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TAXONOMIC REVISION OF CENTRATHERUM AND PHYLLOCEPHALUM (COMPOSITAE:VERNONIEAE)

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Centratherum has generally been treated as a widely distributed tropical genus of the tribe Vernonieae, family Compositae, found in Central and South America, the West Indies, Australia, the Philippines, India, and Java. Willis (1973) recognized approximately 20 species for the genus. A historical record of about 90 names associated with this genus since it was first described by Cassini in 1817 complicates its taxonomic history. For the most part, descriptions of taxa have been scattered in the literature. DeCandolle excluded Old World species from *Centratherum*, placing them in the genus *Decaneurum* (1834). However, the basis for his classification was not presented. Bentham's revisionary treatment followed (1873) and united the two taxa into the single genus *Centratherum,* a group having large pedunculate heads subtended by foliaceous bracts, and uniseriate pappus bristles. While *Centratherum* species have been treated in various geographical floras, no comprehensive evaluation of the group has been undertaken since that of Bentham and Hooker.

The tribe Vernonieae is highly diversified, but is basically characterized by discoid heads, basally sagittate anthers, and long, slender, hirsute styles flattened on the inner side (Jones, 1977). As noted by Jones, delimitation of the genus *Centratherum* is nebulous, as is that of numerous other genera of the tribe (many of which are very small or monotypic), and the genus itself is in need of comprehensive taxonomic treatment.

The present revisionary study involves a traditional herbarium-

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based analysis of the gross-morphologic characters combined with pollen and chromosome studies. The goal is to understand better the taxonomic status and phylogenetic position of this complex.

MORPHOLOGICAL AND CYTOLOGICAL EVIDENCE

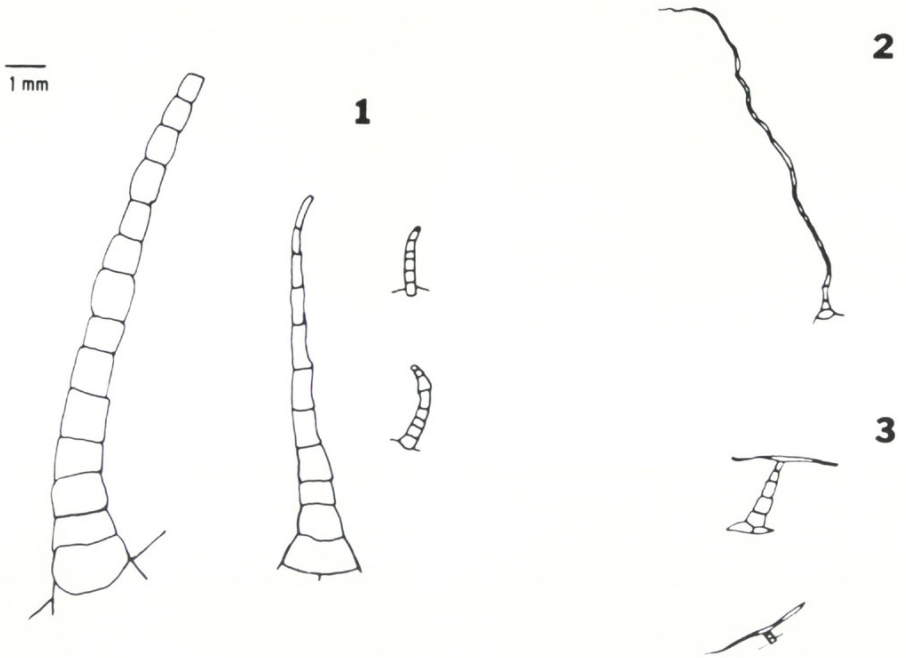
Herbarium specimens were obtained on loan from B, BLAT, BM, BR, BRI, CA, F, G, GH, K, L, LE, LP, M, MO, MPU, NSW, NY, OXF, P, RB, S, SP, SRGH, TEX, UB, and US. Morphological characteristics, such as the length and width of leaves and phyllaries, length of achenes, pappus, style, corolla, involucre, and shape of bracts were recorded for at least ten specimens per country for each taxon (when possible). Otherwise, all available specimens were measured and scored. Means and ranges for the measurements were calculated for each character.

Trichomes. Leaf trichomes were examined after clearing. Leaves from herbarium specimens were cleared in 1% aqueous NaOH at 60° C and transferred to 75% lactic acid at 60° C. Next, the leaves were stained in safranin and fast green and mounted in Hoyer's solution.

Camera lucida drawings of characteristic trichomes are presented (Figs. 1–3). Three types of trichomes were found. T-shaped and uniseriate trichomes, which occur in *Vernonia* as described by Faust and Jones (1973), are also found on species of *Centratherum* from the New World, Philippines, and Australia. All specimens from the Philippines (= *C. punctatum* Cass. ssp. *fruticosum* (Elmer) Kirkman) have both t-shaped and uniseriate trichomes on the veins of the lower leaf surface, the petiole and the peduncle, and rarely, t-shaped trichomes on the upper leaf surface. *Centratherum confertum* Kirkman also has both trichome types present on the leaves, stems, and petioles. Specimens from Australia (= *C. punctatum* Cass. ssp. *australianum* Kirkman) and some from South America (= *C. punctatum* Cass. ssp. *punctatum*) have t-shaped trichomes on the stem only.

Notably, only the Old World species have on the lower leaf surface a type of hair termed by Payne (1978) as flagelliform. Both New World and Old World species have uniseriate trichomes, but such hairs on Old World species are much longer.

Pollen. Pollen samples of each taxon were acetolyzed by



Figures 1–3. Camera lucida drawings of trichomes types of *Centratherum* and *Phyllocephalum*, 10 × : **1.** flagelliform (*Phyllocephalum*); **2.** uniseriate (both genera); **3.** t-shaped (*Centratherum*).

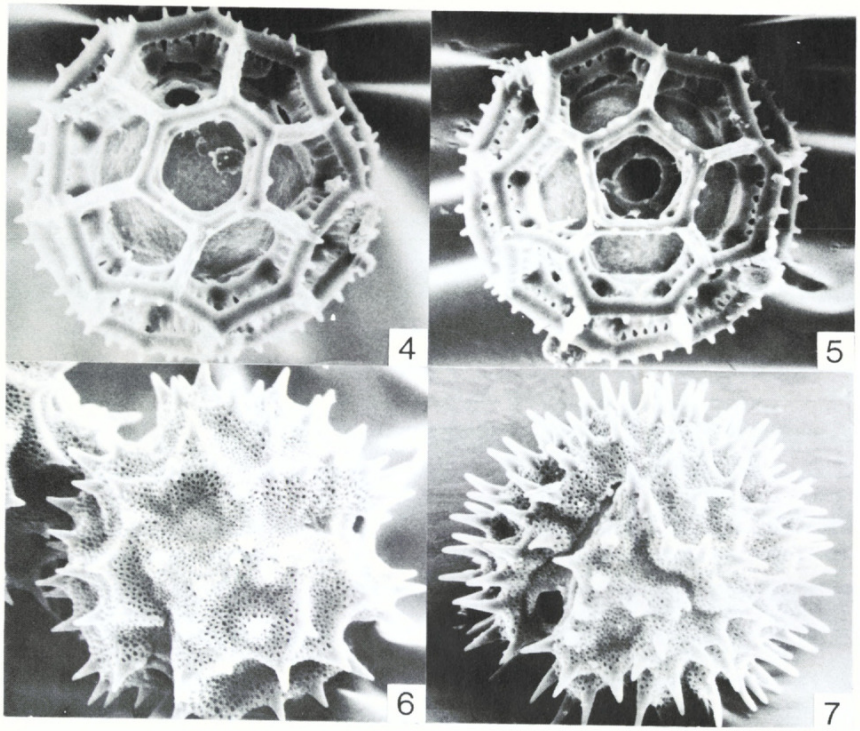
Erdtman's procedure (1966) prior to examination by scanning electron microscopy. Major morphological differences were found between *Centratherum* pollen grains of the New World and those of the Old World. This variation in pollen morphology was previously noted by Kingham (1976). However, one of the species she examined, *C. angustifolium* (Benth.) Adams, is actually a *Vernonia*.

Basically, two types of pollen grains were found. Species of *Centratherum* from India and Java have polyhedral-shaped tricolporate pollen grains with minute spines approximately 1 μm in length along pronounced muri. This type of grain lacks micropuncta. In contrast, New World and Australian species have tricolporate, echinolophate pollen grains (spines up to 5 μm) with a continuous micropunctate tectum (Fig. 4–7).

For examination with light microscope under oil immersion, acetolyzed pollen grains were mounted in glycerin jelly on glass slides. Diameters (spine tip to spine tip at the equatorial view) of 25 pollen grains were measured per sample. The diameter measurements of the spiny pollen grains ranged from 37 to 70 μm. Polyhedral-shaped pollen varied from 47–60 μm in diameter.

Chromosome numbers. Previous reports of chromosome numbers for *Centratherum* include $n = 9$ for *C. rangacharii* Gamble and *C. phyllolaenum* (DC.) Benth. (both = *Phyllocephalum scabridum* (DC.) Kirkman) (Mehra & Remanandon, 1969; Shetty, 1967). Published counts of *C. punctatum* Cass. and *C. muticum* (H. B. K.) Less. (= *C. punctatum* Cass.) indicate $n = 16$ (Coleman, 1970; Gadella et al., 1969; Turner & King, 1964) and $n = 32$ (Jones, 1977). Using the usual acetocarmine squash technique, chromosome numbers of $n = 16$ and $n = 32$ were determined for *C. punctatum* from Brazilian accessions grown from seed in the greenhouse, supporting the report of polyploidy in the *C. punctatum* complex from South America (Fig. 8–9, 10). Some variation is recognizable in bract shape among the greenhouse specimens from South America that have different ploidy levels; however, herbarium specimens demonstrate a continuum between these different involucral phyllaries and no significance is attached to this variation.

Pollen stainability. Pollen fertility was estimated for the greenhouse accesions by determining percentage of pollen stained with 1% aniline blue in lactophenol for 24 hours. A minimum of 150 grains was counted for each slide. Darkly stained pollen grains were considered fertile and lightly stained or unstained grains were scored



Figures 4–7. Scanning electron photomicrographs of *Centratherum* and *Phyllocephalum* pollen grains. **4.** Type A pollen, equatorial view, ca. 50 μm. **5.** Type A polar view. **6.** Type B pollen, equatorial view, ca. 55 μm. **7.** Type B polar view.

Figures 8–9. Camera lucida drawings of PMC with chromosomes. **8.** *C. punctatum* ssp. *punctatum*, $n = 16$; 1000 ×: Voucher: *Jones 22674*. **9.** *C. punctatum* ssp. *punctatum*, interpretation of photo in Fig. 10.

Figure **10.** Photograph of PMC with chromosomes of *C. punctatum* ssp. *punctatum*, $n = 32$; 1000 ×; Voucher: *Kirkman 78–11* GA.

infertile. The sample (*Jones 22682*) having a chromosome number of $n = 16$ had a mean of 57.9% fertile pollen ranging from 41.8–90.9%. Samples (*Kirkman 78–11* and *Jones 22674*) having chromosome number $n = 32$ had means of 28.9% and 34.3% with respective ranges of 17.2–48.8% and 25.3–43.2%. Estimated fertility of pollen from plants grown from self-fertilized achenes averaged 26%, ranging from 16.2–41.4%. The parent of the plant had a chromosome number $n = 32$. This small sample suggests that polyploids in *Centratherum* have a lower pecentage of viable pollen than the plants of a lower ploidy level.

GENERIC CONCEPTS

The fact that the genus *Centratherum* as defined by Bentham has two types of pollen grains geographically correlated with chromosome number strongly suggests that the taxon is heterogeneous.

A strikingly parallel situation is found in the closely related genus *Vernonia*. Chromosome counts reported in New World species include $n = 17$, 34, 51, and 68, whereas Old World species have chromosome numbers of $n = 9$ or 10 and polyploids of 18, 20, and 30 (Jones, 1977). Among the various types of *Vernonia* pollen grains, two resemble the polyhedral *Centratherum* pollen. The polyhedral-shaped *Vernonia* pollen is found in S.E. Asia and Africa, whereas the corresponding spiny *Vernonia* pollen grains are found throughout the range of the genus (S. B. Jones, personal communication). The value of palynology as an aid to the systematics of *Vernonia* has been demonstrated by Jones (1970) and Keeley and Jones (1977). Although pollen morphology alone is not a definitive criterion for taxonomic decisions, it is of value in interpreting phylogenetic relationships in conjunction with other characters.

The genus *Centratherum* has traditionally been held together by characteristics of leafy outer involucral bracts and caducous pappus bristles. However, in view of the evidence obtained from pollen grain morphology, chromosome numbers, geographical distribution and morphological differences (Table I), it is likely that two taxa having different pollen types were independently derived from *Vernonia* and that their common characters are due to convergent evolution rather than to development from a common ancestor. Based on the presented evidence indicating a polyphyletic origin of

the group, generic distinction of the respective taxa is proposed, i.e., *Centratherum* from the New World, Australia, and Philippines, and *Phyllocephalum* from India and Java.

Summary of Generic Character Differences

	Centratherum	*Phyllocephalum*
Reported chromosome number	$n = 16, 32$	$n = 9$
Leaf trichome types	t-shaped, uniseriate	flagelliform, uniseriate
Pollen type	spiny	polyhedral
Distribution	New World, Australia, Philippines	India, Java

SPECIES CONCEPTS

In this revisionary study, species and subspecies are delimited mainly by megamorphological characters. Field population studies and further biosystematic studies are needed to assess variability within species as well as to verify suspected hybrids (by putative parent crosses and backcrosses.) Greenhouse-grown *Centratherum punctatum* ssp. *punctatum* ($n = 32$) self-fertilizes and produces viable offspring. The percentage of fertile achenes to the total number of achenes per head averaged 3.7%, ranging from 0–9.8%. Accessions of *C. punctatum* ssp. *punctatum* ($n = 16$) averaged .068% fertile achenes due to self-fertilization. These plants self-fertilize rarely or not at all.

TAXONOMIC TREATMENT OF PHYLLOCEPHALUM

Phyllocephalum Bl., Bidjr. fl. Ned. Ind. p. 888. 1826. TYPE SPECIES: *P. frutescens* Bl.

Decaneurum DC. ex Wight, Contrib. bot. ind. p. 7–8. Oct. 1833. TYPE SPECIES: *D. reticulatum* DC. ex Wight.

Herbs or subshrubs; stems glabrous, hispid, or woolly. Leaves alternate, petiolate or sessile; blades elliptic to obovate, acute to acuminate at the apex, obtuse or attenuate at the base, marginally serrate and sometimes revolute, pubescent or rugose above, puberulous to tomentose beneath. Inflorescences terminal on axillary branches (rarely spikelike). Heads with numerous florets,

involucre cylindric-campanulate; phyllaries imbricate in several series, glabrous to long ciliate, the inner membranaceous, the outer foliaceous. Pappus of bristles, stramineous to reddish, deciduous. Corollas tubular, reddish-purple (infrequently white). Achenes ribbed, obconic.

Phyllocephalum is a genus of three species found in India and Java. Their distribution is shown in Fig. 11.

1. Leaves white-tomentose beneath, nerves not conspicuously raised. ..... 1. *P. scabridum.*
1. Leaves either white-tomentose beneath with conspicuously raised nerves, or merely puberulous.
    2. Leaves sessile, margins of blades revolute; India 2. *P. indicum.*
    2. Leaves with petioles 0.5–2 cm long, margins of blades not revolute or only minutely so; Java .... 3. *P. frutescens.*

1. **Phyllocephalum scabridum** (DC. in Wight) Kirkman, *comb. nov.*

Ampherephis mollis Wall., cat. n. 2957. 1831. nom. nud.

Decaneurum scabridum DC. in Wight, Contrib. bot. ind. p. 7. 1834. TYPE: *Wight cat. n. 1392* (LECTOTYPE here designated: LE!. ISOLECTOTYPE: BR! 1393 apparently mislabeled on herbarium sheet at BR.)

D. epilejum DC. in Wight, Contrib. bot. ind. p. 7. 1834. TYPE: *Wight cat. n. 1393* (LECTOTYPE here designated: K!. ISOLECTOTYPES: BM!, G!, OXF!).

D. molle (Wall.) DC. var. *scabridum* DC., Prod. **5:** 66. 1836.

D. molle (Wall.) DC. var. *epilejum* DC., Prod. **5:** 66. 1836.

D. phyllolaenum DC., Prod. **7:** 264. 1838. TYPE: *Roux s.n.* (LECTOTYPE here designated: G-DC, as microfische!. ISOLECTOTYPE: G!).

Gymnanthemum molle (DC.) Sch.-Bip., in Walp. Rep. **2:** 948. 1843.

G. phyllolaenum (DC.) Sch.-Bip., in Walp. Rep. **2:** 948. 1843.

Decaneurum courtallense Wight, Icon. **3**(4): 6 tab. 1081. 1846. TYPE: the illustration.

Centratherum molle (Wall.) B. & H., Gen. Pl. **2:** 225. 1873.

C. phyllolaenum (Wall.) B. & H., Gen. Pl. **2:** 225. 1873.

C. courtallense (Wight) B. & H., Gen. Pl. **2:** 225. 1873.

C. molle (Wall.) B. & H. var. *epilejum* (DC.) Clarke, Comp. Ind. p. 4. 1876.

C. tenue Clarke, Comp. Ind. p. 4. 1876. TYPE: INDIA: Concan, *Law s. n.* (LECTOTYPE here designated: K!. ISOLECTOTYPES: GH!, L!).

C. hookeri Clarke, Comp. Ind. p. 4. 1876. TYPE: INDIA: Bombay: Concan, *Law s. n.* (LECTOTYPE here designated: P!. ISOLECTOTYPE: L!).

C. ritchiei Hook., Fl. Brit. Ind. p. 228. 1881. TYPE: INDIA: Canara, no collector cited *93a* (LECTOTYPE here designated: BM!. ISOLECTOTYPE: G!).

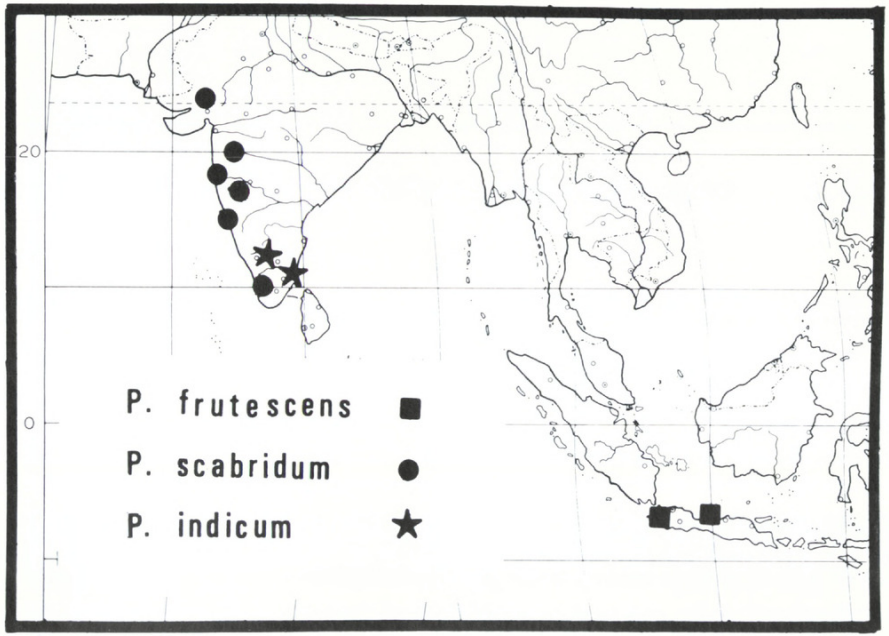


Fig. 11. Distribution of *Phyllocephalum scabridum*, *P. indicum*, and *P. frutescens*.

C. metzianum Sch.-Bip. ex Hook., Fl. Brit. Ind. p. 228. 1881. TYPE: INDIA: Canara, *Metz 175* (LECTOTYPE here designated: P!. ISOLECTOTYPES: BM!, G!, L!, LE!, MPU!, NY!, OXF!, P!, S!, UC!, US! Only the specimen from LE had the collector's name on the label).

C. rangacharii Gamble, Kew Bull. p. 338. 1920. TYPE: INDIA; Tinnevelly District, *Rangachari 13195* (LECTOTYPE here designated: K!).

Suffrutescent, erect herb; stems glabrous to hispid, furrowed when dry. Leaves evenly scattered on stem; petioles indistinct to 4 cm long; leaf blades elliptic to obovate, acute to acuminate at the apex, attenuate at the base, 3.5–15.5 cm long, 3.5–9 cm broad, serrate on the margins, hispid above, white-tomentose beneath. Inflorescences terminal on axillary branches (rarely spikelike). Heads with many florets; peduncles 0–8.5 cm; involucre cylindric-campanulate, 0.5–1.5 cm long; phyllaries imbricate in several series, glabrous to long-ciliate, loosely appressed, greenish; innermost phyllaries 6–10 mm long, linear, membranaceous, tips acute to cuspidate, occasionally reddish, the intermediate ones intergradient from membranaceous to foliaceous, the outer foliaceous. Pappus bristles stramineous to reddish, often extremely numerous, 2–6.5 mm long. Corollas 7–11.5 mm long, purplish (infrequently white). Achenes 1.5–3 mm long, cylindric to obconic, ribbed. $n = 9$.

Native to India. Flowering and fruiting from June to October.

Representative specimens examined include: INDIA: Concan, *Stocks s. n.* (BM, MPU, L, NY, P, US). Kerala: Portland abandoned estate, Thenmala, no collector cited *17* (K). Madras: Tinnevelly (Tirunelveli) Hills, no collector cited *4009* (BM). Myosore: North Kanara, *Talbot 1319* (K); Canara, *Stocks 132* (P). Rajasthan: Mount Abu, *Raizada 20594* (L).

This species is highly variable in size, shape and pubescence of the leaves, resulting in many past nomenclatural proposals. The variation observed from herbarium specimens does not appear to be correlated with geographical distribution and therefore does not warrant subspecific classification.

2. **P. indicum** (Less.) Kirkman, *comb. nov.*

Ampherephis indica Less., Linnaea **6**: 686. 1831. TYPE: *Leehenault s. n.* (HOLOTYPE: probably not extant. NEOTYPE here designated: *Noton s.n.* G-DC as I-DC microfiche!).

Decaneurum reticulatum Wight, Contrib. bot. ind. p. 7. 1834. TYPE: *Wight 1391.* (LECTOTYPE here designated: K!. ISOLECTOTYPES: BM!, BR!, G!, NY!, P!).

Rolfinkia centaurioides Zenker, Pl. Ind. 13, tab. 14. 1837. TYPE: the illustration!

Gymnanthemum reticulatum (Wight) Sch.-Bip. ex Walp. Rep. **2**: 948. 1843.

Centratherum reticulatum (Wight) B. & H., Gen. Pl. **2**(165); 225. 1873.

C. indicum (Less.) Fischer, Kew Bull. p. 44. 1940.

C. mayurii Fischer, Kew Bull. p. 45. 1940. TYPE: *Mayuranathan s. n.* The holotype for this species is apparently not extant; however, the description indicates the specimen is *P. indicum*.

Shrub; stems crisply-hairy pubescent especially near inflorescence, channeled when dry. Leaves sometimes crowded; petioles lacking; leaf blades elliptic, acute at the apex (revolute margin giving blunt appearance), obtuse at base, 3–6 cm long, 1.5–3 cm broad, margins revolute, appearing scalloped, hirsute, often rugose above, dirty-white tomentose beneath with light brown crisped hairs on conspicuously raised veins. Inflorescences terminal on axillary branches, usually subtended by leaves similar to cauline ones. Involucre campanulate, 1.5–1.8 cm long; phyllaries loosely appressed, imbricate; inner phyllaries 9.5–15 mm long, linear, straw-colored, membranaceous, fringed at the tips; outer ones 5–9 mm long, ovate, foliaceous, constricted, membranaceous at the base, ciliate, tips acuminate to mucronate. Pappus straw-colored, bristles 3–4 mm long. Corollas (10.7) 11–16.2 mm long, purple. Achenes 3–3.4 mm long, obconic, ribbed.

This species occurs in southern India along weedy roadsides and shady areas. Flowering and fruiting occur from May to October.

Representative specimens examined include: INDIA: Madras: In Montibus Nilagiri, *Hohenacker 1036* (BM, G, GH, K, L, M, MPU, S); Nilghiri, *Wight 1534* (GH, L, M, NY, S).

This species appears to be very closely related to and sometimes resembles *P. frutescens,* but can be distinguished by its sessile leaves and revolute leaf margin.

3. **P. frutescens** Bl., Bidjr. fl. Ned. Ind. p. 888. 1826. TYPE: None cited. (LECTOTYPE here designated: JAVA, *Blume 1400.,* L!. ISOLECTOTYPE: L!).

Decaneurum frutescens (Bl.) DC., Prod. **5:** 66. 1836.

Gymnanthemum frutescens (Bl.) Sch.-Bip. ex Walp. Rep. **2:** 948. 1843.

Decaneurum javanicum Miq. in Pl. Jung, p. 496. 1853. TYPE: Malabar, *Junghin s. n.* (HOLOTYPE: L!).

Centratherum frutescens (Bl.) Boerlage, Handleiding **2:** 234. 1899.

Decaneurum frutescens (Bl.) DC. var. *javanicum* (Miq.) Koster, Blumea **1:** 379. 1935.

Decaneurum frutescens (Bl.) DC. var. *papandaianense* Koster, Blumea **1:** 379. 1935. TYPE: *Went s. n.* (HOLOTYPE: L!).

Herb; stems puberulous to woolly, deeply grooved or sometimes slightly flattened upon drying. Leaves cauline, even spaced; petioles usually distinct, 0.5–2 cm long; leaf blades elliptic, widest at the middle, acuminate at the apex, obtuse at the base, 5–13 cm long, 1.5–3.9 cm broad, margins serrate, occasionally slightly enrolled but marginal teeth protrude, blades puberulous to villous above, puberulous to brown-white tomentose beneath. Heads solitary or in clusters of 2 or 3 heads on axillary branches. Heads with numerous florets; involucre campanulate, 0.8–1.5 cm long; phyllaries imbricate, loosely appressed, brownish when dried; inner phyllaries 6.4–10.4 mm long, linear, membranaceous, tips mucronulate, outer ones ovate to elongate, ciliate, distally foliaceous, basally membranaceous, tips mucronulate to cuspidate, intergrading to the inner. Pappus bristles straw-colored, 1.9–3.5 mm long. Corollas 8.1–12 mm long, purple. Achenes 2.5–3.7 mm long, obconic, ribbed.

Java; mountainous, humid forests and water edges. Flowering and fruiting all year.

Representative specimens examined: JAVA: *Blume 146* (BM). Preanger: G. Papandajan, Boshranden, *Van Steenis 12227* (GH, L). Priangan: G. Patoeha, W., *Van Steenis 4427* (L).

This species is extremely variable. Some specimens are very similar to *Phyllocephalum indicum* in regard to leaf shape and tomentose lower leaf surface, while others appear almost glabrate. A continuum of leaf characteristics is evident in herbarium specimens studied, which does not support subspecific classification within *P. frutescens.*

TAXONOMIC TREATMENT OF CENTRATHERUM

Centratherum Cass., Dict. Sci. Nat. **7:** 384. 1817. TYPE SPECIES: *C. punctatum* Cass.

Spixia Schrank, Pl. Rar. Hort. Monac. tab. 80. 1819. TYPE SPECIES: *S. violacea* Schrank.

Ampherephis H. B. K., Nov. Gen. Sp. Pl. **4:** 31. 1820. TYPE SPECIES: *A. mutica* H. B. K.

Amphibecis Schrank, Syll. Ratisb. 1: 86. 1824. TYPE SPECIES: *A. violacea* Schrank.

Crantzia Vell., Fl. Flum. Ic. 8, tab. 153. 1827. TYPE SPECIES: *C. ovata* Vell.

Herbs or subshrubs, often-branched stems glabrescent to villous.

Leaves alternate, petiolate to sessile; petioles often indistinct; blades ovate, linear, or oblanceolate, obtuse to sub-acute at the apex, cuneate to attenuate at the base, margins serrate or lobed, blades glabrous, punctate, or pubescent above and beneath. Heads terminal on axillary branches, occasionally 2 or 3 clustered together, many-flowered, sessile; involucre cylindric-campanulate, 8–25 mm wide; phyllaries in several series, outer foliaceous, intergrading to firm scales, tips variable, rounded to long-awned. Pappus bristles straw-colored, deciduous, occasionally absent. Corollas tubular, 5-lobed, reddish-purple, glandular, tube sometimes pubescent. Achenes cylindric to obconic. $n = 16, 32$.

Centratherum is a genus of two species found in the tropics of the New World, Australia, and the Philippines. Their distribution is shown in Fig. 12.

1. Achenes less than 3 mm long.
   2. Leaves serrate, teeth with minute mucro; South and Central America and Philippines.
      3. Phyllaries membranaceous; New World. ..... 1a. *C. punctatum* ssp. *punctatum.*
      3. Phyllaries indurate at the base; Philippines. ..... 1b. *C. punctatum* ssp. *fruticosum*
   2. Leaves shallowly lobed; Australia. ... 1c. *C. punctatum* ssp. *australianum.*
1. Achenes 3 mm or longer.
   4. Leaves mostly linear or at least many times longer than wide (rarely elliptical), blunt at apex; phyllaries awned; S. America. ..... 2. *C. confertum.*
   4. Leaves rhombic to elliptic, broadly acute at apex; phyllaries not awned; Philippines. ..... 1b. *C. punctatum* ssp. *fruticosum.*

1. **Centratherum punctatum** Cass., Dict. Sci. Nat. **7:** 384. 1817. TYPE: none cited. (NEOTYPE here designated: BRAZIL: Maranhão: Loreto, *Eiten 4042* SP!. ISONEOTYPE: BRI!, G!, NY!, US!).

Synonymies and typifications are given under subspecific heading.

Sprawling to erect herb, suffrutescent with age; stems strigose, often ridged upon drying. Leaves cauline, often crowded, short petiolate to sessile; blades ovate to elliptic, spatulate, or rhombic,

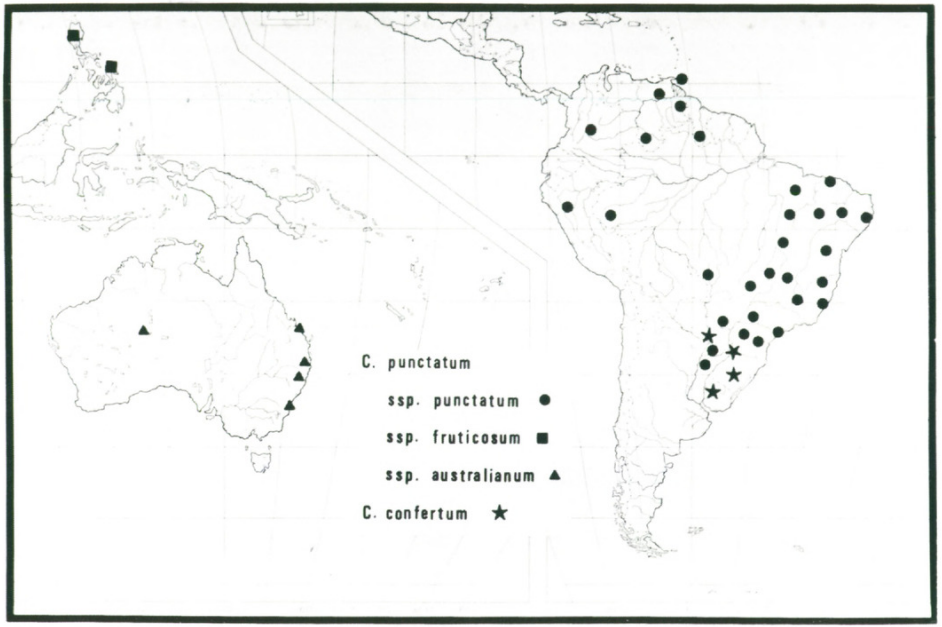


Fig. **12.** Distribution of *Centratherum punctatum* ssp. *punctatum*, *C. punctatum* ssp. *australianum*, *C. punctatum* ssp. *fruticosum*, and *C. confertum*.

obtuse to broadly acute at the apex, cuneate to attenuate at the base, 1–8.3 cm long, 0.5–3.9 cm broad, margins serrate or shallowly lobed, often ciliate, glandular punctate, often pubescent (especially on veins) above and beneath. Inflorescences of terminal, many-flowered heads. Involucre cylindric-campanulate; phyllaries imbricate in several series, outer ones foliaceous. Pappus bristles straw-colored, deciduous. Corollas 5–14.2 mm long. Achenes cylindric to obconic.

Three subspecies of *Centratherum punctatum* have been distinguished in the key. Their distributions are shown in Fig. 12.

The three taxa, although distinct, appear to be very closely related and are probably derived from one source; and are therefore accorded subspecific designation rather than specific rank. It is likely that they were originally dispersed along trade routes between Europe and the Orient. Merrill (1954) discusses the probable introduction of tropical American plants into the Philippines and Australia via definite trade routes which were established by the Portugese in 1500 A.D. and the Spaniards in 1565 A.D., and which lasted for 250 years. These geographically distinct taxa have become somewhat differentiated yet have maintained a close resemblance to each other. Specific recognition would tend to obscure their close phylogenetic relationship.

a. **Centratherum punctatum** Cass. ssp. **punctatum**.

Spixia violacea Schrank, Pl. Rar. Hort. Monac. tab. 80. 1819. TYPE: the illustration!

Ampherephis aristata H. B. K., Nov. Gen. Sp. **4:** 31. 1820. TYPE: none cited. (LECTOTYPE here designated: *Bonpland s. n.* P, seen as photo TEX!. ISOLECTOTYPE: P!).

Ampherephis mutica H. B. K., Nov. Gen. Sp. **4:** 31. 1820. TYPE: none cited. [LECTOTYPE here designated: Herb. H. B. K., (no collector cited), P, as photo GH!].

Amphibecis violacea Shrank, Syll. Ratisb. **1:** 86. 1824. TYPE: none cited.

Crantzia ovata Vell., Fl. Flum. Ic. **8**, tab. 153. 1827. TYPE: the illustration!

Ampherephis pulchella Cass., Dict. Sci. Nat. **57:** 346. 1828. TYPE: *d'Urville and Lesson s. n.*, not seen.

A. pilosa Cass., Dict. Sci. Nat. **57:** 346. 1828. TYPE: same as *A. mutica* H. B. K. (Cassini merely suggested a more "descriptive" name).

Centratherum brevispinum Cass., Dict. Sci. Nat. **57:** 346. 1828. TYPE: same as *A. aristata* H. B. K.

C. longispinum Cass., Dict. Sci. Nat. **57:** 346. 1828. TYPE: same as *C. punctatum* Cass.

Ampherephis intermedia Link, Abbild. **5** tab. 29. 1829. TYPE: not seen.
Centratherum muticum (H. B. K.) Less., Linnaea **4:** 320. 1829.
C. intermedium (Link) Less., Linnaea **4:** 320. 1829.
C. pulchellum (Cass.) Steud., Nom. Bot. ed. **2.** p. 324. 1840.
C. punctatum Cass. var. *parviflorum* Baker in Mart. Fl. Bras. **6**(2): 12. 1873. TYPE: BRAZIL: Bahia, *Blanchet 3689* (LECTOTYPE here designated: K!. ISOLECTOTYPES: BR!, F!, G!, LE!, MO!, P!).
C. holtoni Baker in Mart. Fl. Bras. **6**(2): 12. 1873. TYPE: BRAZIL: Ibague, *Holton 301* (HOLOTYPE: K!).
C. brachylepis Sch.-Bip. ex Baker in Mart. Fl. Bras. **6**(2); 12. 1873. TYPE: BRAZIL, *Martius 461* (LECTOTYPE here designated: M! as photo GH!, NY!, TEX!. PARATYPE: K!. ISOPARATYPES: G!, GH!, LE!).
Baccarodes holtonii (Bakér) O. Ktze., Rev. Gen. **1:** 320. 1891.
B. brachylepis (Sch.-Bip. ex Baker) O. Ktze., Rev. Gen. **1:** 320. 1891.
B. violaceum (Schrank) O. Ktze., Rev. Gen. **1:** 320. 1891.
B. punctatum (Cass.) O. Ktze., Rev. Gen. **1:** 320. 1891.
B. muticum (H. B. K.) O. Ktze., Rev. Gen. **1:** 320. 1891.
Centratherum aristatum non Cass., Index Kew. **1:** 478. 1895.
C. punctatum Cass. var. *foliosa* Chod., Bull. Herb. Boissier **2**(2): 298. 1902. TYPE: PARAGUAY: Capibuy, *Hassler 4378.* (LECTOTYPE here designated: BM!. ISOLECTOTYPES: G!, K!, NY!, P!).
C. punctatum Cass. ssp. *camporum* Hass. var. *viscosissimum* Hass. f. *foliosum* (Chod.) Hass., Feddes Repert. Spec. Nov. Regni Veg. **12:** 369. 1913.
C. punctatum Cass. ssp. *camporum* Hass. var. *viscossissimum* Hass. f. *brachyphyllum* Hass., Feddes Repert. Spec. Nov. Regni Veg. **12:** 369. 1913. TYPE: PARAGUAY: In regione vicine Igatimi, *Hassler 4768* (LECTOTYPE here designated: GH!. ISOLECTOTYPES: BM!, G!, MO!, MPU!, NY!, P!, S!).
C. punctatum Cass. ssp. *camporum* Hass. var. *longipes* Hass., Feddes Repert. Spec. Nov. Regni Veg. **12:** 369. 1913, TYPE: PARAGUAY, *Fiebrig 4532* (LECTOTYPE here designated: B, as photo GH!, TEX!. ISOLECTOTYPES: G!, GH!, K!, L!, M!, US!).
C. vioalaceum (Schrank) Gleason, N. Amer. Fl. **33:** 49. 1922.
C. camporum (Hass.) Malme var. *longipes* (Hass.) Malme, Arkiv. Bot. 24A **6:** 15. 1931.

Sprawling to erect herb, suffrutescent with age; stems strigose, often deeply grooved upon drying. Leaves cauline, often crowded; short to indistinctly petiolate; blades ovate to elliptic to spatulate, obtuse at the apex, cuneate to attenuate at the base, (1)2–7 cm long, (0.5)0.8–3 cm broad, marginally serrate and often ciliate, glandular-punctate, often sparsely pubescent (especially on veins) above and beneath. Heads terminal, many flowered, solitary or occasionally 2–3 clustered together, peduncles 2–7 cm long. Involucre cylindric-campanulate, 0.5–1.2 cm long; phyllaries imbricate in several series, glandular, membranaceous, the outer foliaceous, greenish, the inner purplish, rounded to aristate (when awned, awns to 3 mm). Corollas

5–8(10) mm long, glandular. Achenes (1.2)1.6–2.6 mm long, 8–10 ribbed, occasionally with minute pubescence on ribs. Pappus bristles numerous, stramineous, deciduous, 1.5–2.8(3.5) mm long, or rarely absent. $n = 16, 32$.

South and Central America and the West Indies; pastures and waste places. Flowering all year. Sometimes cultivated as an ornamental.

Representative specimens examined: ARGENTINA: Corrientes: Estancia Tuyuti, Itati, edge of woodland by the river, *Pederson 5530* (GH, LP, P, S, US). Misiones: Candelaria, Loreto, *Montes 1785* (F, SP, US). BOLIVIA: Velasco: Longlais, *Kuntze s. n.* (NY). BRAZIL: Acre: Estrada Alemanha, Cruzeiro do Sul, roadside, *Prance et al. 11965* (F, G, GH, M, MO, NY, S, US). Amazonas: Rio Curuquetê, vicinity of Cachoeira, Santo Antonio, *Prance et al. 14359* (F, GH, NY, S, US). Bahia: *Rose 20136* (NY, US). Ceará: Acude, São Bento Municipio de Maranguape, wet places below dam, *Drouet 2191* (F, NY, S, US). Espirito Santo: Afonso Cladio, *Pereira 9856* (M). Federal District: Lagôa Feia, ca. 10 km E of Sobradinho, elevation 1000 m, *Irwin, Souza, Santos 13168* (NY, SP, UB, US). Goiás: Serra dos Pirineus, Capoeira, ca. 12 km S. of Corumbá, *Irwin, Souza, Santos 10956* (NY, S, UB). Maranhão: Municipio de Lorêto, "Ilha Balsas": region between the Rios Balsas and Parnaiba, *Eiten & Eiten 4712* (NY, SP, US). Matto Grosso: Corumba, *Malme 3012* (GH, S). Minas Gerais: Faxenda do Paraiso, Pau de Paina, grazed hillside, above stream, *Mexia 5388* (F, GH, NY, MO, S, UC, US). Pará, *Martius s. n.* (G). Paraná: Parque Nacional do Iguacú, near Aranha, roadside at edge of forest, *Lindeman & de Haas 3403* (GH, NY, US). Pernambuco: Vitoria de Sto. Antão, *Tavares s. n.* (US). Piauhy: Floriano to Oeiras, wet swampy places, *Swallen 4161* (GH, US). Rio de Janeiro: vicinity of Monte Serrat, Mt. Itatiaya, Estacão Biolôgica, roadside weed, *Smith 1588* (F, GH, S, US). Santa Catarina: Mina Velha, Garuva, S. Francisco do Sul, *Reitz & Klein 4.993* (NY, UC, US). São Paulo: Municipio de Caraguatatuba; at station of Reserva Florestal, 3.5 km NNW of Caraguatatuba, at base of Serra do Mar. Along path in secondary forest, *Eiten & Eiten 2845* (US). BRITISH GUIANA: Dorusfruit, Berbice R., *Morgan 3* (K, NY). COLOMBIA: Departmento Tolima, sterile fields, Piedras, *Haught 2405* (NY, US). PARAGUAY: Alto Paraná, *Fiebrig 5374* (BM, G, GH, K, US). Caaguazú, *Hassler 8892* (G, GH, MO, NY, S, UC). Caazapa: Borja, open camps, *West 8518* (UC). Guaira: Villarrica, gregarious in humid thickets (forests), *Jorgenson 3479* (F, GH, MO, NY, S, US). Misiones: Estancia La Soledad Santiago, dry, rough grasslands, *Pederson 4321* (BR, G, GH, MO, NY, S, US). Paraguari: Camino Ipacaray-Pirayú, *Schinini 4296* (LP). PERU: no locality cited, open roadside spot, *Woytkowski 7643* (MO). VENEZUELA: Amazonas: Orinoco Delta, *Bond, Gillin, & Brown 133* (NY, US). Bolívar: woods, northwest of Upata on road to San Felix, between Upata and Altagracia, *Steyermark 57694* (F, US). Monagras: rocky open slopes between Caripe and San Augustin, *Steyermark 61781* (F, MO, NY, US). Sucre: rocky limestone, steep slopes along headwaters of Rio Manzanares (Rio de la Cuesta) along highway between Cumanacoa and Cocollar, *Steyermark 62431* (F, US). WEST INDIES: Trinidad: Blanchisseuse village, north coast on banks, *Broadway 9149* (BM, TEX).

This subspecies is variable in regard to involucral bract shape and size of heads and leaves. The large number of synonyms for this taxon is a reflection of the variability within the group. Prior to a comprehensive examination of numerous herbarium specimens, distinct taxa were recognized in the extreme polymorphological characters. Observation of a continuum of characters without a corresponding geographical distributional pattern indicates a variable taxonomic unit.

1b. **Centratherum punctatum** Cass. ssp. **fruticosum** (Elmer) Kirkman, *comb. nov.*

C. fruticosum Elmer Leafl. Philipp. Bot. **1:** 88. 1906. TYPE: *Cuming 1556* (LECTOTYPE here designated: G!. ISOLECTOTYPE: K!, LE!).

Herb, suffrutescent with age; stems hispid, becoming glabrate. Leaves crowded, short internodes often appear fascicled; petioles up to 0.8 cm long, often indistinct; leaf blades rhombic, sometimes elliptic, broadly acute at the apex, attenuate and hispid at the base, (1.5)2–8.3 cm long, (0.5)1–3.9 cm broad, margins serrate, darkened above when dried, glandular-punctate above and below, canescent, minutely villous on nerves beneath with uniseriate and t-shaped hairs. Inflorescences terminal on axillary branches. Heads with many florets; peduncles 3.5–10.5 cm; involucre cylindric-campanulate, 0.8–1.2 cm long; phyllaries imbricate in several series, loosely appressed, often glandular, stramineous to green, the inner ones (6.1)7.5–10.6 mm long, linear, membranaceous, 3-veined in lower half, scarious and purple colored at the tips, the intermediate ones 2.8–6 mm long, pandurate, indurate at base, at the tip foliaceous to scarious, mucronate. Pappus bristles straw-colored, 2.4–3.9 mm long. Corollas 8.5–14.2 mm long, purple, glandular hairs on tips of corolla limb. Achenes 2.5–3.9 mm long, glabrous, finely ribbed.

The Philippines; on mountain slopes. Flowering and fruiting all year.

Representative specimens examined. PHILIPPINES: Rizal, Mt. Canumay, Luzon, *Ramos 13769* (G, S). Trinidad Valley, Mt. Province, mountain road on hilltop, *Quisumbing 18823* (L).

This subspecies is distinguished by large achenes and phyllaries with a strong indurate base.

1c. **Centratherum punctatum** Cass. ssp. **australianum** Kirkman *ssp. nov.* TYPE: AUSTRALIA: New South Wales, Sydney, *Vickery 23846* (HOLOTYPE: NSW!. ISOTYPES: L!, MO!).

Herba erecta. Caulis ramosus, usque ad 0.5–1 cm altus, puberulus Folia 1.9–6 cm longa, 0.6–2 cm lata, lobis apice obtusis vel subacutis, basi attenuatis. Capitula ramos axillares terminantia. Involucra 0.5–1 cm longa. Phyllaria acuminata vel aristata, margine ciliata. Pappi setae straminei. Achaenia glabra, 2–2.6 mm longa.

Supine-erect herb, 0.5–1 m tall; stems puberulous, grayish, slightly ridged. Leaves evenly spaced, sometimes crowded at intervals; petioles 0–1.2 cm long, often indistinct; leaf blades bluntly serrate to lobed, oblanceolate to spatulate, subacute to blunt at the apex, attenuate at the base, 1.9–6 cm long, 0.6–2 cm wide, glabrous, gland-dotted above and beneath; t-shaped and nonglandular uniseriate trichomes on leaves, stems and petioles. Inflorescences terminal to axillary branches, often dichotomously branched. Heads many-flowered; peduncles 4–13 cm. Involucre cylindric-campanulate, 0.5–1 cm long; phyllaries imbricate in several series, loosely appressed at maturity, membranaceous, golden brown, the tip often dark brown or reddish, the inner ones 5–7 mm long, pandurate, glandular, the tip often fringed, narrower than the base, intermediate ones 1–1.7 mm long, triangular or occasionally constricted at middle, glandular, the tip acuminate to spine tipped, the margin slightly ciliate. Pappus bristles stramineous, 2–3 mm long. Corollas 4.2–6 mm long, purple, glandular hairs at the tip. Achenes 2–2.6 mm long, glabrous, ribbed.

Australia (New South Wales, Queensland and Northern territory); on rocky slopes, roadsides and *Eucalyptus* forests. Flowering and fruiting from February to May.

Representative specimens examined: AUSTRALIA: Queensland: Belmont near Brisbane, *White 6671* (GH, K, S). New South Wales: West of Wingham on Bulga Road, *Vickery 23846* (L, MO). Northern Territory: Mt. Lindsay, *Boorman 139922* (NSW).

The narrow, oblanceolate to spatulate leaves with bluntly serrated or shallowly lobed margins are distinctive.

2. **Centratherum confertum** Kirkman, *nom. nov.* TYPE: PARAGUAY: Regione fluminis Yhu, *Hassler 9572* (LECTOTYPE here desig-

nated: K!. ISOLECTOTYPES: BM!, G!, GH!, MO!, MPU!, NY!, P!, S!, UC!).

C. punctatum Cass. ssp. *camporum* Hass. var. *albicans* Hass., Feddes Repert. Spec. Nov. Regni Veg. **12:** 369. 1913. TYPE: PARAGUAY: Regione fluminis Yhu, *Hassler 9572* (LECTOTYPE here disignated: K!. ISOLECTOTYPES: BM!, G!, GH!, MO!, MPU!, NY!, P!, S!, UC!).

C. camporum (Hass.) Malme var. *albicans* Hass., Arkiv. Bot. 24A **6:** 15. 1931.

Herb, from thickened rootstock, 15–60 cm; stems usually with grayish-white appressed pubescence. Leaves very crowded, appearing fascicled; petioles lacking; blades linear and oblanceolate (rarely elliptical), obtuse and serrate at the apex, attenuate at the base, linear ones 0.5–2 cm long, 0.1–0.3 cm wide, the oblanceolate ones 1.1–3.6 cm long, 0.2–2 cm broad, margins dentate, punctate above and beneath, grayish-white with appressed pubescence. Inflorescences terminal on axillary branches. Heads with many florets; peduncles 3–6 cm long; involucre cylindric-campanulate, 3.5–8 cm long; phyllaries imbricate in several series, loosely appressed, purplish with scattered glandular hairs; the inner ones 4–7.7 mm long, linear, membranaceous, purplish, tips mucronate; the outer ones 3–6 mm long, the intermediate ones intergradient with outer foliaceous ones, base indurate, constricted below the middle, distally foliaceous. Pappus bristles straw-colored, 1.8–3 mm long. Corollas 6.8–13 mm long, purple, glandular, tube pubescent. Achenes (3.3)3.5–4.6 mm long, ribbed.

Argentina, southern Brazil, and Paraguay. Flowering and fruiting occur from October to January.

Representative specimens examined include: ARGENTINA: Corrientes: Berón de Astrada, Loc Ruta Nac. No. 12, Yahape (21 km W de Itá Ibaté), *Krapovickas, et al. 16549* (UC); Concepción, Tabay, *Arbo 10* (P), *Arbo 876* (LP); General Paz, *Ibarrola 3549* (BM, F, K, RB); General Paz, *Ibarrola 3594* (S); Ituzaingó, Estancia Puerto Valle, *Pederson 2956* (P, S, US); Mburucuyá, Estancia Santa Teresa, *Pederson 512* (BR, G, K, MO, P, S, US); *Krapovickas 13622* (G, LP, MO, RB). Santa Fé: Mocove, *Venturi 122* (G, GH, UC, US); Reconquista, *Burkart 5717* (F); Roe Camino de Reconquista, *Job 787* (S); *Parodi 11160* (F, NY). BRAZIL: Rio Grande do Sul: Belisanio, *Rau 88* (RB); Cruz Alta, *Malme 1109* (S), *Pereira 8585* (K, LP, M, RB), *Rambo 50019* (S); Gomez, *Bornmüller 266* (GH); Tupaceretan, *Archer 4433* (B, US); Tupaceretan, *Rambo 9911* (SP). PARAGUAY: Cordillera do Altos, *Fiebrig 496* (BM, F, G, GH, L). Corrientes, *Hassler 5881* (G).

This species appears to be variable in length and width of leaves. From observation of herbarium specimens, I suggest that it may

hybridize with *C. punctatum* ssp. *punctatum*; however, hybridization has not been experimentally demonstrated. Population studies in the field and crossing experiments are needed.

DOUBTFUL AND EXCLUDED SPECIES

Gymnanthemum fimbrilliferum Cass., Dict. Sci. Nat. **10:** 109. 1817. This species is the type of genus *Gymnanthemum,* which was, along with the genus *Phyllocephalum*, united into the single genus *Decaneurum. Decaneurum* was later transferred to *Centratherum. Gymnanthemum fimbrilliferum* is a *Vernonia*, and therefore is not only excluded as a species from the genus *Centratherum,* but also eliminated as priority for a generic name of the Old World taxa.

Wightia formosa Spreng. This species was never validly published; it was merely cited by DeCandolle in Prod. **5:** 67. 1836 "as correspondence".

Centratherum grande (DC.) Nob, Mem. Couronnes Autres Mem. Acad. Roy. Sci. Belgique p. 53. 1895. This species is a *Vernonia.*

C. englerianum Muschler, Bot. Jahrb. **46:** 57. 1911. It is doubtful that this species is *Phyllocephalum*. The type specimens are apparently not extant and according to Bot. Jahrb. Syst. **53:** 367, 1914, Muschler, besides being declared insane, is reported to have falsified much of his data, including that for *C. englerianum.*

C. burmanicum Gamble, Kew Bull. p. 90. 1915. This species is not *Phyllocephalum*. The large solitary heads are reminiscent of *Phyllocephalum,* but the leaves do not have the correct pubescence and the involucral bracts do not resemble stem foliage.

C. angustifolium (Benth.) Adams, J. W. Afr. Sci. Ass. **3:** 122. 1957. This species is a *Vernonia*.

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