyllaries 6–7-seriate; corollas pale lavender or pale pink, 8–14 × 1 mm, corolla tube 3–5 mm long; corolla lobes short, strongly recurved; styles 15 mm long; villose pappus with pink bristles and white hairs, 8–10 mm long; northern Peru and southern and coastal Ecuador …………… F. laurifolia

Fulcaldea stuessyi Roque & V.A. Funk, sp. nov. (Figs. 4–7)

– Type: BRAZIL. Bahia, Municipality of Rio de Contas, Arapiranga district, on the road beside Brandão Farm, floresta estacional, 9 August 2010, I. Abreu 123 (holotype: ALCB); isotype: US!

Frutax axillaris gemelis spinis; capitulum uno flosculo; involucrum 15–17 mm longum, bractae imbricature 10–13 seriebus; corollae rubrae, 20–23 mm longae; stylus glaber, minute divisus, tumidos modo infra furca; pappus plumosus, rubescens, 15–16 mm longus; corollae acheniae cum trichomati Denis, unicellularibus, longis, gracilibus, basi tumidos.

Shrub ca. 3 m tall, trunks to 25 cm diameter, paired axillary spines usually present, 6–7 cm long and somewhat variable in their direction, branches pubescent. Leaves alternate, spiraled, subsessile, petiole 2–5 mm long; blade slightly discolorous, elliptic, 3-veined, 8–12 × 3–4.5 cm, base cuneate, margins entire, apex acute to apiculate, mucronate (mucro up to 1 mm long). Inflorescences terminal, paniculate, with leafy bracts, bracts ca. 4, ovate, acute, acuminate, pubescent; 2–5 clusters (corymb) of capitula in each inflorescence, each cluster with up to 6 capitula. Capitula disced, homogamous, 1-flow ered; involucres narrowly cylindrical, 15–17 × ca. 3 mm; phyllaries 10–13-seriate, 25–28 in number, imbricate, apressed, green and straw colored, turning pale purple near apex, scarious, abaxial surface sericeous, apex with a micro or spine, reflexed, the outer 2–6 × 1–2 mm, broadly ovate to ovate, apex acute, inner 10–15 × 2–2.5 mm, gradually lengthening to narrow-lanceolate or linear, apex acute, white villose at apex and margins; receptacle convex, epaleaceous, glabrous. Florets bisexual, 25–28 mm long; corollas red, actinomorphic, long-exserted from involucre (10–15 mm), tubular, narrowly cylindrical, 20–23 × 2 mm; corolla lobes long, 6–7 × 1 mm, erect, acute; corolla tube 7–8 mm long, densely white villose outside; stamens 9–11 mm long, anther thecae 4 mm long, dark purplish-brown, filaments free, ca. 7 mm long, flattened in cross section, inserted at apex of tube, apex elongate but acute, ca. 1 mm long, base of pollen sacs truncate; style terete, 27–30 mm long, exserted (up to 12 mm long), white to cream, apex purple, branches shortly bifid, acute, papilllose and distinctly swollen directly below branches. Achenes ca. 5 mm long, cylindrical, inconspicuously ribbed, densely villous, hairs white; pappus uniseriate, bristles 34–40 in number, 15–16 mm long, “plumose” (villose bristles), subequal, basally connate, “róseo” (bristles red, hairs white giving it a light red appearance).

Pollen. – The pollen of Fulcaldea laurifolia has been part of several studies; most recently it was discussed by Hansen (1991), Urtubey & Telleria (1998), and Stuessy & al. (2009). These studies show a type of pollen often found in the basal grade of the family: slightly prolate, radially symmetric, isopolar, tricolporate, without intercolpor depressions, and spinulose or psilate; dry grains were estimated to be approximately 40 µm long and 30 µm in diameter (Urtubey & Telleria, 1998). A quick examination of the pollen of F. stuessyi showed a very similar grain (Fig. 7A). The only difference is that the acetylated pollen of F. laurifolia is slightly prolate and the unacetylated grains of F. stuessyi appeared more or less spherical but this may be the result of the different preparations. In the SEM images (Fig. 7A) the F. stuessyi grains measured 35–38 µm long and 36–39 µm in diameter. What is interesting is that F. stuessyi and its most closely related genera (Arnaldoa and Dasyphyllum as reported by Urtubey & Telleria, 1998) have a single-layered exine that is at least partially caveate (Fig. 7B). Urtubey & Telleria (1998) did not report that F. laurifolia was partially caveate but it appears to be from available images. If so, the partially caveate, single-layered exine could serve as a synapomorphy for a Dasyphyllum-Arnaldoa-Fulcaldea clade (Fig. 1) but further study is needed.

Distribution and ecology. – Known only from the type collection, this species is restricted to Bahia occurring in seasonally deciduous forest called floresta estacional (Fig. 2).

Phenology. – Flowering in August. We know little about the pollination of the new species but the long exerted styles, red color, and damage to the styles hint at possible hummingbird pollination (Fig. 6).

Etymology. – Fulcaldea stuessyi is named in honor of Prof. Tod F. Stuessy, University of Vienna, a student of the subfamily Barnadesioideae who has made many valuable contributions to our understanding of Compositae and who has served as the Secretary General of the International Association for Plant Taxonomy (IAPT) for 12 years (1999–2011) during which time he helped transform both IAPT and its journal Taxon.
Fig. 4. Illustration of *Fulcaldea stuessyi* Roque & V.A. Funk: A, habit; B, stem; C, undersurface of leaf. Illustration by Alice Tangerini (US).
Fig. 5. Illustration of *Fulcaldea stuessyi* Roque & V.A. Funk: A, 1-floret capitulum; B, base of the involucres; C, phyllary; D, floret; E, corolla opened to show anthers; F, anther; G, style; H, style apex; I, achene and pappus; J, base of pappus. Note the white “barnadesioid” hairs on the bracts, florets, achenes, and pappus bristles, and the swollen area below the very short branches of the style. Illustration by Alice Tangerini (US).
Fig. 6. Images of *Fulcaldea*: **A–B**, *F. laurifolia* (Bonpl.) Poir.: **A**, inflorescence; **B**, fully developed pappus; **C–E**, *F. stuessyi* Roque & V.A. Funk: **C**, inflorescence; **D**, stem with paired axillary spines; **E**, leaves; note the 3-veined blades. Photo credits: **A** by G. Lewis (K); **B** by M. Dillon (F); **C–E** by I. Abreu.

Fig. 7. Pollen of *Fulcaldea stuessyi* Roque & V.A. Funk: **A**, whole grain; **B**, broken grain; note that it is partially caveate.
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LITERATURE CITED


NOTE ADDED IN PROOF

The illustration of *Fulcaldea stuessyi* Roque & V.A. Funk was made using traditional and digital methods. Alice Tangerini began with sketches in pencil which were composed into a layout. These sketches were traced onto drafting film using special drafting film pencils. The finished pencil drawing was scanned into Photoshop and the color was added. Colors were selected from digital photographs provided by the authors. The choice of the background color was selected to highlight the important character of the white hairs on the inflorescence, disk flowers, and achene.