

Home at last: the enigmatic genera *Eriachaenium* and *Adenocaulon* (Compositae, Mutisioideae, Mutisieae, Adenocaulinae)

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Abstract

The genera *Eriachaenium* and *Adenocaulon* (Compositae) have distinct but complex histories and both have been placed in a number of tribes across the family. For the first time the two genera are included in a molecular study and the results show that they are best placed in the tribe Mutisieae s.s. and are the only genera in the re-instated subtribe Adenocaulinae. When described, this subtribe contained only *Adenocaulon* and was found in the Inuleae. The study also confirms one of the conclusions of a recent morphological study that *Eriachaenium* and *Adenocaulon* are sister taxa. Past difficulties in tribal assignment are attributed to the distinct and unusual morphology of each genus. Both genera and the subtribe are described and a key to separate the genera is provided.

Keywords

Asteraceae, dimorphic flowers, endemism, Patagonia, Asia-North America disjunct

Introduction

Eriachaenium Sch. Bip. and *Adenocaulon* Hook. (Figs 1–5) are perennial herbs that were left unplaced in the most recent genus level classification of the Compositae family (Hind 2007). More recent phylogenies, based on molecular data, have divided the Compositae into 42–43 tribes; about half of them are small (Panero and Funk 2008; Funk et al. 2009). Within these family level phylogenies there are four main areas (as well as a number of very small subfamilies), beginning with the crown group: the highly nested subfamily Asteroideae (asters, ragworts, sunflowers: monophyletic) which contains about 65% of the species in the family; the subfamily Cichorioideae s.l. (gazanias, dandelions, ironweeds: monophyletic); the subfamily Carduoideae (thistles and African Mutisieae: monophyletic), and finally there is a paraphyletic basal area of the phylogeny that contains most of what used to be the tribe Mutisieae s.l. (*Gerbera* daisies) whose former members are now in 15 tribes (Funk et al. 2009). Throughout its history *Eriachaenium* has been placed in three tribes in the subfamily Asteroideae and one in the basal grade; *Adenocaulon* has previously resided in six tribes in the Asteroideae and two in the basal grade.

Unlike many taxa that are difficult to place, *Eriachaenium* is rarely discussed or debated. Perhaps its remote location (endemic to Patagonia; Fig. 3) or the fact that it is monospecific (*Eriachaenium magellanicum* Sch. Bip) and relatively rare, has fostered this lack of attention. This small herb has an unusual compressed underground stem and staminodes in the marginal florets (Figs 1, 2). The species was described by Schultz Bipontinus (1855) who placed it near *Osteospermum*, an African genus in an almost exclusively African tribe (Asteroideae: Calenduleae). Although today this placement is difficult to understand it was probably based on the long corolla lobes and short anther bases. Bentham (1873) and Hoffman (1894) did not disagree with this placement and there it remained until Cabrera (1961) in his key to the Argentine genera of Asteraceae moved it to the Inuleae (Asteroideae) without comment, but in the subtribe Adenocaulinae along with *Adenocaulon*. Gray described Adenocaulinae (1873) but included only the type. *Eriachaenium* was left in the Inuleae by Muñoz Pizarro (1966) as well as Moore (1983). Robinson and Brettell (1973) moved the genus to the Mutisieae s.l., based mainly on pollen characters and Bremer (1994) put the genus in the Mutisieae subtribe Nassauviinae (now tribe Nassauvieae). *Eriachaenium* was not included in recent molecular phylogenies such as Funk et al. (2005), Panero and Funk (2008), Funk et al. (2009, 2014).

Adenocaulon has five species that grow in temperate forests (Fig. 4A) in four widely disjunct areas (Fig. 3): Northwest USA and adjacent Canada (1 species), East Asia (2), Mesoamerica (1), and Patagonia (1) (Bittman 1990a, b). In contrast to *Eriachaenium*, *Adenocaulon* has received quite a bit of attention possibly because it is more widespread and most of its taxa are found in areas with numerous botanists. These various studies have moved the genus from tribe to tribe; in fact, over the years it has been placed in eight tribes. Along with a few other genera, *Adenocaulon* was unplaced to tribe by Bremer (1994). The various placements are as follows:

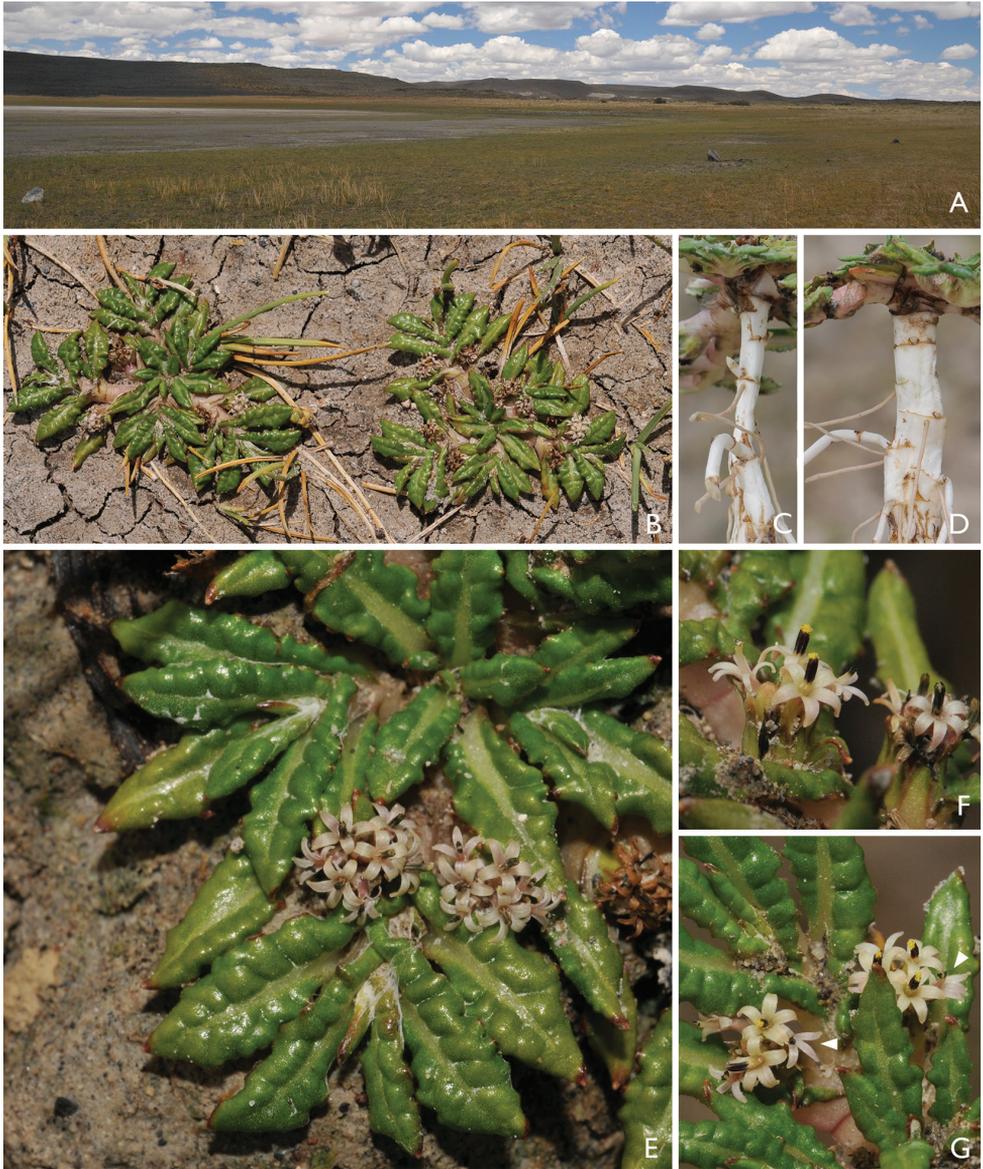


Figure 1. *Eriachaenium*. **A** General habitat, muddy shores of temporal lakes; central Chubut (Argentina) **B** Habit detail; notice stems adpressed to the ground **C** Lateral view of rhizome **D** Dorsal view of rhizome; compare with C and note the flattened nature of rhizome **E** Close up of leaves, note the bullate condition. **F** Detail of heads **G** Detail of heads; arrows point marginal florets. (Photos by M. Bonifacino)

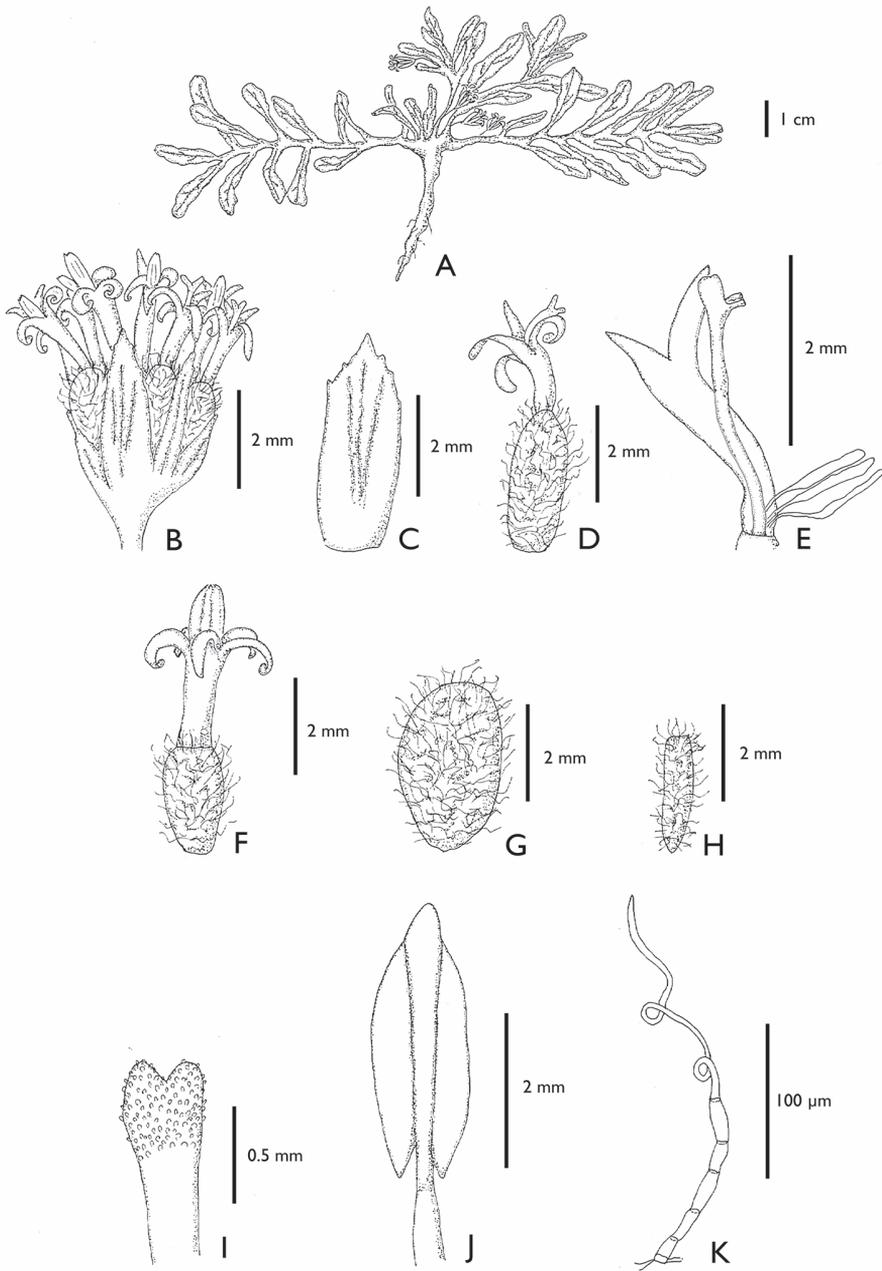


Figure 2. *Eriachaenium magellanicum* (from Katinas 2000). **A** habit **B** head **C** involucral bract **D** marginal floret **E** marginal floret opened showing the staminodes **F** central floret **G** marginal achene **H** central achene **I** upper part of style **J** stamen **K** cypselid hair flagellate, filiform. (*E. magellanicum*: **A** Birabén and Birabén 242 LP; **B–F, I–K** Sleumer 908 LP; **G–H** LP *s.n.* ex LPS 13745)

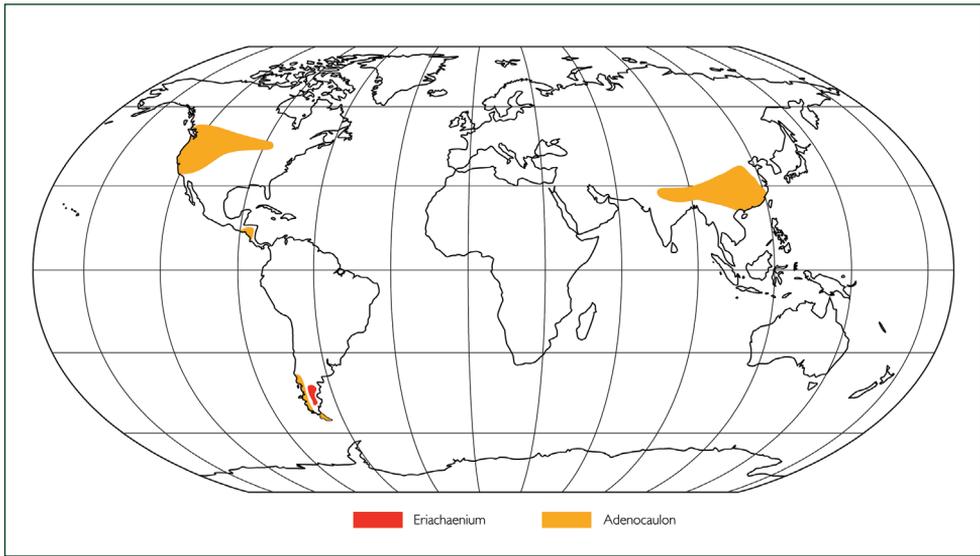


Figure 3. Map showing distribution of *Eriachaenium* and *Adenocaulon*.

(1) EUPATORIEAE: Edgeworth (1851); (2) HELIANTHEAE s.l. (in tribe Millerieae): Bentham and Hooker (1873), followed by Gardner (1977); (3) INULEAE: Gray (1873, as the separate subtribe Adenocaulinae), followed by Hoffmann (1894), Britton and Brown (1943), Cabrera (1961, 1971), Muñoz Pizarro (1966), Merxmüller (1977), and Moore (1983); (4) ADENOCAULEAE: Rydberg (1917), monogeneric; (5) SENECEONEAE: Cronquist (1955), followed by Wagenitz (1964), and Morton (1978); (6) ANTHEMIDEAE: Stix (1960), followed by Leins (1968), and Skvarla et al. (1977); (7) MUTISIEAE: Stebbins as quoted in Ornduff et al. (1967), followed by Nordenstam (1977), Bittman (1990a,b), Bremer (1994), Jansen and Kim (1996), Panero and Funk (2008); Katinas et al. (2008) and (8) CARDUEAE: Maximova (1999).

Cabrera (1961) and Katinas (2000) were the only ones to consider the two genera together. Cabrera (1961) published a key to the genera of Asteraceae of Argentina and, probably following the classification of Gray (1873) who placed *Adenocaulon* in the subtribe Adenocaulinae of the tribe Inuleae. Cabrera (1961) accepted that placement and also included *Eriachaenium* in the subtribe. Katinas (2000) conducted a cladistic analysis using 38 morphological characters and 52 genera from across the family to investigate whether or not *Adenocaulon* and *Eriachaenium* were closely related to one another and to determine a tribal assignment for the two genera. Her study showed that the two genera were closely related based on sharing four characters: 1) involucre bracts in 1–2 series, 2) length/width ratio of anthers was 2.5–4.5, i.e., very small; this

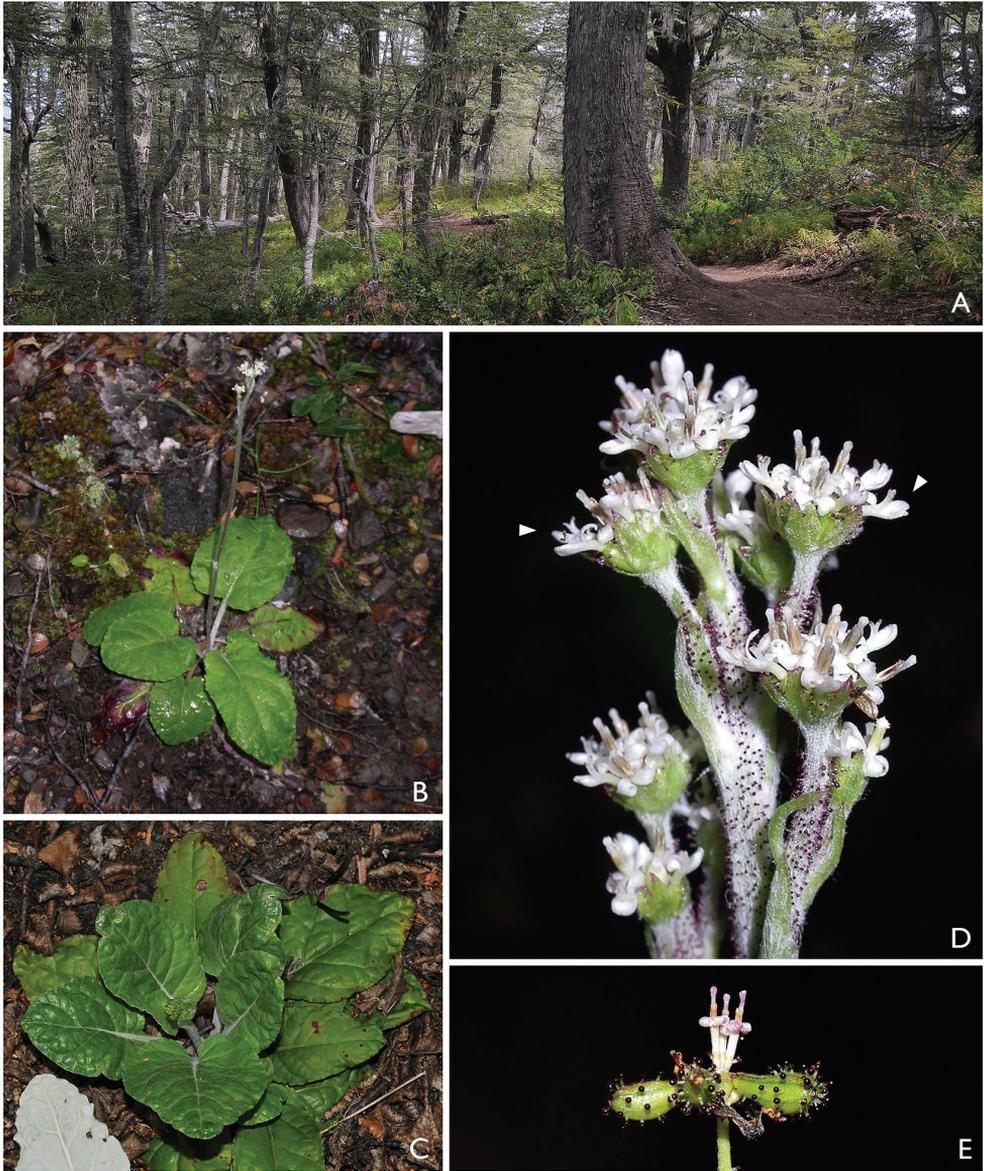


Figure 4. *Adenocaulon*. **A** Habitat, understory of *Nothofagus* dominated forest (Araucanía Region, Chile) **B** Habit **C** Close up of rosette, note the bullate leaves **D** Close up of heads; arrows indicate marginal florets, note the conspicuous glandular trichomes on peduncles and other parts of the inflorescence **E** Close up of fruiting head; note the same trichomes on fruits. (Photos by M. Bonifacino)

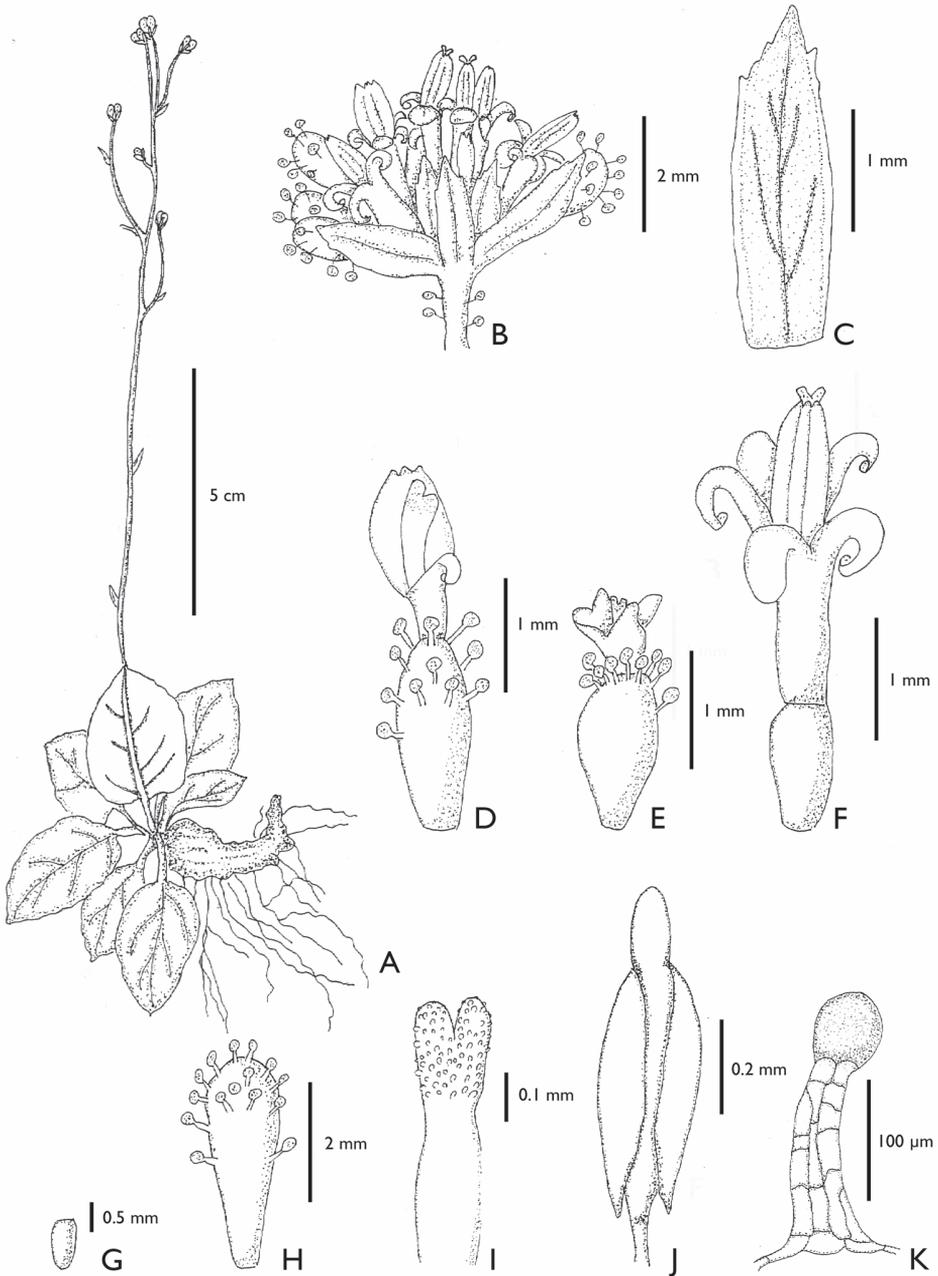


Figure 5. *Adenocaulon* (from Katinas 2000). **A** habit **B** head **C** involucral bract **D–E** marginal florets **F** central floret **G** central achene **H** marginal achene **I** upper part of style **J** stamen **K** achene hair multiseriate, capitate, glandular. (*A. chilense*: **A** LP s.n. ex LPS 16554; **B–D, F** Cabrera et al. 23066 LP; **G–H** Riccardi et al. 1983 LP. *A. bicolor*: *E* Hedgcock s.n. LP, **I–K** Morrison 121 LP)

ratio was only found in members of Anthemideae, 3) the lack of a pappus (characters that are found in other parts of the phylogeny), and 4) a re-occurrence of the plesiomorphic short bifid style. As far as placement in the family, Katinas results showed that ‘floret dimorphism’ and ‘pseudobilabiate florets shared with Anthemideae, *Adenocaulon* and *Eriachaenium* that are female or neuter and the tubular and/or pseudobilabiate florets’ place them above the Mutisieae and Cardueae. Also they share two synapomorphies, ‘floret dimorphism’ and ‘marginal florets female or neuter’, that group them with the Liabeae, Arctotideae, and Asteroideae. The placement of the two genera was determined to be (in today’s classification) in the Cichorioideae (s.s.) above the Lactuceae/Vernonieae clade and the sister group of the Liabeae. This was yet another new position for both of these genera. *Adenocaulon* was included in the chloroplast DNA phylogenies of Panero and Funk (2008) and Funk et al. (2009) and placed in the Mutisieae s.s. but the generic representation from the Mutisieae s.s. was not extensive and *Eriachaenium* was not included.

In order to ascertain the best placement for *Eriachaenium* and *Adenocaulon* and to test the proposed sister group relationship between the two genera we used a molecular approach that included species of both taxa and a wide sampling of outgroups. In 2009, the members of a collecting expedition to Patagonia located populations of *Eriachaenium* and *Adenocaulon* (*A. chilense* Less.) and this fresh material combined with two additional herbarium specimens (*Adenocaulon*: *A. bicolor* Hook., and *A. lyratum*) has allowed us to fully discuss these two genera and to provide an estimate on where they should be placed in the phylogeny of the family.

Materials and methods

We sequenced the nuclear ITS and the plastid molecular markers *trnL-trnF* and *rpl32* of two different populations of *Eriachaenium magellanicum*, one each of *Adenocaulon chilense*, *A. lyratum* and *A. bicolor*, the sequences are deposited in GenBank and the numbers will be included in Pasini et al. (MS submitted). These data were shared with the authors of a separate study that encompassed a broad selection of taxa from the Mutisioideae and related tribes (Pasini et al. MS submitted) in order to determine the proper placement for these problematic genera. The molecular dataset contained species of the three tribes of the subfamily Mutisioideae (Mutisieae—8 genera, 21 species, Onoserideae—four genera, four species, and Nassauvieae—13 genera, 25 species) and four species of the subfamily Barnadesioideae. These data contain new sequences generated for the Pasini et al. (MS, submitted) as well as sequences from GenBank generated for several publications (Katinas et al. 2008; Simpson et al. 2009; Baird et al. 2010; Funk et al. 2014).

Details of the sampling strategy, DNA extraction, amplification, and sequencing methods and data analysis discussion are included in the Pasini et al. paper (MS, submitted). Here we show a part of the final cladogram that highlights the placement of *Eriachaenium* and *Adenocaulon* (Fig. 6).

Results and discussion

Phylogeny

The results of all three datasets, the *matK*, the combined ITS-trnL-F, and the total combined show *Eriachaenium* and *Adenocaulon* forming a clade nested in the Mutisieae s.s. (Fig. 6). The support values of the clade formed by these two genera are high (Bayesian inference of 1) but the relationships among the three species of *Adenocaulon* sampled in the analysis and *Eriachaenium magellanicum* are not clear. Here we show a section of the phylogeny (Fig. 6) for the purpose of facilitating the discussion in this paper. For the complete phylogeny based on the combined ITS, *trnL-F*, *matK*, and *trnL-rpl32* markers see Pasini et al. (MS, submitted).

Morphology

Most of the confusion in the placement of *Eriachaenium* and *Adenocaulon* is caused by a lack of understanding of character evolution within the family complicated by the fact that the characters that were most often used to define the Mutisieae s.l. are often missing or modified in both genera. Now that *Eriachaenium* and *Adenocaulon* form a clade nested in the tribe Mutisieae s.s. (Mutisioideae) we can re-examine the morphology of the two genera and how their characters fit with those of the Mutisieae s.s.

Prior to the advent of molecular data, the Mutisieae s.l. were considered to be highly derived because some were humming bird pollinated and many had some form of colorful and/or dimorphic corollas (especially bilabiate or pseudo-bilabiate), long tails on the anthers, short bifid styles often with a rounded apex, and psilate or microechinate pollen. Later characters such as anthemoid (ecaveate) pollen (Ornduff et al. 1967, Robinson and Brettell 1973), testa epidermis type (Grau 1980); chromosome number ($n = 23$; Ornduff et al. 1967), and “thickened apical appendage on anthers” and “obtuse-rounded style hairs” (Bremer 1994), were added to the list. These were thought to be derived characters because they were uncommon in the family and restricted, for the most part, to South American taxa, and because it was commonly believed by many taxonomists that studied the Compositae that the Heliantheae s.l. represented the ancestral morphology. Since the groundbreaking work of Jansen and his co-authors (Jansen et al. 1987, 1990, 1991, 1996) and subsequent contributions by Panero and Funk (2008) and Funk et al. (2009) we now know that the Mutisieae s.l. are actually a number of independent lineages strung out along the basal area of the phylogeny; some are even part of the thistle subfamily (Carduoideae) or independent lineages (Pertyeae; Pertyoideae).

Within the latest classification the tribe Mutisieae s.s. falls into the subfamily Mutisioideae with two additional tribes: Onoserideae, Nassauvieae. This more restricted version of the tribe is defined by the presence of many of the same characters mentioned above because many of the taxa that lack those characters are now placed elsewhere.

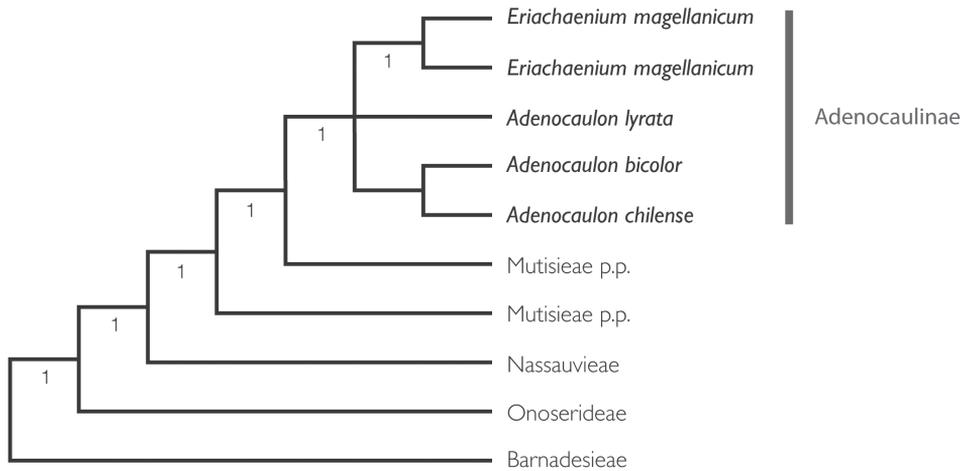


Figure 6. Simplified phylogeny showing placement of *Eriachaenium* and *Adenocaulon*.

However, as Katinas et al. (2008) correctly pointed out, some of these characters are found in other tribes. *Eriachaenium* and *Adenocaulon* have some of these characters (dimorphic corollas; short bifid styles with a rounded apex; microechinate, ecavate pollen) but lack others (colorful corollas, long tails on anthers). While *Adenocaulon* has bilabiate corollas, *Eriachaenium* does not, however it does have a variable number of corolla lobes (4 or 5) so technically they both have dimorphic corollas.

Pollen and chromosome numbers

The pollen grains of *Eriachaenium* and *Adenocaulon* (Fig. 6) are very similar to one another differing only in the size of the grain and the thickness of the exine and both genera have some grains with a compact aspect and Anthemoid pattern (see also Skvarla et al. 1977; Bittmann 1990a). A study by Zhao et al. (2006) has the only SEM images that show the exine structure that we know of for both genera and they appear to be of the standard pollen type for the Mutisioideae. *Adenocaulon* and *Eriachaenium* have pollen of medium size ($P \times E = 26\text{--}32 \times 26\text{--}30 \mu\text{m}$ in *Adenocaulon*, and $30\text{--}36 \times 24\text{--}30 \mu\text{m}$ in *Eriachaenium*), are tricolporate, with the colpi long with thin margins and a microgranulate membrane and a diffuse mesoaperture (Katinas et al. 2008). Both genera have a *Mutisia* type exine (Tellería et al. 2003). Overall the pollen grains of both genera are similar to that of *Artemisia verlotiorum* (Anthemideae) a condition that exemplifies one of the major problems with trying to identify unique morphological characters to define groups within the family (Hansen 1991). Ornduff et al. have a very interesting quote in their 1967 paper (page 212):

“We are not convinced that *Adenocaulon* belongs in Senecioneae where it has been placed by various workers (Ornduff et al. 1963), but the count of $n = 23$ for the very local and distinctive Central American *A. lyratum* is a report for the fourth ... member of the genus to be examined. Each species has consistently had $n = 23$... Stebbins (personal communication) has suggested that *Adenocaulon* shows affinities with Mutisieae on the basis of a common possession of distinctive pollen characters. The bilabiate tendencies of marginal corollas, the shape and pubescence of leaves, and the chromosome number of *Adenocaulon* further suggest relationships to Mutisieae....”

Taxonomy

Subtribe Adenocaulinae A. Gray, *Syn. Fl. N. Amer.* 1(2): 59. 1884 (as “Adenocaulinae”). **TYPE:** *Adenocaulon* Hook.

Description. *Herbs* perennial, dwarf or scapiform with cylindrical or planate rhizomes, stems simple, erect or prostrate to ascending, glabrous or with stipitate-glandular hairs. *Leaves* glabrous to subglabrous above, tomentose beneath; basal leaves alternate or rosulate to sub-rosulate; sessile or petiolate to pseudopetiolate; blades oblanceolate, elliptic, ovate, obovate, to deltoid, margin entire to lyrate, pinnately or palmately veined, glabrous to subglabrous above, tomentose beneath. *Inflorescences* terminal or axillar, monocephalous or laxly racemose to corymbose, pedunculate; heads heterogamous, disciform; receptacle epaleate; involucre uniseriate. *Florets* dimorphic; marginal florets female, with or without staminodes, corolla sub-bilabiate (3+1 corolla lips), tubular-funnelform, shortly to deeply 4- to 5-lobed, rarely bilabiate; central florets bisexual or male with a rudimentary ovary, corolla tubular-funnelform, deeply 5-lobed; anther apical appendages rounded to acute at the apex, basally constricted and demarcated from the thecae, basally auriculate with tails very short, smooth to slightly papillose, filament with anther collar; style shortly bifid, branches dorsally papillose. *Achenes* truncate at the apex, densely pubescent, shaggy (long, filiform, uniseriate hairs) or glandulose (glandular multiseriate capitate hairs), dimorphic, marginal cypselae conspicuously bigger than the central ones; pappus absent. Pollen spheroidal to prolate, tricolporate, exine *Mutisia* type, microechinate.

The subtribe Adenocaulinae was described by Gray (1873), on the basis of the genus *Adenocaulon*, for the tribe Inuleae. Rydberg (1917) raised the subtribe to the independent tribe Adenocaulinae, also with *Adenocaulon* as its only genus. Further, Cabrera (1961) returned to Gray's concept and re-described the subtribe Adenocaulinae for the tribe Inuleae, but this time the subtribe included the genera *Adenocaulon* and *Eriachaenium*. Despite the addition of *Eriachaenium*, no emendation of Gray's subtribe concept is needed because the short and general description of Gray includes the features common to both genera.

Key to genera

- 1 Herbs prostrate to ascending with leaves alternate; blades oblanceolate. Heads solitary. Achenes shaggy, covered by long, filiform hairs ***Eriachaenium***
 - Herbs scapiform with leaves rosulate; blades elliptic to deltoid. Heads laxly racemose or corymbose. Achenes covered by glandular hairs ***Adenocaulon***

***Eriachaenium* Sch. Bip.**

Figures 1, 2

Eriachaenium Sch. Bip. *Flora* 38: 120. 1855. TYPE: *Eriachaenium magellanicum* Sch. Bip.

Etymology. From the Greek *erion*, wool, and the Latin *achaenium*, a type of fruit, describing the villose fruits.

Description. *Herbs* perennial, dwarf, with stout, oblique to vertical rhizomes that are compressed laterally, stems prostrate to ascending. *Leaves* alternate; sessile, clasping; blades oblanceolate, pinnately veined, margin entire to undulate-dentate, glabrous to subglabrous above, tomentose beneath. *Inflorescence* monocephalous, axillar; heads pedunculate, heterogamous, disciform; receptacle epaleate; involucre uniseriate. *Florets* dimorphic; marginal florets female with staminodes, corolla tubular-funnelform, deeply 4-lobed; central florets bisexual or male with a rudimentary ovary, corolla tubular-funnelform, deeply 5-lobed; anther apical appendages rounded to acute, basally constricted and demarcated from the thecae, anthers dark, basally auriculate with tails very short, smooth to slightly papillose; style bilobed, dorsally papillose. *Achenes* truncate at the apex, densely pubescent, dimorphic, the marginal achenes conspicuously bigger than the central ones; pappus absent. [modified from Katinas et al. 2008]

Pollen spheroidal to prolate, spheroidal or elliptic in equatorial view, circular in polar view, medium size, $P \times E = (30\text{--}36 \times 24\text{--}30) \mu\text{m}$. Tricolporate, colpi long with thin margin and microgranulate membrane, mesoaperture diffuse. Exine *Mutisia* type, microechinate, 2–6 μm thick, slightly slender at the poles. Ratio ectosexine/endosexine: 1:1.5; 1:2. Nexine 1.5 μm thick. SEM: tectum punctate.

Habitat and distribution. Genus with only one species, *Eriachaenium magellanicum* Sch. Bip., endemic to Patagonia in Argentina and Chile (Fig. 3). It grows in mud, sand, and pebbles either along the margins of inland somewhat saline lakes or near the coast in estuaries (Morore 1983 and field observations).

Species list. *Eriachaenium magellanicum* Sch. Bip., *Flora* 38: 121. 1855.

***Adenocaulon* Hook., 1829**

Figures 4, 5

Adenocaulon Hook., Bot. Misc. 1: 19. 1829. TYPE: *Adenocaulon bicolor* Hook.

Etymology. From the Greek *aden*, gland, and *kaulos*, stalk, stem, describing the stalked glandular hairs.

Description. *Herbs* perennial, scapiform with stout rhizomes, stems simple, erect, with stipitate-glandular hairs. *Leaves* glabrous to subglabrous above, tomentose beneath; basal leaves rosulate to sub-rosulate; petiolate to pseudopetiolate; blades elliptic, ovate, obovate, to deltoid, margin entire to lyrate, pinnately to palmately veined; upper leaves similar to the basal ones but few and reduced. *Inflorescence* terminal, laxly racemose to corymbose, on long peduncles; heads pedunculate, heterogamous, disciform; receptacle epaleate; involucre uniseriate. *Florets* dimorphic; marginal florets female, without staminodes, corolla sub-bilabiate (3+1 corolla lips), tubular-funnelform 4- to 5-lobed, rarely bilabiate; central florets male with a rudimentary ovary, corolla tubular-funnelform, deeply 5-lobed; anther apical appendages rounded to acute at the apex, basally constricted and demarcated from the thecae, anthers light colored and basally auriculate with tails very short, smooth; style bilobed, branches dorsally papillose. *Achene* truncate at the apex, pubescent (glandular multiseriate capitate hairs), dimorphic, marginal achenes conspicuously bigger than the central ones; pappus absent. [modified from Katinas et al. 2008]

Pollen spheroidal, circular in polar view, medium size, $P \times E = (26-32 \times 26-30)$ μm . Tricolporate, colpi long with thin margin and microgranulate membrane, mesoaperture diffuse. Exine *Mutisia* type, microechinate, 4–5 μm thick, slightly slender at the poles. Ratio ectosexine/endosexine: 1:1.5; 1:2. Nexine 1.5 μm thick. SEM: tectum punctate. Note: pollen of *A. bicolor* was found to be identical to that of *A. chilense* Less.

Habitat and distribution: Genus of five species with a disjunct distribution in Patagonia, Mesoamerica, northern United States and southern Canada, and temperate southeastern Asia (Fig. 3). Inhabits moist forests in the shade of *Pinus* spp., *Quercus* spp. and *Nothofagus* spp. (Bittmann 1990a, b, and field observations). Details of the flower morphology, including the differences between the male and female flowers, can be found in Ayers (1900).

Species list: five species falling into three morphological groups that are biogeographically distinct (according to Blake 1934):

Group A: North America and East Asia

1. *Adenocaulon bicolor* Hook., Bot. Misc. 1: 19. 1830. (British Columbia to south central California, eastward to Montana and sparingly to Michigan)
Adenocaulon integrifolium Nutt.
2. *Adenocaulon himalaicum* Edgew., Trans. Linn. Soc. London 20: 64. 1851. Himalayan region and Japan
Adenocaulon adhaerescens Maxim. (described from Japan)
3. *Adenocaulon nepalense* M. Bittmann, Candollea 45: 403. 1990. Nepal

Group B: Chiapas, Mexico & Guatemala

4. *Adenocaulon lyratum* S. F. Blake, J. Wash. Acad. Sci. 24: 435 1934.

Group C: South America

5. *Adenocaulon chilense* Less., *Linnaea* 6: 107. 1831. (Southern Chile and the Magellan region)
Adenocaulon lechleri Sch. Bip.

Conclusion

Perhaps the best conclusion is to review synapomorphies for the *Eriachaenium* + *Adenocaulon* clade. With the phylogeny available we can examine the characters that group the two genera. That does not mean that none of the other species in the family or even in the Mutisioideae have these characters, it means that, when examined in the light of the phylogeny they are deemed synapomorphies for the *Eriachaenium* + *Adenocaulon* clade.

1. Within the Mutisioideae s.s. the tails are short only in *Adenocaulon* and *Eriachaenium* (Figs 2J, 5J).
2. Within the Mutisieae s.s. the anther collar is only found in *Adenocaulon* and *Eriachaenium*.
- 3 & 4. Two synapomorphies that are most likely linked are the dimorphic florets and achenes: the marginal, functionally female florets (Figs 2D, E, 5D, E) have larger achenes (Figs 2D, G, 5D, G) and the central, functionally male florets (Figs 2F, 5F) have smaller achenes (Figs 2H, 5G).
5. It is interesting to note that in these two genera the florets' dimorphism is not conspicuous, while in all the other genera of the tribe it is. In fact, within the Mutisieae s.s. there is an impressive variety of colors of the marginal florets which easily distinguishes them from the central florets. Therefore the character of "inconspicuously dimorphic florets" found in the *Eriachaenium* + *Adenocaulon* clade and not found in the Mutisieae s.s., can also be considered as a synapomorphy.
6. The presence of tubulose 4-lobed corollas in the marginal florets in both genera indicates a strong affinity between the two genera because while tetramerous central florets are common in Compositae, such corollas rarely occur as marginal ones.
7. Even though *Eriachaenium* and *Adenocaulon* have a *Mutisia* exine type of pollen, the grains are small and spheroid with a thin exine, whereas those of Mutisioideae (excluding Nassauvieae) are usually large and elliptic with a thick exine. This type of pollen grain is unique in the Mutisieae and it approaches the *Artemisia* exine type (Anthemideae).
8. Both genera lack a pappus (Figs 2D–H, 5D–H). The absence of a pappus is widespread in other tribes of Compositae (e.g., Heliantheae s.s.) but it is very rare in Mutisioideae (only found in Adenocaulinae and *Cephalopappus* and *Panphalea* of the tribe Nassauvieae).

9. Both genera have their achenes covered with unusual pubescence: *Eriachaenium* has multicellular, flagellate, filiform hairs that are confined to the achene (Fig. 2D, F–H, K) and *Adenocaulon* has multiseriate, capitate, glandular pubescence (the glands are dark purple) and this pubescence is found on other parts of the inflorescence (Figs 4D, E, 5B, D, E, H, K).
10. *Eriachaenium* and *Adenocaulon* both grow in habitats that are unusual for the family: *Eriachaenium* practically buries itself in the sandy mud (Fig. 1B, E) and when we found it, it was a few feet above the water line of some, but certainly not all, lakes/ponds in the mountains of Patagonia (Fig. 1A); *Adenocaulon* inhabits the floor of relatively moist forests (Fig. 4A–C). Both of these are rather extreme limits of the habitat for the family. Perhaps this movement into these habitats has triggered their unusual morphology.

Another potential synapomorphy is the bullate leaves found in both genera. But, more data need to be gathered to be sure of its distribution in the Mutisioideae.

We can also list some characters that we now think are plesiomorphic for the *Eriachaenium* + *Adenocaulon* clade in that they are shared with other parts of the basal grade: central corollas deeply lobed; style shortly bifid with an apex that is rounded or slightly acute; style apex shortly papillose; pollen with exine psilate or microechinate and pollen of the Anthemoid pattern. The pollen grains in *Eriachaenium* and *Adenocaulon* share features with many taxa in the Mutisioideae and with Anthemideae. However, at this point, the occurrence of the “anthemoid” pollen in the Anthemideae is considered to be independent of its occurrence in the Mutisioideae.

In future studies we hope to expand these lists as well as determine the point on the cladogram where the plesiomorphic characters are actually apomorphic.

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Coprosma kawaikiniensis (Rubiaceae) a new species from the *Dubautia-Sadleria* shrubland-fernlend community on Kaua‘i, Hawaiian Islands

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Abstract

Coprosma kawaikiniensis K.R. Wood, Lorence & Kiehn (Rubiaceae), a rare endemic tree from Kaua‘i, Hawaiian Islands, is described and illustrated along with a previously undescribed endemic plant community, the *Dubautia-Sadleria* shrubland-fernlend (DSSF). The new species differs from Hawai‘i congeners by its combination of opposite, long, elliptic to narrowly elliptic or ovate-elliptic leaves with revolute margins; caducous stipules 7–10 mm long, externally glabrous, densely hirtellous-pilose near the margins of the inner surface; unbranched inflorescences with peduncles 20–28 mm long; flowers 6–8 per cluster; and persistent calyx tube with 4–8 irregular dentate lobes. Known only from the windward slopes and ridges of southeastern Kaua‘i below the Kawaikini summit, *Coprosma kawaikiniensis* falls into the IUCN Critically Endangered (CR) Red List category.

Keywords

Rubiaceae, *Coprosma*, new species, *Dubautia-Sadleria* shrubland-fernlend, Hawaiian Islands, Kaua‘i, high endemism, Critically Endangered

Introduction

Coprosma J.R.Forst. & G.Forst., in the family Rubiaceae, is a genus of approximately 110 species of dioecious wind-pollinated shrubs or small trees widely distributed on Pacific islands, with a primary center of diversity in New Zealand (ca. 50 spp.), and secondary centers of diversity in the Hawaiian Islands (13 spp.), New Guinea (11 spp.), and Australia (8 spp.) (Wagner and Lorence 2011; Cantley et al. 2014). The remaining species are scattered over a wide area of the Pacific Basin, extending from Borneo and Java to Rapa Nui in southeastern Polynesia, and the Juan Fernández Islands (Smith 1988). There are six endemic *Coprosma* in the Marquesas Islands including three newly described by Wagner and Lorence (2011), four in the Society Islands (Welsh 1998), three in the Australs, two in Samoa, and one each in the Tuamotu Islands, Pitcairn Island, and Cook Islands.

Oliver (1935) divided the genus into seven groups, most of which were subdivided into smaller groups of presumably closely related species. He placed all southeastern Polynesian species then known into his *Coprosma pyriformis* (Hook. & Arn.) Skotts. group characterized by relatively large, usually obovate to ovate leaves with finely reticulate venation, entire to denticulate triangular stipules, male flowers in small clusters with a calyx present, and three female flowers per cluster, the calyx lobes as long as or shorter than the tube, and fruit red or orange. He hypothesized that this group was related to similar species in New Zealand. Florence (1986) described two new Marquesan species and suggested they and the one other known Marquesan species were allied with the orange-fruited Hawaiian species. Although Heads (1996) included no Polynesian *Coprosma* species in his sparse sampling of the genus, he supported Florence's hypothesis by placing the three known Marquesan species in a group along with the Hawaiian species, rather than the *C. pyriformis* group where all of the other southeastern Polynesian species were placed. A molecular study of Tribe Anthospermeae (Anderson et al. 2001), in which 6 of 16 of the taxonomic groups recognized by Heads (1996) were sampled, indicates an apparent Australian origin of *Coprosma* and possible independent colonization of Fiji and Hawaiian Islands from New Zealand. Based on molecular phylogenetic analyses of ITS and ETS regions Cantley et al. (2014) provided new biogeographic insights into Pacific *Coprosma* species. Their analyses suggest two independent colonizations of *Coprosma* to the Hawaiian Islands. The majority (12) of the 13 Hawaiian species form a monophyletic group closely related to red- and orange-fruited species from the Marquesas and Austral Islands, whereas the single black-fruited species (*C. ernodeoides* A.Gray) represents a separate colonization to Hawai'i from an unknown origin, perhaps New Zealand or Tasmania (Wagner and Lorence 2011). This view is also corroborated by the fact that *C. ernodeoides* is a very high polyploid ($2n \geq 220$), whereas all other cytologically investigated Hawaiian taxa are tetraploids with $2n = 44$ chromosomes (Kiehn 2005). The discovery and publication of *C. kawaikiniensis*, a member of the red- and orange-fruited group, now brings the number of Hawaiian *Coprosma* species to 14.

Methods

All measurements and descriptions were taken from dried herbarium specimens or from notes made in the field and are presented in the descriptions as follows: length × width, followed by units of measurement (mm or cm).

Taxonomic treatment

Coprosma kawaikiniensis K.R. Wood, Lorence & Kiehn, sp. nov.

urn:lsid:ipni.org:names:77152891-1

Figs 1, 5

Diagnosis. Differs from Hawai'i congeners by its combination of opposite, long, elliptic to narrowly elliptic or ovate-elliptic leaves with revolute margins; caducous stipules 7–10 mm long, externally glabrous with dense hirtellous-pilose hairs near the margins of the inner surface; unbranched inflorescences with peduncles 20–28 mm long; flowers 6–8 per cluster; and persistent calyx tube with 4–8 irregular dentate lobes.

Type. USA. Hawai'i. **Kaua'i:** Lihue District, ridge below Kawaikini, Ioli headwaters, 26 Aug 1999, K.R. Wood & M. Query 7978, (holotype: PTBG-050238; isotypes (to be distributed): BISH, MO, P, US, WU).

Description: *Trees* 2–4 m tall, dioecious, bark grey-brown, trunk with branches or knobby protuberances; branchlets glabrous, light brown, 3–4 mm diam., nodose with leaf and stipule scars. *Leaves* opposite, decussate, glabrous, blades elliptic to narrowly elliptic or ovate-elliptic, 40–76 × 11–22(–26) mm, pinnately veined with 8–10 pairs of secondary veins, higher level venation conspicuously reticulate, occasionally impressed adaxially, small pit domatia often present located abaxially along midrib near juncture with secondary veins, sometimes absent, margins slightly revolute, apex acute, base attenuate and decurrent; petioles 5–11 mm long, narrowly winged distally, purple-brown; stipules 7–10 mm long, connate for 1/3–1/2 of their length into a cylindrical sheath (1–)2–4 mm long, free apical portion (3–)4–6 mm long, acuminate to a conspicuous, thickly carinate-subulate apex with a claw-like appendage, externally glabrous, internally densely hirtellous-pilose distally, sheath margins with shortly ciliate fringe and sometimes a few short callous protuberances or glandular appendages 0.1–0.2 mm long, as long as the ciliate hairs. *Inflorescences* axillary, mostly simple and capituliform, subtended by a pair of connate, broadly ovate bracts, 6–8-flowered, peduncles 20–35 mm long, or rarely bearing an additional peduncle with one additional pair of subsessile, 3–5-flowered cymules subtended by connate, broadly ovate bracts 2–3 × 2–3 mm with ciliate margins. *Flowers:* staminate flowers mostly in groups of 6–8 on peduncles 20–28 × 0.7–0.8 mm, subtended by a pair of connate, broadly ovate bracts 2–3 × 2–3 mm with ciliate margins; flowers subsessile, the calyx cup-shaped, irregularly (4–)8-lobed, cup 0.8–1 mm long, the lobes 1–2.2 × 0.8–1.5 mm, apex entire



Figure 1. *Coprosma kawaikiniensis* K.R.Wood, Lorence & Kiehn, sp. nov. (holotype: PTBG).

or irregularly 2–4-dentate, glabrous or sparsely hirtellous; corolla (only seen in bud) glabrous, 6–6.5 mm long, the tube 2–3 mm long, 4–5-lobed, the lobes 3.5–4 mm long, stamens 8, the staminal filaments 1.5–2 mm long, the anthers 3.6–4 mm long, apex acuminate, base sagittate, the pistillode 2.5 mm long. Female flowers and inflorescence not seen. **Infructescences** with peduncle 20–28 mm long, flattened, fruits in terminal cluster of 3–6 subtended by cupuliform pair of connate bracts 2–3 × 2–2.5 mm, margins ciliolate; fruits orange when fresh, broadly ellipsoid to broadly obovoid, 5.5–6 × 4.5–5 mm, glabrous, surface drying wrinkled, weakly 4-ribbed, apex with persistent irregularly lobed calyx 1.5 mm long. **Pyrenes** 2, broadly ellipsoid to broadly obovoid, plano-convex, 5.7–6 × 4.1–4.5 mm, brown, with low dorsal ridge in distal 1/3–1/2.

Phenology. To date, *Coprosma kawaikiniensis* has been observed in flower during early April, and with fruit from late August to mid-September.

Etymology. The new species is named after the holotype locale, Kawaikini, the highest peak on Kaua‘i and one of the rainiest places on earth (Juvik and Juvik 1999). Literally, Kawaikini means “the multitudinous waters” in Hawaiian (Pukui et al. 1974).

Distribution and ecology. The volcanic island of Kaua‘i is the oldest of the main high Hawaiian Islands (ca. 5 Ma) featuring a physical geography that is quite variable with deeply eroded drainages, well-defined canyons, and tall coastal seacliffs. It is also the most floristically rich Hawaiian Island (Wagner et al. 1990, Imada 2012) exemplified by high levels of habitat diversity and endemism, which includes ca. 244 single island vascular plant endemics (Wood 2015). Careful botanical research conducted over the last few decades by staff of the National Tropical Botanical Garden (NTBG), especially around cliffs and remote regions, has contributed 32 new published plant taxa from Kaua‘i (Imada 2012).

The recent discovery of *Coprosma kawaikiniensis* was made around extremely steep, narrow wind swept ridges, slopes, and boulder strewn stream banks below Kawaikini, the highest peak on Kaua‘i which summits at 1598 m elevation (Figures 2–4). This particular habitat is the remotest of Kaua‘i’s eco-regions and can be further characterized by its mist-shrouded, dark, narrow basalt canyon walls seeping with springs, and having the distinction of being one of the rainiest places in the world (Juvik and Juvik 1998). The holotype region represents a previously undescribed plant community dominated by two Hawaiian endemic genera, namely *Dubautia* Gaudich. (Asteraceae) and *Sadleria* Kaulf. (Blechnaceae), referred to as the *Dubautia-Sadleria* shrubland-fernland (DSSF) community (Wood 2013; Figures 2, 3). To date, fewer than 50 individuals of *C. kawaikiniensis* have been documented, occurring in elevations between 1035 to 1350 m.

The DSSF community is predominantly low-statured at 1–2(–4) m tall and is composed of several species of *Dubautia* including *Dubautia imbricata* H.St.John subsp. *acronaea* G.D.Carr, *D. knudsenii* Hillebr. subsp. *nagatae* (H.St.John) G.D.Carr, *D. laxa* Hook. & Arn. subsp. *hirsuta* (Hillebr.) G.D.Carr, *D. paleata* A.Gray, *D. railardioides* Hillebr., and on rare occasions *D. pauciflorula* H.St.John & G.D.Carr. The four species of *Sadleria* that also dominate this community are *Sadleria cyatheoides*



Figure 2. Landscape habitat where *Coprosma kawaikiniensis* was discovered below Kawaikini, Kaua'i, showing rugged terrain and the *Dubautia-Sadleria* shrubland-fernland (DSSF) community.

Kaulf., *S. pallida* Hook. & Arn., *S. souleyetiana* (Gaudich.) T.Moore, and occasionally *S. squarrosa* (Gaudich.) T.Moore.

Some of the more common herbs, shrubs and trees, the latter depauperate in physical stature, of the DSSF community include *Antidesma platyphyllum* H.Mann var. *hillebrandii* Pax & Hoffm., *Astelia argyrocoma* A.Heller ex Skottsbo., *Bidens forbesii* Sherff, *Broussaisia arguta* Gaudich., *Coprosma kauensis* (A.Gray) A.Heller, *Ilex anomala* Hook. & Arn., *Pritchardia hardyi* Rock, *Syzygium sandwicensis* (A.Gray) Nied., along with several to numerous species of *Cheirodendron* Nutt. ex Seem., *Cyanea* Gaudich., *Cyrtandra* J.R.Forst. & G.Forst., *Labordia* Gaudich., *Kadua* Cham. & Schldtl., *Lobelia* L., *Melicope* J.R.Forst. & G.Forst., *Metrosideros* Banks ex Gaertn., *Myrsine* L., *Peperomia* Ruiz & Pav., *Pipturus* Wedd., *Platydesma* H.Mann, *Polyscias* J.R.Forst. & G.Forst., *Psychotria* L., *Scaevola* L., and *Vaccinium* L.

Common sedges and grasses of the DSSF are *Cyperus sandwicensis* Kükenth., *Eragrostis grandis* Hillebr., *Gahnia vitiensis* Rendle subsp. *kauaiensis* (Benl) T.Koyama, *Machaerina angustifolia* T.Koyama, *Panicum lineale* H.St.John, along with several species of *Dichantheium* (Hitchc. & Chase) Gould.

Besides the dominant *Sadleria*, there are a number of other common associated ferns found in the DSSF such as *Cibotium glaucum* (Sm.) Hook. & Arn., *Dicranopteris linearis* (Burm.f.) Underw., *Diplopterygium pinnatum* (Kunze) Nakai, *Sphenomeris chinensis* (L.) Maxon ex Kramer, as well as several species of *Adenophorus* Gaudich., *Asplenium* L., *Dryopteris* Adans., *Elaphoglossum* Schott, and *Hymenophyllum* Sm.



Figure 3. The *Dubautia-Sadleria* shrubland-fernland (DSSF) community below Kawaikini, Kauaʻi.

Kaua`i

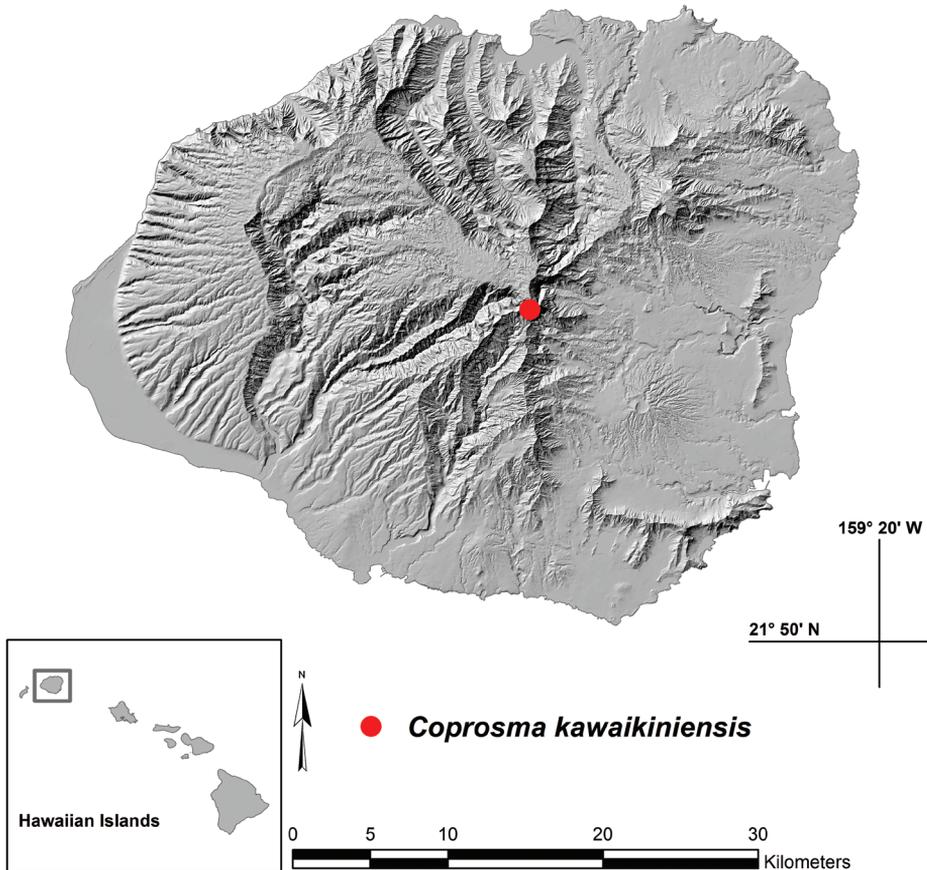


Figure 4. Map showing location of *Coprosma kawaikiniensis* near Kawaikini summit, Kaua`i, Hawai`i.

Plant communities of the nearby surrounding region are all montane windward wet habitat associations. Open bogs occur in scattered locations along the main upper headwater ridge line and are dominated by genera such as *Metrosideros*, *Rhynchospora* Willd., *Dichantheium*, *Gabnia* J.R.Forst. & G.Forst., *Machaerina* Vahl, *Plantago* L., *Viola* L., and *Oreobolus* R.Br. Several very rare species associated with bogs and bog margins were also discovered, namely *Keyseria helenae* (C.N.Forbes & Lydgate) Cabrera and *Lysimachia venosa* (Wawra) H.St.John, a member of the Primulaceae family undocumented since 1911 (Wood 2013). Occasional stands of *Metrosideros-Cheirodendron* forest with low-statured canopies of 5–7 m also occur in a mosaic of random patches surrounding the DSSF community, and *Coprosma kawaikiniensis* has also been observed ranging into this habitat. These forests are usually dominated by a significant diversity of mixed understory associates very similar to that of the DSSF. The ripar-

ian regions that dissect these relic *Metrosideros-Cheirodendron* forests and form the headwater drainages that feed the respective lower elevation valleys retain a flourishing treasure trove of rare plant taxa along nearby stream banks, including endangered species of *Cyanea*, *Cyrtandra*, *Hesperomannia* A.Gray, *Isodendrion* A.Gray, *Labordia*, *Melicope*, *Phyllostegia* Benth., *Platydesma*, and *Polyscias*.

Vegetation cover on several nearby steep slopes is composed of just a few species of matting ferns (i.e., *Dicranopteris linearis*, *Diplopterygium pinnatum*, and *Sticherus owhyhensis* (Hook.) Ching) and may be the resulting succession of past landslides. Vertical wet cliff communities of sedges, herbs, and ferns, accentuated with numerous waterfalls form the prevalent back-drop that tower over and surround these habitats below Kawaikini (Wood 2014) (Figure 2).

The holotype region of *Coprosma kawaikiniensis* has very few non-native plants and animals, however, *C. kawaikiniensis* is susceptible to catastrophic extinction through environmental events such as hurricanes, landslides, and flash floods in addition to the incursion of threats from nearby regions. Native habitats in the adjacent lower elevation regions, especially below 730 m, are intensely threatened by habitat degradation from feral goats (*Capra hircus* L.) and pigs (*Sus scrofa* L.), predation of seeds by rats (*Rattus rattus* L. and *R. exulans* Peale), and competition with non-native plant taxa, especially *Axonopus fissifolius* (Raddi) Kuhlman., *Blechnum appendiculatum* Willd., *Buddleia asiatica* Lour., *Clidemia hirta* (L.) D.Don, *Cyperus meyenianus* Kunth, *Erigeron karvinskianus* DC., *Juncus planifolius* R.Br., *Melastoma septemnerium* Lour., *Paspalum conjugatum* P.J.Bergius, *Psidium cattleianum* Sabine, *Rhodomyrtus tomentosa* (Aiton) Hassk., *Rubus rosifolius* Sm., *Sacciolepis indica* (L.) Chase, and *Sphaeropteris cooperi* (Hook. ex R.Muell.) R.M.Tryon. These highly invasive weeds possess the ability to spread rapidly (Smith 1995) and have begun to ingress into the upper watershed habitats of *C. kawaikiniensis* (Wood 2014).

Conservation status. *IUCN Red List Category.* When evaluated using the World Conservation Union (IUCN) criteria for endangerment (IUCN 2001), *Coprosma kawaikiniensis* falls into the Critically Endangered (CR) category, which designates this species as facing a very high risk of extinction in the wild. Our formal evaluation can be summarized by the following IUCN hierarchical alphanumeric numbering system of criteria and subcriteria: CR B1ab(i,ii,iii,v)+2ab(i,ii,iii,v); C2a(ii); D; which reflects a severely limited Extent of Occurrence (EOO) and Area of Occupancy (AOO) of less than 3 km² and a population of less than 50 individuals.

Discussion. All species of *Coprosma* from Kaua'i have stipules shorter than 4.5 mm except for *C. kawaikiniensis* and *C. kauensis*. The features distinguishing those two species are the number of the flowers per partial inflorescence [6–8, sometimes with an additional pair of 3–5 flowered cymules in *C. kawaikiniensis* vs. 3(–5) flowered in *C. kauensis*], the length of the calyx in staminate flowers (1.8–3.2 mm in *C. kawaikiniensis* vs. 0.4–0.6 mm in *C. kauensis*), the length of the staminate peduncle (20–28 mm in *C. kawaikiniensis* vs. 4–8 mm in *C. kauensis*), the pubescence of the stipules (externally glabrous in *C. kawaikiniensis* vs. densely strigose on both surfaces in *C. kauensis*), and the number and form of the stipular appendage(s) [only 1 terminal



Figure 5. Stipules and petiole bases of *Coprosma kawaikiniensis* (**A** Wood 3539, paratype PTBG) and *C. kauensis* (**B** Perlman 18645, PTBG). Scale bars in mm.

claw-like appendage and occasionally a few short, rounded appendages or callous protuberances 0.1–0.2 mm long c. equaling the ciliate marginal hairs in *C. kawaikiniensis*, vs. (3–)5–7(–8) pairs of thickly ovoid to digitate, shiny dark brown-black marginal appendages 0.3–0.5 mm long in *C. kauensis*] (Figure 5).

Species of *Coprosma* that have stipules of 4.5 mm or greater from the remaining Hawaiian Islands include: *C. longifolia* A.Gray, *C. ternata* W.R.B.Oliv., *C. rhynchocarpa* A. Gray, *C. montana* Hillebr., and *C. ochracea* W.R.B.Oliv. *Coprosma kawaikiniensis* differs from *C. longifolia* and *C. ternata* in having opposite vs. usually ternate leaves (with only occasionally opposite leaves on some stems). *Coprosma kawaikiniensis* has peduncles 20–28 mm long vs. 2.5–16 mm long in *C. rhynchocarpa* and only 0–1(–4) mm long in *C. ochracea*. The new species differs from *C. montana* in having 6–8 flowers per cluster, sometimes with an additional pair of 3–5 flower cymules vs. 1–2 per cluster. In terms of morphology, *C. kawaikiniensis* most closely resembles *C. longifolia* (Oahu), but differs from the latter in having opposite vs. usually ternate leaves, stipules with a shorter sheath (1–)2–4 mm long, and free apical portion (3–)4–6 mm long terminated by a thickly carinate-subulate apex with a claw-like appendage, vs. sheath 7–9 mm long and free apical part 2–3 mm long with short-attenuate, acute tip.

The following couplets can be inserted into the existing key to Hawaiian *Coprosma* by Wagner et al. (1990: 1123) to accommodate *C. kawaikiniensis*.

- 4(2) stipules 4.5–11(–15) mm long..... **5**
- 4 stipules 1.5–4 mm long **9**
- 5(4) Staminate calyx 1.8–3.2 mm long; staminate corolla lobes ca. 3.5–6 mm long **5a**
- 5 Staminate calyx 0.4–2 mm long; staminate corolla lobes 2–4.5 mm long ... **6**
- 5a(5) Staminate calyx ca. 3 mm long; staminate corolla lobes ca. 5–6 mm long; pistillate calyx urceolate, 2–4 mm long, enlarging to 5–10 mm long in fruit; H..... **11. C. rhynchocarpa**

- Staminate calyx ca. 1.8–3.2 mm long; staminate corolla lobes 3.5–4 mm long; pistillate calyx unknown, but not enlarging in fruit; K.....
 **14. *C. kawaikiniensis***
- 6(5) Stipule margins without appendages except 1 at apex, short-ciliate, base puberulent; flowers 1–2 per cluster; usually subalpine, above 1,830 m, EM, H. .
 **8. *C. montana***
- (6) Stipule margins with conspicuous appendages, but often obscured by pubescence in *C. ochracea*, and sparsely ciliate, pilose, or long-hirsute to short-hirsute, base strigose, appressed or spreading hirsute, short-hirsute, pilose or glabrous; flowers 3–6 per cluster **7**
- 7(6) Peduncles 0–1 mm long **9. *C. ochracea***
- 7 Peduncles 4–28 mm long **7a**
- 7a(7) Staminate calyx 1.8–3.2 mm long..... **14. *C. kawaikiniensis***
- 7a Staminate calyx 0.4–1 mm long..... **8**

Additional specimens examined (paratypes). United States of America. Hawai‘i. Kaua‘i: Lihu‘e District, ridge running south of Kawaikini, above Ililiula and Ioli drainage, 1035 m elev., 19 Sep 1994, *K.R. Wood, P. Wood, S. Perlman 3539*, (BISH, PTBG, US); ridge just south below Kawaikini, 1130–1350 m elev., 03 Apr 2013, *K.R. Wood 15460* (BISH, PTBG, US); loc. cit., 03 Apr 2013, *K.R. Wood 15463* (PTBG, US, WU).

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New and resurrected Hawaiian species of pilo (*Coprosma*, Rubiaceae) from the island of Maui

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Abstract

Two species of *Coprosma* (Rubiaceae) J.R.Forst. & G.Forst. are described from the island of Maui of the Hawaiian Archipelago. A newly described taxon, *Coprosma cordicarpa* J.Cantley, Sporck-Koehler, & M.Chau, **sp. nov.** is locally common in medium to high elevation dry forests and shrublands of leeward East Maui. The second taxon is resurrected from the synonymy of *C. foliosa* A.Gray as *C. stephanocarpa* Hillebr. and occurs in mesic to wet rainforests of both East and West Maui. Both taxa are segregated from *C. foliosa*, with which they share similar morphological characters. A conspicuous and persistent calyx of the fruit and various floral characters most easily differentiate both taxa from other Hawaiian taxa. The newly described *Coprosma cordicarpa* is further distinguished from *C. stephanocarpa* by a central constriction of the fruit with a depressed apex, which gives it a characteristic heart shape. Furthermore, the taxa are largely separated phenologically, ecologically, and geographically. Descriptions, conservation status, and specimens examined for the new species are included.

Keywords

Auwahi, *Coprosma*, *Coprosma cordicarpa*, *Coprosma stephanocarpa*, East Maui, Haleakalā, Hawaiian Islands, Kanaio, Maui, pilo, Rubiaceae, West Maui

Introduction

There are more than 110 species in the genus *Coprosma* J.R. Forst. & G.Forst., which consists of species that are predominantly dioecious and wind pollinated. Species range in habit from trailing woody plants to large trees and produce many various colored fruits (e.g. black, blue, orange, red, yellow, and translucent), which are most often two-seeded drupes. The genus is Oceanic in distribution with a primary center of diversity in New Zealand (ca. 55 spp.: Glenny et al. 2010), and secondary centers of diversity in the Hawaiian Islands (13 spp.: Wagner et al. 1999), New Guinea (15 spp.: Garner 2002), Australia (8 spp.: Thompson 2010) and the Marquesas Islands (6 spp.: Wagner and Lorence 2011). Elsewhere, species are scattered widely across many islands and archipelagos of the Pacific Ocean from Borneo to the Juan Fernández Islands, but each island or archipelago has only one or two endemic species.

Cantley et al. (2014) indicate from their molecular phylogeny that the Hawaiian Islands were colonized by *Coprosma* during two independent colonization events: once for the black-fruited *C. ernodeoides*, and secondly for all orange-fruited species. The orange-fruited Hawaiian *Coprosma* taxa—known locally as pilo in the Hawaiian language—were determined to be most closely related to the six Marquesan species and one (of two) species from Rapa Iti of the Austral Islands. Together, these taxa (from the Hawaiian Islands, Marquesas Islands, and Rapa Iti) were found to be more closely related to taxa in New Zealand than to other species on islands elsewhere in the Pacific where *Coprosma* taxa occur (i.e. Austral Is., Cook Is., Fiji, Kermadec Is., Lord Howe I., Norfolk I., Pitcairn I., Samoa, Society Is., and Vanuatu). Cantley et al. (2014) also determined that Hawaiian taxa were not closely related to Australian or Malesian taxa. Within the Hawaiian Islands, *Coprosma* taxa occur on all major islands except for Ni‘ihau and Kaho‘olawe. All taxa are endemic to the archipelago, but some maintain distributions across multiple islands. The intra-archipelago relationships among these taxa are not known. No resolution among Hawaiian taxa was recovered by Cantley et al. (2014), which they suggest is because the colonization event to the Hawaiian Islands by the orange-fruited *Coprosma* ancestor occurred after the emergence of Kaua‘i (≈ 5 Ma). Therefore, few detectable genetic mutations have since accumulated, which made it difficult to resolve recently diverged evolutionary relationships from the methodology that was used.

Species belonging to the genus *Coprosma* were first formally described in the Hawaiian Islands by Asa Gray in 1858 from material gathered by Nelson on Cook’s last voyage to the islands, and by Menzies during Vancouver’s voyage (Gray 1858). The descriptions of the taxa were brief, but included seven from the Hawaiian Islands. Following this, a number of individuals described additional taxa including: Wawra (1872), Hillebrand (1888), Heller (1896), Lévillé (1911), Rock (1913), and Oliver (1935, 1942). No new species of *Coprosma* have been described from the Hawaiian Islands since Oliver (1942). Only one comprehensive monograph of the genus was published (Oliver 1935), and therein was provided a thorough discussion of Hawaiian taxa, which highlighted Oliver’s dissatisfaction with attempting to fully delineate them with limited material, and without field observations. The most recent taxonomic treatment including all Ha-

waiian *Coprosma* taxa was by Wagner et al. (1999). In this treatment, six species and all varieties were sunk into synonymy. The resulting treatment details 13 endemic Hawaiian species in total from what was previously more than 20 taxa. Many taxa in Wagner (1999) are described as having a wide range of morphological diversity—such as for *C. foliosa* A.Gray, *C. ochracea* W. Oliver, and *C. pubens* A.Gray. These species occur across multiple islands, whereas single island endemic taxa have much better defined morphologies (ex. *C. ellpitica* W. Oliver of Kaua‘i or *C. longifolia* A. Gray of O‘ahu). In some cases, Wagner et al. (1999) note at the end of the taxonomic descriptions that various Hawaiian *Coprosma* taxa are in need of fieldwork in order to better understand precise relationships and probable segregate taxa. In the field, Hawaiian *Coprosma* are notoriously difficult to quickly distinguish from one another as diagnostic characters among taxa are minute, and boundaries among species are not always clearly defined. Further complicating proper identification is that taxa are often found growing sympatrically, and are thought to hybridize occasionally. Without knowledge of variant morphologies of populations on different islands, it is often difficult to accurately identify a particular taxon in the field, even with the most current key to species (J. Cantley, pers. obs.).

Such is the case for currently described *C. foliosa*, which is a widespread taxon occurring on islands of Kaua‘i, O‘ahu, Moloka‘i, Maui, and Lana‘i (Wagner 1999). It is effectively replaced on Hawai‘i Island by the morphologically similar *C. menziesii* A.Gray. *Coprosma foliosa* was first described by Gray (1858), as a shrub with glabrous lanceolate to oblanceolate leaves and obovate to globose fruit with a naked apex. Following this, Hillebrand (1888) described a similar species, *C. stephanocarpa* Hillebr. from Moloka‘i, Maui, and Kaua‘i, indicating the species had—as the name suggests—a fruit with a persistent calyx on the apex that is connate, forming a crown-like structure. The Kaua‘i specimens considered to represent *C. stephanocarpa* were recognized by Gray (1858) as *C. pubens* A.Gray var. *kauensis* A.Gray, and later were elevated to species level by Heller (1896). Hillebrand (1888) indicated the fruit of *C. stephanocarpa* was globose or obovate with a depressed apex becoming bisulcate, and crowned by the spreading discreet calyx lobes. Rock (1913) then described *C. vontempskyi* Rock from rainforests above Olinda, Maui, which shared similar morphological characters of Hillebrand’s *C. stephanocarpa*, yet he made no mention of *C. stephanocarpa* in his description. Oliver (1935) recognized this oversight by Rock and sank *C. vontempskyi* into *C. stephanocarpa* as he deemed them indistinguishable. Oliver revised the description of *C. stephanocarpa* and restricted the fruit morphology to a “drupe [that is] ovoid...[and] crowned by the persistent calyx, 5-6 mm long.” However, the new restricted description of *C. stephanocarpa* failed to mention Hillebrand’s fruit characters describing the fruit as sometimes “obovate with a depressed apex, becoming bisulcate.” The bisulcate character was never again noted in further Hawaiian *Coprosma* taxonomic descriptions, including in Wagner et al. (1999) where *C. stephanocarpa* (plus *C. fauriei* H. Lév. and *C. skottsbergiana* W. Oliver) was officially lumped into *C. foliosa*. Oliver (1935) notes that his descriptions of *C. stephanocarpa* were not fully satisfying to him as he felt unable to disentangle the diverse series, subspecies, forms, and potential hybrids of *C. stephanocarpa*, particularly on East Maui, with only limited

material, which was provided to him from his collaborator Harold St. John at the Bishop Museum in Honolulu.

The (re)discovery of bisulcate fruit with a depressed apex and a persistent crown-like calyx from a locally common *Coprosma* taxon in the Kanaio Natural Area Reserve on leeward East Maui, plus the difficulty in keying these individuals to the species level, prompted this detailed investigation by the authors. The investigation included in-depth herbarium research, as well as fieldwork to validate findings and to assess the taxon's abundance and distribution on Maui. This paper recognizes one new distinct species, *C. cordicarpa*, and unexpectedly confirms the need to resurrect *C. stephanocarpa* from synonymy. Both taxa are segregated from *C. foliosa* using morphological, ecological, phenological, and geographical lines of evidence. This study, plus a concurrent study of a new taxon from Kaua'i (D. Lorence, pers. comm.), increases the total number of endemic *Coprosma* species in the Hawaiian Islands to 16.

Methods

All measurements given herein are taken from dried herbarium specimens. Field observations were performed in September 2013, September 2014, and May 2015 to assess abundance and to take field notes and digital photos. Seeds of *C. cordicarpa* were collected from two populations at Kanaio Natural Area Reserve and Auwahi totaling 609 seeds from 32 individual plants. All seeds were deposited for long-term germplasm storage at the Seed Conservation Laboratory at Lyon Arboretum. Measurements are presented in the descriptions as follows: length, then width, each followed by units of measurement (mm or cm). More than 80 specimens (including type specimens) from the BISH herbarium were studied and measured. Validations were also garnered from PTBG specimens. The area of occupancy (distribution) for each species was calculated using herbarium collection data and field observations. The conservation status is proposed following the IUCN Red List Category criteria (IUCN 2001; www.iucnredlist.org/info/categories_criteria2001). A file including measurements and notes taken from herbaria specimens is provided as supplemental data (See Suppl. material 1: *Coprosma* Morphology Data Matrix).

Taxonomic treatment

Coprosma J.R. Forster & G. Forster

Lectotype species (designated by Rehder 1949, pg. 597): *Coprosma foetidissima* J.R.Forst. & G.Forst.

Description. Shrubs, multi-branched, erect, occasionally creeping and sometimes rooting at the nodes, or occasionally trees, often foetid when bruised. Leaves simple,

opposite or rarely ternate, margins entire, petiolate or sessile; stipules interpetiolar, distinct or partly connate, entire or dentate with tooth-like marginal colleters. Flowers unisexual (and the plants dioecious or rarely monoecious), rarely polygamous or in one species perfect, axillary, solitary or in cymes; calyx 4–5(–10)-toothed, often reduced or absent in male flowers; corolla funnelform or campanulate, 4–5(–10)-lobed, lobes valvate in bud; stamens 4–5(–10), inserted at base of corolla tube; filaments long-exserted, erect or pendulous; ovary 2(–4)-celled, ovule 1 per cell, basal, anatropous; style 2(–4)-lobed, divided nearly to base; stigmas long-exserted, papillose-hirsute. Fruits drupaceous, fleshy, ovoid to globose, with 2(–4), 1-seeded, plano-convex pyrenes.

Key to the Hawaiian species of *Coprosma* previously treated as *C. foliosa* s.l.

- 1 Fruit reddish-orange, ovoid, lacking a central constriction between the two seeds, apex not depressed, calyx conspicuous or not..... (2)
- Fruit reddish-orange to yellow, cordate (heart-shaped) with a central constriction between the two seeds, apex depressed, calyx conspicuous and persistent, leeward East Maui..... *C. cordicarpa*
- 2 Fruit reddish-orange to yellow, fruit calyx conspicuous and persistent and >1.5 mm long, East and West Maui *C. stephanocarpa*
- Fruit reddish-orange to yellow, persistent fruit calyx not present or sometimes minute (<1.5 mm), Kaua‘i, O‘ahu, Moloka‘i, Lana‘i, West Maui... *C. foliosa* s.l.

***Coprosma cordicarpa* J.Cantley, Sporck-Koehler, & M.Chau, sp. nov.**

urn:lsid:ipni.org:names:77152890-1

Figure 1A–F; Figure 2

Type. USA. Hawai‘i: Maui: East Maui: Kanaio Natural Area Reserve, near cabin, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau* JC-479 (holotype: BISH 763458).

Diagnosis. Differs from other currently recognized species of *Coprosma* in the Hawaiian Islands primarily by its cordiform fruits formed by a depressed apex and central constriction on female plants, and by large calyces (lobes 2–4 mm vs., for example, 0.25–2.00 mm of *C. stephanocarpa* and *C. foliosa* s.l.) on male flowers.

Description. *Shrubs to trees* 2–7 m tall, with one to many main stems; young stems sparsely pubescent to puberulent; *Seedlings* and *Juveniles* with significantly more trichomes than mature individuals; *Leaves* opposite, blades 20–56 × 8–25 mm, lanceolate, both surfaces sparsely pilose or glabrous, midrib sparsely puberulent towards base, domatia present on abaxial surface in secondary vein axils, blade apex acute or sometimes rounded, base cuneate; petioles 5–12 mm long; stipules deltate 2–3 mm long, connate 25–50% of their length, base puberulent to lanate with band of glabrous tissue immediately below margin, margin lanate with a conspicuous apical colleter sometimes obscured by two marginal colleters. *Inflorescences* axillary; male inflorescences a

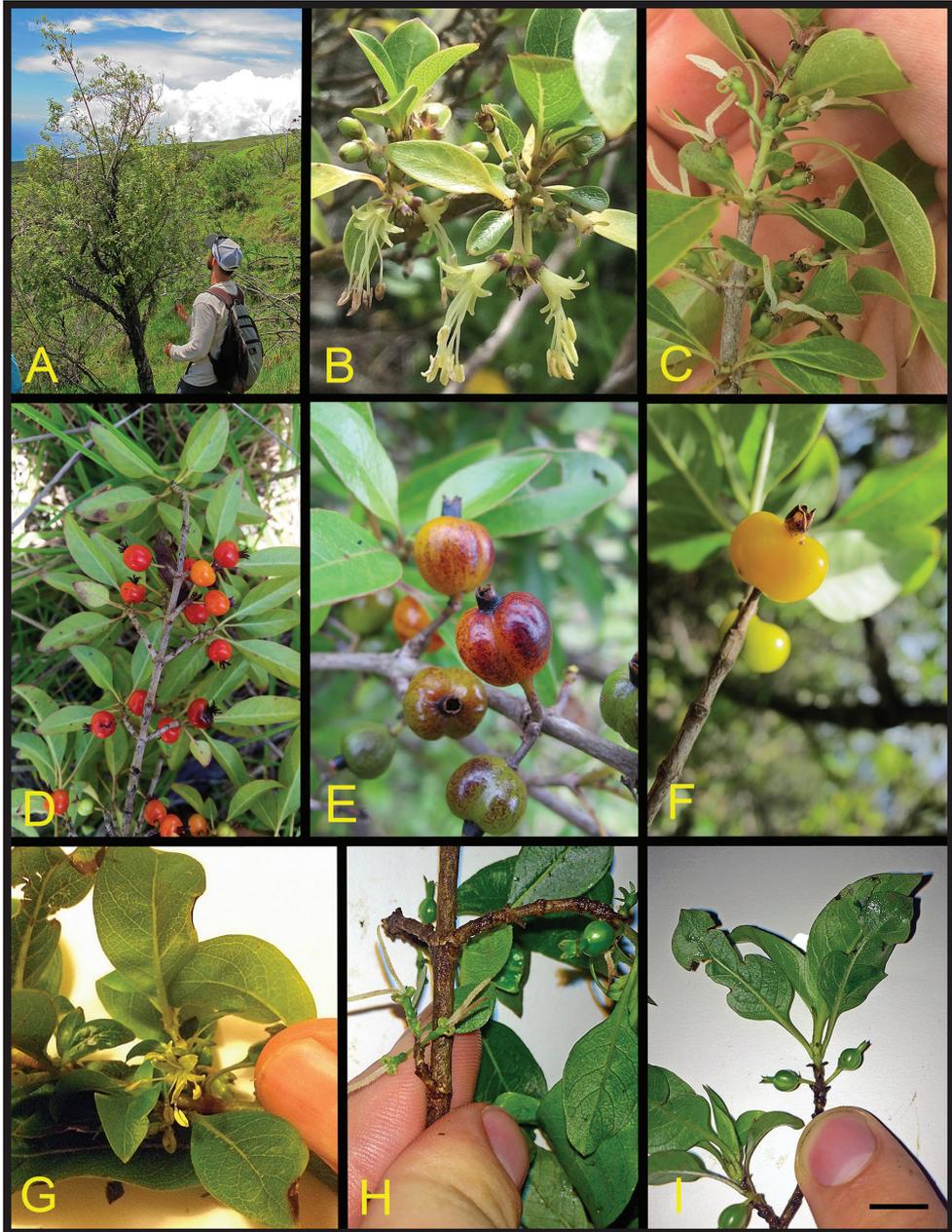


Figure 1. Field images of *C. cordicarpa* and *C. stephanocarpa*. **A–F** *Coprosma cordicarpa*. **A** habit and habitat of whole plant with JTC **B** male stem and inflorescences **C** female stem and inflorescences **D–F** fruits illustrating population variation in color and degree of calyx connation **G–H** *Coprosma stephanocarpa* **G** male stem and inflorescence **H** female stem and inflorescences **I** immature fruits. All images were taken by the authors, **A–C, E** from Kanaio Natural Area Reserve **D, F** from Auwahi **G–I** from Makawao Forest Reserve. Black scale bar at bottom right indicates the following lengths: 0.5 m (**A**), 1.5 cm (**B–C, E–F**), 5 cm (**D**), 2 cm (**G–I**).

3-flowered cyme on an unbranched peduncle (3–)7–9(–17) mm long or sometimes trichotomously branched at base, with flowers terminal in groups of 3 on each branch, internodes 5–25 mm long, central branch up to twice as long; female inflorescence solitary, 3–7(–13) mm long or sometimes trichotomously branched at base with solitary flowers terminally occurring on lateral branches and central branch a 3-flowered cyme with sessile central flower, and two lateral flowers on short pedicels, internodes 5–25 mm long, central branch up to twice as long. *Flowers*: male calyx irregularly toothed, urceolate to campanulate in early development, becoming deeply split due to corolla growth, 2–4 mm long, sheathing basal 1/8–1/4 of the mature corolla, apex red-purple at maturity, corolla 5–6(–8)-merous, campanulate to widely funnelform, lobes 3 × 0.5 mm, stamens 5–6, inserted at base of corolla, filaments exerted to 7 mm, pendulous at maturity; female calyx irregularly toothed at margin, completely connate or nearly so, forming a cylindrical tube around the corolla or occasionally only 1/4 connate, 1.5–3.5 mm long, corolla 5–6-merous, narrowly funnelform to tubular, only lobes exerted beyond calyx, recurving 360 degrees at maturity, lobe apices often touching upper calyx near teeth, styles 2, divided to base, 3 cm long, ca. 0.5 mm diam. *Fruit* reddish-orange to lemony-yellow, sometimes with red to reddish-purple colored epidermal flecks, cordiform, tapering towards the base, 7–10 × 5–7 mm when dry, with central constriction (furrow) from base to apex present between two seeds, apex depressed between the two seeds, crowned with a conspicuous persistent calyx, drying brown. *Seeds* 2(–3) plano-convex pyrenes, yellowish-white, 2.3–6.3 × 2.5–5.0 mm × 1.0–3.0 mm, seed operculum 0.5–2.1 mm long.

Phenology. Flowering specimens were collected from August to September except for one individual in March. Field observations of September 2013 and 2014 found that most individuals of the population at Kanaio Natural Area Reserve and Auwahi were fruiting, and only few flowering. Fruiting specimens were collected across many months, but it is unknown how long fruits were mature on individuals prior to collection.

Distribution. Known only from southern, leeward slopes of East Maui (Haleakalā) at elevations of approximately 1000–2000 m, roughly spanning east to west from the Kanaio Natural Area Reserve to the Kaupō Gap Trail. The linear distance is estimated at approximately 21 km, but populations may be disjunct, especially in poor, degraded habitat where ungulates and invasive plant species (i.e. *Cenchrus clandestinus* (Hochst. ex Choiv.) Morrone) are dominant. Known locations include Kanaio Natural Area Reserve, Auwahi, Kahikinui Forest Reserve, Nu‘u, and the Kaupō Gap Trail. Modern observations of abundance (2013–2015) at Kanaio Natural Area Reserve, Auwahi and Kaupō Gap Trail indicate that it is locally common at all sites. Its present abundance in Nu‘u and Kahikinui Forest Reserve is not known.

Ecology. In native habitats, *Coprosma cordicarpa* occurs in dry forest/shrubland habitat with *Chrysodracon auwahiensis* (H. St. John) P.L.Lu & Morden, *Dodonaea viscosa* Jacq., *Euphorbia celastroides* (Boiss) Croizat & Degener var. *lorifolia* A.Gray, *Osteomeles anthyllidifolia* (Sm.) Lindl., *Leptecophylla tameiameiae* (Cham. & Schltldl.) C.M.Weiller, and an understory of *Carex wahuensis* C.A.Mey. It is often present in in-



Figure 2. Photo of the holotype specimen of *Coprosma cordicarpa* (BISH).

vaded habitats with *Cenchrus clandestinus*. It occurs primarily in open habitat receiving direct sunlight, but was observed in gulches and high elevation forests along the Kaupō Gap Trail (Seana Walsh, pers. comm.). The rainfall in the distribution of *C. cordicarpa*

varies from 700 to 1900 mm annually with the highest rainfall occurring from December to January (Giambelluca et al. 2013). Flowering occurs during the dry season, and fruits appear to mature shortly preceding the wettest months, which may represent a germination strategy for this dry habitat taxon.

Etymology. The specific epithet refers to the heart-shaped fruit, which is a product of the central constriction of the fruit and depressed apex. This character is unique among Hawaiian *Coprosma* taxa.

Conservation status. This taxon occurs as scattered individuals that are locally common within five populations on one volcano. When evaluated using the IUCN criteria for extinction risk (IUCN 2012), *C. cordicarpa* falls into the Vulnerable (VU) category under Criterion B1ab(iii)+2ab(iii). The VU designation is the lowest of three threatened categories, but indicates the taxon still faces a high risk of extinction in the wild. It has an area of occupancy < 2000 km² and extent of occurrence < 20,000 km², less than 10 known locations that are possibly fragmented, and an observed continuing decline in habitat quality overall. Such suitable habitat may continue decreasing in size without active conservation management. In areas where the landscape has been actively managed for ungulates and invasive plant species (i.e. Auwahi, Kanaio Natural Area Reserve), *C. cordicarpa* purportedly has displayed a marked natural increase in population size. Further conservation measures may lower extinction risk and change the threatened status of *C. cordicarpa*.

Specimens examined. United States of America. Hawai'i: Maui: East Maui: Hana District, Kaupo Gap, ≈1.75 mi S of Paliku Cabin, alt. 5000 ft, 16 Jul 1969, *J.S. Henrickson 5000* (BISH); Haleakalā, Kaupo Gap, 2nd cove S of Waikeke'ehia, 6000 ft, 27 Jun 69, *H. St. John 21189* (BISH); Auwahi, 4000 ft, 30 Jun 72, *H. St. John 26860* (BISH); Auwahi District, S slope, 18 Dec 1981, *A.C. Medeiros 195* (BISH); Auwahi District, S slope, 18 Dec 1981, *A.C. Medeiros 195* (BISH); Auwahi, 0.5 km SE of Pu'u O'uli, alt. ca. 4000 ft, 24 Jun 1980, *P.K. Higashino 9254* (BISH); Auwahi, 24 Nov 1920, *C.N. Forbes 2096M* (BISH); Auwahi, 20 Mar 1920, *C.N. Forbes 2043M* (BISH); Auwahi, 1 Feb 1953, *J.F.C. Rock 27003* (BISH); 8 mi. E of Ulupalakua, S slope of Haleakalā, alt. 3000-3500 ft, 26 Aug 1976, *E.L. Little Jr. 31132* (BISH); SW slope of Haleakalā, Kahikinui FR, S of Kahua Cabin Rd, alt. ca. 4900 ft, 24 Jun 1980, *F.R. Warshauer 2684* (BISH); Kahikinui, S Haleakalā, 0.1-0.5 km W of Manawainui Gulch, alt. ca. 4840 ft, June 20, 1980, *P.K. Higashino 9234* (BISH); Kanaio NAR, 13 Sept 2013, *M.J. Sporck-Koehler s.n.* (BISH); Nui, S slope of Haleakalā, 6 Mar 1920, *C.N. Forbes 1858M* (BISH); Near Kanaio NAR Cabin, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau JC-475* (BISH); Near Kanaio NAR Cabin, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau, JC-476* (BISH); Near Kanaio NAR Cabin, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau JC-477* (BISH); Near Kanaio NAR Cabin, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau JC-478* (BISH); Near Kanaio NAR Cabin, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau JC-479* (Holotype: BISH); Auwahi restoration unit #1, 29 Sep 2014, *J.T. Cantley, M.J. Sporck-Koehler & M.M. Chau JC-480* (BISH); Kahikinui, area east of Manawainui, alt. 5000-6000 ft, *K.R. Wood 6247* (PTBG).

***Coprosma stephanocarpa* Hillebr.**

Figure 1G–I; Figure 3

Type. United States of America. Hawai‘i: Maui, East Maui, Haleakalā, alt. 3000–6000 ft, 1888, *J. Hillebrand* s.n. (lectotype, designated by Oliver 1935, pg. 164: isolectotype: BISH!)

Description. *Shrubs to small trees* 2–6 m tall, with one to many main stems; young stems sparsely pubescent. *Leaves* opposite, blades 6–50 × 4–15 mm, elliptic or sometimes lanceolate, sparsely pilose on both surfaces, midrib puberulent, domatia present on abaxial surface in secondary vein axils, apex acute, base cuneate to attenuate, petioles 3–5(–10) mm long; stipules narrowly deltate, often recurving away from stem, 2–4 × 2–3 mm, connate 1/4 to 1/2 of their length, base puberulent to lanate, margins lanate with one apical colleter and no marginal collectors, band of glabrous tissue immediately below the margin. *Inflorescences* axillary, male inflorescence a 3(–5) flowered cyme on an unbranched peduncle 3–5 mm long; female inflorescence solitary or occasionally 2–3, sessile or subsessile, peduncle 0–3(–6) mm long, unbranched, flowers terminal. *Flowers* male calyx lobes 3–5, irregularly toothed 0.25–2 mm long, corolla 5–6-merous, funnellform, 3–4 mm long, lobes 0.5–1.5 mm long, tube 3–4 mm long beyond calyx, stamens 5–6, anthers inserted at base of corolla, filaments 7–13 mm long, exerted beyond corolla, pendulous at maturity; female calyx 3–5 lobes 0–2 mm long, corolla funnellform to campanulate, only lobes exerted beyond calyx, recurving 360 degrees at maturity, lobe apices often touching calyx, styles 2, divided to base, exerted 3–4 mm beyond corolla. *Fruit* reddish-orange to yellow, ovoid, 4–10 × 3.5–6 mm, crowned with a conspicuous persistent calyx. *Seeds* 2 plano-convex pyrenes, yellowish-white.

Phenology. Most flowering specimens were collected from December to February and a lesser number from July to August. Specimens from Lihau (West Maui) are only known to flower in July. No individuals were fruiting or flowering in late September 2014 in Makawao Forest Reserve, but immature fruits and flowers were observed in May 2015. Most fruiting specimens occurred in July, but collections were made across many months.

Distribution. Known from East and West Maui, but apparently more prevalent on East Maui. The taxon occurs from approximately 975m to 1700m elevation. On East Maui, it is known from mesic sites from Kipahulu Valley to Olinda. Collections on West Maui are collected from Lihau and Honokawai.

Ecology. Found in mesic to wet forests and shrublands with both native and non-native plant communities. Occurs primarily as an understory shrub to small tree. The rainfall varies dramatically across its distribution and precise collection localities should be geo-referenced to provide an accurate range of precipitation requirements for this taxon’s distribution.

Etymology. The specific epithet refers to the persistent calyx on the fruit apex that looks like a crown (crown in Greek = stephanos) due to its persistence, connation, and irregular dentations.

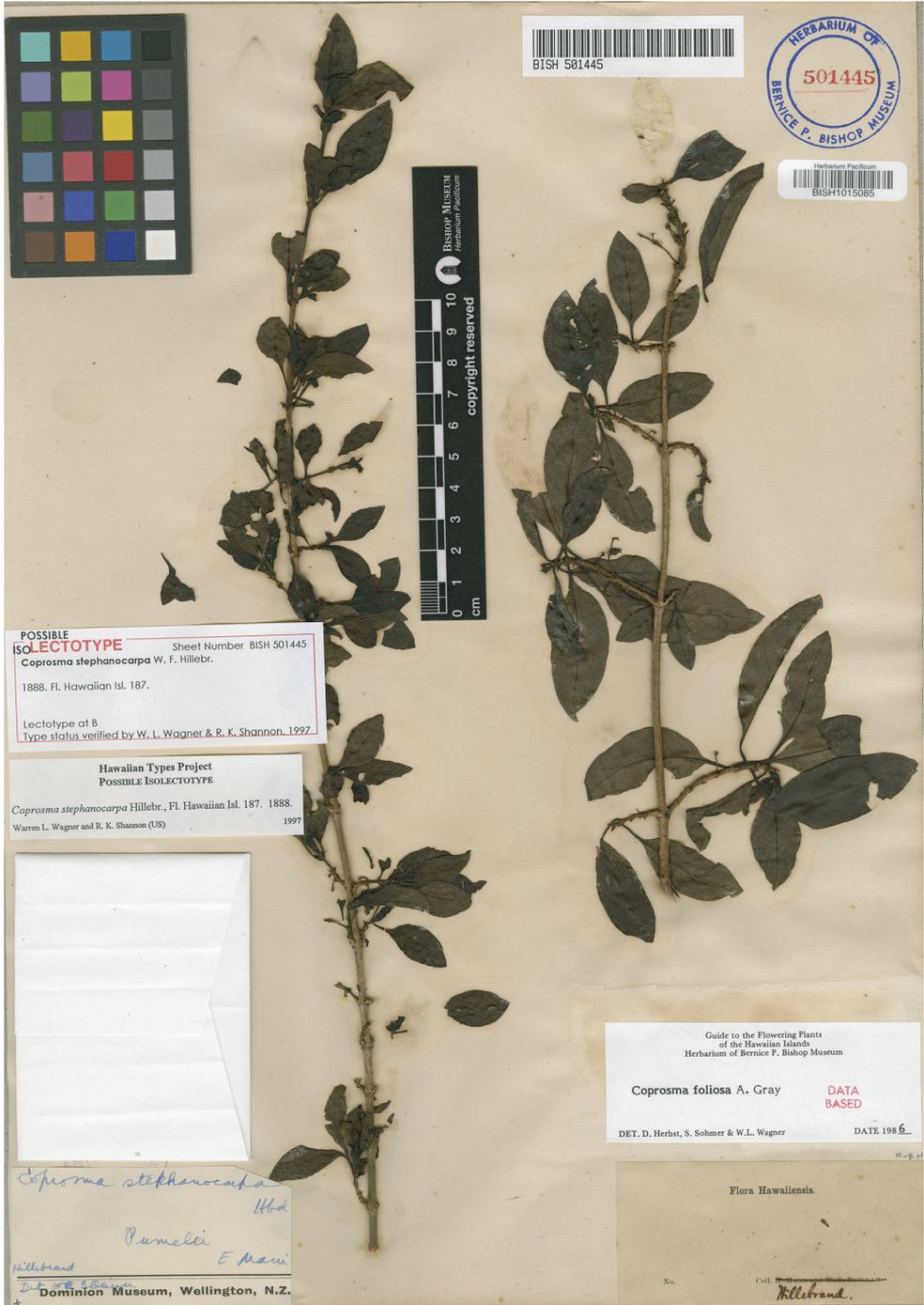


Figure 3. Photo of the holotype specimen of *Coprosma stephanocarpa* (BISH).

Conservation status. This taxon occurs as scattered individuals that are locally common on two volcanoes within one island. When evaluated using the IUCN criteria for extinction risk (IUCN 2012), *C. stephanocarpa* falls into the Vulnerable (VU) category under Criterion B1ab(iii)+2ab(iii). The VU designation is the lowest of three threatened categories, but indicates the taxon still faces a high risk of extinction in the wild. It has an area of occupancy < 2000 km² and extent of occurrence < 20,000 km², less than 10 known locations, and an observed continuing decline in habitat quality overall. Suitable habitat may continue decreasing in size without active conservation management, and currently none of the populations occur in protected areas.

Specimens examined. United States of America. Hawaii: Maui: West Maui: edges of Honokowai gulch, alt. 4500 ft, 24 Aug 1910, *J.F.C. Rock 8189* (BISH); Manawai-nui Gulch, alt. 820 m, 8 Mar 1988, *W.L. Wagner 5857* (BISH, PTBG); Lahaina District, Lihau, alt. 3200 ft, 28 Oct 1991, *P. Welton 1379* (BISH); Lahaina District, Lihau, alt. 3250 ft, 9 May 1991, *P. Welton 911* (BISH); Lahaina District, Lihau, alt. 3700 ft, 9 May 1991, *P. Welton 954* (BISH); Lahaina District, Lihau, alt. 3800 ft, 25 Aug 1991, *P. Welton 1237* (BISH); Lahaina District, Lihau, alt. 3800 ft, 26 Aug 1991, *P. Welton 1261* (BISH); Lahaina District, Lihau, alt. 3900 ft, 9 May 1991, *P. Welton 955* (BISH); Lahaina District, Lihau, alt. 4000 ft, 24 Aug 1991, *P. Welton 1177* (BISH); Lahaina District, Lihau, alt. 4000 ft, 24 Aug 1991, *P. Welton 1178* (BISH); Lihau, alt. 4100 ft, 13 Jul 1991, *P. Welton 1091* (BISH); Lahaina District, Lihau, alt. 4120 ft, 25 Aug 1991, *P. Welton 1200* (BISH); Kukui watershed area, ridge towards Kahana Valley between Kahana and Kahana Iki valleys, *M. Kiehn MK-990913-2/4* (PTBG). **East Maui:** Olinda Forest Reserve, 26 Mar 1952, *O. Degener 22116* (BISH); Olinda Forest Reserve, 26 Mar 1952, *O. Degener 22116* (BISH); Makawao, Olinda pipe line road, lower fork, alt. 4650 ft, 25 Dec 1951, *A.K. Chock 298* (BISH); Olinda FR, Waikamoi Flume, 12 Jan 1985, *L. Pyle & W. Takeuchi 1923* (BISH); Olinda FR, alt. 4025 ft, 12 Jan 1985, *L. Pyle & W. Takeuchi 1922* (BISH); Olinda, 24 Apr 1918, *G.C. Munro 482* (BISH); Olinda, 3 May 1967, *N.L.H. Krauss 1128* (BISH); 2 mi. E of Olinda, alt. 4200 ft, 27 Jun 1969, *J.S. Henrickson 3738* (BISH); Haleakalā, below Olinda, 24 Apr 1918, *G.C. Munro 648* (BISH); lower Olinda Flume, between gate and road, alt. ca. 4000 ft, 19 Jul 1964, *M.R. Crosby 1804* (BISH); above Olinda, alt. 4200 ft, 30 Sep 1945, *A.L. Mitchell 65* (BISH); Kula pipe line, Olinda, 4500 ft, 11 Feb 1930, *H. St. John 10296* (BISH); Kula Pipe Line, 25 May 1930, *O.H. Swezey s.n.* (BISH); Makawao Forest Reserve, Olinda pipe line, alt. 4300 ft, 25 Dec 1955, *H.A. Woolford 137* (BISH); Makawao, Olinda pipe line road, lower fork, alt. 4650 ft, 25 Dec 1951, *A.K. Chock 298* (BISH); Kula pipe line, 18 Oct 1922, *C.J.F. Skottsberg 892* (BISH); Makawao Forest Reserve, alt. 4300 ft, 16 Jul 1980, *K.T. Adee s.n.* (BISH); Makawao District, Kalialinui, NW Haleakala, Pu'u Luau, ca. 5720 ft, 10 Jun 1980, *P.K. Higashino 9340* (BISH); Ko'olau Forest Reserve, S of W Wailuaiki Stream on pali, alt. ca. 5310 ft, 31 May 1980, *P.K. Higashino 9047* (BISH); E of Ukulele, 17 Jul 1919, *C.N. Forbes 816M* (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes 748M* (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes 758M* (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes 769M* (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes 936M* (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes 748M* (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes*

738M (BISH); Ukulele, 1 Jul 1919, *C.N. Forbes* 7 69M (BISH); above Ukulele, 1 Jul 1910, *C.N. Forbes* 215M (BISH); Ukulele, *C.N. Forbes* s.n. (BISH); Pu'u Pani, 4 Mar 1920, *C.N. Forbes* 1836M (BISH); Waikamoi, alt. 4250 ft, 14 Aug 1933, *M.C. Neal* s.n. (BISH); Makawao Forest Reserve, Waikamoi Flume Rd, 9 Jan 1997, *C.R. Annable* 3231 (BISH); N slope of Haleakalā, between Hanawī and E fork of Kopiliula streams, alt. ca. 5750 ft, 13 Jul 1980, *P.K. Higashino* 9375 (BISH); Hana, E of Kuhiwa Stream and Valley, ca. 5540 ft, 13 Jun 1980, *P.K. Higashino* 9146 (BISH); Kīpahulu, L side of valley, 15 Nov 1919, *C.N. Forbes* 1639M (BISH); Kīpahulu, ridge L side of valley, 15 Nov 1919, *C.N. Forbes* 1648M (BISH); Hana, ridge of central part of Kīpahulu Valley, alt. 3780 ft, 22 Jul 1980, *P.K. Higashino* 9407f (BISH); Kīpahulu Forest Reserve, ridge N of Pu'u Ahuli'i, alt. ca. 5400 ft, 23 Aug 1980, *F.R. Warshauer* 3113 (BISH); 1-3 km E of Kaupo Gap, Kīpahulu Forest Reserve, alt. ca. 5750 ft, 27 May 1980, *F.R. Warshauer* 2560 (BISH).

Discussion. When numerous collections of *Coprosma foliosa* from Maui were run through the most current key to Hawaiian *Coprosma* (Wagner et al. 1999), it was clear that at least two taxa subsumed under that species merited taxonomic recognition. Both taxa failed to key out, and specimens did not closely match the taxonomic description of *C. foliosa* or any other species. After multiple field visits, herbarium specimen measurements, and an in-depth literature review, it was concluded that the two *C. foliosa* segregates, *C. cordicarpa* and *C. stephanocarpa*, maintain rather consistent morphologies on leeward East Maui (*C. cordicarpa*) and mesic areas of East and West Maui (*C. stephanocarpa*). They can easily be segregated from the variable *C. foliosa* s.l. found on other islands and effectively replace *C. foliosa* s.l. on East Maui, although at least one form of *C. foliosa* s.l. is still found on West Maui. *Coprosma cordicarpa* is most easily distinguished from *C. foliosa* s.l. by its heart-shaped fruit characters, which include a depressed apex crowned by a persistent connate calyx and the tendency to become bisulcate, particularly when dry. Male individuals of *C. cordicarpa* are easily differentiated as the calyx is nearly double in size (2-4 mm) than that of *C. foliosa* s.l. (0.25-2 mm), and *C. stephanocarpa* (0.25-2 mm). The male calyx ontogeny of *C. cordicarpa* is quite striking; the irregularly toothed calyx initially appears to be completely connate (or nearly so) when in bud, but due to expansion of the growing corolla, the calyx is mechanically split (often in two locations) becoming deeply incised, and then brown callus tissue forms. Ecologically, *C. cordicarpa* is found in a unique habitat niche (dry forest/shrubland) compared to *C. foliosa* s.l. and *C. stephanocarpa*. The niche requirements of *C. cordicarpa* should be studied in more detail, but it is clear that the areas where it occurs receive much less precipitation than *C. stephanocarpa* habitat, which include mesic to wet locations of East and West Maui.

Phenological observations suggest that *C. cordicarpa* and *C. stephanocarpa* have different flowering periods that are primarily non-overlapping. *Coprosma cordicarpa* has a primary flowering period in late summer (August to September). The flowering period of *C. stephanocarpa* is primarily the winter (December to February), with a less pronounced period of flowering from July to August. Scant information about Hawaiian *Coprosma* phenology has been published, but *C. ochracea* and *C. rhynchocarpa* from Hawai'i Island

have a peak flowering period during early spring months (March to May; Lamoureux 1973), which is different from the summer flowering *C. cordicarpa*, and winter flowering *C. stephanocarpa*. Phenological differences among the evolution of Lord Howe Island species of *Coprosma* have proven to be evolutionarily significant (Papadopolos et al. 2011), and a similar case could also be true for Hawaiian taxa. However, it should be noted that while most, if not all, taxa of Hawaiian *Coprosma* have a primary robust flowering period each year, a small percentage of individuals in any population can occasionally be sporadically flowering across many different months (J. Cantley, pers. obs.). The stochasticity of flowering times could help explain the presence of occasional hybrids that are thought to exist among many sympatrically occurring *Coprosma* taxa in Hawai'i.

The taxonomic boundaries between *Coprosma stephanocarpa* and *C. foliosa* s.l. are less easily defined, especially from populations of *C. foliosa* s.l. occurring on the islands of Moloka'i and Lana'i. However, *C. stephanocarpa* is here restricted to Maui only, as taxa elsewhere appear to maintain consistent morphological differences. On Moloka'i, at least two morphotypes of *C. foliosa* s.l. exist that are similar to *C. stephanocarpa*. One of these taxa has smaller fruits that are globose with a naked apex, smaller floral characters, and smaller leaves in general, but other vegetative characters (e.g. stipule size & pubescence) are similar to *C. stephanocarpa*. The second Moloka'i *C. foliosa* s.l. morphotype has broad stipules that are more or less glabrous and ellipsoid to globose fruits with a small persistent crown that is not longer than 0.75 mm in length. Concerning Lana'i specimens, few collections have been made, but these agree in morphology with the former described small-fruited, small-leaved Moloka'i taxon, although much less morphological variation was noted. Fieldwork is needed on both islands to better understand these taxa and their relationship with *C. stephanocarpa*.

Conclusions. The recognition of *C. cordicarpa* and *C. stephanocarpa* brings the total number of *Coprosma* species described in the Hawaiian Islands to 15. A concurrent study of material collected on Kaua'i will increase the total number of taxa described to 16 (D. Lorence, pers. comm.). Ongoing investigation of the *C. foliosa* s.l. complex on Maui and other islands (Kaua'i, O'ahu, Moloka'i, and Lana'i) is currently being pursued by the authors. Preliminary investigation suggests that perhaps morphology is correlated with geographical location, which may support the need for resurrection of other currently synonymized or novel taxa not discussed in this paper. Moreover, detailed investigations of other currently valid taxa, such as the variable *C. pubens* and *C. ochracea*, could reveal cryptic taxa by understanding their diversity in better detail at the population level. Ultimately, it is suggested that a molecular study be undertaken to help shed light on the interesting evolutionary patterns of speciation for this dynamic genus in the Hawaiian Islands.

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Supplementary material I

***Coprosma* Morphology Data Matrix**

Authors: Jason T. Cantley, Margaret J. Sporck-Koehler, Marian M. Chau

Data type: Measurement

Explanation note: Measurements and notes taken from herbaria specimens.

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Vernonieae (Asteraceae) of southern Africa: A generic disposition of the species and a study of their pollen

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Abstract

Current and previously included members of the Tribe Vernonieae (Asteraceae) of southern Africa are listed in their presently recognized genera with complete synonymies and keys to genera and species. The genus *Vernonia*, as presently delimited, does not occur in Africa. Genera of the Vernonieae presently recognized from southern Africa are *Baccharoides*, *Bothriocline*, *Cyanthillium*, *Distephanus*, *Erlangea*, *Ethulia*, *Gymnanthemum*, *Hilliardiella*, *Oocephala*, *Orbivestus*, *Parapolydora*, *Polydora*, *Vernonella*, *Vernoniastrum*, plus two genera that are named as new: *Namibithamnus* and *Pseudopegolettia*. Twelve new combinations are provided and two species, *V. potamiphila* and *V. collinii* Klatt., hom. illeg., remain unplaced because of a lack of material.

Pollen types are illustrated including previously recognized types: non-lophate, sublophate, tricolporate lophate, and non-colpate triporate lophate. A type previously unknown in the Asteraceae is described here and in a separate paper for *Oocephala* and *Polydora*; a non-colpate pantoporate lophate type with pores not strictly equatorial.

Keywords

Asteraceae, *Baccharoides*, *Bothriocline*, Botswana, Compositae, *Cyanthillium*, *Distephanus*, *Erlangea*, *Ethulia*, *Gymnanthemum*, *Hilliardiella*, Lesotho, Namibia, *Namibithamnus*, new combinations, new genera, *Oocephala*, *Orbivestus*, *Parapolydora*, pollen, *Polydora*, *Pseudopegolettia*, South Africa, Swaziland, *Vernonella*, *Vernonia*, *Vernoniastrum*, Vernonieae

Introduction

Attempts to revise the generic concepts of the tribe Vernonieae (Asteraceae: subfamily Cichorioideae) in Africa have proven difficult, but it is now possible to resolve nearly all of the generic limits within the tribe in the more limited area of southern Africa here defined as including the following: Botswana, Lesotho, Namibia, Republic of South Africa, and Swaziland. This treatment is the latest in a series of papers revising the generic limits in the Vernonieae, a series that includes an initial summary of eastern hemisphere taxa (Robinson 1999a), a summary of western hemisphere taxa, (Robinson 1999b), the Vernonieae of China (Robinson and Skvarla 2010) and the Vernonieae of Thailand (Bunwong et al. 2014). As elsewhere in the series, changes are necessitated by the discovery of the natural limits of the genus *Vernonia* Schreb., typified by *V. noveboracensis* (L.) Michx., which is now known to be almost entirely restricted to North America (Robinson 1999a, b) and is native only in the western hemisphere. Thus, many older as well as recent generic segregates in the tribe are now recognized. In addition, in this treatment, two genera are described as new, older names are recognized for two species, and new combinations are provided for 13 species that have previously been placed in *Vernonia*. The pollen of the revised southern African genera is described and illustrated. During the course of the study a new species of *Gymnanthemum* has been found and described elsewhere (Robinson and Funk 2014) and a previously unknown form of pollen for the Asteraceae has been recognized (Robinson and Skvarla 2014).

The initial reference used for members of the Vernonieae in southern Africa was *Flora Capensis* by Harvey and Sonder (1894). Additions have been made using Jeffrey and Leistner (2000), Pooley (1991) and Retief and Hermann (1997), and especially Arnold and De Wet (1993). Also helpful were the treatments of *Flora Zambesiaca* (Wild 1978a, 1978b, Wild and Pope 1977) and Madagascar (Humbert 1960). Subtractions from the Vernonieae, as listed by Harvey and Sonder, include the discovery that *Corymbium* L., *Hoplophyllum* DC., *Litogyne* Harv., and *Platycarpha* Less. are not members of the Vernonieae. According to the latest molecular phylogenies (Keeley and Robinson 2009; Funk et al. 2009), *Corymbium* is in the tribe Corymbieae, at the base of the subfamily Asteroideae, *Hoplophyllum* is in the tribe Eremothamneae in the subfamily Cichorioideae, *Litogyne* is in the tribe Inuleae in the subfamily Asteroideae, and *Platycarpha* is in the tribe Platycarphaeae in the subfamily Cichorioideae. The first three of these genera have totally non-lophate pollen (see below). In southern Africa, the Vernonieae now contain 13 genera. These include *Ethulia*, recognized by Harvey and Sonder, plus the various old and new segregates of *Vernonia sensu lato*, i.e. *Distephanus* Cass., *Gymnanthemum* Cass., *Hilliardiella* H. Rob., *Ocephala* H. Rob., *Vernonella* Sond., *Orbivestus* H. Rob. and *Parapolydora* H. Rob. Also present in southern Africa, but with species not listed by Harvey and Sonder (1894) are *Polydora* Fenzl, *Bothriocline* Oliv. ex Benth. in Hook., *Cyanthillium* Blume, and *Erlangea* Sch. Bip. Most of the taxa involved in the study are found in southern Africa, but a few species are mentioned that are not known from southern Africa but occur in Angola, Mozambique or Zimbabwe, and many subspecific

taxa mentioned in synonymies are based on type specimens that were not collected in or near southern Africa.

Some of the proper generic dispositions were established in various papers such as Robinson and Kahn (1986) dealing with *Distephanus* Cass. plus one species of *Gymnanthemum*, and by Robinson (1999a) dealing with many genera of the paleotropical region. Some of the genera have been discussed in individual papers, *Parapolydora* in Robinson (2005) and Robinson and Funk (2011), *Orbivestus* in Robinson (2009) and *Vernonella* in Robinson and Skvarla (2010a). The present paper disposes of all but two of the southern African species now known that were previously placed in the genus *Vernonia*.

Material and methods

In the following treatment, each genus is described or redescribed with general habit, types of vegetative trichomes, head structure, achene setulae and other trichomes, idioblasts and raphids, pappus form, and pollen form. Secondary metabolite chemistry is indicated based on data from two rather extensive summaries of constituents in the tribe by Bohlmann and Jakupovic (1990) and Herz (1996).

Figures are numbered in the order of the taxonomic treatment. Among the characteristics used in the classification, some special comments are in order.

Trichomes

The trichomes of the African Vernonieae may be simple or with transversely affixed cap-cells as indicated below in the key and descriptions (Robinson 1999a). There are no stellate or goblet-formed trichomes such as those found in the American Vernonieae of the subtribe Piptocarphinae (Robinson 1999b).

Pollen variation

The pollen is complicated, showing variation from nearly non-lophate to sublophate or lophate with or without colpi (Figs 3, 4, 8, 10, 14, 16, 18, 19, 21, 22, 24, 25; see Appendix A for definitions). In addition, grains show various degrees of loss of the perforated tectum. The structure of the muri and distribution of columellae also varies, and there is a variation from the usual tricolporate or non-colpate triporate conditions to a previously unknown form with pores greater in number and non-equatorial in distribution known as pantoporate.

Regarding the lophate condition, in reality, none of the grains in the Vernonieae has completely evenly spaced spines or columellae, and thus none are completely non-lophate. *Lophate*, in the Vernonieae, is defined as: pollen having the perforated tectum non-continuous in the intercolpar areas (Fig. 3A-E, 4A, B, D-F). In what is

called lophate in many Lactuceae or Arctoteae taxa, the perforated tectum is always continuous in all non-colpar areas. This same structure in the Vernoniae is called *sublophate*: having the perforated tectum continuous between the colpi, supported by massive columellae or baculae, with spines being almost always present over the baculae. These sublophate forms differ from truly *non-lophate* forms in having the arrangement of the spines somewhat to distinctly uneven, leaving incipient lacunae. Examples of this sublophate morphology are seen in southern African Vernoniae in *Distephanus angustifolius* (O. Hoffm.) H. Rob. & B. Kahn (Fig. 4G–I), *Gymnanthemum capense* (A. Spreng.) J.C. Manning & N. Swelankomo (Fig. 10A–C), *Hilliardiella capensis* (Houtt.) H. Rob., Skvarla & V.A. Funk (Fig. 14A–F), *Orbivestus cinerascens* (Sch. Bip. in Schweinf.) H. Rob. (Fig. 19A–C), and *Pseudopogolettia* (Fig. 24A–F). In *Gymnanthemum* (Fig. 10A–C), the incipient lacunae in the intercolpi are in a pattern of 1-2-2-1, a pattern like that seen in the fully developed lacunae of lophate colpate grains in *Linzia* and *Baccharoides*. The pollen of *Gymnanthemum* might be referred to as lophate in other tribes. Its grains are totally radially symmetrical. The baculae in all of these sublophate forms are freestanding and are firmly attached to the footlayer. All of these above mentioned grains also seem to grade into forms of lophate grains that are highly perforate and spinose. These grains are referred to here as sub-echinolophate (Fig. 4G–I, 10A–C, 14A–F, 19A–C, 24A–F).

In addition to the sublophate pollen types described above, there are many variations of lophate grains, grains with ‘perforated tectum lacking’ to various degrees in the lacunae or even on the muri. Of these lophate types, one variant, represented by *Baccharoides* (Fig. 3 A–I), *Bothriocline* (Fig. 4 A–C) and *Cyanthillium* (Fig. 4 D–F), has prominent highly perforate lophae (muri) with sharply projecting spines. The lophae and supporting thickened columellae or baculae are similar to those in the mentioned above: *Distephanus*, *Gymnanthemum*, *Hilliardiella*, *Orbivestus*, and *Pseudopogolettia*. These grains are termed *echinolophate* (Fig. 3A–E). A variant of the echinolophate types is seen in *Linzia* where the surface of the lophae is highly perforate and supported by massive columellae or baculae, but is without spines and is classified as *psilolophate* (Fig. 16A, B, D).

Pollen and Subtribal Classification

The most systematically important subdivision among the lophate types of pollen are the strongly colpate types as seen in *Baccharoides* and *Linzia* of the subtribe Linziinae (Figs 3 A–H, 16 A–E) as distinguished from the non-colpate porate forms of the genera of the subtribes Erlangeinae or Centrapalinae (see below). The Linziinae genera have either a distinct polar lacuna or an orderly arrangement of lacunae at the polar junctures of the three colpi. The patterns of distribution of these characters suggest that the sublophate pollen of all members of the Vernoniae may be reversion types from various lophate types. It is thus notable that the lophate types and sublophate types of the Linziinae and Gymnantheminae all have radially symmetrical organization with regular arrangement

of lacunae or incipient lacunae in both lophate and sublophate forms. The non-colpate lophate pollens of the Centrapalinae and Erlangeinae treated below also have sublophate types that are colpate but have smaller and more irregularly arranged incipient lacunae.

Linzia has baculae that are connected to each other at their bases and have fewer and weaker attachments to the footlayer. This latter condition approximates what is referred to as the rhizomate or two-layered lophae in some members of the Erlangeinae and Centrapalinae treated below, and what is common in the New World subtribe Lepidaploinae (Keeley and Robinson 2009) previously placed in the Vernoniinae (Robinson 1999b).

A different pattern is seen in the many members of the subtribes Erlangeinae and Centrapalinae, where in both the sublophate tricolporate and lophate triporate forms, the incipient lacunae of the sublophate forms and the lacunae of the lophate forms are as mentioned above, smaller and in no regular pattern. The rather irregular disposition of lacunae is especially noticeable at the poles of the grains. For these latter forms, two other terms must be added, tricolporate sublophate (Fig. 10A–C) and triporate lophate (Fig. 4A, B, D–F).

The triporate grains in the Erlangeinae and Centrapalinae have subtypes. *Cyanthillium* (Fig. 4 D–F) has baculae only at the intersections of the muri or lophae, and *Bothriocline* (Fig. 4 A–C), *Erlangea* (Fig 8 A–C.), and *Namibithamnus* (Fig. 16 F–H) have baculae that intrude upon the submural space (the space under the lophae) but tend to leave an ogee-shaped gap in the middle (Fig. 16 F–G). *Bothriocline* is distinct in the triplet of slightly connected lacunae that represent a minimal incipient colpus (Fig. 4 A–C). *Namibithamnus*, *Oocephala* and *Polydora* have pollen with greatly reduced perforated tectum and may be completely non-microporate. *Oocephala* (Fig. 18 B–E) and *Polydora* (Fig. 22 A–I) have many evenly spaced baculae or columellae subtending each of the muri or lophae. The baculae of these latter two genera are subtended by a continuous “rhizomate” structure that is itself only weakly attached to the footlayer (Figs. 18 F, 22 C). This structure of the lophae could be described as having two equally thick layers separated by numerous very short evenly spaced columellae. In all of these listed lophate non-colpate genera, the columella or baculae under the lophae or muri tend to be in a single row. *Vernoniastrum* differs by the irregularly aligned or double-rowed columellae under the muri (Fig. 25 I).

The genera *Oocephala* and *Polydora* have the most distinctive pollen of all genera presently known in the Asteraceae. They have a 5–8-porate condition with pores distributed non-equatorially in noncontiguous (Fig. 18) or sometimes contiguous lacunae (Figs. 18A, B, 22B). These grains are not radially symmetrical but essentially spherically symmetrical or totally asymmetrical, termed pantoporate (Robinson and Skvarla 2014). This differs from the 6-pores in three equatorial pairs found in the southeast Asian genus *Camchaya* Gagnep. in Lecomte (Bunwong and Chantaranothai 2008, Robinson and Skvarla 2010b).

The genera discussed in the section below fall into a number of subtribes. Some genera, from the more basal subtribes (based on DNA studies by Keeley et al. 2007), i.e. Distephaninae (*Distephanus*), Linziinae (*Baccharoides*, *Linzia*), and Gymnantheminae (*Gymnanthemum*), all have tricolporate pollen grains that are either lophate or sublophate.

Pollen and Chemistry

The Distephaninae, Linziinae, and Gymnantheminae, have tricolporate sublophate or lophate forms of pollen and contain elemanolide sesquiterpene lactones as secondary metabolites. In contrast, two of the genera are in the more highly nested subtribe Centrapalinae (*Hilliardiella*, *Parapolydora*) and have weakly sublophate, tricolporate pollen and glaucolide/hirsutanolide sesquiterpenes. According to results from DNA studies combined with some obvious relationships based on pollen, two other genera with lophate, pantoporate pollen also belong to the Centrapalinae (*Oocephala* and *Polydora*).

Most of the remaining genera in the study, on the basis of DNA, structural or other evidence are presently placed in the subtribe Erlangeinae (*Bothriocline*, *Cyanthillium*, *Erlangea*, *Ethulia*, *Namibithamnus*, *Orbivestus*, *Pseudopegolettia*, and *Vernoniastrum*) which includes all the genera that contain the non-sesquiterpenoid 5-alkylcoumarin secondary metabolites.

The genus *Vernonella* has been placed in the subtribe Linziinae with some question by Robinson and Skvarla (2010a).

Results

Disposition of the genera of southern African Vernonieae into subtribes

Subtribe Centrapalinae: *Hilliardiella*, *Oocephala*, *Polydora*, *Parapolydora*

Subtribe Distephaninae: *Distephanus*

Subtribe Erlangeinae: *Bothriocline*, *Cyanthillium*, *Erlangea*, *Ethulia*, *Namibithamnus*, *Orbivestus*, *Pseudopegolettia*, *Vernoniastrum*

Subtribe Gymnantheminae: *Gymnanthemum*

Subtribe Linziinae: *Baccharoides*, *Linzia*, *Vernonella*-placement uncertain

Subtribe Unknown: *Vernonia potamophila*

The presently recognized genera of the Vernonieae in southern Africa can be distinguished by the following key.

Key to the genera of the Vernonieae in southern Africa

- 1 Leaf venation triplinervate; flowers usually yellow or orange, sometimes purple or white (Subtribe Distephaninae).....***Distephanus***
- Leaf venation pinnate or without evident secondary veins; flowers usually purple or blue, sometimes white, never yellow or orange**2**
- 2 Plants woody, shrubs or small trees; outer surfaces of involucral bracts with broad smooth shields, without evident strong midveins or keels (Subtribe Gymnantheminae)..... ***Gymnanthemum***

- Plants herbaceous or small shrublets; outer surfaces of involucre bracts narrow or with midveins or keels **3**
- 3 Involucre bracts usually with rounded tips and with the scarious margin continuous across tip *Vernonella*
- Involucre bracts with acute or awned tips; without continuous scarious margins across tips **4**
- 4 Plants with either involucre bracts with spicules on margins or with broad flattened pappus bristles; pollen lophate and tricolporate, sometimes not echinate (subtribe Linziinae) **5**
- Plants with neither involucre bracts with spicules on margins nor with broad flattened pappus bristles; pollen nearly nonlophate or sublophate and echinate or triporate, not lophate combined with tricolporate **6**
- 5 Involucre bracts without spicules along margins; basal tubes of corollas slender with expanded throat longer than the lobes; pappus bristles broad and flattened outside; pollen with polar lacunae, without spurs projecting into colpi *Baccharoides*
- Involucre bracts with spicules along lateral margins; corollas funnel-form with lobes longer than throat; pappus bristles capillary, not flattened outside; pollen without polar lacunae, with spurs projecting into colpi above and below pores *Linzia*
- 6 Setulae of achenes deeply divided, sometimes with single cell from near base; hairs of stems simple; pollen tricolporate, non-lophate (typical element of subtribe Centrapalinae) *Parapolydora*
- Setulae of achenes, when present, with pairs of cells not or scarcely divided at tips; hairs of stems simple, T-shaped or L-shaped; pollen triporate or polyporate without colpi or non-lophate and tricolporate (some Centrapalinae and members of subtribe Erlangeinae) **7**
- 7 Pappus bristles elongate and subplumose *Oocephala*
- Pappus bristles absent, short, scabrid or barbellate **8**
- 8 Involucre bracts ca. 80 in ca. 6 series; stems with asymmetrical L-shaped hairs, with cap-cell mounted near one end; pollen pantoporate *Polydora*
- Involucre bracts less than 50 in less than 5 series; stems with variously shaped hairs; pollen triporate **9**
- 9 Pollen sublophate, without distinct polar lacunae **10**
- Pollen lophate and triporate, with irregular cluster of polar lacunae **14**
- 10 Pappus totally lacking or present as cylindrical collar *Ethulia*
- Pappus with capillary bristles **11**
- 11 Heads few or solitary at tips of long branches or peduncles; stems with short often asymmetrically capped hairs *Pseudopegolettia*
- Heads clustered at tips of branches; stems usually with T-shaped hairs **12**
- 12 Stems with yellowish-brown-velutinous pubescence (unplaced) *Vernonia potamophila*
- Stems with sericeous to hirsute pale pubescence **13**

- 13 Inflorescences with heads in corymbiform cymes; stems, involucre and corollas with symmetrically T-shaped hairs ***Hilliardiella***
 – Inflorescence with heads in seriate cymes; corollas without T-shaped hairs
 ***Orbivestus***
- 14 Pappus bristles much shorter than corollas or lacking, easily deciduous; achenes short and broad, narrowed greatly apically to the narrow insertion of the corolla **15**
 – Pappus bristles about as long as corolla, rather persistent; achenes not greatly narrowed distally to insertion of corolla **16**
- 15 Hairs of stems often T-shaped with long arms; leaves alternate, opposite or whorled; corolla lobes without long hairs at apex; achenes with few raphids or thick sclerified layer inside of wall; pollen with 2 or 3 lacunae with incomplete muri adjacent to pores ***Botbriocline***
 – Hairs of stems and branches simple with short basal cells and long flexuous terminal cell; leaves alternate; corolla lobes with long hairs at apex; achenes without thick sclerified layer inside, with well-developed layer of dense subquadrate cells containing subquadrate or short-oblong raphids; pollen strictly triporate ***Erlangea***
- 16 Hairs of stems simple or asymmetrical; achenes with numerous idioblasts densely clustered in transverse bands ***Vernoniastrum***
 – Hairs of stems symmetrically T-shaped; achenes with idioblasts not in distinct transverse bands **17**
- 17 Short-lived herbs; hairs with long armed cap cells, forming hirsute or pilose indument ***Cyanthillium***
 – Small subshrubs; hairs of stems and bracts with small or elongate cap-cells, forming dense tomentellous or sericeous cover ***Namibithamnus***

Taxonomy

***Baccharoides* Moench, 1794**

Figures 1 A, B; 2 A; 3 A–I

Baccharoides Moench, *Methodus* 328 (1794). – Type: *Conyza anthelmintica* L.

Ascaricida Cass., *Dict. Sci. Nat.* 3, suppl. 38 (1817), nom. superfl. – Type: *Conyza anthelmintica* L.

Candidea Tenore, *Atti Reale Accad. Sci. Sez. Soc. Reale Borbon* 4 (CI. Botan.): 104, t. 1, 2 (1839). – Type: *Candidea senegalensis* Tenore.

Vernonia subsect. *Stengelia* Sch. Bip. ex Walp., *Repert. Bot. Syst.* 2: 946 (1843). – Type: *Vernonia adoensis* Sch. Bip. ex Walp.

Stengelia Steetz in Peters, *Reise Mossamb.*, Bot. 360. 1864. – Type: *Vernonia schimperi* DC.

Vernonia sect. *Stengelia* (Sch. Bip. ex Walp.) Benth. in Benth. & Hook.f., *Gen. Pl.* 2: 127 (1873).



Figure 1. Photographs of *Baccharoides*, *Bothriocline*, and *Vernonia potamophila*. *Baccharoides adoensis* (Sch. Bip. ex Walp.) H. Rob. **A** Habit **B** Close up of flowering head: note that the corollas are narrowed near the apex and have an lengthened throat that is much longer than the short lobes and the involucre bracts have a differentiated margin that is often pale or reddish; *Bothriocline laxa* N.E. Br. **C** Immature heads; *Vernonia potamophila* Klatt. **D** Image of herbarium specimen (PRE). See Appendix C for citation details.

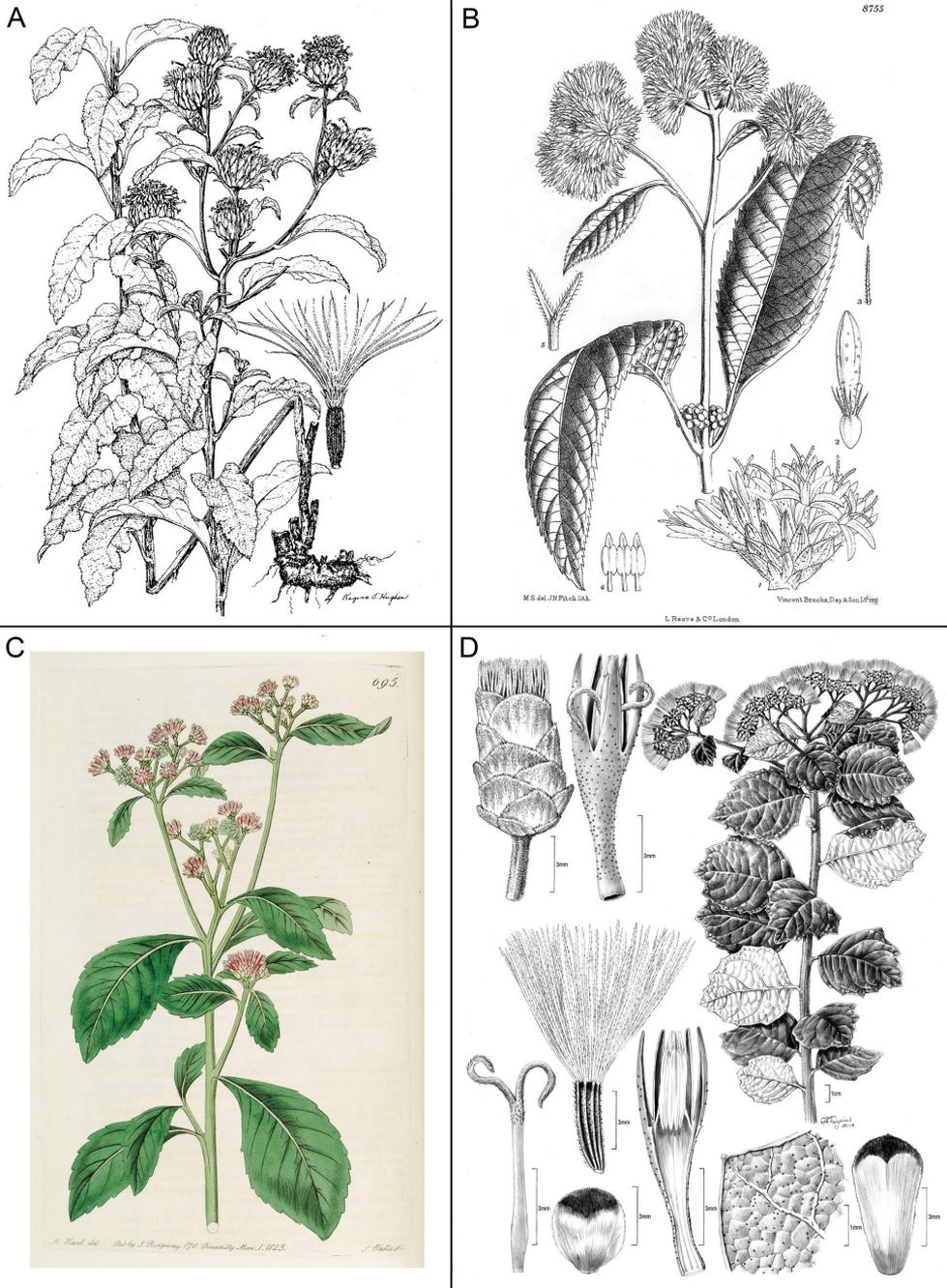


Figure 2. Illustrations: **A** *Baccharoides adoensis* (Sch. Bip. ex Walp.) H. Rob. **B** *Bothriocline aggregata* Hutch., note: this taxon is not found in southern Africa **C** *Ethulia conyzoides* L.f., note: lack of pappus; and **D** *Gymnanthemum koekemoerae* H. Rob. & V. Funk, note: broad involucre bracts without a high midrib. See Appendix C for citation details.

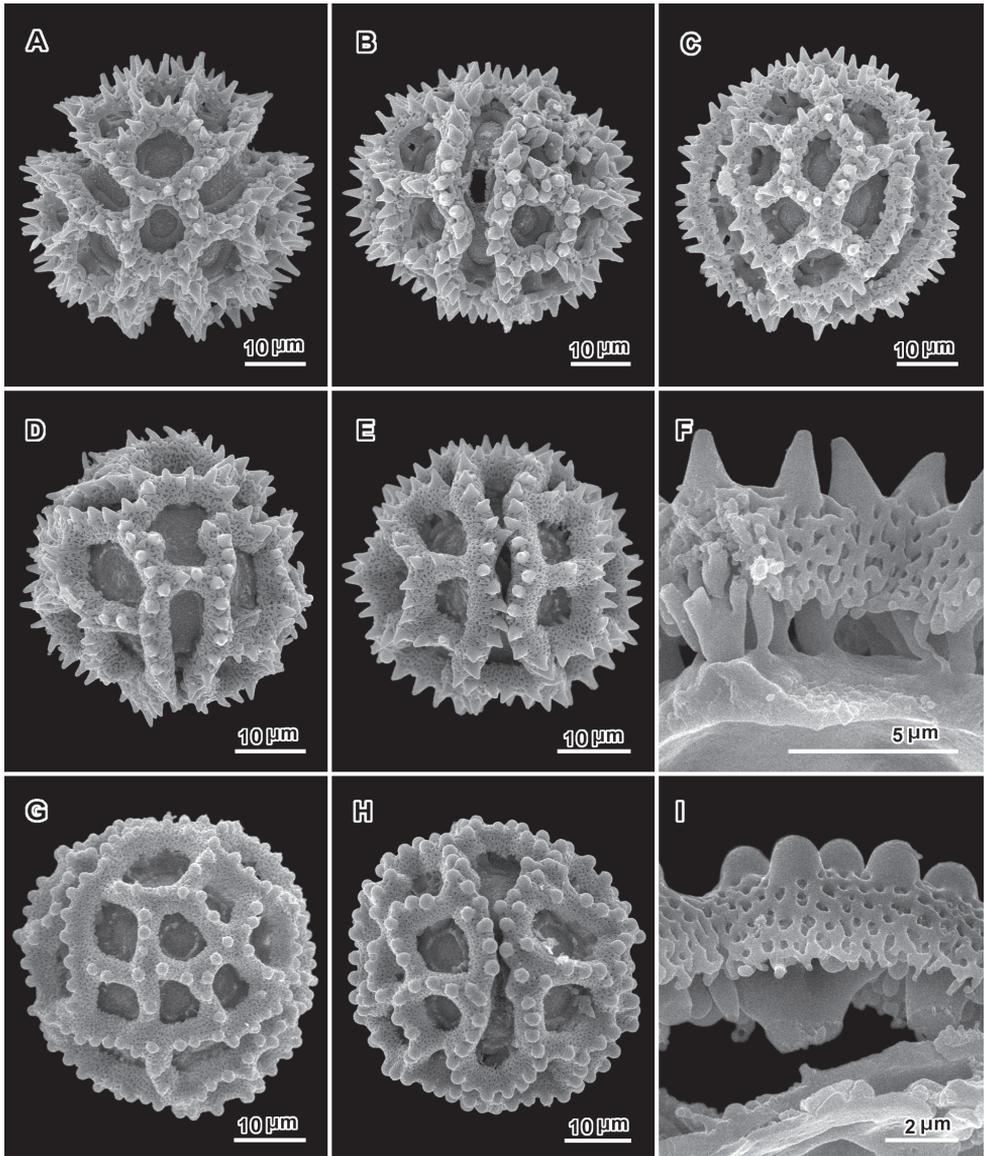


Figure 3. Scanning electron electron micrographs from three collections of acetolyzed echinolophate *Baccharoides* pollen showing variations in spine shape from acute to markedly blunt. **A–H.** *Baccharoides anthelmintica* (L.) Moench. **A** polar view **B** Equatorial view **C** Lateral view **D** Near polar view **E** Equatorial view **F** Fractured grain **G** Lateral view **H** Equatorial view **I** Fractured grain. (A–C, USDA P.I. 283729; D–E, Cooray 70031701R; G–I, Koelz 7469). [Views from Robinson and Skvarla (2010); Figure 1 B = original Figure 1G; Figure 1C = original Figure 1H; and Figure 1H = original Figure 1J.]

Resources. Treatment by Isawumi et al. (1996).

Descriptions. Annual or perennial herbs, suffruticose; stems erect or reclining; hairs short-stalked with an erect, elongate apical cell. Leaves alternate, narrowly petiolate; blades chartaceous, ovate to elliptic, serrate, secondary veins pinnate, ascending at 45° angles or more. Inflorescence with single lateral or terminal head or heads in corymbiform groups; peduncles usually solid, sometimes fistulose. Heads with involucre broadly campanulate or hemispherical; bracts 25–100 in 4–8 series, mostly gradate but with outer bracts sometimes elongate and foliiform, tips of bracts appendaged, white or colored; receptacles epaleate. Florets 25–100 in a head; corollas reddish or lavender to white, with long slender basal tube, limb abruptly expanded at base, cylindrical, with lobes about as long as throat, erect, with various hairs and glands outside, inside with cells elongate, transversely striate; anther thecae spurred with small tails; endothelial cells with nodular thickenings on transverse walls; apical appendages oblong-ovate, rounded or acute at tips, glabrous; nectary elongate, cylindrical; style base without node; sweeping hairs acicular. Achenes cylindrical or turbinate, 8–20-costate, glabrous or with setulae distinctly cleft or with glands or idioblasts, carpodium annuliform, large to obsolete, with thickened porose walls, raphids in ovules elongate, with rhomboid tips; pappus pluriseriate, persistent or caducous, inner capillary, flattened, barbellate on margins, sometimes shortly connate at base, sometimes with outer row of small scales. Chromosome number $x = 10$ (Jones 1970, Mathew and Mathew 1983)

Pollen. 43.5–72.0 μm diam. (Isawumi et al. 1996); tricolporate, echinolophate; lacunae regularly disposed, one at each pole, 2 across intercolpus; tectum restricted to muri, with distinct microperforations; stout baculae under muri firmly attached to footlayer (Fig. 3A–I).

Most notable secondary metabolites, sesquiterpene elemanolides (Bohlmann and Jakupovic 1990, as *Vernonia anthelmintica* (L.) Willd., *V. hymenolepis* A. Rich., *V. lasiopis* O. Hoffm.), eudesmanolide (Bohlmann and Jakupovi 1990, as *Vernonia adoensis* Sch. Bip. ex Walp.).

Key to the species of *Baccharoides*

- 1 Leaf blades sessile or subsessile *B. benguelensis*
- Leaves distinctly petiolate 2
- 2 Branching perennial herbs from large root crown; fusiform tubers often present; peduncle not enlarged or fistulose distally *B. adoensis*
- Annual herbs; without tubers; peduncles often somewhat enlarged and fistulose distally *B. anthelmintica*

***Baccharoides adoensis* (Sch. Bip. ex Walp.) H. Rob., 1990**

- Vernonia adoensis* Sch. Bip. ex Walp., Repert. Bot. Syst. 2: 946. 1843.
Stengelia adoensis Sch. Bip. ex Hochst., Flora 24: Intelligenzbl. 1841: 1(2): 26. 1841, nom. nud.
Vernonia kotschyana Sch. Bip. ex Walp., Repert. Bot. Syst. 2: 947. 1843.
Vernonia macrocephala A. Rich., Tent. Fl. Abyss. 377. 1847, nom. illeg., non Less.
Ascaricida adoensis (Sch. Bip. ex Walp.) Steetz in Peters, Reise Mossamb. 358. 1864.
Ascaricida mossambiquensis Steetz in Peters, Reise Mossamb. 358. 1864.
Ascaricida richardi Steetz in Peters, Reise Mossamb. 358. 1864.
Vernonia grantii Oliv., Trans. Linn. Soc. London 29: 92. 1873.
Vernonia polymorpha var. *adoensis* (Sch. Bip. ex Walp.) Vatke, Linnaea 39: 476. 1875.
Vernonia polymorpha var. *accedens* Vatke, Linnaea 39: 477. 1875.
Vernonia polymorpha var. *ambigua* Vatke, Linnaea 39: 477. 1875.
Vernonia tigrensensis Oliv. & Hiern in Oliv., Fl. Trop. Africa 3: 290. 1877.
Vernonia shirensensis Oliv. & Hiern in Oliv., Fl. Trop. Africa 3: 291. 1877.
Vernonia mossambiquensis (Steetz) Oliv. & Heirn in Oliv., Fl. Trop. Afr. 3: 292. 1877, non *V. mossambicensis* Busc. & Muschler 1913.
Vernonia whyteana Britten, Trans. Linn. Soc., London, ser. 2, 4: 17. 1894.
Vernonia leptolepis Bak., Bull. Misc. Inf. Kew 1898: 147. 1898, nom. illeg., non O. Hoffm. 1895.
Vernonia woodii O. Hoffm. in Engl., Bot. Jahrb. 38: 198. 1906.
Vernonia integra S. Moore, J. Bot. 46: 39. 1908.
Vernonia bequartii De Wild., Feddes Repert. 13: 206. 1914.
Vernonia integra S. Moore, J. Bot. 46: 39. 1918.
Candidea stenostegia Stapf, Bot. Mag. 149: t. 8981. 1923.
Vernonia latisquama Mattf., Bot. Jahrb. Syst. 59: Beibl. 133: 5. 1924.
Vernonia fulviseta S. Moore, J. Linn. Soc. Bot. 47: 266. 1925-27.
Vernonia stenostegia (Stapf) Hutch. & Dalz., Fl. W. Trop. Africa 2: 164. 164, in key 166. 1931.
Vernonia adoensis var. *mossambiquensis* (Steetz) G.V. Pope, Kew Bull. 43(2): 284. 1988.
Vernonia adoensis var. *kotschyana* (Sch. Bip. ex Walp.) G.V. Pope, Kew Bull. 43(2): 285. 1988.
Baccharoides adoensis (Sch. Bip. ex Walp.) H. Rob., Proc. Biol. Soc. Washington 103(1): 250. 1990.
Baccharoides adoensis (Sch. Bip. ex Walp.) H. Rob. var. *kotschyana* (Sch. Bip. ex Walp.) Isawumi, El-Ghazaly & B. Nord., Grana 35. 219. 1996.
Baccharoides adoensis (Sch. Bip. ex Walp.) H. Rob. var. *mossambiquensis* (Steetz) Isawumi, El-Ghazaly & B. Nord., Grana 35. 219. 1996.

Distribution. Ivory Coast, Ethiopia, Malawi, Mozambique, Zimbabwe, South Africa.

***Baccharoides anthelmintica* (L.) Moench, 1794.**

Conyza anthelmintica L., Sp. Pl. ed 2, 1207. 1763.

Baccharoides anthelmintica (L.) Moench, Method. 578., 1794.

Vernonia anthelmintica (L.) Willd., Sp. Pl. 3: 1634. 1803.

Vernonia stenolepis Oliv., Trans Linn. Soc. ser 2, 2: 337. 1887.

Dolosanthus sylvaticus Klatt, Bull. Herb. Boiss. 4: 473, t. 5. 1896.

Centratherum anthelminticum (L.) Gamble, Fl. Pres. Madras 2: 667. 1921.

Distribution. Congo, Kenya, Tanzania, Uganda, Malawi, Zambia, Zimbabwe, Botswana, Namibia, Sri Lanka, Nepal, Pakistan, India, China.

***Baccharoides benguellensis* (Hiern) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152894-1

Vernonia benguellensis Hiern, Cat. Afr. Pl. 1: 536. 1898.

Vernonia limosa O. Hoffm. in Warburg, Kunene-Sambesi Exped. 400. 1903.

Distribution. Angola, also cited from SW Africa, but that locality probably not intended in the restricted sense.

Note. The species is known from photographs of types and from descriptions deposited at US by C.E. Smith. The type photographs – as well as Fig. 1 B (for corollas) – clearly show the corolla form and flattened pappus bristles of *Baccharoides*, and the species is not accounted for elsewhere. The type specimen of *Vernonia benguelensis* is collected in Angola, ad lacum de Ivantola, Feb. 1860, *Wehwitsch 3276b* (BM, photo seen). The lectotype of *Vernonia limosa* is cited as Südwest Afrika, am Longa unterh. Chijija, Jan. 1900, *Baum 624* (BM, photo seen; Smith 1917). This locality is situated in Angola (Figueiredo et al. 2009).

***Bothriocline* Oliv. ex Benth.**

Figures 1C; 2B; 4A–C

Bothriocline Hooker's Icon. Pl. 12: 30, t. 1133. 1873. – Type: *Bothriocline schimperi* Oliv. & Hiern ex Benth.

Volkensia O. Hoffm., Bot. Jahrb. Syst. 20: 219. 1894; Engl. & Prantl, Natürl. Pflanzenfam. iv. 5: 387. 1893. – Type: *Volkensia argentea* O. Hoffm.

Resources. Many species are keyed in Jeffrey's (1988) treatment of Vernonieae in East Africa and in Wild and Pope (1977), Wild (1978a, 1978b).

Descriptions. Perennial herbs (up to 1 m) to subshrubs, branching sparse, stems erect with a solid pith and long-armed T-shaped hairs with short 2-celled stalks. Leaves

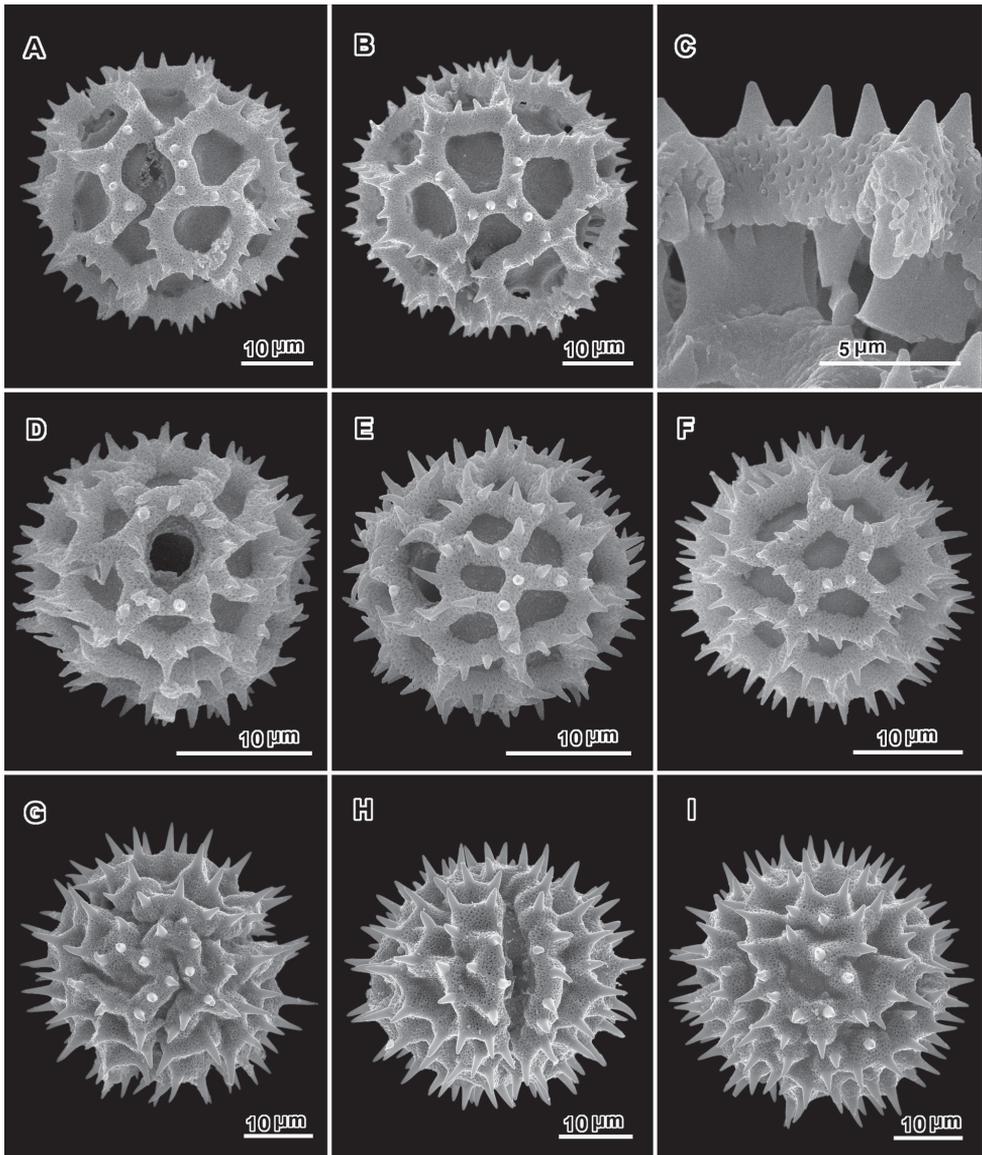


Figure 4. Scanning electron micrographs of acetolyzed pollen of echinolophate *Bothriocline* and *Cyanthillium* and sublophate-lophate *Distephanus*. **A–C** *Bothriocline schimperi* Oliv. & Hiern ex Benth. **A** Equatorial view, note incipient colpus of 3 connected lacunae centered on pore **B** Near polar view **C** Fractured grain **D–F** *Cyanthillium cinereum* (L.) H. Rob. **D** Equatorial view **E** Lateral view with apertures on sides **F** Lateral view **G–I** *Distephanus angustifolia* (DC.) **H** Rob. & B. Kahn. **G** Polar view **H** Equatorial view **I** Lateral view. (A–C, *F. Meyer 8159*; D–F, *Evans 344*; G–I, *Sidley 2211*).

alternate, opposite or whorled, sessile to short petiolate, blade narrow to ovate or elliptical, pinnately veined, often paler or tomentose to sericeous below. Inflorescence laxly to densely corymbiform or thyriform cymes; heads pedunculate. Involucres campanulate, bracts ca. 50–60, gradate in 3–4 series, cuspidate at apex, with distinct pale or reddish lateral margins, nearly glabrous to pilosulous outside; receptacle convex, epaleaceous, with glabrous reticulum. Florets 3–100 or more in a head; corollas purplish, funnellform, basal tube slender with small stipitate glands, throat shorter than 1 mm, lobes, linear-lanceolate, with glandular dots and often with stiff subapical hairs; anther thecae blunt at base with few sterile cells; apical appendages ovate-oblong, with thin cell walls; style base with minimal annuliform node; sweeping hairs acicular, mostly restricted to branches. Achenes prismatic, short and broad with 3–6(–9) ribs, setuliferous with sparse short setulae scarcely split at tips, often densely covered with idioblasts and with scattered subquadrate raphids. Pappus of few or no short easily deciduous bristles narrowed at base, without obvious shorter outer series or outer pappus a rim or collar. Chromosome number $n = 9, 10, 18–20$ (Jones 1979, 1982). Pollen grains ca. $47 \mu\text{m}$ in diam, lophate to rarely sublophate, finely echinate, pores in triplet of connected colpar lacunae, perforated tectum usually restricted to muri (Fig. 4 A–C).

Notable secondary metabolites include 5-alkylcoumarins and sesquiterpene glucolides/hirsutanolides [Bohlmann and Jakupovic 1990, as *Bothriocline laxa* N.E. Br., *B. longipes* (Oliv. & Hiern) N.E. Br.], and 5-alkylcoumarins (Bohlmann and Jakupovic 1990, as *Erlangea fusca* S. Moore, *E. rogersii* S. Moore).

***Bothriocline laxa* N.E. Br., 1894.**

Bothriocline laxa N.E. Br., Bull. Misc. Inf. Kew 1894: 388. 1894.

Distribution. Tanzania, Zambia, Malawi, Zimbabwe, Congo, Angola, South Africa (Transvaal).

***Cyanthillium* Blume, 1826**

Figures 4 D–F; 5 A–C

Cyanthillium Blume, Bidjr. 889. 1826. – Type: *Cyanthillium villosum* Blume
Isonema Cass., Bull. Soc. Philom. Paris 1817: 152. 1817, nom. illeg., non *Isonema* R.
Br., 1810. – Type: *Isonema ovata* Cass.

Cyanopsis Blume ex DC., 5: 69. 1836, nom. illeg. superfl., non Cass. 1817.

Vernonia sect *Tephrodes* DC., Prodr. 5: 24. 1836. – Lectotype: *Conyza cinerea* Blume
(Jones 1981a).

Claotrachelus Zoll. & Moritz ex Zoll., Natuur-Geneesk. Arch. Ned. Indie 2: 263, 565.
1845. – Type: *Claotrachelus rupestris* Zoll. & Moritz ex Zoll.



Figure 5. Photographs of *Cyanthillium cinereum* (L.) H. Rob: **A** Inflorescence, **B** habit, **C** Close up of heads in fruit. See Appendix C for citation details.

Seneciodes L. ex Post & O. Kuntze, Lex. Gen. Phan. 2: 515. 1903. – Type: *Conyza cinerea* L.

Triplotaxis Hutch., Bull. Misc. Inform. 1914: 355. 1914. – Lectotype: *Herderia stellulifera* Benth. in Hook. (Robinson 1990a).

Vernonia subsect. *Tephrodes* (DC.) S.B. Jones, *Rhodora* 83: 70. 1981.

Resources. Traditionally treated as part of *Vernonia*.

Descriptions. Annual or short-lived perennial herbs to 1 m tall; stems erect or spreading; hairs symmetrically or asymmetrically T-shaped with short stalk. Leaves alternate; petioles narrow; blades membranaceous, ovate to narrowly lanceolate. Inflorescences terminal, moderately densely to laxly branching, distinctly cymiform or with rather corymbiform branches, with minute bracteoles; peduncles rather short to elongate. Heads narrowly campanulate, involucre bracts ca. 30 in 3(–5) series, gradate, thinly chartaceous, green with pale or purplish margins, persistent, often with pilose to sericeous pubescence; receptacles epaleaceous. Florets 15–94 in a head; corollas bluish to lavender, funnelliform with slender lower tubes, throat a third as long to nearly as long as lobes, lobes with simple hairs especially near tips; anthers without tails; apical appendages oblong-ovate, glabrous, with thin cell walls; style base with broad node; style branches with acicular sweeping hairs. Achenes 5-ribbed, or terete, setulae shortly cleft at tips, with idioblasts, sometimes with glands, raphids elongate; inner pappus of many long, sometimes rather fragile, slender-tipped capillary bristles, outer series of persistent squamellae, one species with callose ring. Chromosome number $n = 9, 18, 20$ (Turner and Lewis 1965, Mathew and Mathew 1976, Jones 1979).

Pollen ca. 30 μm in diameter (dry); triporate, echinolphate, ca. 21 lacunae rather irregularly disposed at poles and in intercolpi; perforated tectum restricted to ridges of muri, with distinct microperforations; spinules of muri short, shorter than width of mural ridge, pointed, without columellae under each murus; baculae single at junctures of muri and no baculae between junctures, each intersection of muri with stout columella that is firmly attached to footlayer (Fig. 4 D–F).

Notable secondary metabolites, 5-alkylcoumarins, sesquiterpene glaucolides, guanolides (Bohlanmn and Jakupovic 1990, as *Vernonia chinensis* Less., *V. cinerea* Less.).

Key to the species of *Cyanthillium*

- 1 Plants perennial, weakly frutescent, often scrambling..... *C. wollastonii*
- Plants annual **2**
- 2 Inner pappus absent or of few dissected scales; outer pappus forming a collar *C. stelluliferum*
- Inner pappus of many bristles; outer pappus not forming a collar **3**
- 3 Outer pappus of short oblong often rounded scales less than 0.2 mm long...
..... *C. vernonioides*
- Outer pappus of narrow lanceolate scales 0.2 or more long.....
..... *C. cinereum*

***Cyanthillium cinereum* (L.) H. Rob., 1990**

Conyza cinerea L. Sp. Pl. 862. 1753.

Vernonia cinerea (L.) Less., Linnaea 4: 291. 1829.

Vernonia lentii O. Hoffm. in Engl., Pflanzenw. Ost-Afr. C: 404. 1895.

Seneciodes cinerea (L.) Post & Kuntze, Lex. Gen. Plan. 2: 515. 1903.

Cyanthillium cinereum (L.) H. Rob., Proc. Biol. Soc. Wash. 103: 252. 1990

Distribution. Widely introduced weed, pantropical.

***Cyanthillium stelluliferum* (Benth.) H. Rob., 1990**

Herderia stellulifera Benth. in Hook.f. & Benth., Niger Fl. 425. 1849.

Triplotaxis stellulifera (Benth.) Hutch., Bull. Misc. Inf. Kew 1914: 356. 1914.

Cyanthillium stelluliferum (Benth.) H. Rob., Proc. Biol. Soc. Wash. 103(1): 252. 1990.

Distribution. Tropical Africa south to Angola.

***Cyanthillium vernonioides* (Muschl.) H. Rob., 1999**

Erlangea vernonioides Muschl., Bot. Jahrb. Syst. 45: 62. 1911, non *V. vernonioides* (A.Gray) Bacigalupo 1931.

Vernonia meiostephana C. Jeffrey, Kew Bull. 43: 225. 1988.

Cyanthillium vernonioides (Muschl.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 229. 1999.

Distribution. Tropical Africa from Congo, Uganda and Kenya south to Zambia, Zimbabwe and South Africa (Transvaal), Madagascar.

***Cyanthillium wollastonii* (S. Moore) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152895-1

Vernonia wollastonii S. Moore, Journ. Linn. Soc. 38: 257. 1908.

Vernonia gracilipes S. Moore, Journ. Linn. Soc. 40: 105. 1911.

Vernonia heterocarpa Chiov., Nuov. Giorn. Bot. Ital, n.s. 36: 365. 1929.

Vernonia transvaalensis Hutchinson, Botanist S. Afr. 347. 1946, in note.

Vernonia umbratica Oberm., J. S. Afr. Bot. 2: 164. 1936.

Distribution. Abyssinia, Malawi, Sudan, Swaziland, Tanzania, South Africa (Transvaal), Uganda, Zimbabwe.

***Distephanus* Cass., 1817**

Figures 4 G–I; 6 A–H

Distephanus Cass. Bull. Soc. Philom. Paris 1817: 151. 1817.*Gongrothamnus* Steetz in Peters, Reise Mossamb., Bot.: 336. 1864. – Type: *Gongrothamnus divaricatus* Steetz in Peters*Newtonia* O. Hoffm. in Engler & Prantl, Natürl. Pflanzenfam. 4(5): 285. 1892, nom. illeg., non Baill. 1888. – Type: *Newtonia angolensis* O. Hoffm.*Antunesia* O. Hoffm., Bolet. Soc. Brot. 10^o 178. 1893 (“1892”), nom. nov. for *Newtonia*.

Resources. For discussion and numerous transfers of species see treatment by Robinson and Kahn (1986). For a recent treatment of the genus in southern Africa see Swelankomo and Manning (2014).

Descriptions. Shrubs or vines; hairs arachnoid, contorted or asymmetrically T-shaped. Leaves alternate; petioles short; blades ovate to rounded, often with truncate to subcordate bases, less often narrow with cuneate bases, margins usually entire or subentire, venation usually with stronger more ascending basal pair or strongly triplinervate, less often irregularly pinnate. Inflorescences terminal on stems or branches, with single heads or usually branching, corymbiform with minute bracts or thyrsoid with foliose bracts; peduncles usually short. Heads with campanulate involucre; bracts 21–24(–75) in 4–6(–7) gradate series, without appendaged tips; receptacles epaleaceous. Florets 10–16(–75) in a head; corollas usually yellow, purplish in a few continental African species; anther thecae with distinct broad often sclerified basal appendages; endothecial cells with simple, broad, non-contiguous, sclerified shields; apical appendages without glands; style base with large abruptly distinct node; style branches with obtuse sweeping hairs. Achenes cylindrical to prismatic, sometimes subtriquetrous or quadrangular, with 5–12 ribs, usually 10, setulae or glands present or absent, raphids elongate; carpodium turbinate; pappus of many capillary bristles, outer series of squamellae. Chromosome numbers $n = 9, 10, 15$ (Jones 1982, Gill and Omoigui 1992).

Pollen: 30–36 μm in diameter (dry); tricolporate, sublophate to lophate; lophate forms with muri projecting as spurs into colpus, with echinate or with nearly psilate ridges; tectum continuous in intercolpi and at poles, or in pockets surrounded by ridges, with distinct perforations; with columellae under spines or with muri granular inside, without distinct baculae (Figs. 4 G–I).

Notable secondary metabolites: sesquiterenes, elemanolides (Bohlmann and Jakupovic, as *Gongrothamnus aurantiaca* N.E. Br.), guaianolide (as *Gongrothamnus sublutea* Elliot., guaianolides (Bohlmann and Jakupovic 1990, as *Vernonia anisochaetoides* Sond., glaucolides/hirsutanolides (Bohlmann and Jakupovic 1990, as *Vernonia angulifolia* DC., *V. tufrnellae* S. Moore).

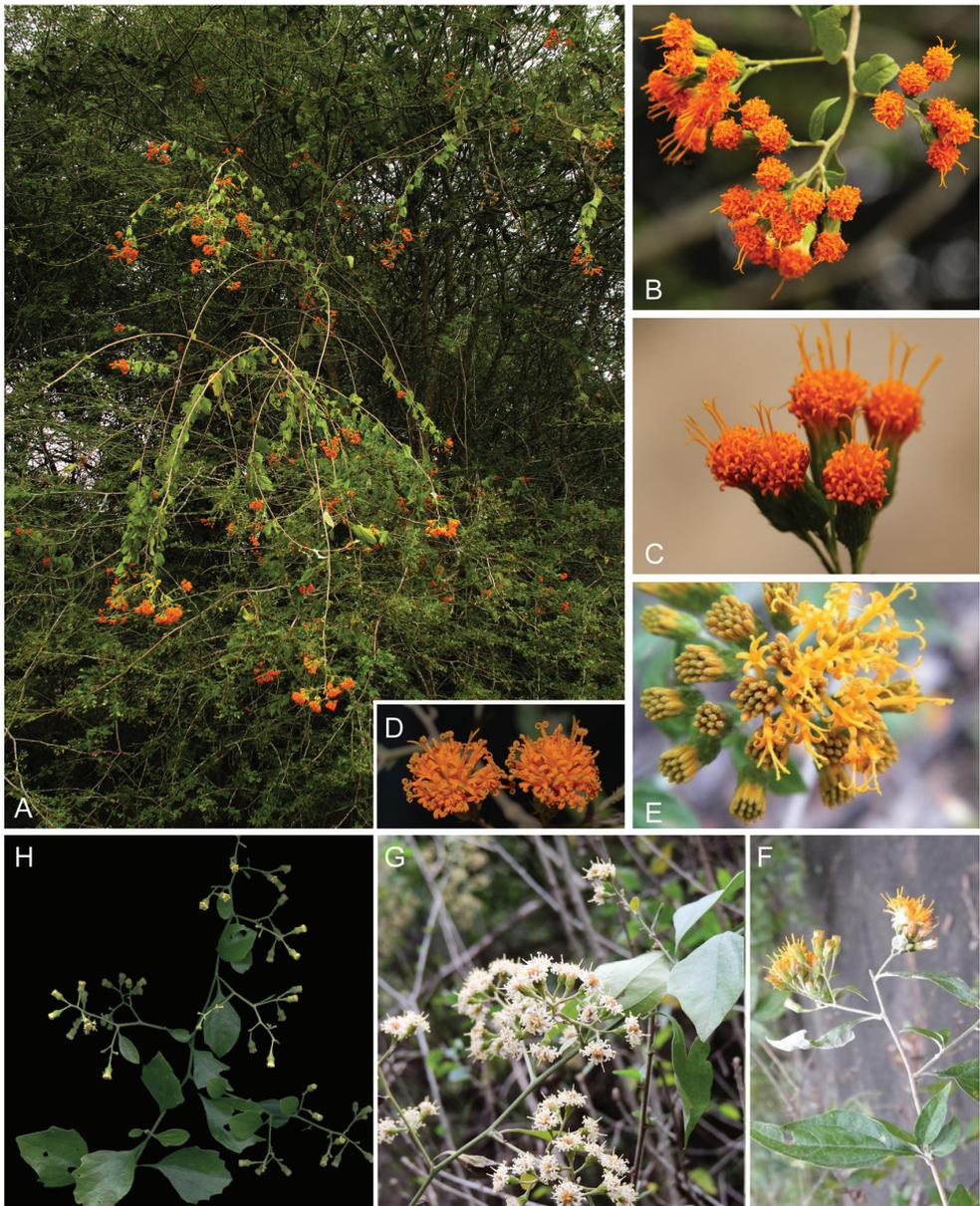


Figure 6. Photographs of *Distephanus*: **A–F** *Distephanus divaricatus* (Steetz) H. Rob. & B.Kahn; **G–H** *Distephanus anisochaetoides* (Sond.) H. Rob. & B.Kahn. Note the variable flower color in *D. divaricatus*. Note: trinervate venation, lack of lavender corollas and presence of yellow and orange. See Appendix C for citation details.

Key to the species of *Distephanus*

- 1 Involucral bracts oblong with obtuse or shortly acute tips.....2
 – Involucral bracts lanceolate, narrowly acute 3
 2 Leaf blades ovate, with marginal lobes; branches of inflorescence essentially straight; corollas purple or yellow.....*D. angulifolius*
 – Leaf blades rhomboidal, cuneate proximally; inflorescence branches with strong zigzag pattern; corollas white.....*D. anisochaetoides*
 3 Corollas purple or white *D. inbacensis*
 – Corollas yellow or orange..... 4
 4 Stems and abaxial surfaces of leaves not tomentellous; leaf blades oblong or ovate-elliptical, often blunt at tip *D. angolensis*
 – Stems and abaxial surfaces of leaves with fine tomentellum; leaf blades ovate, broadest at or below proximal third*D. divaricatus*

***Distephanus angolensis* (O. Hoffm.) H. Rob. & B. Kahn, 1986**

Newtonia angolensis O. Hoffm., Natürl. Pflanzenfam. 4(5): 285. 1892.

Antunesia angolensis (O. Hoffm.) O. Hoffm., Bolet. Soc. Brot. 10: 178. 1893.

Gongrothamnus angolensis (O. Hoffm.) Hiern, Cat. Welw. Afr. Pl. 1: 592. 1898.

Vernonia angolensis (O. Hoffm.) N.E. Brown, Kew Bull. 1909: 116. 1909.

Vernonia lutea N.E. Brown, Kew Bull. 1909: 116. 1909.

Distephanus angolensis (O. Hoffm.) H. Rob. & B. Kahn, Proc. Biol. Soc. Wash. 99(3): 498. 1986. SW Africa.

Distribution. Angola, Namibia.

***Distephanus angulifolius* (DC.) H. Rob. & B. Kahn, 1986**

Vernonia angulifolia DC., Prodr. 5: 29. 1836.

Distephanus angulifolius (DC.) H. Rob. & B. Kahn, Proc. Biol. Soc. Wash. 99(3): 499. 1986.

Note. Jeffrey (1988) mentioned *Vernonia biafrae* Oliv. & Hiern in Oliv. was once placed in the synonymy of this species by Maquet in Troupin (1985), but cited a number of differences that did not include the strictly pinnate venation of the more northern *V. biafrae* [= *Distephanus biafrae* (Oliv. & Hiern in Oliv.) H. Rob.].

Distribution. Mozambique, South Africa (Natal, Transkei).

***Distephanus anisochaetoides* (Sond.) H. Rob. & B. Kahn, 1986**

Vernonia anisochaetoides Sond., Linn., 23: 61. 1850.

Distephanus anisochaetoides (Sond.) H. Rob. & B. Kahn, Proc. Biol. Soc. Wash. 99(3): 499. 1986.

Distribution. South Africa (Cape colony, Natal).

***Distephanus divaricatus* (Steetz) H. Rob. & B. Kahn, 1986**

Gongrothamnus divaricatus Steetz in Peters, Reise Mossamb. Bot. 242. 1864.

Gongrothamnus aurantiacus O. Hoffm., Bot. Jahrb. Syst. 30: 433. 1902.

Vernonia aurantiaca (O. Hoffm.) N. E. Brown, Kew Bull. 1909: 116. 1909.

Vernonia vitellina N. E. Brown, Kew Bull. 1909: 117. 1909.

Gongrothamnus corradianus Cufod., Nuovo Giorn. Bot. Ital. n.s. 1: 111. 1943.

Distephanus divaricatus (Steetz) H. Rob. & B. Kahn, Proc. Biol. Soc. Wash. 99(3): 499. 1986.

Distribution. Angola, Botswana, Congo, Ethiopia, Kenya, Malawi, Mozambique, Namibia, Tanzania, South Africa (Transvaal), Zambia, and Zimbabwe.

***Distephanus inhacensis* (Pope) Boon & Glen, 2013**

Vernonia inhacensis G.V. Pope, Kew Bull. 43(2): 280. 1988.

Distephanus inhacensis (Pope) Boon & Glen, Bothalia 43: 94. 2013.

Distribution. Mozambique and South Africa (Natal).

***Erlangea* Sch. Bip., 1853**

Figures 7 A, B; 8 A–C

Erlangea Sch. Bip., 1853, Flora 36: 34. 1853. – Type: *Erlangea plumosa* Sch. Bip.

Resources. Species treatment based on Wild and Pope 1977.

Descriptions. Annual or short-lived perennial herbs; stems erect, branching near base; hairs on vegetative parts simple, uniseriate, multicellular, with a straight elongate apical cell. Leaves alternate, sessile or subsessile, pinnately veined with weak secondary veins, margins serrulate, apices obtuse. Inflorescence with single terminal head or laxly cymiform with narrowly pedunculate heads. Heads campanulate; involucre bracts 45–60 in 3–4 series, gradate, cuspidate apically, with distinct pale or reddish lateral



Figure 7. Photographs of *Erlangea* and *Ethulia*: **A–B** *Erlangea misera* S. Moore, and **C–E** *Ethulia conyzoides* L.f. subsp. *conyzoides*, note: *Ethulia* has no capillary pappus. See Appendix C for citation details.

margins, pilose to lanulose outside; receptacle convex, epaleaceous, with glabrous reticulum. Florets 50–75 or more in a head; corollas reddish, funnelform, with slender basal tube bearing small stipitate glands, throat shorter than lobes, lobes linear-lanceolate, with stiff hairs distally or apically; anther thecae short-acute with small sterile margin at base; apical appendage, oblong-ovate, glabrous, with thin cell walls; style base with nar-

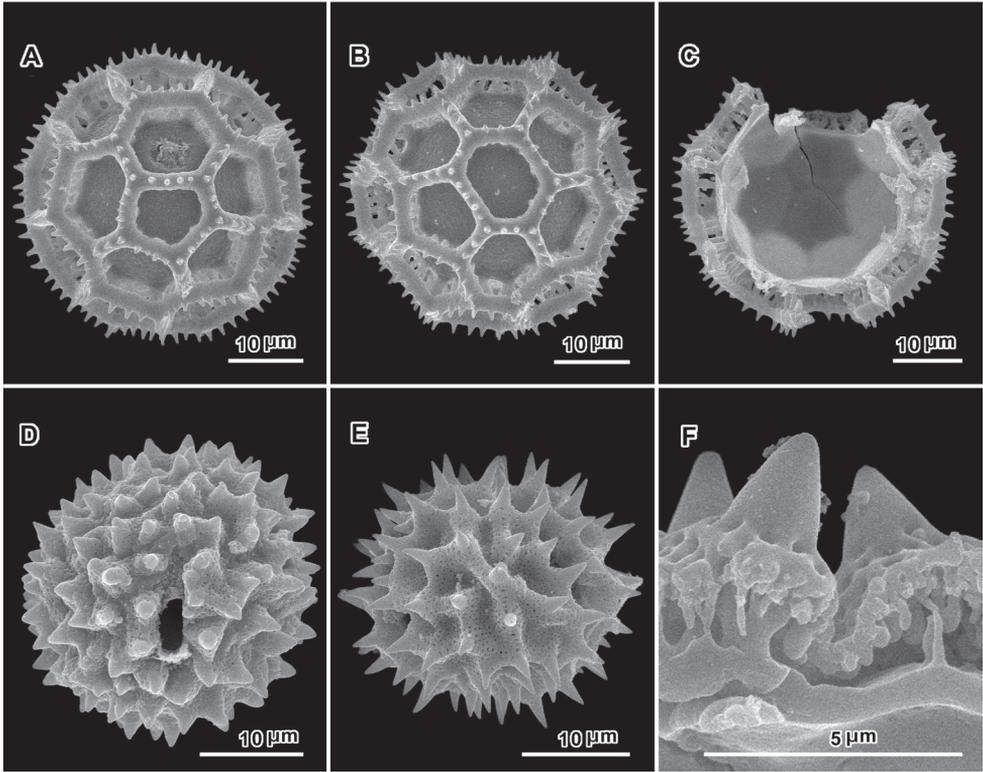


Figure 8. Scanning electron micrographs of acetolyzed echinolophate pollen of *Erlangea* and sublophate pollen of *Ethulia*. **A–C** *Erlangea misera* (Oliv. & Hiern) S. Moore. **A** Poral view **B** Near polar view **C** Grain fragment. **D–F** *Ethulia conzjooides* L.f. **D** Equatorial view, showing comparatively blunt spines **E** Lateral view **F** Grain fragment. (**D–F** Funk 12708 **G** *Petelot* 4047 **H** *Lewis* 6025; *Ethulia* views from Robinson and Skvarla (2010)).

row annuliform sclerified node; sweeping hairs acicular, at lowest level scarcely extending to top of shaft. Achenes shortly obconic, abruptly narrowed distally to insertion of corolla, 3-6-ribbed, setulae restricted mostly to broad ribs, setulae not split at tips, sides with scattered isolated idioblasts, raphids subquadrate or short oblong in dense inner layer of short to quadrate cells in achene wall; pappus of less than 20 easily deciduous barbellate bristles, bases narrow and weakly attached, distinct outer series not evident. Chromosome number $n = 10$ (Turner and Lewis 1965, Nordenstam 1967).

Pollen ca. 47 μm in diameter in fluid, lophate, triporate, with group of polar lacunae, perforated tectum restricted to muri, baculae centered at junctures of muri, leaving ogee-shaped gaps under the centers of the muri (Figs. 8 A–C).

Notable secondary metabolites, eudesmanolide sesquiterpene lactones, Bohlmann and Jakupovic 1990, as *Erlangea remifolia* Wild & Pope).

Key to the species of *Erlangea*

- 1 Leaves sessile or subsessile; blades linear to oblong or ovate-oblong.....
 *E. misera*
- Leaves distinctly petiolate, with petioles to 1.5 cm long; blades ovate.....
 *E. remifolia*

***Erlangea misera* (Oliv. & Hiern) S. Moore, 1902**

Vernonia misera Oliv. & Hiern in Oliv., Fl. Trop. Afr. 3: 278. 1877.

Erlangea schinzii O. Hoffm., Bull. Herb. Boiss. 1: 71. 1893

Bothriocline misera (Oliv. & Hiern) O. Hoffm., Bot. Soc. Brot. 13: 11. 1896.

Erlangea misera (Oliv. & Hiern) S. Moore, J. Linn. Soc., Bot. 35: 310. 1902.

Bothriocline schinzii (O. Hoffm.) O. Hoffm. in Warburg, Kunene-Sambesi Exped. 398. 1903.

Erlangea sessilifolia R.E. Fr., Wiss. Ergebn. Schwed. Rhodesia-Kongo-Exped. 1911–1912, 1: 319. 1916.

Vernonia merenskiana Dinter ex Merxm., Mitt. Bot. München 2: 38. 1954, nom. nud. in syn.

Distribution. Botswana, Mozambique, Namibia (Caprivi strip), Zambia, Zimbabwe.

***Erlangea remifolia* Wild & G.V. Pope, 1977**

Erlangea remifolia Wild & G.V. Pope, *Kirkia* 10(2): 317. 1977.

Distribution. Botswana.

***Ethulia* L.f.**

Figures 7 C–E; 8 D–F

Ethulia L.f. Dec. Prima Pl. Rar. Horti Upsal. 1 (1762); L.f. ex L., Sp. Pl. ed. II: 1171 (1763). – Type: *Ethulia conyzoides* L.f.

Hoehnelia Schweinf. in Höhnel, Zum Rudolf-See und Stephanie-See 86 (1892). – Type: *H. vernonioides* Schweinf. in Höhnel.

Resources. Treatment of the genus by Gilbert and Jeffrey (1988).

Descriptions. Annual or short-lived perennial herbs, rarely rhizomatous; stems terete and usually striate, with broad solid pith; hairs uniseriate with erect apical cells, with glandular dots. Leaves alternate, sessile or short petiolate; blades thinly

herbaceous, ovate to linear lanceolate, base cuneate or continuous onto stem, margins subentire to serrate or dentate, apex acute to obtuse, surfaces glabrous to densely pubescent; venation pinnate with ascending secondary veins. Inflorescence terminal, corymbiform to rather cymiform, lower bracteoles a reduced foliiform, peduncular bracteoles filiform. Heads rather small, with broadly campanulate involucre; involucre bracts 15–40 in 2–3 usually subequal series; receptacle flat or slightly convex, epaleaceous. Florets 3–100 in a head, strongly exserted; corollas white or pink to purple, with glandular dots on surface, with a narrow cylindrical base, limb narrowly funneliform to narrowly campanulate; lobes lanceolate, without apical hairs; bases of anther thecae rounded, not tailed; apical appendages glabrous; style base without node; branches with sweeping hairs shortly acute. Achenes cylindrical with 2–6 usually paler ribs, sides with glandular dots, rarely with short white setulae; raphids short-oblong; pappus lacking or a coroniform rim. Chromosome number $n = 10, 20$ (Pilz 1980; Gilbert and Jeffrey 1988).

Pollen: ca. 35 μm in diam. in fluid; tricolporate, sublophate, echinate, spines long; tectum continuous in intercolpi and at poles, distinctly microperforate; columellae below spines firmly attached to footlayer (Fig 8 D–F).

Notable secondary metabolites: 5-alkylcoumarins (Bohlmann and Jakupovic 1990, as *Ethulia conyzoides*).

***Ethulia conyzoides* L.f., 1762**

Ethulia conyzoides L.f., Decas Prima Pl. Rar. Horti Upsal. 1, pl. 1. 1762.

Ethulia ramosa Roxb., Hort. Beng. 61. 1814.

Ethulia gracilis Delile in Cailliaud., Voy. Meroe 4: 398. 1827.

Distribution. Tropical and southern Africa, Asia to China, introduced in Brazil.

***Gymnanthemum* Cass., 1817**

Figures 9 A–D; 10 A–E

Gymnanthemum Cass. Bull. Soc. Philom. Paris 1817: 10. 1817. – Type: *G. cupulare* Cass. = *Baccharis senegalensis* = *Gymnanthemum coloratum* (Willd.) H. Rob. & B. Kahn

Bracheilema R. Br. ex Salt., Abyss. Append. 65. 1814, nom. nud.

Decaneurum DC., Arch. Bot. (Paris) 2: 516. 1833, nom. superfl., type same as *Gymnanthemum*.

Plectreca Rafin., Fl. Tellur. 4: 119. 1838. – Type: *Staezelina corymbosa* Thunb.

Keringa Rafin., Sylva Tellur. 144. 1838. – Type: *Vernonia amygdalina* Del.

Cheliusia Sch. Bip. in Hochst., Flora 24 [Intell. 1(2)] 26. 1841, nom. nud. – *Cheliusia abyssinica* Sch. Bip. = *Gymnanthemum amygdalinum* (Del.) Sch. Bip. ex Walp.



Figure 9. Photographs of *Gymnanthemum*: **A** *Gymnanthemum corymbosum* (Thunb.) H. Rob. **B–D** *Gymnanthemum capense* (A. Spreng.) J. C. Manning & N. Swelankomo. See Appendix C for citation details.

Vernonia subsect. *Urceolata* S.B. Jones, *Rhodora* 83: 67. 1981. – Type: *Vernonia sphaerocalyx* O. Hoffm.

Descriptions. Shrubs or small trees, moderately to densely branching; stems mostly terete, with solid pith; hairs of stem often forming a felt, with large often contorted

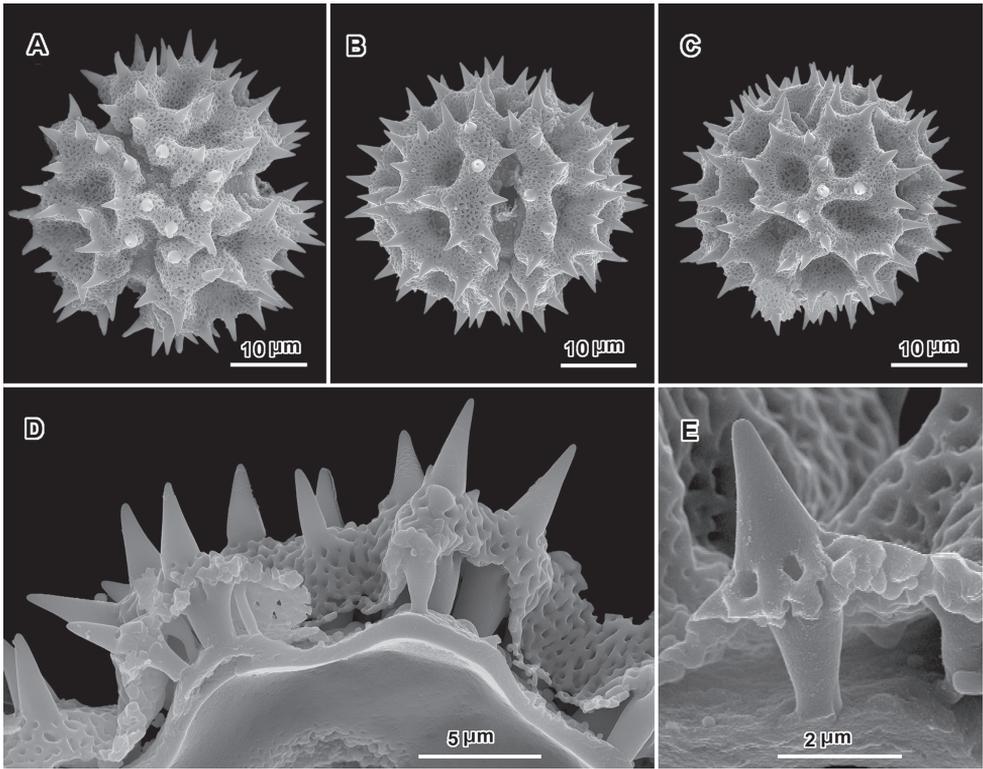


Figure 10. Scanning electron micrographs of acetolyzed pollen of two collections of sublophate echi-nolophate *Gymnanthemum capense* (A. Spreng.) J. C. Manning & N. Swelankomo. **A** Polar view **B** Equatorial view **C** Lateral view **D** Fractured grain structure of exine surfaces **E** Fractured grain showing spine construction. (**A–C** *Schlechter 6644*).

cap cells basally or nearly basally attached. Leaves alternate; petioles short, winged or elongate; blades membranaceous to rather coriaceous, margins entire to serrate or repand dentate, upper surfaces essentially glabrous and somewhat glossy to arachnoid tomentose; secondary veins pinnate, spreading at 30–80° angles, arching nearer margins. Inflorescences terminal, densely corymbiform, with small bracteoles; peduncles short. Heads with campanulate to cylindrical or ovoid involucre; involucre bracts coriaceous to subcoriaceous, appressed, 25–35 in 4–5 gradate series, inner bracts persistent to easily deciduous, outer surface with smooth median shield, without narrow median costa or keel; receptacles epaleaceous. Florets 5–50 in a head; corollas white to violet, basal tube cylindrical, throat longer than the anther thecae or very deeply cut, lobes with glands or spicules on outer surface; anther thecae with base broadly tailed, tails often long; apical appendages glabrous, with rather thick-walled cells; style base without or with scarcely distinct node; style branches with stout, pointed sweeping hairs. Achenes 5–10-costate, with or without setulae, raphids short to elongate, sometimes not evident; pappus of many rather persistent capillary bristles, often with

broadened tips, with outer series of short squamellae. Chromosome numbers $n = 10, 15, 20$ (Jones 1970, 1982; Adegbite and Ayodele 2004).

Pollen: 30–35 μm in diam. (dry); tricolporate, echinate, sublophate; tectum continuous in intercolpi and at poles, with distinct microperforations; spines long, each with single stout columella below firmly attached to footlayer, intervening perforated tectum scarcely mamilllose on inner surface (Fig. 10 A–E).

Generic limits more restricted than given in Robinson (1999a), see Robinson and Skvarla (2006, 2007) and Robinson et al. (2008).

A special effort has been made to resolve the endemic southern African element of *Gymnanthemum* that includes *G. corymbosum* and *G. capense* (Swelankomo et al. 2015).

Key to the species of *Gymnanthemum*

- 1 Capitula with 9–30 florets 2
- Capitula with 2–5 florets 4
- 2 Leaves sessile, usually auriculate at base..... *G. theophrastifolium*
- Leaves with distinct petioles..... 3
- 3 Achenes with setulae on the surface *G. coloratum*
- Achenes without setulae..... *G. amygdalinum*
- 4 Leaf blades elliptical, with sharply serrate margins..... *G. myrianthum*
- Leaf blades suborbicular to narrowly obovate, with repand-dentate distal margins 5
- 5 Leaves sparsely puberulous to essentially glabrous abaxially..... 6
- Leaves hispid to tomentose abaxially 7
- 6 Leaf blades chartaceous, with broadly obtuse bases; stems puberulous with often dark hairs..... *G. koekemoerae*
- Leaf blades rather membranaceous with long-acuminate bases; stems essentially glabrous *G. capense*
- 7 Leaf blades oblong to ovate with obtuse bases; stems hirsute; capitula with 3 florets..... *G. triflorum*
- Leaf blades obovate to oblanceolate with cuneate bases; stems tomentose; capitula usually with 4–5 florets..... 8
- 8 Stems and abaxial surfaces of leaves completely covered with appressed tomentum; inflorescence narrowly corymbose *G. corymbosum*
- Stems with tomentum of cottony hairs, abaxial surfaces of leaves with mixed erect and arachnoid hairs that do not totally obscure green surface; inflorescence broadly corymbose, much broader than high..... *G. crataegifolium*

***Gymnanthemum amygdalinum* (Del.) Sch. Bip. ex Walp., 1843**

Vernonia amygdalina Del., Cent. Pl. Afr. Voy. Méroé 41. 1826.

Gymnanthemum amygdalinum (Del.) Sch. Bip. ex Walp., Rep. 2: 948. 1843.

Gymnanthemum abyssinicum Sch. Bip. ex Walp., Rep. 2: 948. 1843.

Vernonia vogeliana Benth. in Hook., Niger Fl. 427. 1849.

Vernonia condensata Baker, J. Bot. 8: 202. 1875.

Vernonia eritreana Klatt, Bull. Herb. Boiss. 4: 826. 1896.

Vernonia randii S. Moore, J. Bot. 37: 369. 1899.

Vernonia giorgii De Wild., Bull. Jard. Bot. Brux. 5: 92. 1915.

Vernonia bahiensis Toledo, Arq. Bot. Estado Sao Paulo, n.s. 1: 52. 1939.

Vernonanthura condensata (Baker) H. Rob., Phytologia 73: 69. 1992.

Note. The species is used as medicinal plant by both people and animals.

Distribution. Africa and introduced into Brazil.

***Gymnanthemum capense* (A. Spreng.) J. C. Manning & N. Swelankomo, 2015**

Eupatorium capense A. Spreng., Tent. Suppl. 22. 1828.

Vernonia mespilifolia Less., Linnaea 6: 641. 1831, nom. superfl.

Gymnanthemum mespilifolium (Less.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 242. 1999.

Gymnanthemum capense (A. Spreng.) J. C. Manning & N. Swelankomo, S. African J. Bot. 101: 12. 2015.

Distribution. Transvaal, Natal, Swaziland, Cape colony.

Note. Swelankomo et al. (2015) point out that the older name *Eupatorium capense* should have been used for this species, and they make the necessary new combination. The combination *Vernonia capensis* has been used since 1917 for another species (now in *Hilliardiella*). At this time there is still no unpreoccupied name for the species that has been called *V. mespilifolia* in the genus *Vernonia*. Two specimens examined: Rogers 28651 from Grahamstown, and C.E. Smith & Duthie 4678 from Natal, the latter originally distributed as *Vernonia crataegifolia*.

***Gymnanthemum coloratum* (Willd.) H. Rob. & B.Kahn, 1986**

Eupatorium coloratum Willd., Sp. Pl. 3: 1769. 1803.

Baccharis senegalensis Pers., Syn. Pl. 2: 424. 1807.

Gymnanthemum cupulare Cass., Dict. Sc. Nat. ed. 2, 20: 109. 1821.

Vernonia senegalensis (Pers.) Less., Linnaea 4: 265. 1829.

Decaneurum grande DC., Prodr. 5: 67. 1836.

Decaneurum senegalense (Pers.) DC., Prodr. 5: 68. 1836.

- Gymnanthemum grande* (DC.) Sch. Bip. ex Walp., Rep. 2: 948. 1843.
Gymnanthemum senegalense (Pers.) Sch. Bip. ex Walp., Rep. 2: 948. 1843.
Gymnanthemum quercifolium Steetz in Peters, Reise Mossamb. Bot. 334. 1864.
Vernonia oxyura O. Hoffm. in Engler, Pflanzenw. Ost.-Afr. C. 403. 1895.
Vernonia polyura O. Hoffm., Bot. Jahrb. Syst. 30: 422. 1901.
Vernonia cirrifera S. Moore, J. Linn. Soc. Bot. 35: 320. 1902.
Vernonia longipetiolata Muschl., Bot. Jahrb. Syst. 46: 74. 1911.
Vernonia aldabrensis Hemsl., J. Bot. 54: suppl., 2: 20. 1916.
Vernonia grandis (DC.) Humb., Fl. Madag. 189: 44. 1960.
Gymnanthemum coloratum (Willd.) H. Rob. & B.Kahn, Proc. Biol. Soc. Wash. 99: 501. 1986.

Distribution. Tropical and subtropical Africa.

Gymnanthemum corymbosum (L.f.) H. Rob., 1999

- Staehelina corymbosa* L. f., Suppl. 359. 1781.
Vernonia corymbosa (L. f.) Less., Linnaea 6: 647. 1831, nom. illeg., non *Vernonia corymbosa* Schwein. ex Keating, Narr. Exp. Long. 2: 394. 1824.
Plectreca corymbosa (L. f.) Raf., Fl. Tellur. 4: 119. 1838 (“1836”).
Vernonia neocorymbosa Hilliard, Notes Roy. Bot. Gard. Edinburgh 32(3): 385. 1973.
 New name for *Vernonia corymbosa*.
Gymnanthemum corymbosum (L.f.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 241. 1999.

Distribution. Eastern South Africa through Swaziland and Natal, Transkei, s. Mosambique.

Note. Many specimens from South Africa been seen including Schlechter 6644 distributed under the name *Vernonia angulifera* DC., nom. nud.

Gymnanthemum crataegifolium (Hutch.) H. Rob., 1999

- Vernonia mespilifolia* Less. var. *subcanescens* DC., Prodr. 5: 29. 1836.
Vernonia crataegifolia Hutch., Bull. Misc. Inf. Kew 7: 330. 1912.
Vernonia pseudocorymbosa Thell., Vierteljahrsschr. Nat. Ges. Zurich, 68: 440. 1923.
Gymnanthemum crataegifolium (Hutch.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 241. 1999.

Distribution. South Africa (Transvaal, Natal, Swaziland, Cape colony).

Note. The species is known in this study from descriptions, from photographs of the syntype, Clydesdale, *Tyson 1188* (K) deposited at the US by Earl Smith, and one specimen, Sidey 3470 from Natal, distributed originally as *Vernonia corymbosa*.

***Gymnanthemum koekemoerae* H. Rob. & V.A. Funk, 2014**

Gymnanthemum koekemoerae H. Rob. & V.A. Funk, *Phytokeys* 36: 60. 2014.

Type material. Holotype: South Africa. Limpopo Province: Thohoyandou District; Thathe-Vonde Nature Reserve. Grassland at rocky outcrop near entrance, 1233 m, 22°55'10"S, 30°19'36"E [2230CD], 23 March 2002, *Koekemoer 2273* (PRE, isotype US) (Fig. 2D).

The type specimen was distributed as *Vernonia triflora* Brem., which differs by having only 3 florets in its capitula, stiffly and densely hispid stems, and ovate to oblong leaf blades with hispidulous abaxial surfaces.

Distribution. South Africa

***Gymnanthemum myrianthum* (Hook.f.) H. Rob., 1999**

Vernonia myriantha Hook.f., *J. Linn. Soc. Bot.* 7: 198. 1864.

Vernonia podocoma Sch. Bip. ex Vatke, *Linnaea* 39: 476. 1875.

Vernonia subuligera O. Hoffm. in Engler, *Pflanzenw. Ost-Afr. C.* 403. 1895.

Vernonia stipulacea Klatt, *Bull. Herb. Boiss.* 4: 457. 1896.

Vernonia lujae De Wild., *Pl. Nov. Herb. Hort. Then.* 2: 119, t. 96. 1900.

Vernonia ampla O. Hoffm., *Bot. Jahrb. Syst.* 30: 423. 1901.

Vernonia myrianthoides Muschl., *Bot. Jahrb. Syst.* 46: 84. 1911.

Vernonia uhligii Muschl., *Bot. Jahrb. Syst.* 46: 84. 1911.

Vernonia oliveriana Pichi-Serm., *Webbia* 7: 345. 1950, nom. illeg. superfl. for *V. podocoma* Sch. Bip. ex Vatke

Vernonia chlarugii Pichi-Serm., *Miss. Stud. Lago Tana 7, Ricerche Bot.* 1: 155, t. 30. 1951.

Gymnanthemum myrianthum (Hook.f.) H. Rob., *Proc. Biol. Soc. Wash.* 112(1): 242. 1999.

Distribution. West Africa from Guinea and Sierra Leone to Cameroon, Sudan, Ethiopia, Kenya, Uganda, Congo, south to South Africa (Transvaal, Natal), and Swaziland.

***Gymnanthemum theoprastifolium* (Schweinf. ex Oliv. & Hiern) H. Rob., 1999**

Vernonia theoprastifolia Schweinf. ex Oliv. & Hiern, *Fl. Trop. Afr.* 3: 294. 1877.

Vernonia myriocephala A. Rich., *Tent. Fl. Abyss.* 1: 374. 1848, nom. illeg., not DC. 1836.

Cacalia richardiana O. Kuntze, *Rev. Gen. Pl.* 2: 969. 1891, nom. nov. for *V. myriocephala* A. Rich.

Vernonia seretii De Wild., *Ann. Mus. Congo Belge, Bot. ser.*, 5(2): 207. 1907.

Vernonia macrophylla Chiov., Ann. Bot. Roma 9: 70. 1911.

Vernonia richardiana (O. Kuntze) Pichi-Serm., Webbia 7: 340. 1950.

Gymnanthemum theophrastifolium (Schweinf. ex Oliv. & Hiern) H. Rob., Proc. Biol. Soc. Wash. 112(1): 243. 1999.

Distribution. Congo and Nigeria east to Uganda, Kenya, Ethiopia, and south to South Africa.

Gymnanthemum triflorum (Bremek.) H. Rob., 2005

Vernonia triflora Bremek., Ann. Transvaal Mus. 15: 262. 1933.

Gymnanthemum triflorum (Bremek.) H. Rob., Phytologia 87(2): 80. 2005.

Distribution. South Africa (Transvaal).

Note. One specimen has been seen, Stalmans 2430AA, from South Africa (Transvaal), that matched the original description in every respect except for the lack of noticeable pubescence on the involucre bracts.

Hilliardiella H. Rob., 1999

Figures 11 A–D; 12 A–D; 13 A; 14 A–H

Hilliardiella H. Rob. Proc. Biol. Soc. Wash. 112(1): 247. 1999. – Type: *Vernonia piniifolia* (Lam.) Less.

Webbia DC., Prodr. 5: 72. Oct 1836, nom. illeg., not *Webbia* Spach, Jun 1836.

Vernonia subsect. *Hilliardiana* S.B. Jones, Rhodora 83: 66. 1981. – Type: *Vernonia oligocephala* (DC.) Sch. Bip.

Descriptions. Herbaceous perennials to 1 m tall; stems pilose, hairs unequally T-shaped. Leaves alternate; blades abaxially often densely canescent pilose. Inflorescence laxly to subdensely corymbiform-cymose. Heads short-pedunculate; involucre campanulate, bracts 25–40, in ca. 3–4 series, persistent; receptacle epaleaceous. Florets 12–20 in a head; corollas purple, outside with few to many slightly contorted T-shaped hairs; basal tube funneliform above, throat short, lobes linear; anther thecae not or shortly appendaged at base; apical appendages glabrous, with thin walls; style with basal node; style branches with acicular sweeping hairs. Achenes 4–5-costate, densely setuliferous, setulae scarcely divided at tips, idioblasts numerous, raphids elongate, carpodia narrowly cylindrical; pappus bristles white, barbate, tenuous, subpersistent, outer series shortly lanceolate. Chromosome number of $n = 9, 10$, most reports $n = 10$ (Turner and Lewis 1965; Jones 1982).

Pollen grains sublophate, with continuous perforated tectum between colpi, tricolporate to poles, echinate (Fig. 14 A–H).



Figure 11. Photographs of *Hilliardiella*. **A–B** *Hilliardiella aristata* (DC.) H. Rob. **C–D** *Hilliardiella flanagani* (E. Phillips) H. Rob. See Appendix C for citation details.

Notable secondary metabolites; acetones & sesquiterpene glaucolides/ hirsutanolides (Bohlmann and Jakupovic (1990, as *Vernonia sutherlandii* Harv., guaianolides, bisabolene derivatives (Bohlmann and Jakupovic 1990, as *V. hirsuta* Sch. Bip. ex Walp. and *V. oligocephala* (DC.) Sch. Bip. ex Walp.).

Key to the species of *Hilliardiella*

- 1 Leaves mostly basal, not cauline.....***H. nudicaulis***
- Leaves disposed rather uniformly along stems**2**
- 2 Leaf surfaces coarsely pubescent, not sericeous.....**3**
- One or both surfaces of leaves sericeous with silvery pubescence**4**
- 3 Leaves ovate to ovate-elliptic, 1.5–3 times as long as wide....***H. oligocephala***
- Leaves linear, ca. 2 m wide, 12 or more times as long as wide***H. capensis***
- 4 Both leaf surfaces densely silvery sericeous; longest phyllaries 5–8.5 mm long**5**
- Upper leaf surface dark; longest phyllaries 2.3–5 mm long**6**

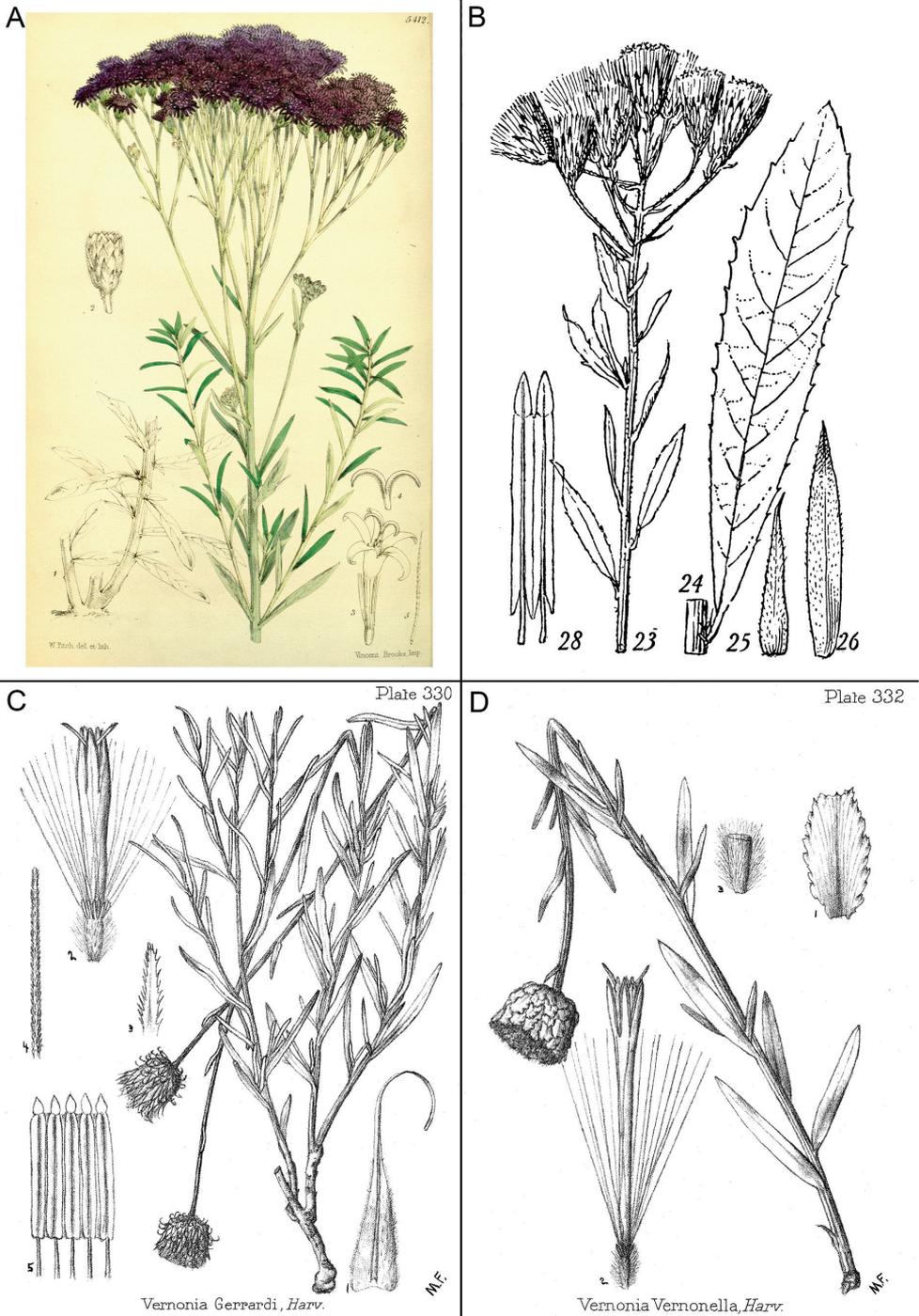


Figure 13. Illustrations *Hilliardiella*, *Linzia*, *Parapolydora*, and *Vernonella*: **A** *Hilliardiella capensis* (Houtt.) H. Rob., Skvarla & V.A. Funk **B** *Linzia glabra* Steetz in Peters, note: characteristic teeth on involucre bracts **C** *Parapolydora gerrardii* (Harv.) H. Rob **D** *Vernonella africana* Sond. See Appendix C for citation details.

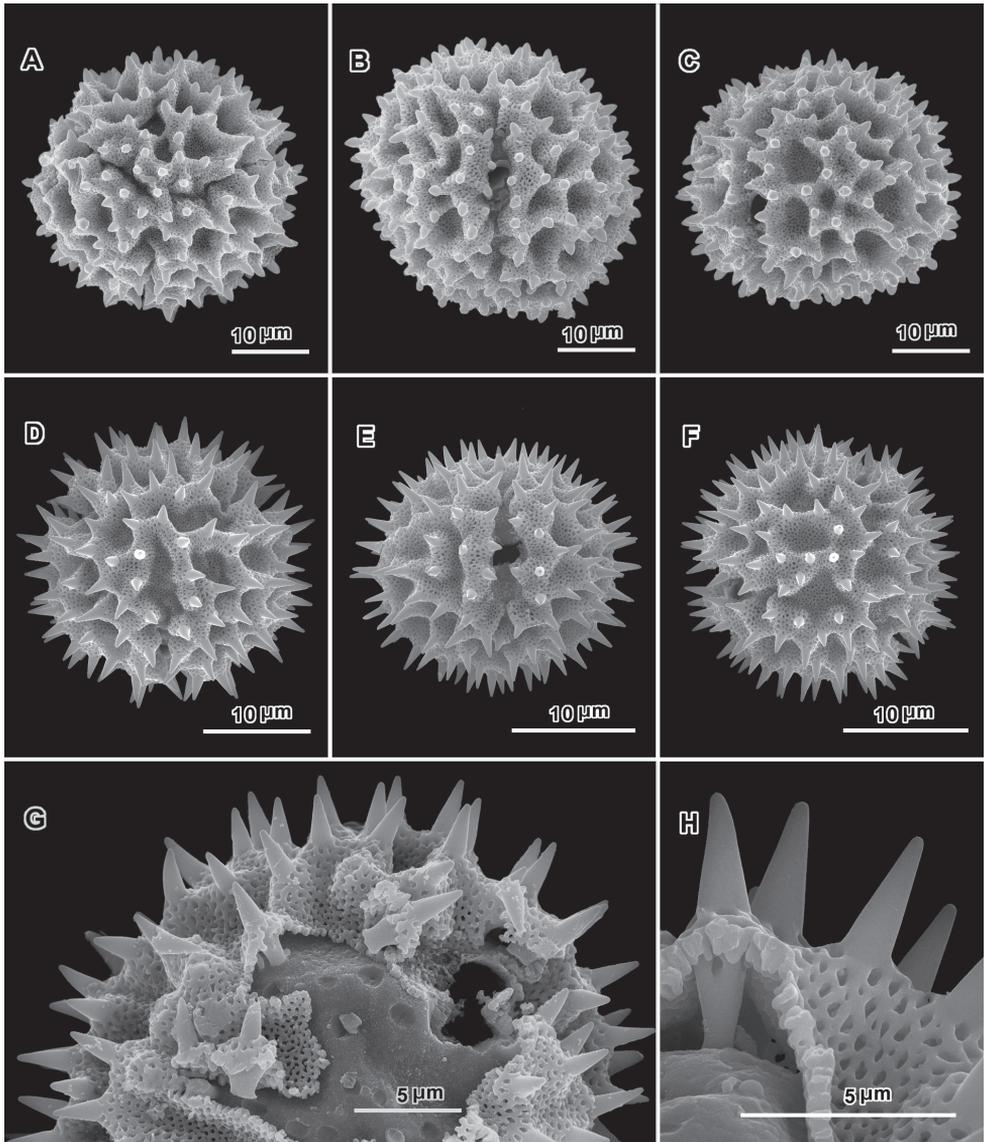


Figure 14. Scanning electron micrographs of acetylyzed pollen from two collections of *Hilliardiella capensis* emphasizing spine variations. The surface seems to vary between sublophate and slightly echinolophate. **A** Polar view **B** Equatorial view **C** Lateral view **D** Polar view **E** Equatorial view **F** Subpolar view **G** Fragmented pollen surface **H** Grain fragment showing structural support of spine. (**A–C** Bayliss BS3686 **D–H** Gentry & Barolas 18914).

- 6 Leaves acute at base; pubescence on leaf surfaces not obscuring the surfaces, numerous large glandular dots visible on abaxial surface *H. sutherlandii*
- At least upper leaves cordate at base, pubescence on abaxial leaf surface mostly obscuring presence of glandular dots.....7

- 7 Bases of lower leaves narrow; tips of phyllaries long-acuminate, equaling or exceeding the pappus *H. flanagani*
 – Bases of lower leaves cordate; phyllaries without long-acuminate tips equaling or exceeding the pappus..... *H. hirsuta*

***Hilliardiella aristata* (DC.) H. Rob., 1999**

Webbia aristata DC., Prodr. 5: 73. 1836.

Vernonia natalensis Sch. Bip. ex Walp., Rep. 2: 947. 1843.

Hilliardiella aristata (DC.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999.

Distribution. Lesotho, South Africa (Transvaal, Orange Free State, Natal, Cape colony), and Swaziland.

***Hilliardiella capensis* (Houtt.) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152896-1

Erigeron capensis Houtt., Handl. Pl.-Kruidk. 10: 629. 1773–1783.

Conyza pinifolia Lam., Encycl. (Lamarck) 2(1): 86. 1786 [16 Oct 1786]

Conyza canescens Thunb., Fl. Cap. 665. 1823.

Vernonia pinifolia (Lam.) Less., Linnaea 4: 257. 1829.

Webbia pinifolia (Lam.) DC., Prodr. 5: 72. 1836.

Vernonia capensis (Houtt.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 1916: 651. 1917.

Hilliardiella pinifolia (Lam.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999.

Distribution. Lesotho, South Africa (Transvaal, Orange Free State, Natal, Cape colony) and Swaziland.

Note. This complete synonymy shows that the oldest name for the species is *Erigeron capensis* Houtt.

***Hilliardiella flanagani* (E. Phillips) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152902-1

Vernonia hirsuta (DC.) Sch. Bip. ex Walp. var. *flanagani* E. Phillips, Ann. S. Afr. Mus. 16(2): 116. 1925.

Vernonia flanagani (E. Phillips) Hilliard, Notes Roy. Bot. Gard. Edinburgh 42(2): 238. 1985.

Note. Distinguished as a variety from typical *Vernonia hirsuta* DC. by Phillips (1925) by the narrow, not cordate, bases of the lower leaves and the long-acuminate tips of the involucre bracts that equal or exceed the pappus.

Distribution. South Africa (Natal).

***Hilliardiella hirsuta* (DC.) H. Rob., 1999**

Vernonia hirsuta (DC.) Sch. Bip. ex Walp., Rep. 2:947. 1843.

Vernonia hirsuta (DC.) Sch. Bip. ex Walp. var. *obtusifolia* Harv. Flora Capensis 3: 52. 1864.

Hilliardiella hirsuta (DC.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999.

Distribution. Lesotho, South Africa (Transvaal, Orange Free State, Natal, Cape colony), and Swaziland.

***Hilliardiella nudicaulis* (DC.) H. Rob., 1999**

Webbia nudicaulis DC., Prodr. 5:73. 1836

Vernonia dregeana Sch. Bip. ex Walp., Rep. 2: 947. 1843.

Hilliardiella nudicaulis (DC.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999.

Distribution. South Africa (Cape colony, Natal, Transvaal).

***Hilliardiella oligocephala* (DC.) H. Rob., 1999**

Webbia oligocephala DC., Prodr. 5: 73. 1836.

Webbia elaeagnoides DC., Prodr. 5: 73. 1836, non *Vernonia elaeagnoides* Kunth in H.B.K.

Vernonia elaeagnoides (DC.) Sch. Bip. ex Walp., Rep. 2: 947. 1843.

Vernonia krausii Sch. Bip. ex Walp., Rep. 2: 947. 1843.

Hilliardiella oligocephala (DC.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999.

Distribution. Tanzania south to South Africa (Transvaal, Orange Free State, Natal, Cape colony), Botswana, Lesotho and Swaziland.

***Hilliardiella pseudonatalensis* (Wild) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152897-1

Vernonia pseudonatalensis Wild, Kirkia 11: 11. 1978.

Distribution. Mozambique, South Africa (Transvaal), and Swaziland.

***Hilliardiella sutherlandii* (Harv. in Harv. & Sond.) H. Rob., 2005**

Vernonia sutherlandii Harv. in Harv. & Sond., Fl. Cap. 3: 52. 1865.

Hilliardiella sutherlandii (Harv. in Harv. & Sond.) H. Rob., Phytologia 87: 82. 2005.

Distribution. South Africa (Natal, Transvaal) and Swaziland.

***Linzia* Sch. Bip. ex Walp., 1843**

Figures 13 B; 15 A–B; 16 A–E

Linzia Sch. Bip. ex Walp., Rep. 2: 948. 1843. – Type: *Linzia vernonioides* Sch. Bip. ex Walp.

Vernonia sect. *Azurae* S.B. Jones, Rhodora 83: 74. 1981. – Type: *Linzia glabra* Steetz in Peters.

Descriptions. Perennial herbs; stems with simple multiseptate hairs. Leaves alternate, subsessile to short-petiolate. Inflorescence corymbiform cymes or single heads with short to long peduncles. Involucre funnellform to campanulate; bracts 50–150 in 5–6 series, often pectinate-denticulate with spicules along lateral margins, outer tips often elongate, green and recurved; receptacle epaleaceous. Florets ca. 20–50 in a head; corollas bluish, tube very long, funnellform near throat; throat very short, lobes apically stiffly pilosulous; anther base rounded; apical appendage glabrous, triangular with thickened ornamentation in center; style base with small annuliform node. Achenes strongly 10-costate, usually with rows of idioblasts or specialized cells along sides of costae, surface setuliferous, setulae slender with pairs of cells not or scarcely separated at tip, raphids subquadrate to short-oblong; pappus of many somewhat persistent long bristles, with outer series short. Chromosome number $n = 10$ (Jones 1979, 1982).

Pollen tricolporate, psilolophate, with spur muri intruding into short colpi above and below pore, single polar lacunae often present, not echinate, with or without micropunctations restricted to muri. Muri showing baculae with broadened base, branching distally into many bacula-like branches (Fig. 16 E), a form that seems almost transitional to a rhizomate condition.

Most notable secondary metabolites, sesquiterpene germacranolides, elemanolides (Bohlman and Jakupovic 1990, as *V. glabra* Vatke & *V. melleri* Oliv. & Hiern).

Key to the species of *Linzia*

- 1 Capitula usually numerous in terminal corymbiform or thyriform cymes, peduncles up to 2–3 times as long as the involucre; plants with rather equally leafy stems ***L. glabra***
- Capitula on long peduncles, 1 or few in open terminal cymes, peduncles mostly 5 or more times as long as the involucre **2**



Figure 15. Photographs of *Linzia* and *Namibithamnus*: **A–B** *Linzia glabra* Steetz in Peters, note that the flowers bloom in two groups with the outer ones blooming first (light colored in 15B) followed by the innermost ones (dark purple in 15B) **C–D** *Namibithamnus obionifolius* (O. Hoffm.) H. Rob. See Appendix C for citation details.

- 2 Leaves in rosettes, arising from a root-crown; capitula to 2.5–3.0 cm high or wide..... *L. gerberiformis*
- Slender leaves on short branches, arising from creeping rhizome; capitula mostly 1.2–1.6 cm high or wide *L. rosenii*

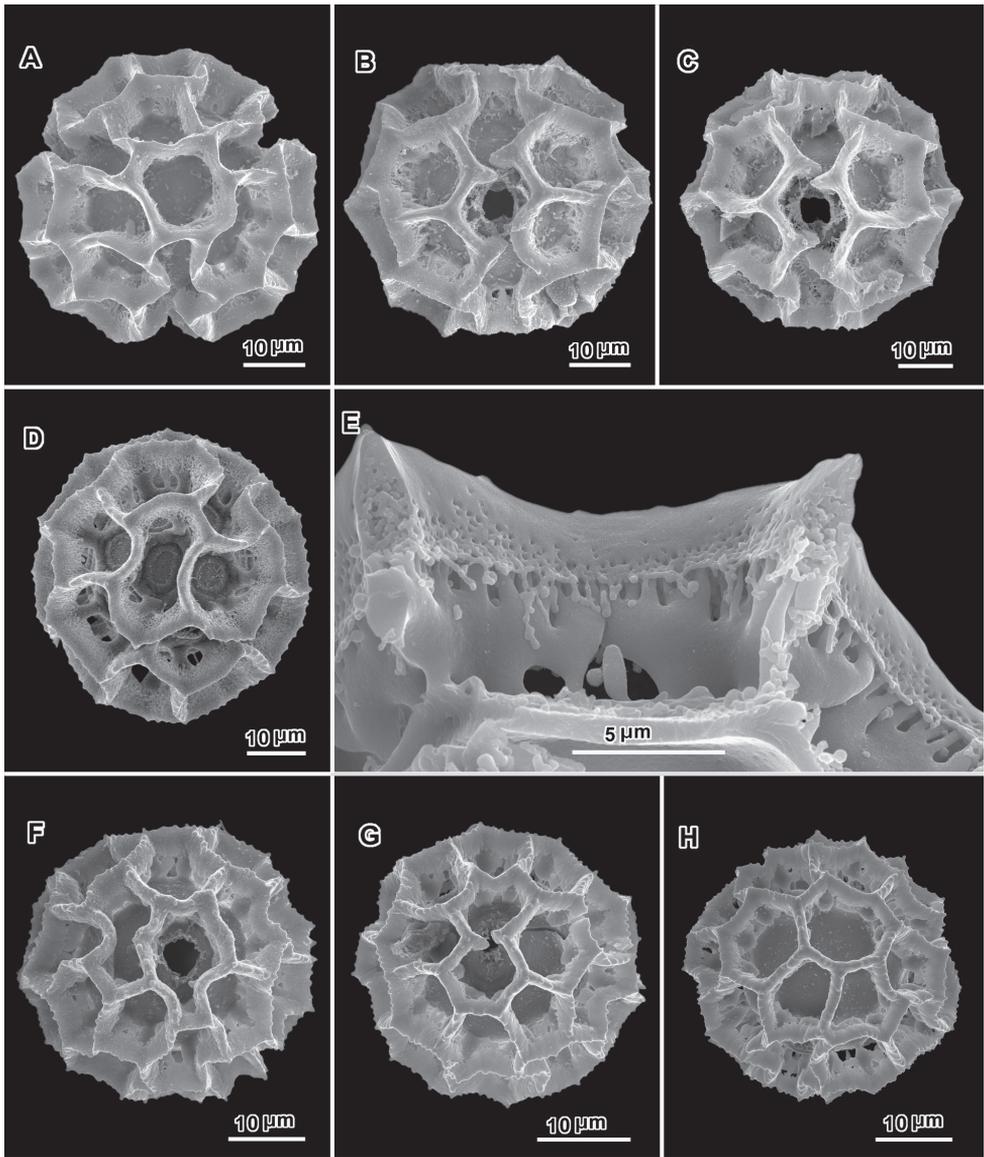


Figure 16. Scanning electron micrographs of *Linzia* and *Namibithamnus* pollen. **A, B, E** *Linzia rosenii*. (R.E. Fries) H. Rob., Skvarla & V.A. Funk. **A** Polar view **B** Equatorial view **C** Equatorial view. Note differences of lophae surrounding pores in **B** and **C**, **D** *Linzia glabra* Steetz in Peters. Lateral view. **E** *Linzia rosenii*. Fractured pollen wall. **F–H** *Namibithamnus obionifolius* (O. Hoffm.) H. Rob., Skvarla & V.A. Funk. **F** Equatorial view. This is the most common form of aperture **G** Equatorial view. Less common form of aperture with broken lophal arms apparent **H** Near polar view (**A–C, E** Jacobsen 3075 **D** West 7292 **F–H** Tölken & Hardy 770).

***Linzia gerberiformis* (Oliv. & Hiern in Oliv.) H. Rob., 1999**

Vernonia gerberiformis Oliv. & Hiern in Oliv., Fl. Trop. Afr. 3: 285. 1877.

Vernonia collina Schlechter, J. Bot. 1898: 374. 1898?

Vernonia gerberiformis var. *hockii* (De Wild. & Muschl.) G.V. Pope, Kew Bull. 43(2): 280. 1988. Distribution: Lesotho, South Africa (Transvaal, Orange Free State, Natal, Cape colony).

Vernonia gerberiformis subsp. *macrocyanus* (O. Hoffm.) C. Jeffrey, Kew Bull. 43: 234. 1988.

Vernonia primulina O. Hoffm. in Warburg, Kunene-Sambesi Exped. 402. 1903.

Vernonia pristis Hutch. & Burt, Rev. Zool. & Bot. Afr. 23: 38. 1932.

Linzia gerberiformis (Oliv. & Hiern in Oliv.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 237. 1999.

Linzia gerberiformis subsp. *macrocyanus* (O. Hoffm.) Isawumi, Comp. Newsl. 40: 38. 2008.

Distribution. Angola, Burundi, Cameroon, Congo, Malawi, Nigeria, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

***Linzia glabra* Steetz in Peters, 1864**

Vernonia glabra (Steetz) Vatke, Oesterr. Bot. Zeitschr. 27: 194. 1877.

Linzia glabra Steetz in Peters, Reise Mossamb. Bot. 353. 1864.

Vernonia obconica Oliv. & Hiern in Oliv., Fl. Trop. Afr. 3: 286. 1877.

Vernonia ondongensis Klatt ex Schinz, Bull. Herb. Boiss. 3: 430. 1895.

Vernonia glabra (Steetz) Vatke var. *laxa* (Steetz) Brenan, Mem. N. Y. Bot. Gard. 8(5): 460. 1954.

Distribution. Burundi, Congo, Kenya, Tanzania, Madagascar, south to Angola, Mozambique, and Namibia, South Africa (Transvaal, Natal) and Swaziland.

***Linzia rosenii* (R.E. Fries) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152903-1

Vernonia rosenii R. E. Fries, Wiss. Ergebn. Schwed. Rhodesia-Congo Exped. 1911–1912, 1: 323. 1916.

Distribution. Botswana.

***Namibithamnus* H. Rob., Skvarla & V.A. Funk, gen. nov.**

urn:lsid:ipni.org:names:77152892-1

Figures 15 C–D; 16 F–H

Type. *Vernonia obionifolia* O. Hoffm.

Descriptions. Small aromatic shrubs to 1.5 m tall; stems, leaves, involucre bracts densely yellowish gray tomentellous or sericeous with crowded T-shaped hairs, hairs with slender 0–2-septate short stalks and small naviculiform or rather elongate cap-cells. Leaves alternate, short-petiolate, with small axillary fascicles usually present, more crowded proximally, smaller distally; blades 5–12 mm long, oblong to obovate, with undulate entire to coarsely dentate margins, basal pair of secondary veins scarcely evident or evident and strongly ascending, minute glandular dots densely disposed on both surfaces. Inflorescences appearing shortly scapose, with numerous pedunculate heads in a corymbiform or partly subumbellate arrangement. Heads campanulate, 6–7 mm wide and high; involucre bracts ca. 60 in ca. 6 strongly gradate series, persistent, oblong ovate with narrow apiculate tips, yellowish with reddish patch or midvein below tip, margins entire, broadly and distinctly thick and pale; receptacle convex, pitted with broad pale network of ridges. Florets 35–40 in a head. Corollas purple, narrowly funnel-shaped from a slender basal tube; throat twice as long as the erect, linear lobes, outer surface of base and throat mostly glabrous, lobes densely glandular-dotted; anther thecae narrow, slightly longer than throat, bases without tails, apical appendages shortly oblong-triangular, glabrous, with thin cell walls; style base with narrow annuliform node; with acicular sweeping hairs almost completely restricted to style branches, a few at top of shaft. Achenes 5-costate, with setulae not divided at tips, surfaces with numerous ungrouped idioblasts, raphids elongate; carpodium turbinate, glabrous; pappus of ca. 35 slender persistent bristles, bristles as wide at tips as at base, densely scabrid on margins and outer surface, outer series of distinct, smooth, lanceolate scales. Chromosome number unknown.

Pollen ca. 45 μm in diam. in fluid, lophate, triporate, not echinate, perforated tectum restricted or lacking, crests of muri sparsely papillose (Fig 16 F–H).

Key to the species of *Namibithamnus*

- 1 Leaves oblong, unlobed to few-lobed on lateral margins; secondary veins obscure; tomentellous with crowded minute trichomes bearing minute naviculiform cap-cells ***N. obionifolius***
- Leaves obovate, with numerous lobes distally; ascending secondary veins evident; trichomes appearing sericeous, with elongate cap-cells ***N. dentatus***

***Namibithamnus obionifolius* (O. Hoffm.) H. Rob., Skvarla & V.A. Funk, comb. nov.**
urn:lsid:ipni.org:names:77152904-1

Vernonia obionifolia O. Hoffm., Bot. Jahrb. Syst. 10: 272. 1888.

Note. With habit remarkably like *Orbivestus cinerascens*, and often in herbaria identified as this species. Differs clearly by non-seriate cymose inflorescence, thicker pale margins on involucre bracts, thicker tips on pappus bristles and lophate/triporate pollen. The margins of the involucre bracts are similar to those of *Erlangea* and *Bothriocline*.

Distribution. Namibia.

***Namibithamnus dentatus* (Merxm.) H. Rob., Skvarla & V.A. Funk, comb. et stat. nov.**
urn:lsid:ipni.org:names:77152905-1

Vernonia obionifolia O. Hoffm. ssp. *dentata* Merxm., Mitt. Bot. Staatssamml. München 3: 608. 1960.

Note. Thoroughly distinct in appearance, having larger more lobed leaves indicative of more moist habitats.

Distribution. Namibia.

***Oocephala* (S.B. Jones) H. Rob., 1999**

Figures 17 A–B; 18 A–F

Oocephala (S.B. Jones) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999. Type species: *Vernonia oocephala* Baker

Vernonia subsect. *Oocephalae* S.B. Jones, Rhodora 83: 72. 1981.

Descriptions. Low, much-branched shrubs to 1 m high, stems with L-shaped hairs on multiseptate stalks, cap-cells one-armed. Leaves alternate, sub-sessile, linear to elliptical, sometimes serrate. Inflorescences corymbiform cymes, with usually shortly pedunculate heads or with heads sessile in apical clusters of leaves. Involucre ovoid or cylindrical; bracts 20–40 in 4–7 gradate series, ovate to oblong, appressed; receptacle without pales. Florets ca. 10–15 in a head; corollas white or lavender, tubular to narrowly funnellform, throat as long as lobes, tips without hairs or with few short biseriate hairs; anther bases rounded, apical appendages glabrous, with thin-walled cells; style base with narrow ring; style branches with acicular sweeping hairs. Achenes weakly 8-ribbed, sericeous with many setulae, idioblasts numerous, raphids narrowly elongate; pappus biseriate, outer shorter and broader, inner setiform, subplumose, glabrous near base. Chromosome number unknown.

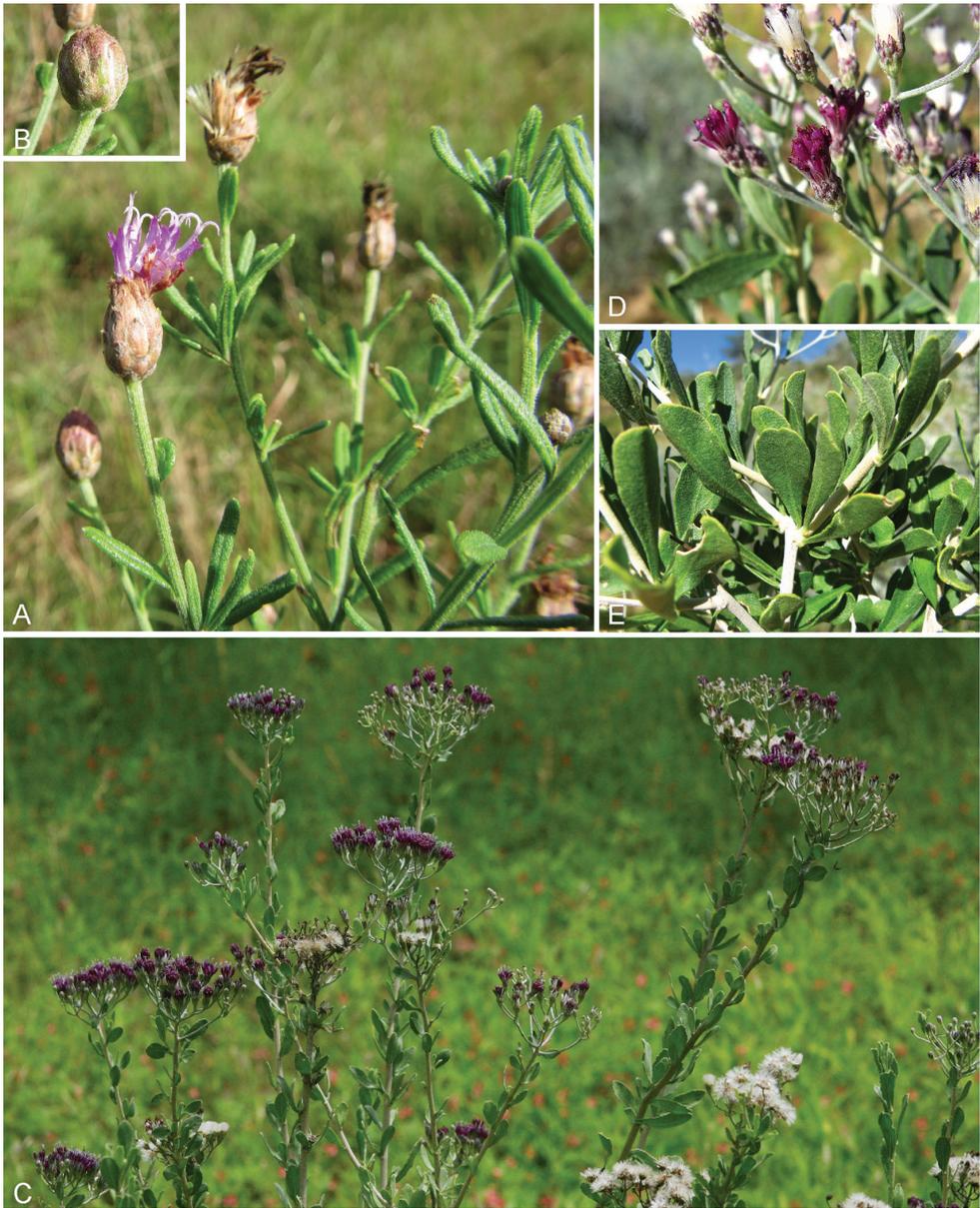


Figure 17. Photographs of *Oocephala* and *Orbivestus*: **A–B** *Oocephala centauroides* (Klatt) H. Rob. & Skvarla, note: egg-shaped head **C–E** *Orbivestus cinerascens* (Sch. Bip. in Schweinf.) H. Rob. See Appendix C for citation details.

Pollen 7–8-porate, with pores scattered over the whole surface in lacunae that are usually not adjacent, lophate (Fig. 18 A–F), minutely papillose on muri, nonperforated tectum restricted to muri, emicropunctate, baculae regularly spaced in single row under muri or lophae, baculae subtended by “rhizomate” structure that is as broad as

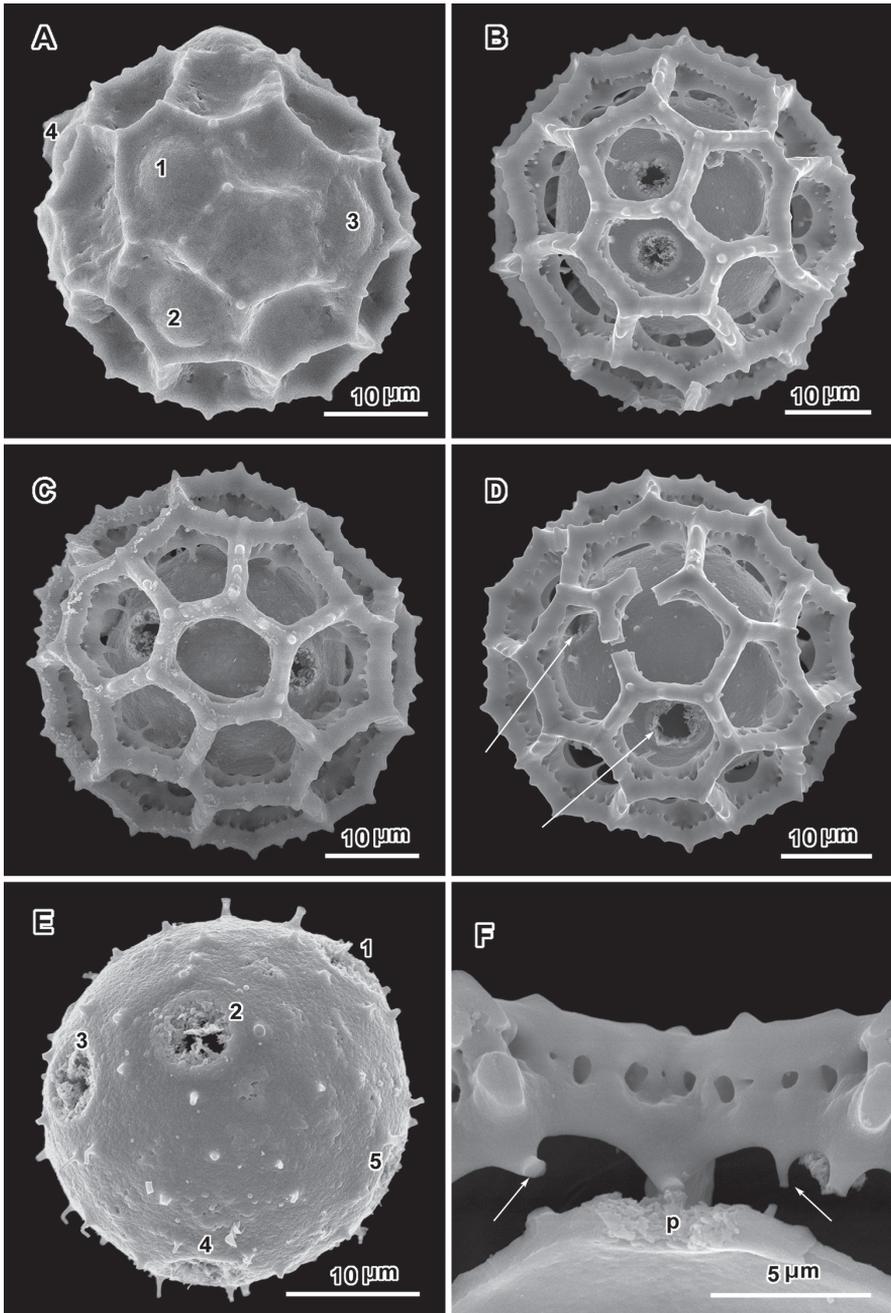


Figure 18. Scanning electron micrographs of *Oocephala staebelinoides* (Harv.) H. Rob. & Skvarla. **A** Unacetylated grain showing three pores with caps intact, two pores in adjacent lacunae **B–D** Intact or nearly intact grains showing pores in both pentagonal and hexagonal lacunae **B** with pores in adjacent lacunae **E** Grain stripped of muri showing five pores and stubs of muri attachments **F** Segment of muri showing rhizomate structure and remnants of weak basal attachments to footlayer, (p) pore. **A–F** are from collection of Liebenberg 8843.

the outer layer, and gives the muri or lophae a two-layered structure with small evenly spaced columellae separating the layers. The rhizomiform base of the muri is weakly attached to the footlayer thus causing muri to easily detach from the core of the grain. Lacunae of exine of pentagons mixed with hexagons. The structure of the bucky ball was a remarkable close approximation of the structure of the pollen. It was study of the toy ball that led to the conclusion that the pollen characteristically had seven or eight pores. Other pollen grains show a somewhat different pattern of pores, where pores occur in pairs, one each in a pair of adjacent lacunae (Fig. 18 B). The polyporate, sub-spherically symmetrical, rhizomate form of pollen in *Oocephala* is shared in a somewhat less symmetrical form by *Polydora*, but as far is currently known, these *Oocephala* and *Polydora* grains, with their non-equatorial pores, are unique in the Asteraceae (Robinson and Skvarla 2014).

Notable secondary metabolites: sesquiterpene glaucolides (Bohlmann and Jakupovic 1990 as *Vernonia staehelinooides* Harv.).

Key to the species of *Oocephala*

- 1 Stems and peduncles sparsely hispid with short spreading hairs; involucre 6–7 mm wide; involucre bracts with mucronate tip ***O. centaureoides***
- Stems and peduncles subcanescent with appressed hairs; involucre 3–4 mm wide; involucre bracts with obtuse or rounded tips ***O. staehelinooides***

***Oocephala centaureoides* (Klatt) H. Rob. & Skvarla, 2014**

Vernonia centaureoides Klatt, Bull. Herb. Boiss. 4: 824. 1896.

Vernonia schlechteri O. Hoffm., Bot. Jahrb. Syst. 24: 466. 1897.

Oocephala centaureoides (Klatt) H. Rob. & Skvarla, Phytokeys 38: 2. 2014.

Distribution. South Africa (Transvaal, Natal), and Swaziland.

***Oocephala staehelinooides* (Harv.) H. Rob. & Skvarla, 2014**

Vernonia staehelinooides Harv., Thes. Cap. 2: 36. 1863.

Oocephala staehelinooides (Harv.) H. Rob. & Skvarla, Phytokeys 38: 2. 2014.

Distribution. South Africa (Transvaal), and Swaziland.

***Orbivestus* H. Rob., 1999**

Figures 17 C–E; 19 A–G

Orbivestus H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999. – Type: *Vernonia karaguensis* Oliv. & Hiern.

Vernonia subg. *Orbivestus* S.B. Jones, Rhodora 83: 60. 1981. – Type: *Vernonia karaguensis* Oliv. & Hiern.

Descriptions. Subshrubs to small shrubs with erect stems from a woody base, not or sparsely branched between base and inflorescence; hairs T-shaped. Leaves alternate, usually decrescent upwardly, sessile or short petiolate, blades elliptical or ovate to oblanceolate, mostly 4–9 cm long, 2–5 cm wide, base short-obtuse to acuminate, margins scarcely repand-dentate, apex short-acute, upper surface with small spinules and few small hairs, lower surface paler, grayish with slender hairs and partially sunken glandular dots; venation pinnate, with up to six or eight lateral veins each side, spreading at 45–60° angles. Inflorescences with leaves of main axis only somewhat to greatly reduced, with only minute bracteoles on branches. Inflorescence shape broadly corymbiform or cylindrical with rounded to flattened top, with lower heads appearing sessile as result of proliferation by immediately subtending branches forming seriate or scorpioid cymes, branches of inflorescence tomentose with T-shaped hairs. Heads broadly campanulate, 4–14 mm high and wide; involucre bracts mostly persistent, innermost somewhat deciduous, ca. 50–100 in 5–7 series, strongly gradate, 1–8 mm long, 1.0–1.5 mm wide, ovate to oblong, subacute and mucronate to apiculate at tip, innermost acute, tips appressed, margins membranous and irregularly denticulate distally, often reddish, with dark median keel extending to apex, scarcely thickened and greenish near keel, with numerous small T-shaped hairs except at margins. Receptacle epaleate and tuberculate. Florets 15–ca. 50 in a head; corollas purplish, narrowly funnelform, 4–8 mm long, with sparsely scattered glandular dots, tube slender, 2–3 mm long, throat 1.5–2.5 mm long, lobes 1.0–2.5 mm long, linear-lanceolate, erect, not recurving, sparsely glanduliferous to distinctly or minutely scabridulous outside, without longitudinal internal ducts filling lobe; anther thecae 1–2 mm long, without glandular dots, calcarate and with long tails at base, endothelial cells short usually with 2–3 nodes on transverse walls; apical appendage 0.5–1.0 mm long, narrowly lanceolate, often sharply acute; style base with distinct expanded node; sweeping hairs on style branches and scarcely extending on to upper style shaft, slender and narrowly acute. Achenes 1.5–2.0 mm long when mature, 5-costate, with few to many setulae when young, often glabrous at maturity, often with numerous glandular dots on sides between costae, surface with numerous idioblasts that are not joined in series, with narrowly rhomboid raphids internally; carpodium stopper-shaped to slightly turbinate, with many series of small thick-walled cells; inner pappus of 25–30 slender capillary bristles, rather flattened outside and barbellate on sides, tips only slightly narrowed, outer pappus of narrow scales 0.5–1.5 mm long. Chromosome numbers $n = 10, 18, 20$ (Mangenot and Mangenot 1962; Bhandari and Singhvi 1977; Morton 1993).

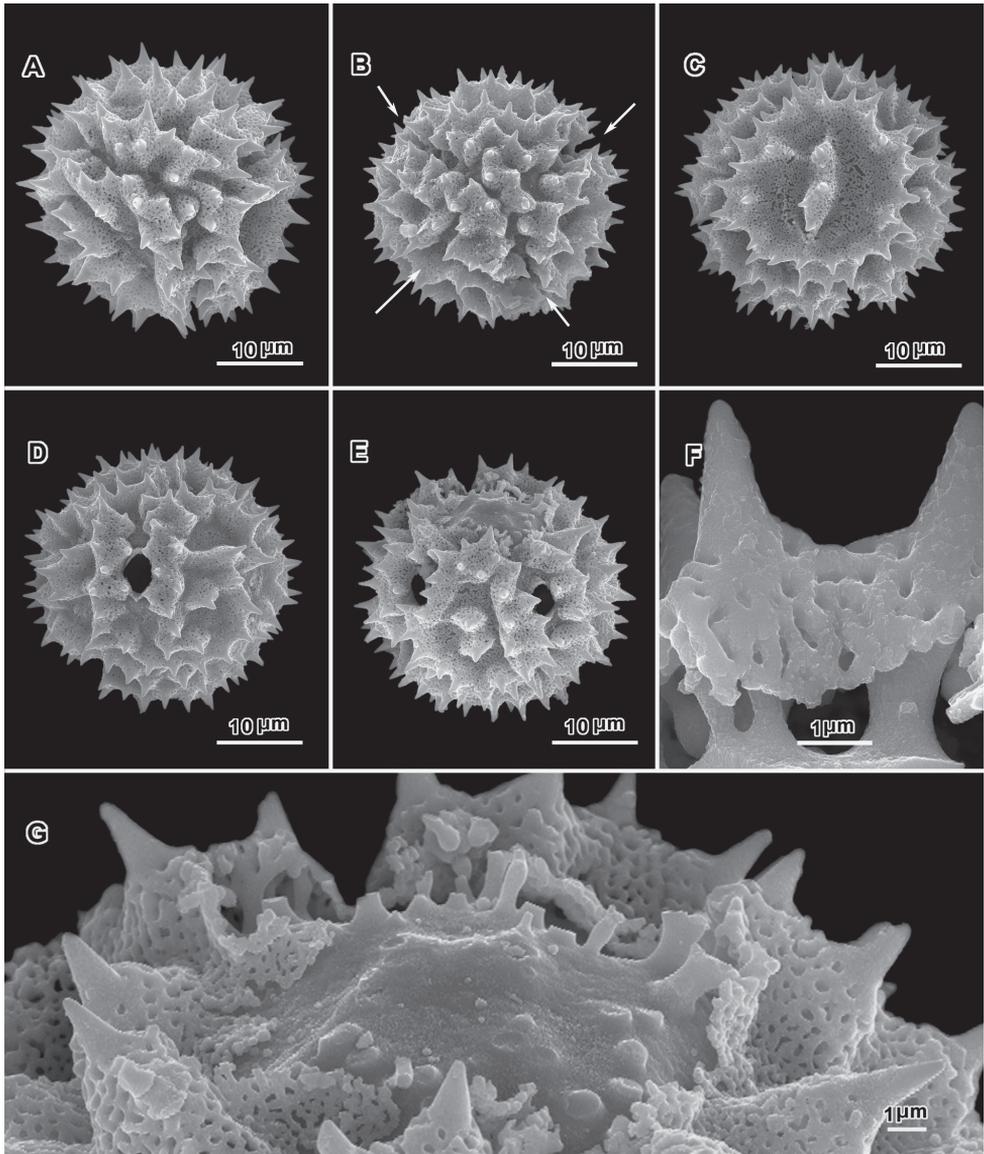


Figure 19. Scanning electron micrographs of *Orvibestus cinerascens* (Sch. Bip. in Schweinf.) H. Rob. **A** Polar view showing 3 colpi **B** Polar view showing 4 colpi **C** Lateral view showing highly perforated sheet-like layers of exine common in many grains of the sample **D** Equatorial view (appearing nearly echinolophate) **E** Lateral/equatorial view showing 2 pores **F** Fractured grain showing thickened columellae supporting a higher perforate surface **G** Fractured polar surface (**A–G** Koekemoer 232).

Pollen grains ca. 50 µm in diameter in fluid, type A, sublophate, tricolporate, echinate, with perforated tectum continuous between colpi (Fig. 19 D–E). The grains may also be somewhat asymmetrical (Fig. 19 A).

Most notable secondary metabolites are 5-alkylcomumarins (Bohlmann and Jakupovic 1990, as *Vernoniia cinarescens* Sch. Bip.) and sesquiterpene glaucolides (Bohlmann and Jakupovic 1990, as *Vernonia cistifolia* O. Hoffm.).

The genus is almost alone in the eastern hemisphere in its seriate cymes, often referred to as scorpioid cymes. Such inflorescences are common in the western hemisphere Vernonieae, occurring in *Vernonia* itself.

Single species in the flora area

***Orbivestus cinerascens* (Sch. Bip.) H. Rob., 1999**

Vernonia cinerascens Sch. Bip. in Schweinf., Beitr. Fl. Aeth. 162. 1897.

Vernonia tephrodioides Chiov., Fl. Somal. 2: 255. 1932.

Vernonia luederitziana O. Hoffm., Bolet. Soc. Soc. Brot. 10: 171. 1892.

Vernonia porta-taurinae Dinter ex Merxm., Mitt. Bot. München 2: 38. 1954, nom. nud. in syn.

Vernonia squarrosa Dinter ex Merxm., Mitt. Bot. München 2: 38. 1954, nom. nud. in syn.

Orbivestus cinerascens (Sch. Bip.) H. Rob., Proc. Biol. Soc. Wash. 112(1): 230. 1999.

Distribution. In Africa in Angola, Botswana, Kenya, Tanzania, Senegal, Uganda, and Zimbabwe; also in western India.

***Parapolydora* H. Rob., 2005**

Figures 13 C; 20 A–C; 21 A–F

Parapolydora H. Rob., Phytologia 87(2): 78. 2005. – Type: *Vernonia fastigiata* Oliv. & Hiern.

Descriptions. Perennial herbs 0.2–1.0 m tall; from slender prostrate or creeping stem or rhizome, erect stems with few to many ascending branches, five-ribbed, sides with numerous glandular dots, glabrous or finely and sparsely puberulous with some simple multiseptate hairs, and some one-armed L-shaped hairs with stalk near one end as in *Polydora*. Leaves alternate, linear to narrowly elliptic-lanceolate, venation pinnate with short, ascending, secondary veins weakly prominulous below, surfaces concolorous, glandular dots more numerous below, sparsely puberulous. Inflorescences of long-pedunculate heads terminal on leafy stems and branches; involucre broadly campanulate to subglobose; involucral bracts 110–130 in ca. six series, persistent, gradate, from 2–12 mm long, bases of bracts oblong, pale, appressed, covered with dense pale tomentum, bracts distally constricted into long glabrous, often reflexed awn, darkened along costa near base of awn; receptacle epaleaceous, alveolate. Florets 45–50 in a head; corollas lav-



Figure 20. Photographs of *Parapolydora* and *Polydora*: **A–C** *Parapolydora fastigiata* (Oliv. & Hiern in Oliv.) H. Rob. **D–F** *Polydora poskeana* (Vatke & Hildebrandt) H. Rob. See Appendix C for citation details.

ender, without hairs, basal tubes narrowly funnellform, glabrous, throats about as long as linear lobes, few glands on throat and glands clustered at lobe tips; thecae of anthers without tails at base; apical appendages ovate-lanceolate, glabrous, with thin-walled cells; style base with distinct annular node; style branches with long acicular sweeping

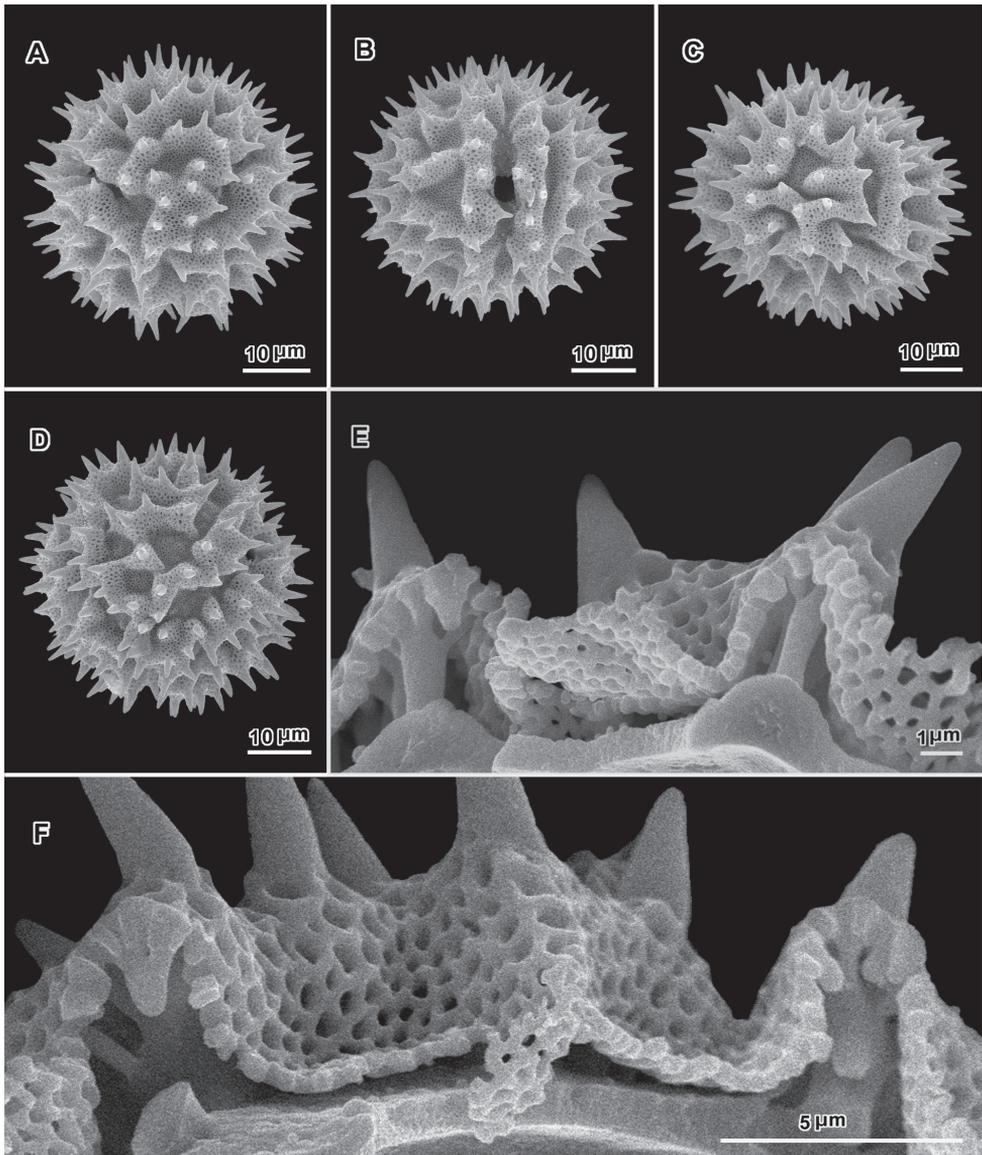


Figure 21. Scanning electron micrographs of acetolyzed sublophate-echinolophate pollen grains of two collections of *Parapolydora fastigata* (Oliv. & Hiern in Oliv.) H. Rob. **A** Polar view **B** Equatorial view showing thickened echinolophate ridges along aperture **C–D** Lateral views showing highly perforate meandering lophal ridges **E** Grain fragment showing thickened columellae underneath two spine regions **F** Grain fragment showing perforate lacunar exine with close parallel proximity to foot layer between thickened columellae supporting spines. (**A** *Pienaar 1073* **B–F** *Seydel 4023*).

hairs scarcely extending below base of branches. Achenes weakly 8–10-veined, with setulae becoming long and uniseriate from near middle or near base, rarely with one long cell and one short cell, idioblasts numerous from base to top of achene, raphids elon-

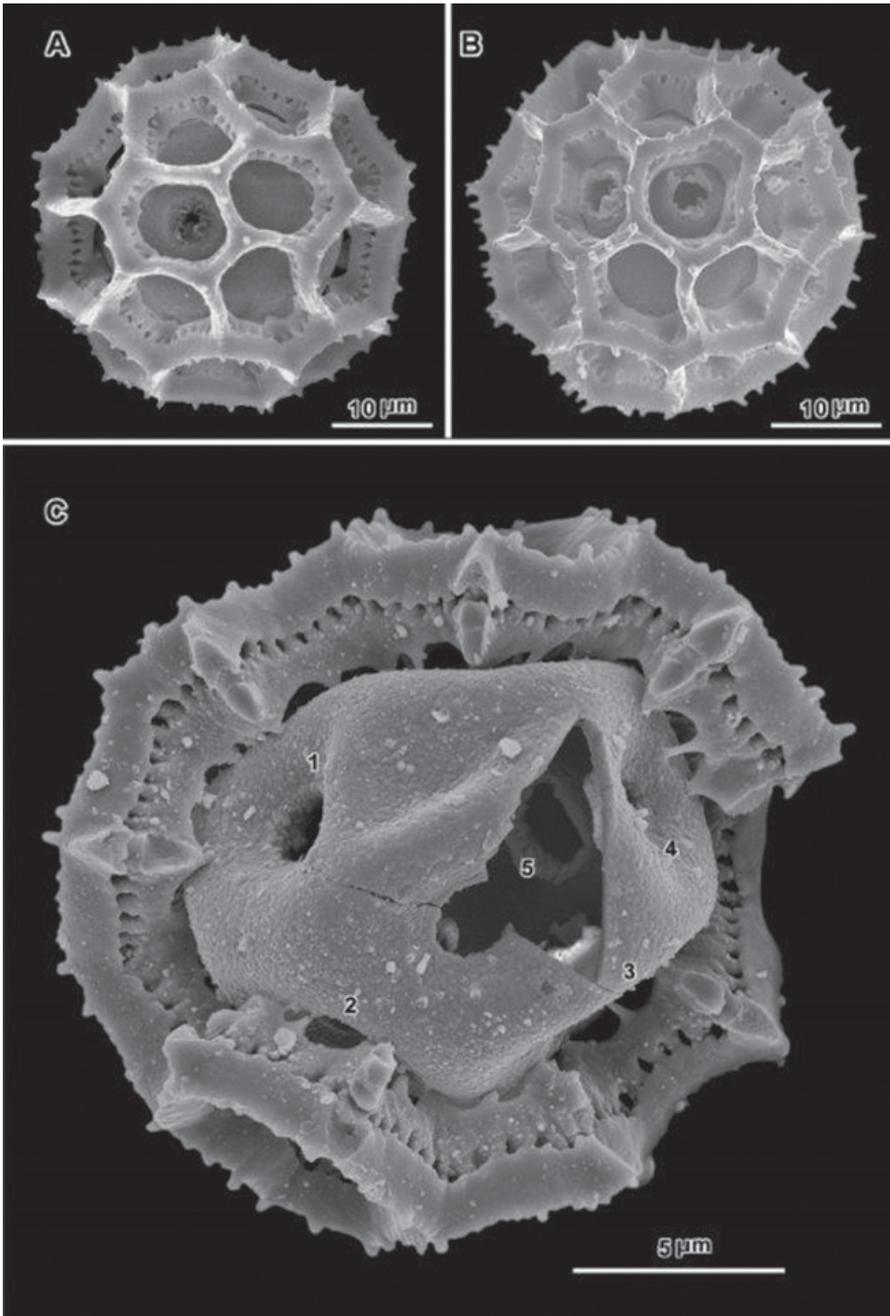


Figure 22. Scanning electron micrographs of *Polydora angustifolia* (Steetz) H, Rob. **A** Intact grain with visible pore **B** Intact grain with 2 visible pores in adjacent lacunae **C** Grain with muri partially removed showing distorted inner surface and five pores, one pore on opposite surface visible through torn area. **A** from *Brass* 16090 **B, C** from *Christensen & Patel* 1457. Views from Robinson & Skvarla, *PhytoKeys* 2014.

Crystallopollen Steetz in Peters, Reise Mossamb. Bot. 363. 1864. – Type: *Crystallopollen angustifolium* Steetz

Resources. Some species of the genus are treated by Pope (1986).

Descriptions. Mostly annuals; stems with L-shaped hairs bearing elongate one-armed cap-cells. Leaves alternate. Inflorescence a thyrsoid panicle with corymbiform cymose branches bearing pedunculate heads or a single terminal head. Involucral bracts ca. 80 in ca, seven series, often with widely scarious margins and awns often black at tips; receptacles epaleaceous. Florets ca. 30 in a head; corollas whitish to purplish, basal tube long, narrowly funnellform distally, throat as long as the narrow glabrous lobes; anther bases plain, not tailed; apical appendage glabrous, with thin cell walls, sometimes weakly ornamented; style base with distinct annular node; branches with acicular sweeping hairs. Achenes 5 or 8–10-ribbed, setuliferous with setulae scarcely divided at tips, idioblasts present but not grouped, raphids elongate; pappus with copious barbelate setae, greenish, yellowish or tawny, rarely white, outer pappus short, squamiform. Chromosome number $n = 9, 10$ (Jones 1979, 1982, Ayodele 1999).

Pollen lophate with ca. 32 lacunae, with five or more pores that seem to be rather asymmetrically distributed on the grains; the pores occur in lacunae that, in a few cases, are adjacent; margins of muri minutely echinate to psilate, without micropunctations, baculae closely spaced in single evenly spaced row under each murus, baculae in turn subtended by “rhizomate” structure that is weakly attached to the footlayer, the muri thus easily stripping away from the footlayer (Fig. 22 C). The pollen of *Polydora* proves to have a lophate condition with well-defined lophae or muro bearing 4–5 spinules on each segment. The lophae are subtended by columellae in a single series not leaving an ogee-shaped gap in the middle.

Notable secondary metabolites: sesquiterpene lactone glaucolides/hirsutanolies (Bohlmann and Jakupovic 1990, as *Vernonia poskeana* Vatke & Hildebr.), elemanolides, eudesmanolides, secoglaucolides (Herz 1996, as *Vernonia poskeana* Vatke & Hildebr.

Polydora angustifolia is the species with which Steetz first introduced the use of pollen structure in the taxonomy of the Asteraceae (Steetz in Peters 1864). The generic name *Crystallopollen* was based on the lophate pattern of the pollen observed by Steetz.

Key to species of *Polydora*

- 1 Base of the involucre with slender lanceolate bracts, bracts with straight or flexuous apical awns..... *P. angustifolia*
- Base of involucre with broad, ovate or oblong bracts, bracts with or without apiculus or mucro **2**
- 2 Tips of involucral bracts erect, mostly without distinct apiculate or mucronate apices *P. poskeana*
- Tips of involucral bracts often with recurved or squarrose apiculate apices....
..... *P. steetziana*

***Polydora angustifolia* (Steetz in Peters) H. Rob., 1999**

Crystallopollen angustifolium Steetz in Peters Reise Mossamb., Bot. 2: 366. 1864. (Type B, destroyed); neotype: Malawi. *Brass* 16090 (neotype SRGH; isoneotypes K, MO, US; see Wild, *Kirkia* 11: 55. 1978b). Originally described as *C. angustifolium* forma *vulgaris*.

Vernonia poskeana Vatke & Hildebr. var. *vulgaris* (Steetz) Hiern, Cat. Afr. Pl. Welw. I, 3: 519. 1898.

Vernonia erinacea H. Wild, *Kirkia* 11: 2. 1978, type same as *Vernonia poskeana* var. *vulgaris*.

Polydora angustifolia (Steetz in Peters) H. Rob., Proc. Biol. Soc. Wash. 112(1): 232. 1999.

Distribution. Tanzania, Mozambique and Natal east to Malawi, Zambia and Zimbabwe.

***Polydora poskeana* (Vatke & Hildebr.) H Rob., 1999**

Vernonia poskeana Vatke & Hildebr., Oesterr. Bot. Zeitschr. 25: 324. 1875.

Vernonia elegantissima Hutch. & Dalz., Fl. West Trop. Africa ed. 1, 2: 164 (in key), 167. 1931.

Vernonia poskeana Vatke & Hildebr. subsp. *bractifimbriata* Mendonça, Contrib. Conhec. Fl. Angola, Compositae. 7. 1943.

Vernonia poskeana Vatke & Hildebr. var. *elegantissima* (Hutch. & Dalz.) C.D. Adams, J. West African Science Assoc. 3(1): 121. 1957.

Vernonia poskeana var. *centauroides* (Klatt) H. Wild, *Kirkia* 11(1): 3. 1978.

Vernonia poskeana var. *botswanica* G.V. Pope, Kew Bull. 41(1): 39. 1986.

Vernonia samfyana G.V. Pope, Kew Bull. 41(1): 42. 1986.

Vernonia poskeana Vatke & Hildebr. subsp. *samfyana* (G.V.Pope) G.V. Pope, Fl. Zambes. 6(1):148. 1992.

Polydora poskeana (Vatke & Hildebr.) H Rob., Proc. Biol. Soc. Wash. 112(1): 233. 1999.

Distribution. Angola, Botswana, Namibia, South Africa (Transvaal), and Zimbabwe.

***Polydora steetziana* (Oliv. & Hiern) H. Rob., 1999.**

Crystallopollen angustifolium Steetz var. *chlorolepis* Steetz in Peters, Reise Mossamb. Bot. 2: 366. 1864, non *Vernonia chlorolepis* S. Moore (Angola).

Vernonia steetziana Oliv. & Hiern in Oliv., Fl. Trop Afr. 3: 278. 1877.

Vernonia poskeana Vatke & Hildebr. var. *chlorolepis* (Steetz) O. Hoffm., Bol. Soc. Brot.10: 171. 1893.

Polydora steetziana (Oliv. & Hiern) H. Rob., Proc. Biol. Soc. Wash. 112(1): 233. 1999.

Distribution. South Africa (Transvaal), Swaziland.

***Pseudopegolettia* H. Rob., Skvarla & V.A. Funk, gen. nov.**

urn:lsid:ipni.org:names:77152893-1

Figures 23 A–E; 24 A–H

Type. *Pegolettia tenella* DC.

Descriptions. Small perennial herbs; stems erect, with short branchlets from lower nodes, puberulous to subsericeous with short-stalked hairs bearing asymmetric cap cells, stalks moderately broad with one or two septae, cap cells short and stout, attached near lower end. Leaves alternate, oblong to linear, essentially sessile, sparsely puberulous, abaxially densely glandular punctate. Inflorescence terminal with 1 or a few heads borne on long peduncles. Heads campanulate, 1.7–2.5 cm. wide; involucre bracts 20–60, in ca. three series, subequal, linear-lanceolate, herbaceous with slender tips, pilosulous outside; receptacle slightly convex, surface with angular thickenings. Florets 15 or more in a head; corollas purple, ca. 1 cm long, narrowly funnel-shaped from a slender base, throat slightly shorter than the moderately distorted, linear-lanceolate lobes, outer surface with short glands on tube and throat, spiculiferous distally on lobes; anther thecae narrowed at base to short lobulate tail; apical appendage glabrous, ovate with rather firm cell walls; style base with narrow annular node; sweeping hairs acicular, restricted mostly to style branches, few on upper shaft. Achenes mostly 6–8-ribbed, to 4.5 mm long, with glandular punctations and scattered idioblasts on sides, rarely without or with many short setulae that are not or scarcely split at apex, inner layer without raphids or with subquadrate raphids, with layer of rather sclerified narrow cells appearing as striations under the glands and idioblasts; carpodium broadly stopper-shaped, sometimes with few short uniseriate hairs on inner surface; pappus of ca. 40 scabrid bristles, mostly in one series, as long as tube and throat of corolla, rather easily deciduous, scarcely narrowed except at tips, with few indistinct short bristles in outer series. Chromosome number unknown.

Pollen ca. 47 μm in diam., tricolporate, sublophate, echinate, with perforated tectum continuous between colpi (Fig. 24 A–H).

Most notable secondary metabolites include sesquiterpene glaucolides (Bohlmann and Jakupovic 1990 as *Vernonia monocephala* Harv.) and 5-alkylcoumarins (Bohlmann and Jakupovic 1990 as *Vernonia galpinii* Klatt).

The genus consists of mostly monocephalous species, but those species have many individual differences such as the restriction of leaves to a basal rosette, capitula structure, and pubescence of the achenes. They do have essentially identical pollen, but it is a widely distributed pollen type in the Erlangeinae. There are no unique or uncommon characteristics that the two species share.



Figure 23. Photographs of *Pseudopegolettia* and *Vernoniastrum*: **A–C** *Pseudopegolettia tenella* (DC.) H. Rob., **D–E** *Pseudopegolettia thodei* (Phillips) H. Rob., Skvarla & V.A. Funk, note: images show the leafy stem of *P. tenella* and the succulent basal leaves of *P. thodei*; **F–G** *Vernoniastrum latifolium* (Steetz in Peters) H. Rob.. See Appendix C for citation details.

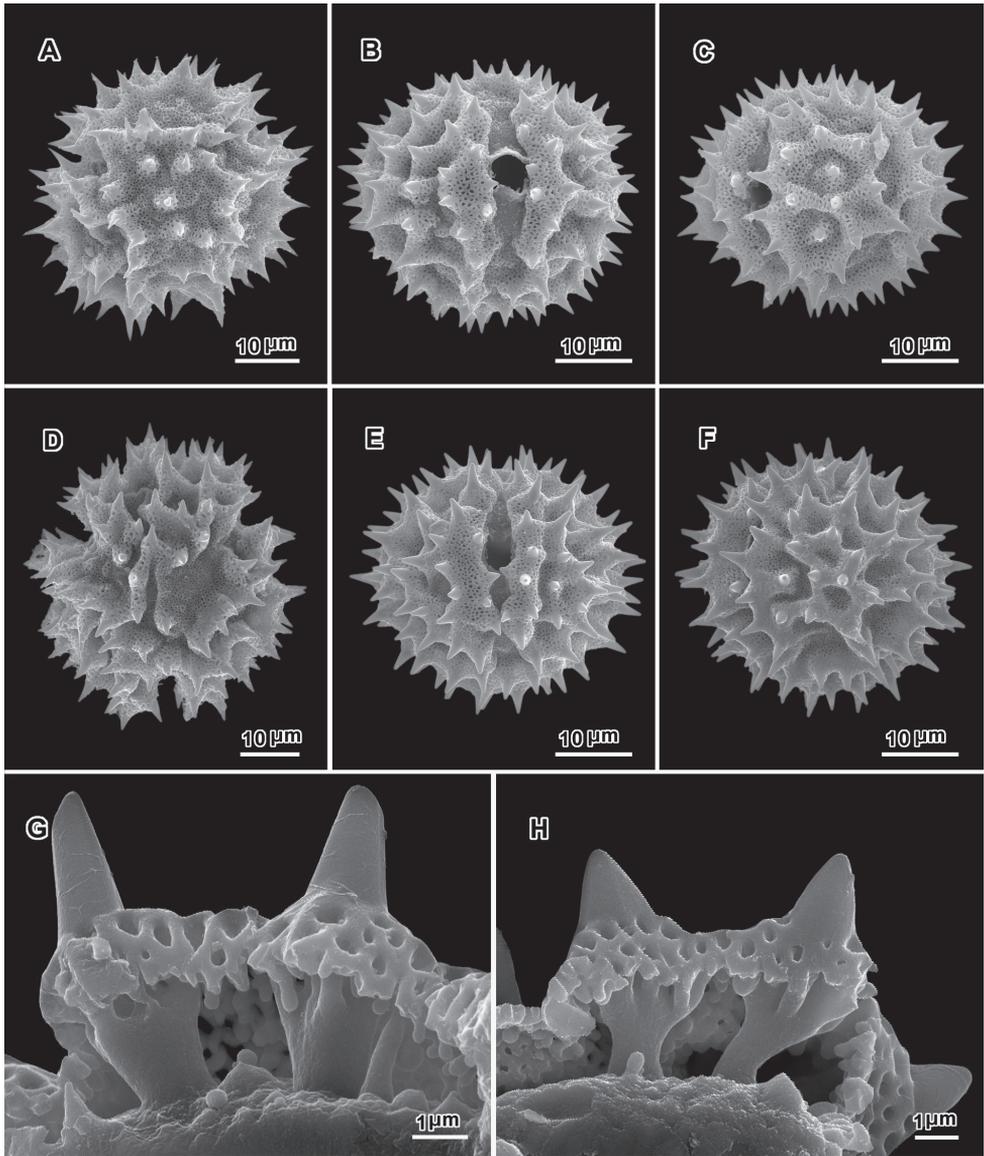


Figure 24. Scanning electron micrographs of *Pseudopegolettia*. **A–H** Scanning electron micrographs of acetolyzed sublophate-echinolophate pollen of *Pseudopegolettia tenella* (DC.) H. Rob. **A** Polar view **B** Equatorial view with prominent lophal ridges surrounding pore **C** Lateral view **D** Polar view, slightly different from **A** **E** Equatorial view **F** Lateral view slightly different from **C** **G** and **H** are fractured grains showing the thickened and distally bifurcated support columellae for the overlying exine. From *Sidley 3904*.

Key to the species of *Pseudopegolettia*

- 1 With numerous cauline leaves; heads with many linear outer involucre bracts; achenes with few or no setulae; setulae not divided at tips *P. tenella*
- With leaves mostly basal; heads without linear outer involucre bracts; achenes with many setulae; setulae with shortly but distinctly divided tips *P. thodei*

***Pseudopegolettia tenella* (DC.) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152899-1

Pegolettia tenella DC., Prodr. 5: 482. 1836.*Vernonia monocephala* Harv. in Harv. & Sond., Fl. Cap. 3: 53. 1865, *nom. illeg.*, non*Vernonia monocephala* Gardn. (1847).*Vernonia galpinii* Klatt, Bull. Herb. Boiss. 4: 827. 1896.**Distribution.** South Africa (Transvaal, Natal).

Note. The older De Candolle name has been placed rather consistently in synonymy, but not adopted. It is only comparatively recently that the combination was occupied in *Vernonia*, as *Vernonia tenella* D.Nash, Fieldiana, Bot. 36: 74. 1974 = *Lepidaploa tenella* (D.Nash) H. Rob. The epithet *tenella* still has priority in almost all other genera. The DeCandolle specimen is known in this study primarily from synonymy, description, and on the basis of microfiche (IDC DeCandolle Herbarium 197: III: 8).

***Pseudopegolettia thodei* (Phillips) H. Rob., Skvarla & V.A. Funk, comb. nov.**

urn:lsid:ipni.org:names:77152900-1

Vernonia collina Schlechter, J. Bot. 1898. 374. 1898, *nom. illeg.*, non *V. collina* Gardn. 1846.*Vernonia thodei* Phillips, J. Bot., Lond. 74: 205. 1936, based on *V. collina* Schlechter.**Distribution.** Zambia, Transvaal (Smith 1971).

Note. The specimen cited by Smith (1971) as *Vernonia nyassae* Oliv. from Transvaal, is *Pseudopegolettia thodei*. The two species have generally similar habits, but they are totally different entities with basically different pollen.

It is evident from the description that *Vernonia collina* of Klatt, based on a Schlechter collection, is not the same as the *V. collina* of Schlechter. See under unplaced species.

***Vernoniastrum* H. Rob., 1999**

Figures 23 F–G; 25 D–I

Vernoniastrum H. Rob.. Proc. Biol. Soc. Wash. 112(1): 233. 1999. – Type: *Crystallopol-
len latifolium* Steetz in Peters.

Vernonia sect. *Lepidella* Oliv. & Hiern, Fl. Trop. Afr. 3: 267. 1877, non *Lepidella* Tiegh.
1912 or *Lepidella* E.J. Gilbert 1925. – Type: *Vernonia petersii* Oliv. & Hiern.

Vernonia subsect. *Lepidella* (Oliv. & Hiern) S.B. Jones, Rhodora 83: 72. 1981.

Descriptions. Annual or perennial herbs 0.3–1.0 m tall; stems pilose, hairs simple with elongate apical cells with slightly asymmetric bases. Leaves alternate. Inflorescence with 1–many heads. Involucre campanulate; involucre bracts ca. 50 in ca. three series, gradate, persistent; receptacle epaleaceous. Florets ca. 50 in a head; corollas reddish-purple, basal tube narrowly funnellform, throat shorter than lobes or anther thecae, lobes pilosulous distally; anther bases acuminate to acutely tailed; apical appendage glabrous, with thin cell walls. Style base with node; style branches with acicular sweeping hairs. Achenes 4–6-angled, setulae aparse on sides, idioblasts usually grouped in transverse bands, raphids elongate; pappus bristles subpersistent, marginally densely barbellate; outer squamae persistent. Chromosome number $n = 10$ (Jones 1979, 1982).

Pollen triporate, lophate, perforated tectum discontinuous in lacunae, muri papillate, with or without micropunctations on muri (Fig. 25 D–I).

With habit similar to *Polydora* but often perennial, lacking L-shaped hairs, having tailed anther bases, and a chromosome number $n = 10$. Also characteristic of the core element of *Vernoniastrum* are the transverse bands of crowded idioblasts in the achene walls.

Key to the species of *Vernoniastrum*

- 1 Perennial herbs *V. nestor*
- Annual herbs **2**
- 2 Apices of involucre bracts straight *V. acuminatissimum*
- Apices of involucre bracts recurved *V. latifolium*

***Vernoniastrum acuminatissimum* (S. Moore) H. Rob., Skvarla & V.A. Funk, comb. nov.**
urn:lsid:ipni.org:names:77152901-1

Vernonia acuminatissima S. Moore, J. Linn. Soc., Bot. 40: 104. 1911.

Vernonia rogersii S. Moore, J. Bot. 52: 183. 1913.

Distribution. Tanzania, Mozambique, Zimbabwe.

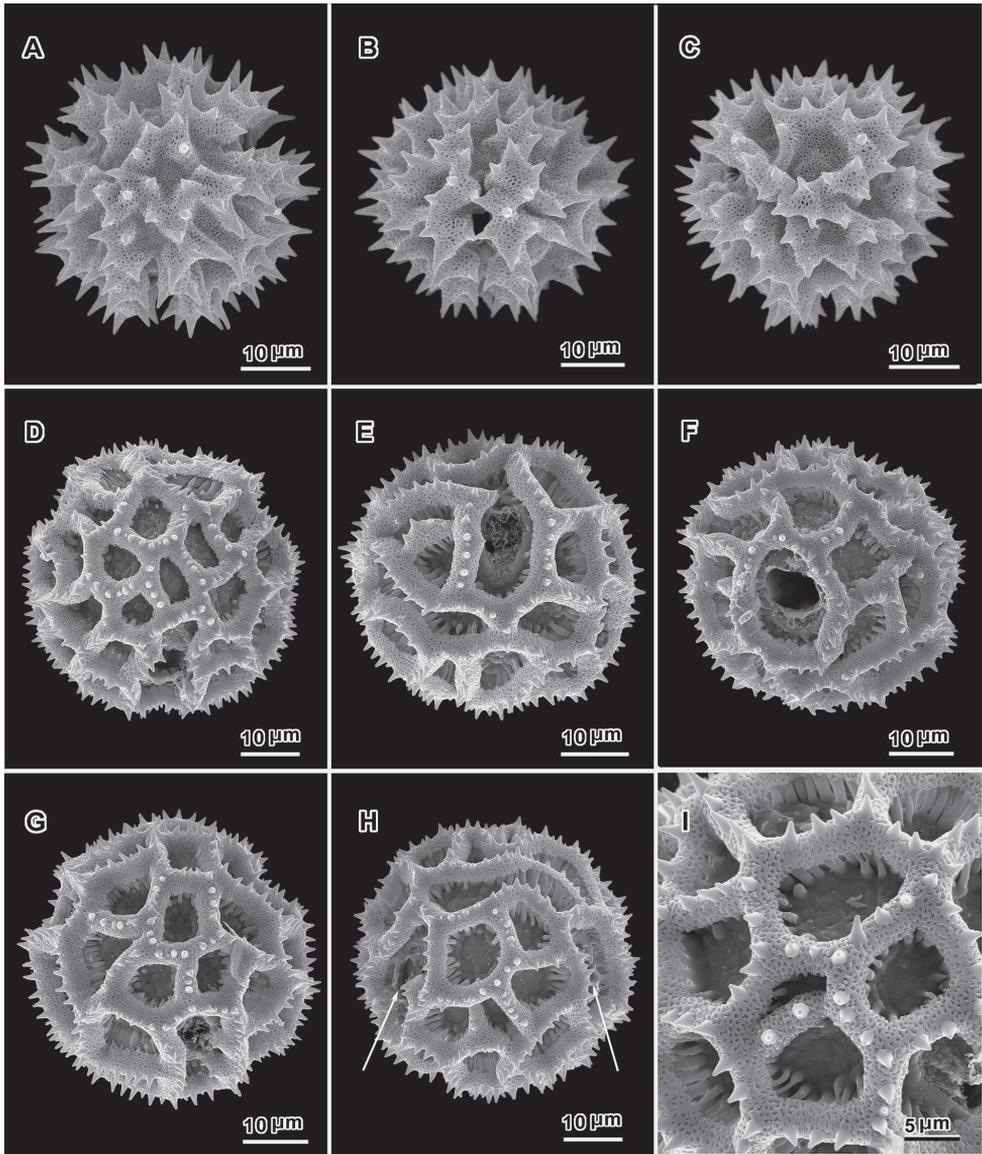


Figure 25. Scanning electron micrographs of *Vernonella* and *Vernoniastrum*. **A–C** Scanning electron micrographs of acetolyzed sublophate-echinolophate pollen of *Vernonella africana* Sond. **A** Polar view **B** Equatorial view **C** Oblique polar view. **A–C** from *Wood 753*. **D–I** Scanning electron micrographs of acetolyzed echinolophate pollen of *Vernoniastrum nestor* (S. Moore) H. Rob., showing diversity of lacunae and lophae. **D–H** Oblique and near polar views showing apertures in markedly long lacunae with irregular lophae **H** Lateral view with apertures (arrows) occupying long lacunar spaces **I** Enlarged section of surface showing columellae in irregular rows under muri). **D–I** from *Reekmans 9185*.

***Vernoniastrum latifolium* (Steetz in Peters) H. Rob., 1999**

Crystallopollen latifolium Steetz in Peters, Reise Mossamb. Bot. 364, t. 48a. 1864, non
Vernonia latifolia Lem. 1855.

Vernonia petersii Oliv. & Hiern, Trans. Linn. Soc. London 29: 90. 1873.

Vernonia eriocephala Klatt, Bull. Herb. Boiss. 4: 826. 1896.

Vernoniastrum latifolium (Steetz in Peters) H. Rob., Proc. Biol. Soc. Wash. 112(1): 234. 1999.

Distribution. Angola and Congo east to Mozambique and Tanzania, Namibia.

***Vernoniastrum nestor* (S. Moore) H. Rob., 1999**

Vernonia nestor S. Moore, J. Linn. Soc. Bot. 35: 317. 1902.

Vernoniastrum nestor (S. Moore) H. Rob., Proc. Biol. Soc. Wash. 112(1): 234. 1999.

Distribution. West Africa east to Tanzania, Mozambique, Zimbabwe, Natal.

***Vernonella* Sond., 1850**

Figures 13 D; 25 A–I

Vernonella Sond., Linnaea 23: 62. 1850. – Type: *Vernonella africana* Sond.

Resources. Species reviewed by Smith (1971) and Robinson and Skvarla (2010a).

Descriptions. Annual or perennial herbs, with leaves rosulate or on leafy stems, basal rosettes often withered at anthesis, bases of plants erect, with or without a dense basal cloak of hairs. Hairs simple or lacking on stems. Inflorescences monocephalic, laxly cymose or densely corymbiform, with short to very elongate peduncles. Heads broadly campanulate; involucre 3–6-seriate, bracts broadly to narrowly oblong, gradate with basal bracts often more lanceolate, tips of inner bracts often obtuse to rounded or apiculate, distally and marginally rather scarious, often purplish. Florets 10–50 or more in a head; corollas purple, with long slender basal tube, throat short, not noticeably broadened at base, lobes linear, usually contorted with age, bearing glands, simple hairs, or L-shaped to T-shaped hairs; anther thecae calcarate and blunt at base, without tails; apical appendage oblong-ovate, with thin cell walls; style base with annulus of thickened, quadrate cells; sweeping hairs slender with sharp, narrow tips. Achenes with ca. 10 ribs, setulose on ribs, setulae with paired cells separated in distal third or less, with numerous idioblasts on surfaces between ribs; raphids in achene wall narrowly elongate. Chromosome number $n = 9$ (Jones 1982).

Pollen ca. 30–40 μm in diameter when dry, tricolporate with short or truncated colpi, sharply echinate with elongate spines, sublophate with large irregularly shaped lacunae, perforated tectum continuous in lacunae (Fig. 25 A–C).

Notable secondary metabolites include sesquiterpene lactones (elemanolides and eudesmanolides).

The genus *Vernonella* is most notable for its often solitary heads, simple vegetative hairs, the comparatively limited differentiation of the involucre bracts, unexpanded corolla throats, and the comparatively small sublophate rather than lophate pollen with uniquely truncated colpi. On the basis of the examination of the type species, the detailed studies of Smith (1971), and reviews of literature, eleven species are recognized in the genus. The genus is restricted to Africa and is distributed from Cameroon and Sudan in the north southward to Natal in South Africa.

One species in the flora area

Vernonella africana Sond., 1850

Vernonella africana Sond., *Linnaea* 23: 62. 1850.

Vernonia vernonella Harv. & Sond., *Fl. Cap.* 3: 53. 1865.

Vernonia africana (Sond.) Druce, *Bot. Exch. Club Soc. Brit. Isles.* 1916: 651. 1917.

Centrapalus africanus (Sond.) H. Rob., *Proc. Biol. Soc. Wash.* 112: 236. 1999.

Distribution. Natal.

Note. Material of the species was sought by Smith from its type locality, but he reported (1971), “I searched the type locality for living plants, but the area is now devoted to sugarcane fields, and the species may have been completely eliminated.”

Species not yet properly placed in a genus

Vernonia potamophila Klatt, 1890

Vernonia potamophila Klatt, *Annal. Naturh. Hofmus. Wien* 7: 100. 1890.

Distribution. Congo, Angola, Namibia (Caprivi strip), Zambia.

Descriptions. The initial assumption, based on the robust habit and the described yellowish brown velutinous pubescence of the stems, was of a relationship to the genus *Gymnanthemum* of the subtribe *Gymnantheminae*. Other features indicate a different relationship. A high resolution image of an herbarium specimen (PRE; Fig 2D) as well as an illustration (Fig. 26), show a somewhat keeled involucre bract with a dark median stripe, a character not found in *Gymnanthemum*. In addition, the pollen totally lacks the strongly developed sublophate pattern that is characteristic of *Gym-*



Ch. Crain et aut. del. et lith.

Ingr. Lemercier, Paris.



VERNONIA POTAMOPHYLLA Klatt.

Figure 26. Illustration of *Vernonia potamophylla* Klatt. See Appendix C for citation details. **1** Habit showing pinnate leaf venation **2** Involucral bracts showing keel and dark line **3** Floret with immature achene **4** Corolla opened longitudinally **5** Anthers **6** Style **7** Achene with pappus **8** Enlarged pappus bristle.

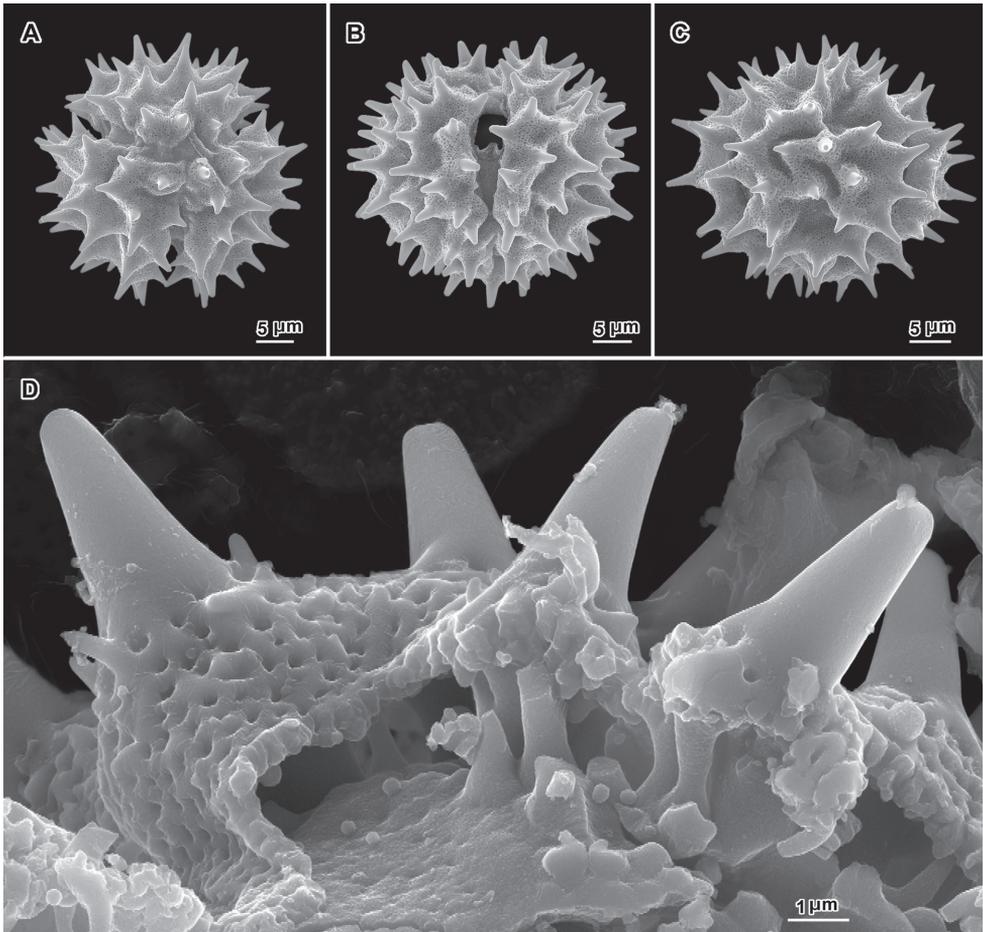


Figure 27. A–D Scanning electron micrographs of acetolyzed sublophate pollen of *Vernonia potamaphylla* Klatt. **A** Polar view **B** Equatorial view **C** Lateral view **D** Grain fragment. From *Killick & Leistner 3277*.

nanthemum (Figs. 10 A–C) and instead is sublophate with small incipient lacunae (Fig. 27). The pollen and involucre characters seem to indicate a position in the subtribe Erlangeinae. This is most likely a new genus but without a more comprehensive study of the more northern members of the African Vernoniae we can only say that *V. potamophila*, while definitely not a true *Vernonia*, is unplaced as to genus.

An examination of limited fragments showed a few additional characters. The abaxial surface of the leaf has a tomentum of long-armed T-shaped hairs and sweeping hairs restricted to the branches of the style and the juncture of the branches at the shaft of the style. The lobes of the corolla had areolae that were reminiscent of the ducts in the corolla lobes of true *Vernonia*, but the areolae do not form continuous elongate ducts. Raphids of the achenes were short-rectangular in elongate cells. Chromosome number unknown.

***Vernonia collina* Klatt, 1896**

Vernonia collina Klatt, Bull. Herb. Boiss. 4: 824. 1896, *nom. illeg.*, non *Vernonia collina* Gardn. 1846.

Distribution. Transvaal (In cliv. Mont. Elandspruitbergen, alt. 7000 ped., leg. R. Schlechter, 2 December 1893, N. 3832).

Note. The name is an illegitimate later homonym and cannot be used, but the species, as described, cannot be placed with other Vernonian species presently known from South Africa. The original description (Klatt 1896) makes no mention of corollas and they may have been absent on the type collection. According to the description, the achenes are ca. 3 mm long and the pappus is 1.5 cm long, suggesting an immature or overly mature condition. From the description it is not certain the species is actually a member of the Vernoniae.

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M. Koekemoer (PRE) is thanked for providing useful scans of some of the unavailable species from South Africa, and also for providing some fragments from which pollen could be extracted and in which some anatomical details could be examined. Carol Kelloff (US) and Alice Tangerini (US) are thanked for help with the figures. We appreciate the efforts of Fabian Michelangeli and Kim Watson (NY) who provided the image of the illustration of *Vernonia potamophila*. We thank Greg Strout (OKL) and Emily Skvarla who went to great lengths to provide the missing pollen images. We thank the many colleagues and nature lovers around the world who sent images and permission to use them – please see Appendix C for information on the photographer or artist and the website addresses. Finally, we thank the editors of the amazing online databases (Index Herbariorum, Thiers continuously updated; IPNI 2012; JSTOR G-P, continuously updated; Compositae Chromosome numbers, Watanabe 2015) that we use daily and often forget to mention.

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Appendix A: Definitions of Pollen Terms (as used in this paper)

As a general rule Vernonieae pollen can be ‘nearly non-lophate’ to ‘sublophate’ to ‘lophate’, however, none of the grains in the Vernonieae are completely non-lophate. Grains can be with or without colpi and they can be tricolporate or triporate to pentaporate.

Columellae: A rod-like element supporting the tectum.

Echinolophate: Among lophate types, one variant has prominent lophae (muri) with sharply projecting spines. The lophae have supporting thickened columellae or baculae.

Lacunae: Areas in lophate pollen surrounded by muri.

Lophate (in the Vernonieae): Pollen having the perforated tectum non-continuous. There are varying degrees of loss of perforated tectum. Grains can have spines (various types of echinolophate) or not (psilolophate).

Muri: partitions or walls forming a network on surface of lophate pollen (Figs. 3 A–I, 4 A–C, and 4 D–F).

Nearly non-lophate: Arrangement of spines is somewhat uneven and the perforated tectum is continuous.

Non-lophate (truly): Completely evenly spaced spines or columellae; the perforated tectum is continuous. [not found in Vernonieae]

Pantoporate: Pores on pollen positioned all over the surface, not strictly equatorial.

Psilolophate: A variant of the lophate types where the surface of the lophae is without spines [Linzia]

Sublophate (as used in the Vernonieae): The arrangement of the spines is somewhat distinctly uneven, leaving incipient lacunae; the perforated tectum is always continuous in all non-colpar areas supported by massive columellae or baculae, and spines being almost always present over the baculae.

Sub-echinolophate: There are varying forms of lophate grains that are highly perforate and spinose.

Tectum: The layer that forms a roof over the columellae. A perforated tectum has perforations smaller than 1 µm in diameter

Tricolporate: Grains with three colpi and a central pore in each colpus. The pore provides a germination point for the emerging pollen tube.

Triporate: Grains without colpi and with three equatorial pores for possible germination.

Appendix B: List of specimens used for pollen images

- Baccharoides anthelmintica* (L.) Moench. Assam, *Koelz 7469* (US)
Baccharoides anthelmintica (L.) Moench., *USDA P.I. 283729*, chromosome voucher, Jones (US)
Baccharoides anthelmintica (L.) Moench., Ceylon (Sri Lanka), 17 March 1970, *G. Cooray 70031701R* (US)
Bothriocline schimperii Oliv. & Hiern ex Benth., Ethiopia, Wllega Prov. 6 Feb. 1962, *F Meyer 8159* (US)
Cyanthillium cinereum (L.) H. Rob., Pacific, Caroline Islands, Fais Isl. *Evans 344* (US)
Distephanus angulifolius (DC.) H. Rob. & B. Kahn, S. Afr., Natal, *Sidley 2211* (US)
Erlangea misera (Oliv. & Hiern) S. Moore, Namibia, Popa Falls, 21 Aug 2007, *Funk 12708* (US)
Ethulia conyzoides L.f., Uganda, *W.H. Lewis 6025* (US)
Ethulia conyzoides L.f., Vietnam, Tonkin, 19 June 1927, *Petelot 4047* (US)
Gymnanthemum mespilifolium (Less.) H. Rob. *Plantae Africae Australe*, *Schlechter 6644* (US)
Hilliardiella capensis (Houtt) H. Rob., Skvarla & V. Funk, S. Africa, Cape Province, *Gentry & Barolas 18914* (US)
Hilliardiella capensis (Houtt) H. Rob., Skvarla & V.A. Funk, Cape Prov., Humansdrap Div., *Bayliss BS 3686* (US).
Linzia glabra Steetz, Zimbabwe, *O. West 7292* (US)
Linzia rosenii (R.E. Fries) H. Rob., Skvarla & V.A. Funk, Botswana, Savuti, Chobi Natl. Park, *Jacobsen 3075* (PE).
Namibithamnus obionifolius (O. Hoffm.) H. Rob., Skvarla & V. Funk, Namibia, *Tölk-en & Hardy 770* (US)
Oocephala centaurioides (Klatt) H. Rob. & Skvarla, Regio oriente et Mosambique, Delagoa Bay, *Schlechter 18138* (US)
Oocephala staehelinoides (Harv.) H. Rob. & Skvarla, Transvaal, *Liebenberg 8843* (US)
Orbivestrus cinerascens (Sch. Bip. in Schweinf.) H. Rob. Transvaal, *Koekemoer 232* (US)
Parapolydora fastigiata (Oliv. & Hiern) H. Rob., Namibia, Vindhuk Bergland 13.5.1964, *Seydel 4023* (US)
Parapolydora fastigiata (Oliv. & Hiern) H. Rob., Tranvaal, *B.J. Pienaar 1073* (US)
Polydora angustifolia (Steetz) H. Rob. (as *erinacea*). Malawi: Zomba District, Likangala, Phalombe Road. 3000 ft. 3/ 12/ 1984. *Christenson & Patel GMC 1357* (US)
Polydora angustifolia (Steetz) H. Rob., *Brass 16090* (US)
Pseudopegolettia tenella (DC.) H. Rob., Skvarla & V. Funk, South Africa: Natal, *Sidley 3904* (US)
Pseudopegolettia thodei (Phillips) H. Rob., Skvarla & V. Funk, *Hilliard & Burt 8374* (PRE)
Pseudopegolettia thodei (Phillips) H. Rob., Skvarla & V. Funk, *Koekemoer 2117* (PRE)
Vernonella africana Sond. Natal, S. Africa, *Wood 753* (US)

Vernonia potamophila Klatt, *SW Africa, Caprivi, Killick & Leistner 3277* (PRE)
Vernoniastrum nestor (S. Moore) H. Rob., Burundi, Prov. Burundi, Gihofi (Mgssso)
 jachere, 20 May 1980, *Reekmans 9185* (US)

Appendix C: Sources for photographs, illustrations, and websites [Plant names are as they were found on the image and may not reflect current taxonomy]

Figure 1:

- A. Blittersdorff R von (2009) “*Vernonia adoensis* Sch. Bip. ex Walp. (photo ID: 23949)”. S. Dressler S, Schmidt M, Zizka G, eds. (2014) African Plants, a photo guide. Forschungsinstitut Senckenberg, Frankfurt/Main, Germany. <http://www.africanplants.senckenberg.de> [date accessed: 23 December 2014]
- B. Hyde M (2014) “*Vernonia adoensis* Sch. Bip. ex Walp. (Record no: 58514)”. Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 23 December 2014]
- C. Hyde M (2014) “*Bothriocline laxa* N.E. Br. (Record no: 158050)”. Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 23 December 2014]
- D. *Vernonia potamophila* Klatt [Image of specimen from PRE]

Figure 2:

- A. Smith CE, Jr (1971) “*Vernonia adoensis* Sch. Bip. Ex Walp., illustrated by Hughes RO”) Observations on stengelioid species of *Vernonia*. USDA (ed.), Agriculture Handbook No. 396, Washington DC, United States Department of Agriculture. 87 Pp.
- B. Prain D (1918) “*Erlangea aggregata* Hutch., illustration no 8755 by Smith M” Curtis’s Botanical Magazine 144 [ser. 4, vol. 14]: t. 8269
- C. Anonymous (1832). “*Ethulia conyzoides* L.f., illustrated by M. Hart” Botanical Register, vol. 9 t. 698.
- D. Robinson H, Funk VA (2014) *Gymnanthemum koekemoerae* H.Rob & V.A. Funk, illustrated by A. Tangerini. *PhytoKeys*: 36: 61.

Figure 5:

- A–C. LeBourgeois T (2008) “*Cyanthillium cinereum* (L.) H. Rob.” Pl@ntNet Web: <http://www.plantnet-project.org/> [date accessed: 23 Dec 2014]

Figure 6:

- A–C. Wursten BT (2014) “*Distephanus divaricatus* (Steetz) H. Rob. & B. Kahn. (Record no: 60279, 60281, 60282)”. Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 16 December 2014]

- D. Creative Commons - Attribution Non-Commercial Share-Alike. *Distephanus divericatus* (Steetz) H. Rob. & B. Kahn. 2011. License Holder: Olivier Maurin, University of Johannesburg, Johannesburg. BOLD Systems. http://www.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxid=349118 [date accessed: 22 Dec 2014]
- E–F. English P (2010) “*Distephanus divericatus* (Steetz) H. Rob. & B. Kahn. (record no: 43443 & 43445).” Web: www.zambiaflora.com [date accessed: 22 Dec 2014]
- G. Graham G (2013) “*Distephanus anisochaetoides* (Sond.) H. Rob. & B.Kahn (image no: 531616). iSpot, share nature. <http://www.ispotnature.org> [date accessed: 19 Dec. 2014]
- H. Anonymous (2012) “*Distephanus anisochaetoides* (Sond.) H. Rob. & B.Kahn (image #521927 by ES). iSpot, share nature. <http://www.ispotnature.org> [date accessed: 19 December 2014]

Figure 7:

- A–B. Schneider B (2013) “*Erlangea misera* S. Moore (image no. 41706)”. Web: <http://www.ispotnature.org/node/508454> accessed date: 2 March 2015
- C–D. Wursten BT (2014) “*Ethulia conyzoides* L.f. subsp. *conyzoides*. (Record no: 40831 & 40832)”. Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 16 December 2014]
- E. Bidault, E. (2015) “*Ethulia conyzoides* L.f.”. <http://tropical.theferns.info/image.php?id=Ethulia+conyzoides> [date accessed: 23 August 2015]

Figure 9:

- A. Villiers F de (2014) “*Gymnanthemum corymbosum*”. iSpot, share nature. <http://www.ispotnature.org> [date accessed: 23 December 2014]
- B–D. Berkel, N van (2013) “*Gymnanthemum mespilifolium*”. iSpot, share nature. <http://www.ispotnature.org> [date accessed: 23 December 2014]

Figure 11:

- A–B. Blittersdorff R von (2008-9) “*Vernonia natalensis* Sch. Bip. ex Walp. Dressler S, Schmidt M, Zizka G (eds.) (2014) African Plant, a photo guide. Forschungsinstitut Senckenberg, Frankfurt/Main, Germany. <http://www.africanplants.senckenberg.de> [date accessed: 23 December 2014]
- C–D. Warren PR (2013) “*Hilliardiella flanaganii*”. iSpot, share nature. <http://www.ispotnature.org> [date accessed: 23 December 2014]

Figure 12:

- A–D Berkel N van (2012) “*Hilliardiella oligocephala*”. iSpot, share nature. <http://www.ispotnature.org> [date accessed: 23 December 2014]

Figure 13:

- Hooker WJ (1863) “*Webbia pinifolia* [*Hilliardiella capensis*] illustration 5412 by W.H. Fitch.” Curtis’s Botanical Magazine 89 [ser. 3, vol. 19]: t. 5412.
- Humbert H (1960) Composees. “*Linzia glabra* Steetz in Peters, Illustrated by J.V. & .G.M.” [as *V. obconica* (Oliv. & Hiern in Oliv.)] in Humbert H (ed.), Flore de Madagascar

et des Comores, Family 189, Tome 1, Fig. VI, Paris, Typographie Firmin-Didot et Cie. <http://www.biodiversitylibrary.org/bibliography/6600#/summary>

Wood JM (1906) "*Vernonia gerrardi* Harv., illustrated by M.F." Natal Plants 4: t. 330.

Wood JM (1906) "*Vernonia vernonella* Harv., illustrated by M.F." Natal Plants 4: t. 332

Figure 15:

A–B. Dressler S, Schmidt M, Zizka G (2014) "*Linzia glabra* Steetz in Peters" Introducing African Plants – A Photo Guide – An interactive photo data-base and rapid identification tool for continental Africa. *Taxon* 63(5): 1159–1161.

C–D. Strohbach B (2014) "*Vernonia obionifolia* O. Hoffm. (photo id: 16480 & 16478)". Jürgens N, Strohbach B, Schmiedel U, Rügheimer S, Erb E, Wesulus D, Schrenk J, Dreber N, Schmidt M, Mayer C, Zizka A, Horn P, Mills A, Etzold S, Schulz A, Beaumont J, Oncken I, Revermann R, Niesler I, Kwembeya E, Deckert J, Kuhlmann M, Reddig C, Miehlich G, Christiaan R, Finckh M, Kruger S, Coetzee M, Fortuin A, Ihlenfeldt H, Le Roux A, Erb P, Groengroeft A, Helme N (2014) Photo Guide to Plants of Southern African plants. BioCentre Klein Flottbek, Hamburg, Germany, www.southernafricanplants.net

Figure 17:

A–B. Taylor R (2014) "*Oocephala (Vernonia) centaureoides* (photographs)". iSpot, share nature. <http://www.ispotnature.org> [date accessed: 23 December 2014]

C. Wursten BT (2007) "*Vernonia cinerascens* Sch. Bip. (Record no: 22771)". Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 16 December 2014]

D–E. Dreyer, A. (2015). "*Vernonia cinerascens* Sch. Bip (Record no: 8879 & 8878)" Kyffhäuser. [online] Kyffhauser.com. Available at: <http://www.kyffhauser.com> [date accessed: 5 Jan 2015]

Figure 20:

A–C. Warren, P.R. (2014) "*Vernonia fastigiata* Oliv. & Hiern". iSpot, share nature. <http://www.ispotnature.org>. [date accessed: 23 December 2014]

D–F. Wursten, B.T. (2014) "*Polydora poskeana* (Vatke & Hildebrandt) H. Rob. (Record no: 25475, 25476)". Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 23 December 2014]

Figure 23:

A. Hankey A (2013) "*Vernonia galpinii* Klatt". iSpot, share nature. <http://www.ispotnature.org>. [date accessed: 23 December 2014]

B–C. Blittersdorff R von (2008) "*Vernonia galpinii* Klatt (photo ID: 24044, 24049)". S. Dressler, Schmidt, M., Zizka, G., eds. (2014) African Plant, a photo guide. Forschungsinstitut Senckenberg, Frankfurt/Main, Germany. <http://www.africanplants.senckenberg.de>. [date accessed: 23 December 2014]

D–E. Warren PR (2013) "*Vernonia thodei*". iSpot, share nature. <http://www.ispotnature.org>. [date accessed: 23 December 2014]

- F–G. Wursten BT (2010) “*Vernonia petersii* Oliv. ♂ *Hiern ex Oliv.* (Record no: 40742, 40745)”. Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2014) Flora of Zimbabwe: species information: individual images. <http://www.zimbabweflora.co.zw> [date accessed: 16 December 2014]

Figure 26

- A. Wildeman E, Durand T (1898) “*Vernonia potamophila* Klatt” (drawn & lithographed from nature by Ch. Cuisin) *Illustrations de la flore du Congo* 1: 35. PL XVIII