

The *Wollastonia*/*Melanthera*/*Wedelia* generic complex (Asteraceae: Ecliptinae), with particular reference to Australia and Malesia

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Abstract

Orchard, A.E. The *Wollastonia*/*Melanthera*/*Wedelia* generic complex (Asteraceae: Ecliptinae), with particular reference to Australia and Malesia. *Nuytsia* 23: 337–466. The generic limits of *Wedelia* Jacq., *Melanthera* Rohr, and *Wollastonia* DC. ex Decne., as currently recognised, are re-examined on the basis of comparative morphology, and a new classification recognising the first two genera in a restricted sense is proposed, with other taxa redistributed through nine genera. In this classification, *Wedelia* (including *Aspilia* Thouars) with c. 100 species, is restricted to the Americas and Africa. *Melanthera* is restricted to c. five species of the Caribbean basin and northern Andes. It is proposed that African species formerly in *Melanthera* be transferred to *Lipotriche* R.Br. and the following new combinations are made: *L. scandens* (Schum. & Thonn.) Orchard; *L. scandens* subsp. *subsimplicifolia* (Wild) Orchard; *L. scandens* subsp. *dregei* (DC.) Orchard; *L. triternata* (Klatt) Orchard; *L. abyssinica* (Sch.Bip. ex Rich.) Orchard; *L. gambica* (Hutch. & Dalziel) Orchard; *L. pungens* (Oliver & Hiern.) Orchard. The autonym *L. scandens* subsp. *scandens* is newly created. *Echinocephalum* Gardner of South America is resurrected, with a single species (*E. latifolium* Gardner). It is proposed that *Wollastonia* be retained as a genus distinct from *Wedelia*, *Melanthera* and *Lipochaeta* DC., with which it has been variously synonymised by recent authors. In Australia two species of *Wollastonia* are recognised, *W. biflora* (L.) DC. and *W. uniflora* (Willd.) Orchard. These species are keyed, described and illustrated. The Hawai‘ian species of *Lipochaeta* sect. *Aphanopappus* (Endl.) Benth. & Hook.f. are transferred to *Wollastonia*, and placement of *Wollastonia lifuana* (Hochr.) Fosb. of New Caledonia and Vanuatu, and the Asian species *Wedelia prostrata* Hemsl. in *Wollastonia* (as *Wollastonia dentata*) is confirmed. New combinations are made for *Wollastonia biflora* var. *ryukyuensis* (H.Koyama) Orchard, *W. bryanii* (Sherff) Orchard, *W. dentata* (H.Lév. & Vaniot) Orchard, *W. fauriei* (H.Lév.) Orchard, *W. integrifolia* (Nutt.) Orchard, *W. kamolensis* (O.Deg. & Sherff) Orchard, *W. lavarum* (Gaudich.) Orchard, *W. micrantha* (Nutt.) Orchard, *W. micrantha* subsp. *exigua* (O.Deg. & Sherff) Orchard, *W. perdita* (Sherff) Orchard, *W. populifolia* (Sherff) Orchard, *W. remyi* (A.Gray) Orchard, *W. subcordata* (A.Gray) Orchard, *W. tenuifolia* (A.Gray) Orchard, *W. tenuis* (O.Deg. & Sherff) Orchard, *W. venosa* (Sherff) Orchard, *W. waimeaensis* (H.St.John) Orchard and *W. uniflora* (Willd.) Orchard. The autonym *W. micrantha* subsp. *micrantha* is newly created. *Lipochaeta* DC. in Hawai‘i is restricted to the species with 4-lobed disc floret corollas, formerly treated as *Lipochaeta* sect. *Lipochaeta*. The Australian and New Guinean species formerly placed in *Wedelia* are transferred to two new genera: *Apowollastonia* Orchard, with eight species, including four new combinations (*A. longipes* (Klatt) Orchard, *A. spilantheidoides* (F.Muell.) Orchard, *A. stirlingii* (Tate) Orchard and *A. verbessinoides* (Benth.) Orchard) and five new taxa (*A. cylindrica* Orchard, *A. hamersleyensis* Orchard, *A. hibernica* Orchard, *A. major* Orchard

and *A. stirlingii* subsp. *fontaliciana* Orchard). The autonym *A. stirlingii* subsp. *stirlingii* is newly created, as is the genus *Acunniana* Orchard, with one species (*A. procumbens* (DC.) Orchard). In Malesia/Asia, two monotypic new genera are proposed, *Indocypraea* Orchard (with a single species, *I. montana* (Blume) Orchard, formerly *Wedelia* (*Wollastonia*) *montana*), and *Quadribractea* Orchard (with a single species, *Q. moluccana* (Blume) Orchard, formerly *Wedelia moluccana*). Five species related to the former *Wedelia urticifolia* (Blume) DC. are transferred to the new genus *Lipoblepharis* Orchard (*L. urticifolia* (Blume) Orchard, with two subspecies *L. urticifolia* subsp. *urticifolia* and subsp. *hortorum* Orchard, *L. thailandica* (Koyama) Orchard, *L. asperrima* (Decne.) Orchard, *L. stenophylla* (Merr.) Orchard and *L. floribunda* Orchard). Lectotypes are chosen for *Verbesina urticifolia* Blume, *V. moluccana* Blume, *V. montana* Blume, *Buphthalmum australe* Biehler (= *Buphthalmum helianthoides sensu* Forster), *Wedelia pilanthoides* F.Muell., *Wedelia verbesinoides* Benth. and *Wedelia stirlingii* Tate.

Introduction

In the course of preparing treatments of the tribe Heliantheae Cass. for *Flora of Australia*, it was found that the plant variously referred to as *Wollastonia biflora* (L.) DC., *Wedelia biflora* (L.) DC. ex Wight and *Melanthera biflora* (L.) Wild in Australia actually comprised two distinct species, separated both morphologically and geographically. While clearly distinct at species level, a problem arose in naming the taxa because of considerable differences of opinion in recent literature on generic delimitation in the wedelioid group of subtribe Ecliptinae Less. of the Asteraceae. In the course of this investigation it also became obvious that the c. eight species from northern Australia currently included within *Wedelia* Jacq. were unrelated to the heterogeneous group of *Wedelia* species of the Americas, Africa and Asia, and that the species of ‘*Wedelia*’ from Malesia and south-east Asia were different from all of the above. To resolve these generic incongruities it became necessary to re-examine the criteria on which the genera *Wedelia*, *Aspilina* Thouars, *Echinocephalum* Gardner, *Lipotriche* R.Br., *Melanthera* Rohr, *Wollastonia* DC. ex Decne., and the Hawai‘ian endemic genus *Lipochaeta* DC. have been delimited. In the course of this re-examination, some new characters were considered, and the conclusion was reached that there was merit in recognising the genus *Wollastonia* as distinct from those above and expanding it to include the Hawai‘ian *Lipochaeta* sect. *Aphanopappus* (Endl.) Benth. & Hook.f., *Wollastonia lifuana* (Hochr.) Fosb. of New Caledonia and Vanuatu, and *Wedelia prostrata* Hemsl. of eastern and south-eastern Asia. As the Hawai‘ian taxa had in recent times been referred to both *Wedelia* and *Melanthera*, a comparison was made of Australian and Malesian/Asian taxa of ‘*Wedelia*’ and ‘*Melanthera*’ with alleged congeners in Africa and the Americas. This revealed that both genera in their currently accepted broad circumscriptions contain a diverse range of taxa, and are extremely difficult to define. Within both taxa there are, however, well-defined assemblages of species that are internally correlated both morphologically and geographically. By recognising these assemblages as distinct genera, a more intuitive and useful (and arguably more natural) classification can be constructed. The remainder of this paper examines morphological characteristics of a number of these subgroups, discusses historical taxonomies, and proposes a new classification reflecting morphology and phylogeography.

Materials and methods

This paper is based upon examination of all available specimens in the major Australian herbaria (AD, BRI, CANB, DNA, HO, MEL, NE, NSW, PERTH), plus large suites of specimens in BM, BO, G, K and L, and on-line scans of type specimens in P, US and elsewhere, as cited below. The morphology of species of *Wedelia*, *Aspilina*, *Melanthera*, *Echinocephalum*, *Lipotriche* and *Wollastonia*, particularly characters of the paleae, achenes, anthers and pappus, and sexuality of the florets, has been examined across the geographical and morphological range of these genera, with particular attention being

given to the types of previously described genera and their synonyms. On the basis of these studies the species have been rearranged into 11 genera that are more easily defined, geographically coherent, and reflect close morphological similarities.

In the lists of specimens examined collections are arranged alphabetically by collector, either within Australian States or Territories, or within countries, while the States or countries are arranged in geographical order, north to south and west to east.

History of generic circumscription in the *Wollastonia/Wedelia/Melanthera* group

Wedelia was described from the Caribbean basin by Jacquin (1760) with a single species *W. fruticosa* Jacq. Additional species were subsequently described from the Americas, Africa, Asia, Malesia, Australia and Oceania. Nearly 700 *Wedelia* names appear in the *International Plant Name Index* (IPNI), with estimates of numbers of accepted names ranging from about 100 to 110, although no complete monograph has been published since Candolle (1836). Bentham and Hooker (1873) recognised *Wedelia* (45 species; widespread in warm areas of the world), *Aspilia* (40 species; tropical Americas and Africa), and *Lipochaeta* (11 species; Hawai'i and Galápagos). The Galápagos species of *Lipochaeta* was subsequently moved to a monotypic genus, *Macraea* Hook.f. (and more recently to *Trigonopterum* Steetz ex N.J. Andersson). Wild (1965, 1966) distributed the African taxa among *Aspilia* and *Melanthera*, leaving no native *Wedelia* species in Africa. Turner (1988, 1989, 1992) and Robinson (1992) transferred *Aspilia* to synonymy under *Wedelia*, thus resurrecting the genus *Wedelia* for Africa. This view was also adopted by Strother (1991) and Karis (1993). Beentje and Hind (2005), however, maintained *Aspilia* for the taxa of tropical east Africa. Bentham (1867) adopted the name *Wedelia* for northern Australian taxa and has been followed by most subsequent Australian authors. The name *Wedelia* has also been applied to Malesian taxa by most authors from Candolle (1836), although Candolle originally included many of them in *Wollastonia*.

Aspilia was described by Du Petit-Thouars (1806), without species, and adopted by Candolle (1836) with two taxa, *A. thouarsii* DC. and *A. bojeri* DC., both from Madagascar. The genus was subsequently greatly expanded to encompass species in the Americas and Africa. It was recognised (with difficulty) as distinct by, for example, Wild (1965, 1966), and Robinson (1984a, 1984b), but was subsumed into *Wedelia* by Strother (1991), Robinson (1992) and Turner (1992). Bremer (1994) commented that this produced a 'large, maybe paraphyletic genus'. Against this consensus, Beentje and Hind (2005) recognised *Aspilia* rather than *Wedelia* for Africa.

Wollastonia was described by Candolle in Decaisne (1834) with three species, increased to 15 in the *Prodromus* (Candolle 1836). It was lectotypified by *W. scabriuscula* DC. ex Decne., *nom. illeg.* (= *W. biflora* (L.) DC.) by Fosberg and Sachet (1980a: 32). *Wollastonia biflora* was transferred to *Wedelia* as *Wedelia biflora* (DC.) Wight by Wight (1834), and in this he was followed by later authors, including Bentham (1867). Wild (1965) transferred *Wedelia biflora* and some African *Wedelia* species to *Melanthera* Rohr.

Lipotriche was described by Brown (1817) to accommodate collections by Smith from the Congo River, although he published no valid species name. Lessing (1831) added two species from Mexico and Hawai'i. In 1836 Candolle validated the African species as *L. brownii* ('*brownei*'), moved the Mexican species to *Perymenium*, and established a new genus *Lipochaeta* for the Hawai'ian species (along with nine other taxa, some from the Americas, some from Hawai'i), leaving *Lipotriche* as an African genus with a single species (*L. brownii*). Bentham (Bentham & Hooker 1873) placed *Lipotriche* (and other genera) in the synonymy of a broadly defined *Melanthera*, where it has remained (e.g. Wild 1965; Beentje & Hind 2005 (by implication)).

Lipochaeta DC. was described by Candolle (1836) as a segregate from *Lipotriche*, with nine (possibly ten) species, five from the Americas (one doubtful) and five from Hawai'i. Subsequently the American species were removed, and additional Hawai'ian species added (see Gardner 1979 for summary), leaving *Lipochaeta* as endemic to Hawai'i. Bentham (Bentham & Hooker 1873) divided the genus into two sections, sect. *Lipochaeta* of about six species and sect. *Aphanopappus* of about 16 species. Wagner and Robinson (2002) restricted the circumscription of *Lipochaeta* to include the allopolyploid races with 4-lobed disc corollas (sect. *Lipochaeta*), and broadened the concept of *Melanthera* to include *Wollastonia* and the 5-lobed *Lipochaeta* sect. *Aphanopappus*. Panero (2007) retained *Wollastonia* for a single species (*W. biflora*), the concept also adopted by Green (1994: 398) in *Flora of Australia*; the name *Melanthera biflora* was used for what was thought to be the same taxon by Du Puy and Telford (1993: 419).

The criteria on which these generic and infrageneric taxa have been recognised are discussed in detail below.

***Wedelia* Jacq.**

This genus was described from the Caribbean and adjacent continental America by Jacquin (1760) with a single species, *W. fruticosa* Jacq. It was described as (translation) 'Receptacle paleaceous. Seed crowned with a 10-toothed calyculus. Calyx [=involucre] 4-foliata, lax.' *Wedelia fruticosa* was described as [symbol for] 'perennial'. A more detailed description (with the spelling *W. frutescens*) appeared in Jacquin (1763); it is a native of the Caribbean island arc, from Puerto Rico to Grenada, and Venezuela. Numerous additional species have been described, principally from the New World, but also from Africa and Asia. IPNI lists over 690 published names in *Wedelia*; estimates of the number of accepted species range from 100 (Bremer 1994) to 110 (Panero 2007).

African species of *Wedelia* were recognised by, for example, Oliver and Hiern (in Oliver 1877), but later were distributed among *Melanthera* and *Aspilia* by Wild (1965, 1966), who recognised only one introduced *Wedelia* species for the continent, *W. trilobata* (L.) Hitchc., now treated as *Sphagneticola trilobata* (L.) Pruski.

In a series of papers, McVaugh (1984) and Robinson (particularly 1984a, 1984b) questioned whether both *Wedelia* and *Aspilia* could be maintained for South America, given that the only substantial difference between them was in the sexuality of the ray florets (pistillate and fertile in *Wedelia*, neuter in *Aspilia*). Turner (1988, 1989) expressed a preference to sink South American *Aspilia* into *Wedelia*, and in Turner (1992) formally transferred these species to *Wedelia*. Robinson (1992) formally transferred the African type species of *Aspilia* (*A. thoursii* DC.) to *Wedelia*. Beentje and Hind (2005) rejected the transfer of African *Aspilia* to *Wedelia*, maintaining the genus as distinct, principally on the character of ray floret sexuality, although admitting that the treatment at species level was unsatisfactory.

Strother (1991) revised the 20 continental North American species of *Wedelia* and related taxa. He defined *Wedelia* as having leaves predominantly cauline and opposite, herbaceous, triplinerved; capitula solitary or in dichasial clusters of two or three to eight, paleate; paleae persistent, linear to lanceolate, conduplicate, navicular, often coloured purple, yellow, or pink, chartaceous to scarious, usually carinate-alate, apically obtuse to acute and often apically erose; involucre bracts in two or three (rarely four) series, deltate to ovate or rotund, never attenuate; disc florets eight to 150+, bisexual and fertile, with yellow to orange 5-lobed corollas; ray florets four to 18 or rarely absent, pistillate and fertile or neuter, with white, yellow, orange, purple, red, or pink 2- or 3-lobed laminas;

pappus persistent, borne on a rostrum and usually cyathiform (i.e., an erose, fimbriate, or lacerate cup or corona, with 0–3 additional awns); achenes stramineous, brown or black, often mottled, outer ones triquetrous, inner biconvex to quadrate, all with or without wings, most bearing oily elaiosomes at the base. Strother included within *Wedelia* most of the North American taxa previously treated as *Aspilia*, and suggested that African *Aspilia* might also belong in *Wedelia*. He recognised within North American *Wedelia* two groups: ‘the *Wedelia acapulcensis* alliance’ with fertile rays and winged achenes, and including some taxa previously placed in *Zexmenia*, and ‘the *Wedelia rosei* alliance’ with neuter rays and wingless achenes, and including most of the taxa previously placed in *Aspilia*. He also segregated two former North American *Wedelia* species as distinct genera: *Pascalialia* Ortega and *Complaya* Strother (now *Sphagneticola* O.Hoffm.). Strother (1991: 14) excluded *Wollastonia biflora* from his concept of *Wedelia*.

Karis (1993) published a cladistic analysis of 97 genera, based on 141 morphological characters. He concurred with Strother (1991) in considering that African species of *Aspilia* were congeneric with *Wedelia*, yet kept them as a separate entity in his analysis. *Wedelia* and African *Aspilia* were found to be sister taxa, and together were sister to the predominantly South American *Zexmenia* La Llave, *Jefea* Strother, *Lasianthaea* Endl. and *Calyptocarpus* Less. Karis did not list the names of the species included in his study, nor voucher specimens; it is unclear whether *Wollastonia biflora* was included in his concept of *Wedelia*.

Panero *et al.* (1999) included two American species of *Wedelia* plus *Wollastonia biflora* in their analysis of chloroplast DNA. *Wollastonia* was well removed from the two *Wedelia* species in their cladogram. This was reflected in Panero (2007) where *Wollastonia* was recognised as a monospecific genus distinct from *Wedelia* (syn. *Aspilia*).

Malesian, Asian and Australian taxa were added somewhat uncritically to *Wedelia* over a long period, by various authors (Wight 1834; Candolle 1836; Mueller 1866; Bentham 1867; Bentham & Hooker 1873; Tate 1896; and others), sometimes as new taxa, sometimes transferred from *Verbesina* or *Wollastonia*, overlooking the fact that in all cases the taxa lacked the key diagnostic character of *Wedelia*, the pappus consisting of a lacinate or fimbriate cup sitting on a rostrum.

In summary, *Wedelia* has had a complicated history. Originally considered to be a New World genus, confined mainly to South America, it has since been expanded by some authors to include American and, sometimes, African *Aspilia*, *Wollastonia*, and a miscellaneous group of Australasian taxa. Its relationship with *Melanthera* and *Zexmenia* is close, but the three are usually kept distinct. Some taxa formerly in *Wedelia* have been removed as distinct genera (*Pascalialia*, *Sphagneticola*). *Wollastonia biflora* has been included in *Wedelia*, as *Wedelia biflora*, in some relatively recent works, including Yuncker (1959) for Tonga, Backer and Bakhuizen van den Brink (1965) for Java, Sykes (1970) for Niue, Parham (1972) for Samoa, Dassanayake (1980) for Ceylon, Ohwi (1984) for Japan, Chowdhery (1995) for India, Peng *et al.* (1998) for Taiwan (with two varieties), and Hu (2009) for Hong Kong, although molecular data (Panero *et al.* 1999) has shown it to be distinct.

Aspilia Thouars

This genus was described from Madagascar by Du Petit-Thouars (1806), but lacked a valid species description. Candolle (1836) adopted the genus, and validly described two species, both from Madagascar. One of these (*A. thouarsii* DC.) is accepted as the type of the genus (Wild 1966). Candolle primarily based his description of the genus on *A. bojeri* DC., as he had no material (only

a description) of *A. thouarsii*. *Aspilia* was described as comprising procumbent herbs with opposite, subsessile, entire or shortly dentate leaves; capitula solitary or few on long peduncles, radiate, with five to ten sterile, yellow ray florets, and hermaphrodite disc florets with yellow 5-lobed corollas. Paleae were oblong, folded and embracing the achenes, with an acuminate apex. The achenes were linear, appressed villous, with a dentate-ciliate coroniform pappus. Additional species were described from Africa, until by 1966 Wild recognised 21 species (with four more insufficiently known). This is the same number recognised by Beentje and Hind (2005). Wild (1965, 1966) discussed the difficulty of separating African *Aspilia* from *Melanthera* (*s. lat.*), but proposed that achene characters were diagnostic, those of *Aspilia* being \pm compressed, with a cupule-like pappus, with or without one or two awns, and uniformly pubescent, while the achenes of *Melanthera* (in which he included *Lipotriche*) were 3- or 4-angled, with pappus absent or of several awns, and were pilose only at the apex. The paleae of *Melanthera* in his concept were many-nerved, with ciliate margins; those of *Aspilia* lacked both these characteristics. Beentje and Hind (2005) adopted Wild's generic distinctions, but differed on species delimitation. Some *Aspilia* species had also been described from South America, where they were distinguished with difficulty from *Wedelia* (e.g. McVaugh 1984; Robinson 1984a, 1984b). Strother (1991) placed 11 American *Aspilia* species names in *Wedelia*, and Turner (1992) formally transferred all remaining South American species to *Wedelia*. Robinson (1992) transferred the African type species of *Aspilia* (*A. thouarsii*) to *Wedelia*.

***Wollastonia* DC. ex Decne.**

This genus was described in a paper on the flora of Timor by Candolle in Decaisne (1834), in which draft accounts destined for Candolle's *Prodromus* (1836) were pre-published. Thus, although the name dates formally from 1834, the 1836 account needs to be read as well to establish Candolle's concept of the genus. In Decaisne (1834) three species were described, but in Candolle (1836) 15 were included, and a fuller description and discussion of the genus was provided. As discussed in Fosberg and Sachet (1980a) it is clear in the 1834 paper that Candolle was basing his new genus principally upon *W. scabriuscula* DC. ex Decne., *nom. illeg.* (= *W. biflora* (L.) DC.), and this name was there (Fosberg & Sachet 1980a) chosen as lectotype.

Candolle considered that his genus fell between *Wedelia* and *Heliopsis* Pers., differing from both in achene structure and pappus. He characterised *Wollastonia* as [translation] shrubs or rarely herbs, with opposite, shortly petiolate, ovate leaves, acute, dentate and triplinerved. Inflorescence [composed] of capitula arranged often ternately on terminal pedicels. Capitula many-flowered, heterogamous, with one series of pistillate ray florets and bisexual disc florets with 5-lobed corollas. Florets yellow. Involucre 2- or 3-seriate, of herbaceous external and membranous internal bracts. Receptacle flat to subconvex and paleaceous. Achenes thick, obovate, or turbinate or compressed, with an umbilicate apex, becoming hairless, often with one to five slender, rigid, fragile awns deciduous at maturity. Candolle divided his species into two sections, '*Wollastoniae verae*' from the Old World, with radiate capitula, and '*Wollastoniae dubiae*', from the Americas, with discoid capitula. The latter comprised two species, *Wollastonia lantanoides* DC., from the Caribbean, a name currently of uncertain application (*vide* World Compositae Checklist), and *Wollastonia prostrata* DC. from Brazil, now included in *Eclipta elliptica* DC. Of the species of the 'true' *Wollastonia*, most were transfers of species previously described in *Buphthalmum* L., *Wedelia*, or *Verbesina* L.

Bentham (1867) included *Wollastonia* within *Wedelia*, commenting 'The *W. biflora* and some other species without any pappus have been separated under the name of *Wollastonia*, but in *W. spilantheidoides* the pappus is often so small as to be quite inconspicuous when the achene is ripe, and in every other respect the species are all too closely allied to be generically separated. It is probable that the several

genera alluded to by A.Gray under *Lipochaeta* will have to be united also with *Wedelia*'. At the same time Bentham included '*Wedelia urticifolia* DC.' in *Wedelia*, a misapplication of Candolle's name, this Benthamian taxon now being recognised as *Blainvillea cunninghamii* (DC.) Orchard (Orchard 2012). Bentham maintained his synonymy in Bentham and Hooker (1873), treating *Wollastonia* as *Wedelia* sect. *Wollastonia*.

Most authors since Bentham have recognised a single taxon for the Australian plants considered in this paper as *Wollastonia*, and they have followed Bentham in calling the species *Wedelia biflora*. One of the few exceptions has been Green (1994) who adopted the name *Wollastonia biflora*.

On a world-wide basis, Robinson (1981) accepted *Wollastonia*, as well as *Lipochaeta*, *Melanthera* and *Wedelia*, as distinct genera within subtribe Ecliptinae. Bremer (1994) also recognised within his '*Wedelia* group' (in the subtribe *Verbesininae*) the genera *Melanthera*, *Wedelia*, *Lipochaeta* and *Wollastonia* as distinct, but noted that the whole group was in need of revision. Panero *et al.* (1999) in a molecular study involving chloroplast DNA, sampled *Wollastonia biflora*, *Lipochaeta integrifolia* (Nutt.) A.Gray (*Lipochaeta* sect. *Aphanopappus*), *Melanthera nivea* (L.) Small, *Wedelia calycina* Rich., and *Wedelia purpurea* (Greenm.) B.L.Turner (among other taxa). All were clustered near the ultimate branches of the resultant phylogenetic tree, with *Wollastonia* sister to *Lipochaeta*, these two genera sister to *Melanthera*, and that group in turn sister to *Wedelia et al.* Thus, outside of Australia, *Wollastonia* has often continued to be recognised. For the most part this has involved only recognition of a single species, *W. biflora*, a strand plant of the Indo-Pacific, with a range from east Africa to the Indian subcontinent, Australia, Malesia, east Asia and the islands of the south Pacific. Examples of this circumscription include Fosberg and Sacht (1980a, 1980b) and Fosberg (1993) for Micronesia, Strother (1991) throughout its range, Smith (1991) for Fiji, and Chen and Hind (2011) for China (two species). Others have adopted the name *Wedelia biflora* or *Melanthera biflora* (L.) Wild for the same taxon (see below).

***Melanthera* Rohr**

The genus *Melanthera* was described by Rohr (1792) from Martinique. Rohr did not cite specimens or a species epithet, but the only species of *Melanthera* on Martinique is *M. aspera* (Jacq.) Spreng., and Rohr's editor, Vahl, included a citation of *Bidens nivea* (which is *M. aspera*) in Swartz (1791). This species has generally been accepted as the type, but see Strother (1970) and Nicholson (1981). A history of the taxonomy and nomenclature of the genus is given in Parks (1973). As originally circumscribed, *Melanthera* was a genus of shrubby perennial plants, with opposite, petiolate, triplinerved, broadly ovate to lanceolate leaves; capitula discoid, terminal, solitary or in loose cymes on long peduncles; involucre 2-seriate; receptacle paleate with oblanceolate, strongly keeled paleae clasping the florets; florets 25–100, all tubular, hermaphrodite; corolla white; achene 2–3 mm long, obpyramidal, 4- or 3-angled, with apex truncate or slightly concave; pappus of two to five weakly barbed, caducous awns.

Bentham (Bentham & Hooker 1873) expanded the circumscription of *Melanthera*, adding species with radiate capitula, in which the ray florets are either pistillate and fertile, or astylous and sterile, and all corollas yellow. These radiate species had previously been recognised as the American genus *Echinocephalum* Gardner, and the three African genera *Lipotriche* R.Br., *Psathurochaeta* DC., and *Wuerschmittia* Sch.Bip. Bentham made no new combinations. He did not include *Wollastonia* as a synonym, this genus being included in *Wedelia*, as mentioned above.

Schulz (1911) revised *Melanthera*, recognising 12 species, all from the Caribbean or nearby American mainland. As his was a regional treatment, he ignored the African and South American taxa and

maintained the original characterisation of the genus, with its white, discoid capitula, merely adding additional species. Subsequent workers found this treatment difficult to apply, leading Standley (1938) to reduce all discoid American taxa to a single species.

Wild (1965) essentially adopted Bentham's circumscription of *Melanthera* in his treatment of African taxa. He recognised 13 species for Africa, all with yellow, radiate capitula, the ray florets being either pistillate or neuter. Some of these taxa had previously been included in *Wedelia*, *Aspilia* or *Lipotriche*. Unlike Bentham (Bentham & Hooker 1873), he also transferred *Wollastonia biflora* to *Melanthera* as *Melanthera biflora* (L.) Wild. He distinguished *Melanthera* from *Aspilia* by achene characters, *Melanthera* being characterised by 'Achenes somewhat (3)4-angled, obovoid, glabrous or nearly so below, ±pubescent near the apex; awns 0–several; receptacular scales strongly many-nerved, marginally ciliate above'. *Aspilia* had 'Achenes somewhat compressed when mature, crowned with a lacerate cupule and 0–2 awns and ±uniform pubescence; receptacular paleae neither strongly many-nerved, nor marginally ciliate above'. No discussion of relationships with *Wedelia* (then represented in Africa only by the introduced tropical American species *Wedelia trilobata* (L.) Hitchc., now *Sphagneticola trilobata* (L.) Pruski), nor other extra-African genera was provided.

Cabrera (1970) formally transferred the South American *Echinocephalum*, with yellow corollas and sterile ray florets, to *Melanthera*.

Parks (1973) re-examined the Caribbean and North American species of *Melanthera*, rejecting many of Schulz's taxa as mere local variants of widespread species. He recognised five species and two varieties, most from the Caribbean, with some reaching Mexico, Central and South America, and south-eastern North America. All were *Melanthera* in the original sense, with white, discoid capitula. Parks also questioned Bentham's (Bentham & Hooker 1873) and Wild's (1965) extension of the limits of *Melanthera* to the yellow, radiate African taxa, pointing out that this then makes difficult the characterisation of the South American genera *Echinocephalum* and *Perymenium*, as well as creating confusion in distinguishing *Aspilia*, *Blainvillea*, *Eleutheranthera* Poit. ex Bosc., *Wedelia*, *Wulffia* Neck. ex Cass. (*Tilesia* G.Mey.), and some *Calea* L. and *Bidens* L. species. Parks did not consider the circumscription of *Wollastonia*. He found that all Caribbean and North American species of *Melanthera* (*s. str.*) had a chromosome number of $n = 15$.

Some subsequent authors have chosen to follow Wild in treating the widespread Indo-Pacific species as *Melanthera biflora* (L.) Wild, unaware of, or discounting, Park's reservations about a broad circumscription for *Melanthera*. In Australia and its territories, Du Puy and Telford (1993) adopted the name *M. biflora* for plants on Christmas Island and Cocos (Keeling) Island, as did Pike and Leach (1997) for Ashmore Reef. Beyond Australia, the name *M. biflora* has also been used recently by, for example, Fosberg and Renvoize (1980) for Aldabra, Arnold and De Wet (1993) for southern Africa, Wagner and Robinson (2002) throughout its Indo-Pacific range, Kress *et al.* (2003) for Burma, and Beentje and Hind (2005) for tropical east Africa.

***Lipochaeta* DC.**

The genus *Lipochaeta* was described by Candolle (1836) to accommodate ten species from Mexico, the Caribbean and Hawai'i. It was characterised by opposite leaves, radiate capitula, yellow corollas, of which the ray florets were fertile, ray achenes 3-angled, 3-awned and somewhat winged, and disc achenes 2-awned and slightly winged. The type is *Lipochaeta lobata* (Gaudich.) DC. from Hawai'i. Bentham (Bentham & Hooker 1873), largely following Gray (1861), recognised two entities (sections)

within *Lipochaeta*: *Microchaeta* (now sect. *Lipochaeta*) with a prominent pappus, and *Aphanopappus* with pappus reduced to a minute crown or entirely absent. Other species were later described, but by 1935 (Sherff 1935) most of the extra-Hawai'ian taxa had been removed to other genera and *Lipochaeta* was considered endemic to Hawai'i (17 spp. with many varieties) and New Caledonia (one sp.).

Gardner (1979) revised *Lipochaeta*, accepting two sections: *Lipochaeta* sect. *Lipochaeta* with nine taxa in six species, and *Lipochaeta* sect. *Aphanopappus* with 18 taxa in 17 species, distinguished principally by the number of lobes on the disc corollas (four in sect. *Lipochaeta*, five in sect. *Aphanopappus*). He considered the genus to be endemic to the Hawai'ian islands, the New Caledonian species (*L. lifuana* Hochr.) being referred to *Wedelia*. The evolutionary significance of 4-merous vs. 5-merous corollas was discussed by Gardner (1977). He (Gardner 1976) considered that the ancestor of *Lipochaeta* was a *Wedelia*-like taxon with buoyant corky achenes, similar to *Wedelia biflora* (= *Wollastonia biflora*). He hypothesised a single introduction to Hawai'i followed by local speciation. In this process, a polyploidy event occurred. The taxa with 5-lobed disc corollas remained as diploids ($n = 15$), while those with 4-lobed corollas are tetraploids ($n = 26$ by reduction from $n = 30$). He found that flavonoid chemistry correlated with ploidy levels and corolla lobe number.

Experimental hybridisation experiments by Rabakonandrianina (1980) and Rabakonandrianina and Carr (1981) confirmed a high level of interfertility within the sections of *Lipochaeta* but sterility of inter-sectional hybrids. As early as 1933, Sherff (1933) had described with Degener a natural hybrid (\times *Lipochaeta procumbens* Degen. & Sherff) between *Lipochaeta lobata* var. *denticulata* (sect. *Lipochaeta*) and *L. integrifolia* var. *megacephala* (sect. *Aphanopappus*) in which hundreds of florets failed to produce a single viable seed. Experimental hybrids were also produced by Rabakonandrianina (1980) and Rabakonandrianina and Carr (1981) between species of the two sections of *Lipochaeta* and two 'Wedelia' species, *Wedelia trilobata* (L.) Hitchc. (= *Sphagneticola trilobata* (L.) Pruski) ($n = 28$) of South America and *Wedelia biflora* (= *Wollastonia biflora*) ($n = 15$). Although all intergeneric hybrids were vegetatively vigorous they had low pollen stainability and failed to produce viable achenes. Levels of chromosomal pairing suggested a close genetic similarity between *Lipochaeta* and both *Sphagneticola* and *Wollastonia*. On the basis of their experimental crosses Rabakonandrianina (1980) and Rabakonandrianina and Carr (1981) suggested that *Lipochaeta* sect. *Aphanopappus* ($n = 15$) was closer to *Wollastonia biflora* than to *Lipochaeta* sect. *Lipochaeta*, and probably arose from colonisation of the Hawai'ian Islands by a species ($n = 15$) akin to *Wollastonia biflora*. On the other hand, *Lipochaeta* sect. *Lipochaeta* ($n = 26$) probably arose from an allopolyploid hybrid between a species akin to *Wollastonia biflora* ($n = 15$) and an unknown wedelioid taxon with $n = 11$. Strother (1991) reported that many of the *Wedelia* species he revised for continental North America had a chromosome number of $n = 11$. Rabakonandrianina and Carr (1981) were unable to produce hybrids between *Sphagneticola trilobata* and *Wollastonia biflora* despite many attempts.

Wagner *et al.* (1990) reduced the number of species in *Lipochaeta* to 20, and the relationships of *Lipochaeta* were again examined by Wagner and Robinson (2002). After reviewing the morphological, biochemical and cytological evidence, they proposed restricting *Lipochaeta* to the six allopolyploid species of sect. *Lipochaeta*. The 14 diploid Hawai'ian species of *Lipochaeta* sect. *Aphanopappus* plus one New Caledonian species (*L. lifuana* Hochr.) were transferred to *Melanthera*. Wild's 1965 transfer of *Wollastonia biflora* to *Melanthera* was also accepted.

In a molecular phylogenetic study of subtribe Ecliptinae based on chloroplast DNA restriction site data, Panero *et al.* (1999) found *Wollastonia biflora* to be sister to *Lipochaeta integrifolia* (sect. *Aphanopappus*), and these two to be sister to *Melanthera nivea* and some *Wedelia* species (among others). A study by Chumley *et al.* (2000) based on ITS sequences delivered a robust clade in which

Wollastonia and *Melanthera* are sister genera, and these together, sister to *Lipochaeta*. This clade was distinct from that containing *Wedelia*. The Chumley *et al.* (2000) results also suggested that *Lipochaeta* may be monophyletic rather than biphyetic as suggested by the hybridisation studies of Rabakonandrianina (1980) and Rabakonandrianina and Carr (1981), although if a *Wollastonia biflora* precursor was involved in the ancestry of both sections, the genetic data may just be picking up this common partial ancestry.

Panero (2007) combined the above two molecular studies in arriving at a generic delimitation that maintained *Lipochaeta* as a single genus, rejecting Wagner and Robinson's (2002) transfer of sect. *Aphanopappus* to *Melanthera*. He also maintained *Wollastonia* as a distinct genus with a single species, *W. biflora*.

***Seruneum* Kuntze**

The generic name *Seruneum*, formerly applied to some Australian taxa, was a pre-Linnaean name coined by Rumphius (1747) with a single species *S. aquatilis* (usually equated with *Wollastonia biflora*), and taken up by Kuntze (1891) as an illegitimate replacement name for *Wedelia* Jacq. and *Wollastonia* DC. ex Decne. Kuntze applied his replacement name (which he also spelled *Serunium*) to a range of taxa from the Americas, Africa, Asia and Australia.

***Nieuhria* Britten**

Britten (1901) validated Necker's generic ('species naturales') name *Nieuhria* for two species, *Nieuhria biflora* (basonym *Verbesina biflora* L., as 'Wedelia biflora DC. apud Wight Contrib. p. 18 (1834)', and here included in *Wollastonia*) and *Nieuhria spilantheidoides* (basonym *Wedelia spilantheidoides* F. Muell., and here included in *Apowollastonia*). Necker's original monomial *Nieuhria* is invalid (the work is listed in Appendix VI of the *Code*). It is also an illegitimate later homonym of both *Nieuhria* Scop. (a superfluous name for *Baltimora* L. (Asteraceae: Ecliptinae)), and *Nieuhria* DC. (Capparaceae). Britten's name is therefore also a later homonym and illegitimate.

Generic circumscriptions adopted in this paper

The initial purpose of the research underlying this paper was to prepare a treatment of the subtribe Ecliptinae for *Flora of Australia*. For most genera this was relatively straight-forward. However, because *Wollastonia biflora* had in recent treatments been included in *Wollastonia*, *Wedelia* and *Melanthera* (see above), and because the eight or so northern Australian species of 'Wedelia' lacked all of the diagnostic characteristics of core *Wedelia* (a pappus consisting of a fimbriate or laciniate cup seated on a rostrum, entirely hairy achenes, elaiosomes on the base of the achenes), generic placement of these Australian taxa was problematic. To try to elucidate this, it was necessary to undertake a wide-ranging morphological survey of the taxa currently included in *Wedelia*, *Aspilia*, *Melanthera* (including the reputed synonymous genera *Lipotriche*, *Psathurochaeta* DC., and *Wuerschmittia* Sch. Bip.), *Wollastonia*, *Lipochaeta* and *Echinocephalum*. The result of this survey revealed that *Wedelia* was heterogeneous, almost certainly polyphyletic, and unrelated, except in the broadest sense, to Australian taxa, or to those of Malesia, Asia and Oceania. The concepts of both *Wedelia* and *Melanthera* seemed to have been expanded by various authors to include so many disparate taxa as to make them almost undefinable. A classification has therefore been developed that greatly restricts both *Wedelia* and *Melanthera*, while recognising several segregate genera. It provides taxa that are both more easily defined, and arguably, more reflective of evolutionary history.

Generic circumscription of *Wedelia/Aspilia*

Wedelia fructicosa (the type of *Wedelia*) is an erect subshrub to 2 m tall, growing in dry woods (Figure 1). It has large ovate to narrowly ovate leaves and yellow, radiate capitula on moderately long peduncles. The involucre is of soft, green, hairy bracts in two series (the inner ones becoming straw-coloured). Ray florets pistillate, corollas yellow, pistillate; disc florets bisexual, fertile, with corollas 5-lobed, yellow, and with black anther thecae. The paleae are linear to lanceolate, conduplicate, clasping the ovary/achene, membranous, hyaline, with a well-developed crest or wing abaxially, almost glabrous, with the tip differentiated into a short, coloured appendage, with margins shortly lobed apically. Achenes are brown, compressed, 2-angled, pilose throughout, with a prominent yellowish swelling(s) at the base (elaiosome); pappus a lobed, lacinate and/or fimbriate cup seated on a rostrum.

Aspilia thoursii (the type of *Aspilia*) is similar in many respects (Figure 2A–H). It is a semi-prostrate subshrub with stems rooting adventitiously. The leaves are small and oblong, and the capitula yellow and radiate on rather short peduncles. The involucre is of soft, green, pilose bracts, the inner bracts becoming straw-coloured with a reddish purple tip. Ray florets are pistillate or neuter (styles apparently abortive), with yellow corollas; disc florets bisexual and fertile, with 5-lobed, yellow corollas and black anther thecae. The paleae are linear, conduplicate, clasping the ovary/achene, membranous (tinted red), hyaline, with a well-developed midrib but hardly crested, glabrous, with a central and two short lateral lobes at the tip. Achenes are yellowish to reddish brown, compressed, 2-angled, pilose throughout, with elaiosomes at the base; pappus a shortly lobed/lacinate cup seated on a short rostrum.

Wedelia and *Aspilia* thus share a suite of diagnostic characteristics that separate them from the *Wollastonia/Melanthera/Lipochaeta* lineage: soft, herbaceous outer involucral bracts; paleae that are hyaline, with a midrib but no other striae, \pm glabrous, sometimes coloured, usually crested abaxially, with a tip differentiated into an appendage, sometimes with lateral lobes; an achene that is compressed, hairy throughout, with elaiosomes basally, and a pappus consisting of a lobed, lacinate or fimbriate cup seated on a distinct rostrum. Achenes are mostly large, 4–5 mm long.

Examination of other North and South American species show a general consistency in these diagnostic characteristics. For example, *Wedelia acapulcensis* var. *hispida* (Figure 3A–K) has paleae with a distinct crest, and the pappus has one or two of its lobes extended as soft ‘awns’, and the disc corollas have clear swollen ‘windows’ at the base of the corolla lobes. The ray florets are pistillate. *Wedelia montevidensis* (Figure 4) has paleae with a very narrow, flattened, almost caudate tip, a distinct crest, and broad lateral lobes. The pappus again has two lobes extended as ‘awns’, and the disc florets have ‘windows’ at the base of the corolla lobes, although not as distinctly as in *W. acapulcensis* var. *hispida*. The ray florets are sterile, and the achenes are densely long-hairy. *Wedelia silphoides* (Figure 3L–U) has paleae in which the apex is an ovate, minutely serrulate appendage, sparsely and shortly hairy, the crest and lateral lobes distinct. The achene is very narrow, almost cylindrical, only slightly compressed and has glandular pits as well as short hairs throughout. The ray florets are neuter. *Wedelia subpetiolata* (Figure 5A–K) and *W. cylindrocephala* (Figure 5L–Q) differ slightly. Involucral bracts are in three or four series, arranged on an elongated receptacle, and have reflexed tips. The palea is hyaline, linear, with the appendage barely differentiated, small lateral lobes, but a very weak crest (in *W. subpetiolata*; stronger in *W. cylindrocephala*). The pappus cupule is barely lobed, although elongated, and the rostrum is obscure. The ray florets are neuter. In *Wedelia latifolia* (Figure 6) the appendage at the tip of the palea and the lateral lobes are less pronounced, but the abaxial crest is very evident.

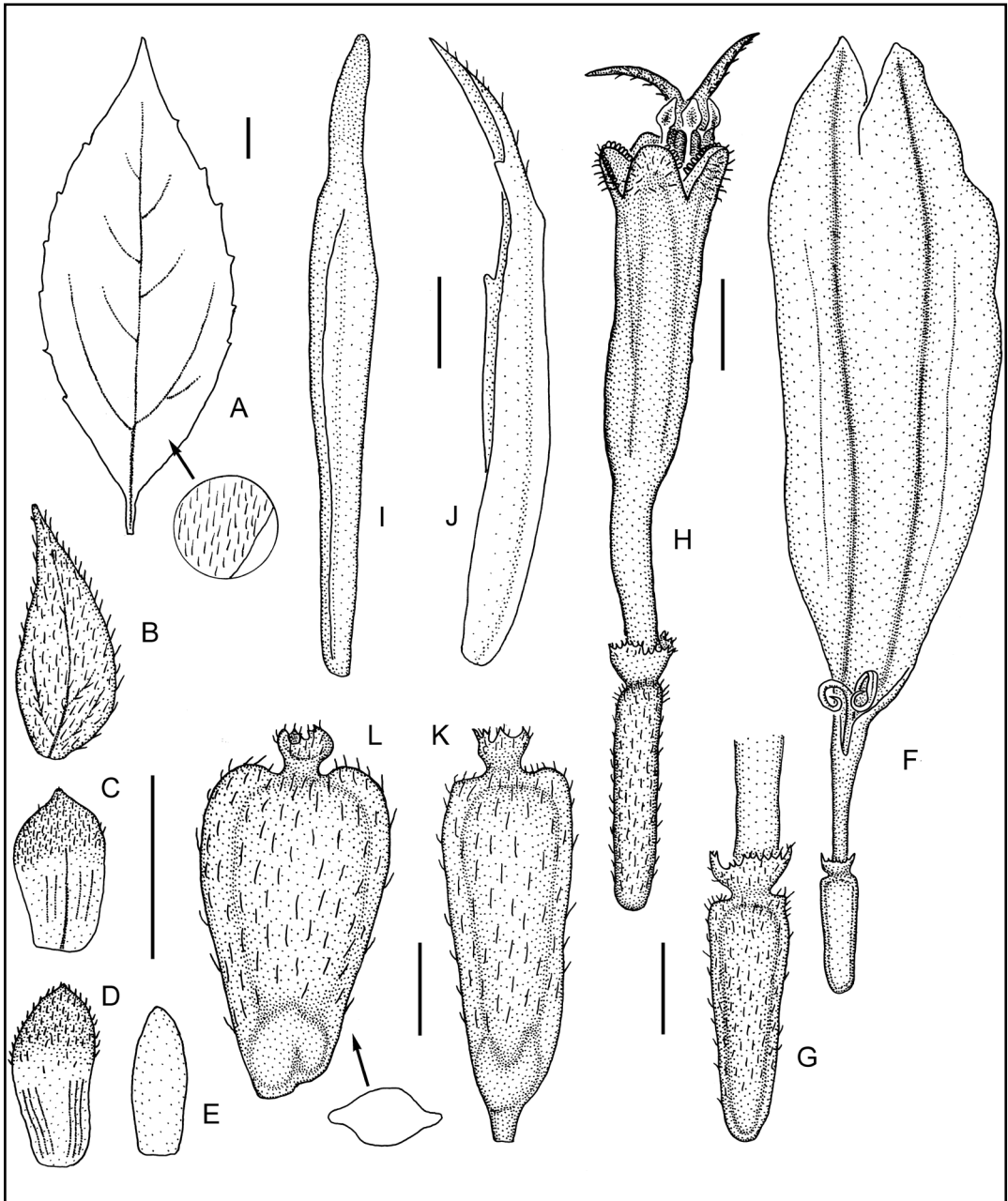


Figure 1. American species of *Wedelia*. *Wedelia fruticosa*. A – leaf; B – outer involucre bract; C – mid-involucre bract; D – inner involucre bract; E – inner involucre bract, transitional to palea; F – ray floret; G – ovary of ray floret; H – disc floret; I – palea, dorsal view; J – palea lateral view; K – slightly immature achene; L – mature achene. (A–J based on *I. Vélez* 3038 (K); K, L based on *W.R. Elliott* 105 (K)). Scale bars: A = 1 cm; B–L = 1 mm. Del. A.E. Orchard.

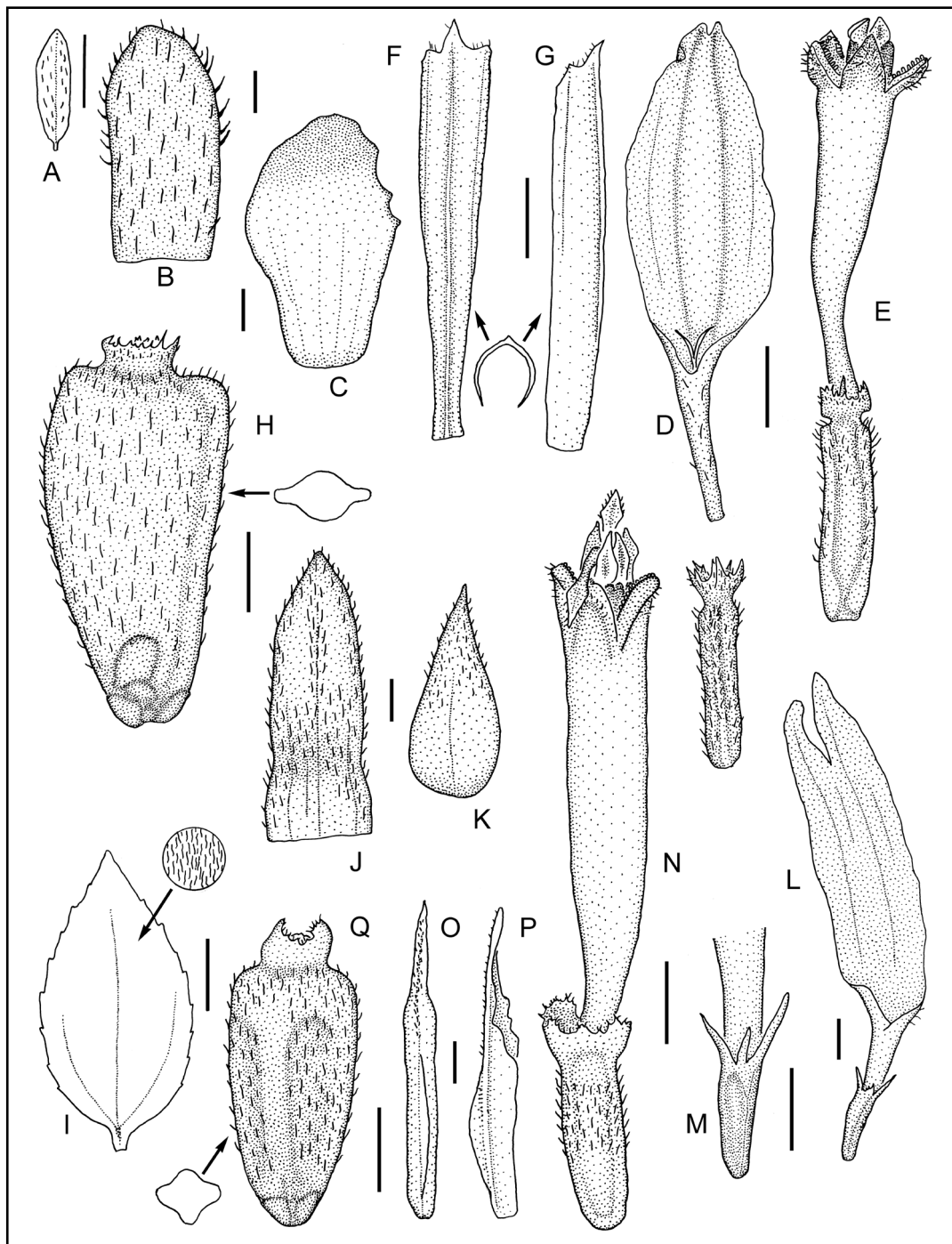


Figure 2. African species of *Wedelia/Aspilia*. A–H. *Wedelia thouarsii*. A – leaf; B – outer involucre bract; C – inner involucre bract; D – ray floret; E – disc floret; F – palea, dorsal view; G – palea, lateral view; H – mature achene. I–Q. *Aspilia plurisetata*. I – leaf; J – outer involucre bract; K – inner involucre bract; L – ray floret; M – disc floret; O – palea, dorsal view; P – palea, lateral view; Q – mature achene. (A–H based on *H.-J. Schleiben* 8006 (K); I–Q based on *G. Troupin* 5872 (CANB)). Scale bars: A, I = 1 cm; B–H, J–Q = 1 mm. Del. A.E. Orchard.

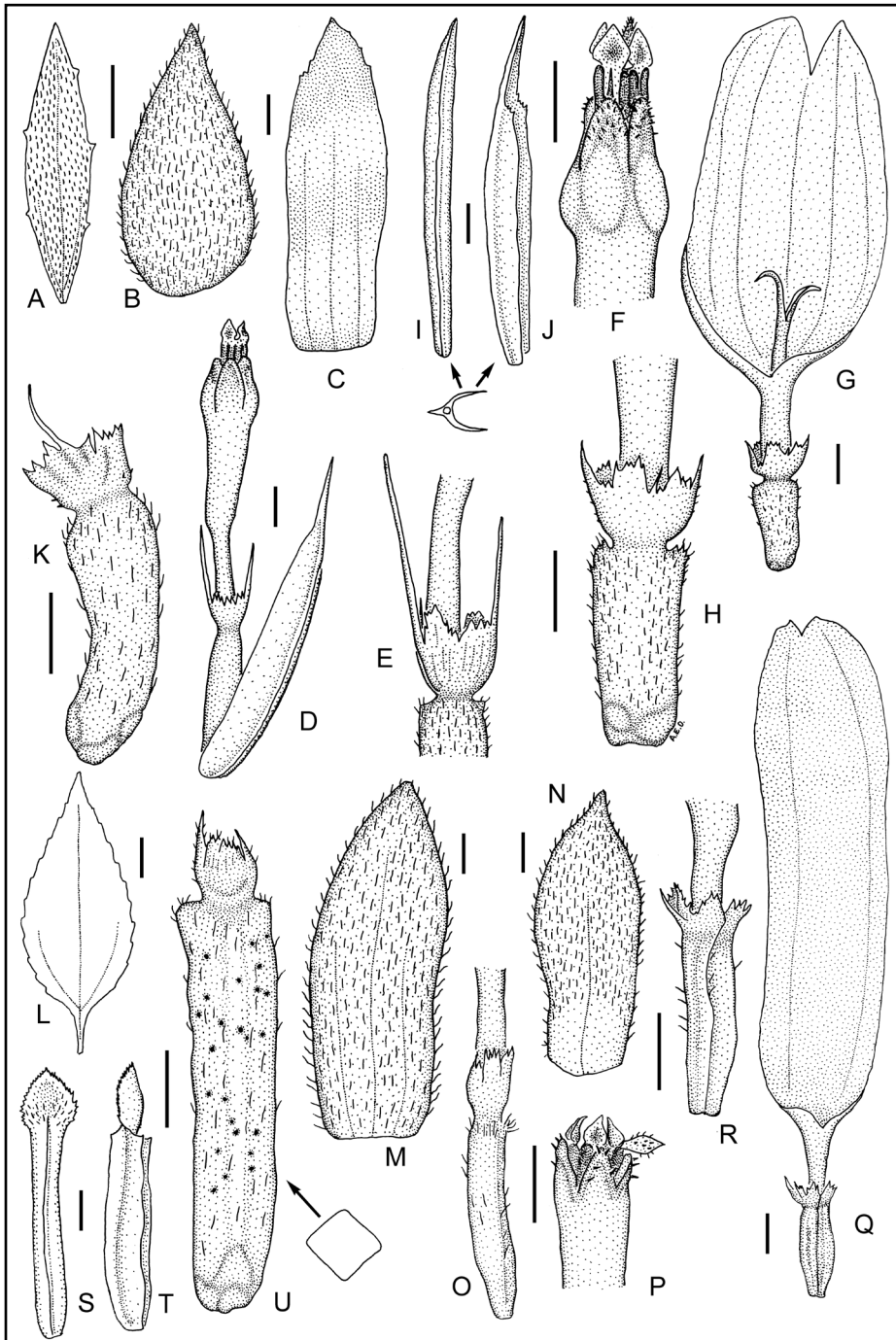


Figure 3. American species of *Wedelia*. A–K. *Wedelia acapulcensis* var. *hispida*. A – leaf; B – outer involucre bract; C – inner involucre bract; D – disc floret included in palea; E – detail of disc floret ovary; F – detail of disc floret corolla lobes, anthers and stigma; G – ray floret; H – detail of ray floret ovary; I – palea, dorsal view; J – palea, lateral view; K – immature achene. L–U. *Wedelia silphoides*. L – leaf; M – outer involucre bract; N – inner involucre bract; O – detail of disc floret ovary; P – detail of disc floret corolla lobes, anthers and stigma; Q – ray floret; R – detail of ray floret ovary; S – palea, dorsal view; T – palea, lateral view; U – mature achene. (A–K based on *M.A. Vincent* 12605 (CANB); L–U based on *A. Schinini* 27532 (CANB)). Scale bars: A, L = 1 cm; B–K, M–U = 1 mm. Del. A.E. Orchard.

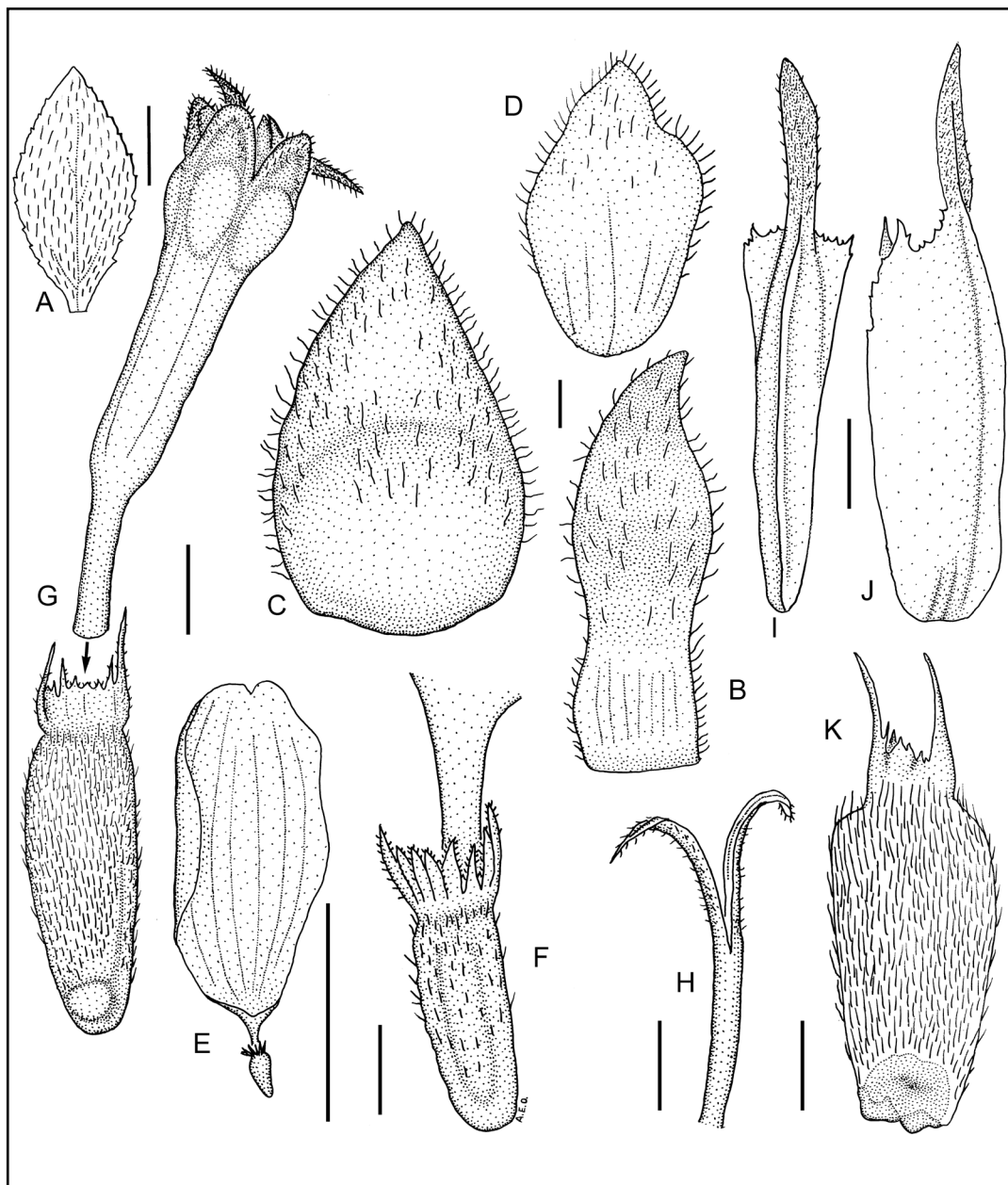


Figure 4. American species of *Wedelia*. *Wedelia montevidensis*. A – leaf; B – outer involucre bract; C – mid-involucre bract; D – inner involucre bract; E – ray floret; F – detail of ray floret ovary; G – disc floret; H – style (disc floret); I – palea, dorsal view; J – palea, lateral view; K – mature achene. (All based on *M.M. Arbo* 5977 (CANB)). Scale bars: A, E = 1 cm; B–D, F–K = 1 mm. Del. A.E. Orchard.

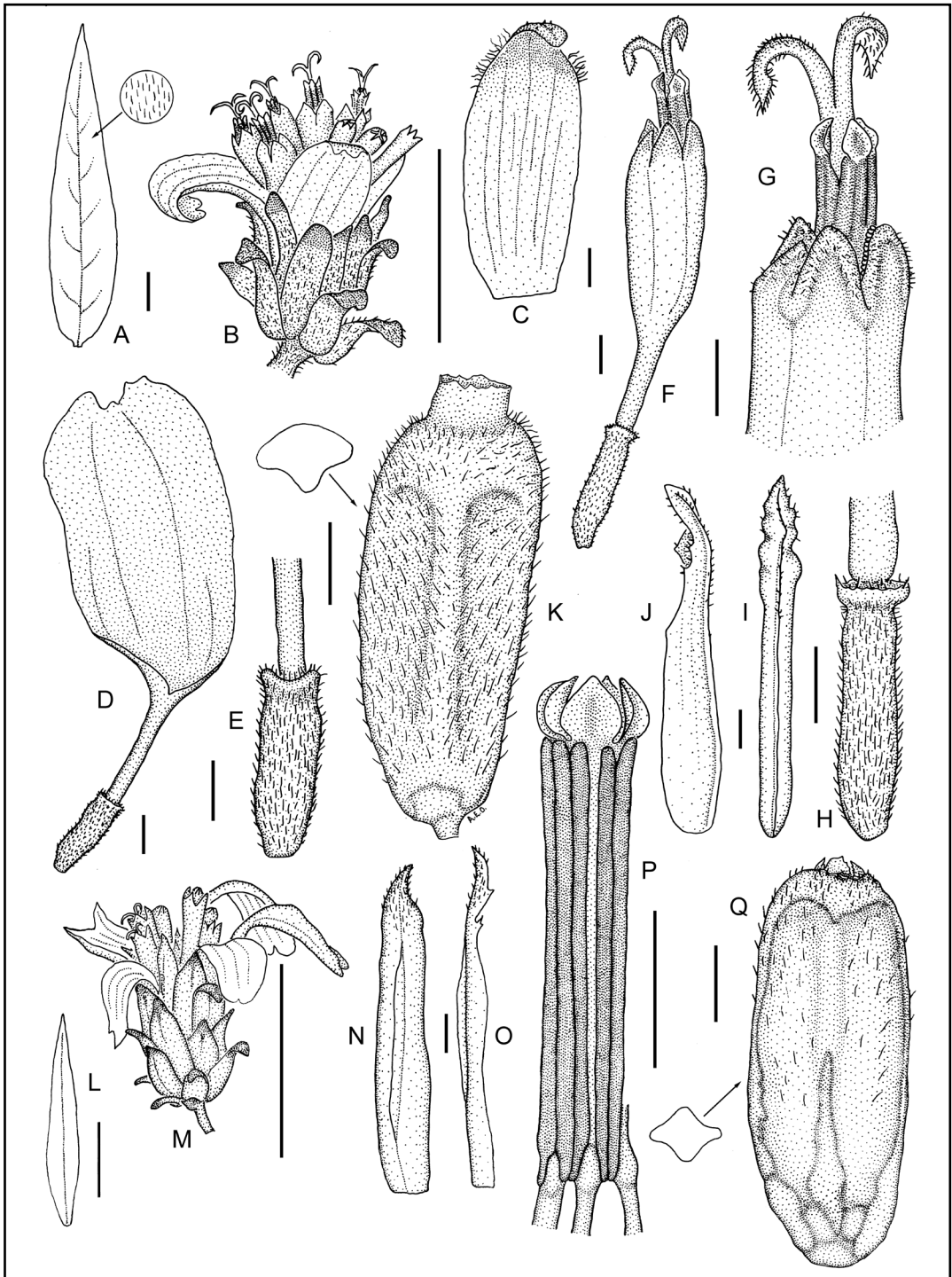


Figure 5. American species of *Wedelia*. A–K. *Wedelia subpetiolata*. A – leaf; B – capitulum; C – involucral bract; D – ray floret; E – detail of ray floret ovary; F – disc floret; G – detail of disc floret corolla lobes, anthers and stigma; H – detail of disc floret ovary; I – palea, dorsal view; J – palea, lateral view; K – mature achene. L–Q. *Wedelia cylindrocephala*. L – leaf; M – capitulum; N – palea, dorsal view; O – palea, lateral view; P – stamens; Q – mature achene. (A–K based on *G. Hatschbach et al.* 67372 (CANB)); L–Q based on *G. Hatschbach et al.* 64713 (CANB)). Scale bars: A, B, L, M = 1 cm; C–K, N–Q = 1 mm. Del. A.E. Orchard.

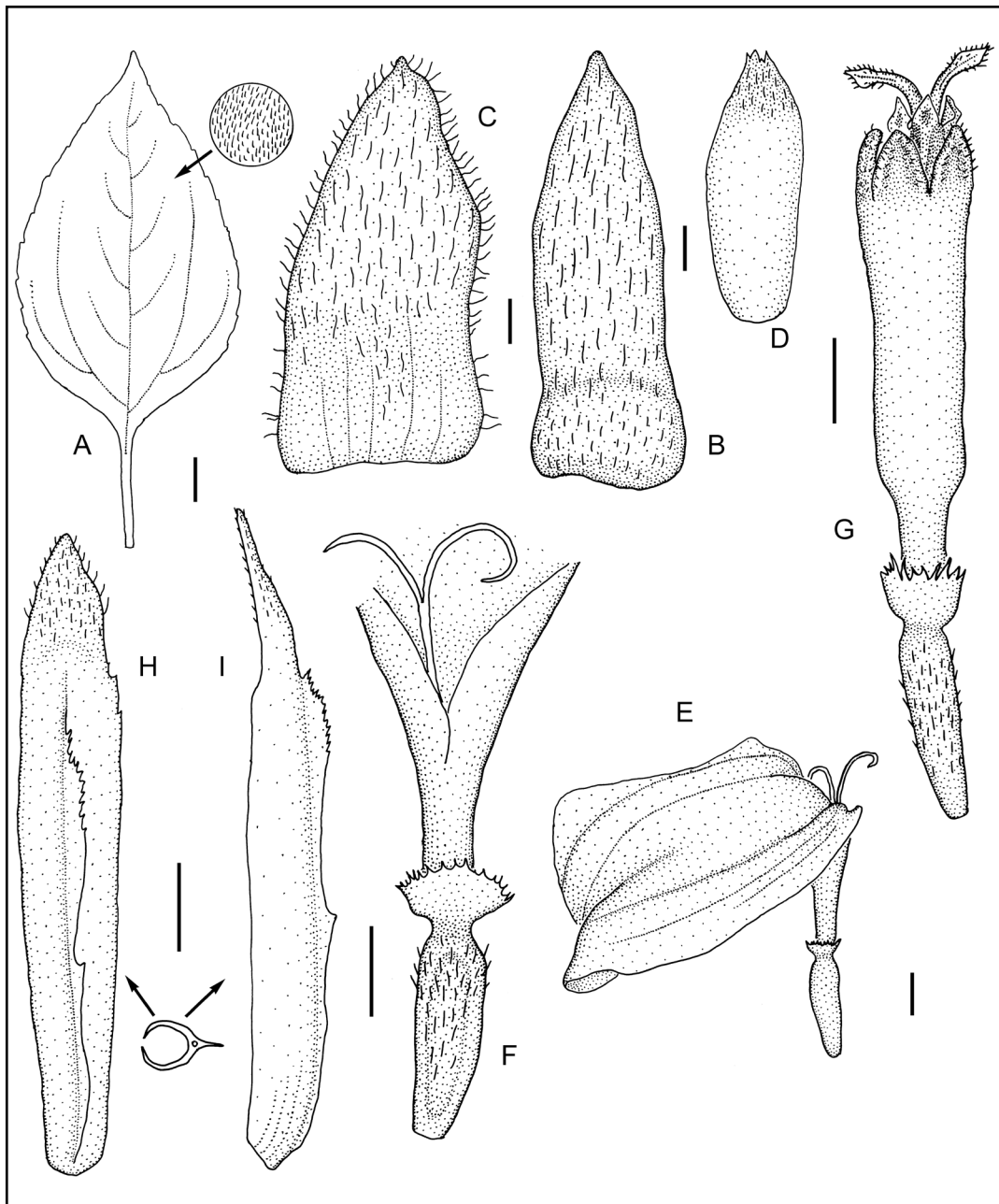


Figure 6. American species of *Wedelia*. *Wedelia latifolia*. A – leaf; B – outer involucre bract; C – mid-involucre bract; D – inner involucre bract; E – ray floret; F – detail of ray floret ovary; G – disc floret; H – palea, dorsal view; I – palea, lateral view. (All based on *J. Campos & P. Diaz* 3267 (CANB)). Scale bars: A = 1 cm; B–I = 1 mm. Del. A.E. Orchard.

African species of *Aspilia*/*Wedelia* follow the same general plan. For example, *Aspilia pluriseta* (Figure 2I–Q) has paleae that are linear, hyaline, with a distinct apical appendage, a crest, and lateral lobes. The achene is hairy throughout, slightly compressed, with a lacinate, cup-shaped pappus seated on a short rostrum. The ray florets are neuter.

Wedelia and *Aspilia* are clearly closely related. Bentham (Bentham & Hooker 1873) separated them on the sexuality of the ray florets, those species with fertile ray florets being placed in *Wedelia*, those with sterile ray florets in *Aspilia*. Bentham subdivided *Wedelia* into four sections. Some of these are now known to belong elsewhere (e.g. *Wollastonia*, *Sphagneticola*). *Aspilia* was divided into three (unnamed) series, two of which had involucre bracts in two series, one with bracts in three series. Unfortunately, later authors have found the sexuality of the ray florets to be rather variable and inadequate to define genera. *Aspilia* is therefore now generally considered to be a synonym of *Wedelia* although the limited number of species studied in detail for this work demonstrates a wide variability and useful, but previously unused, characters available. Resolution of the question as to whether there are one, two, or more genera involved in this complex is beyond the scope of this paper. For convenience, they are all treated below as *Wedelia* (except in cases where the combination in that genus has not been made). They are distinct from the *Wollastonia*/*Melanthera*/*Lipochaeta* lineage, and use of the generic name *Wedelia* for Australasian taxa is incorrect.

Generic circumscription of *Melanthera*

Melanthera aspera (Jacq.) Spreng. (usually considered the type of *Melanthera*, and now included within *M. nivea* (L.) Small), is a low, spreading subshrub. It has large, ovate (sometimes lobed) leaves and white, discoid capitula on medium to long peduncles. The involucre is of green, hairy bracts, somewhat scarious, in two series (the inner ones becoming straw-coloured). Ray florets are absent. Disc florets have corollas that are 5-lobed and white, and are bisexual and fertile, with black anther thecae. The paleae are oblanceolate, conduplicate, clasping the ovary/achene, scarious, green and opaque, striate, with a well developed midrib but no abaxial crest, shortly scabrous apically, tip blunt to acute, not differentiated into an appendage, margins entire. Achenes are reddish brown, ±compressed, 2-angled, apically truncate or slightly sunken, glabrous or shortly pilose apically only, with no elaiosomes; a pappus of few to many short, antrorsely barbellate, caducous awns that are shed at the slightest touch, and no scales or hairs. (Figures 7A–O, 13A)

There are about five species in the Caribbean basin which share with *M. aspera* its diagnostic characters of discoid capitula, white, 5-lobed corollas, anthers with black thecae, oblanceolate, green, scarious, striate, entire paleae lacking lobes, crest and differentiated apiculum, small (1–2 mm long), compressed achenes that are truncate or slightly sunken above, shortly hairy only on the apex, and with a pappus consisting of up to 20 short, erect, shortly barbed, freely caducous awns. One species extends into the northern Andes. All are similar, and the exact number of species has at various times been given as one (Standley 1938), five (Parks 1973), or as many as 12 (Schulz 1911). One species, *M. angustifolia* A. Rich. (Figure 7P–X), differs from *M. aspera* in having narrow leaves and florets in which the corolla lobes are spreading and densely papillose internally, but otherwise agrees with the diagnostic characters above.

Bentham (Bentham & Hooker 1873) greatly expanded the circumscription of *Melanthera* by including taxa with yellow or otherwise coloured, radiate capitula, previously recognised as distinct genera: *Echinocephalum* from South America, and *Lipotriche*, *Trigonotheca* Sch. Bip., *Psathurochaeta* and *Weurschmittia* from Africa. This broadening of the concept of *Melanthera* later induced other authors to expand the genus further, to encompass *Wollastonia*, *Aphanopappus* Endl. (*Lipochaeta* sect.

Aphanopappus), and other taxa from Asia, Malesia and Oceania, creating a heterogeneous genus that is almost impossible to define. On the other hand, recognition of *Melanthera* in its original (i.e. Parks 1973) concept yields a distinctive *Melanthera*, and other genera as discussed below. This is the concept adopted here.

Generic circumscription of *Echinocephalum*

Echinocephalum, with a single species *E. latifolium* Gardner (Figure 8), resembles *Melanthera* in its small (2–3 mm long), truncate achenes with numerous caducous awns, but is distinct in having radiate capitula with yellow to orange corollas. The paleae differ from those of *Melanthera* in being ovate with a caudate tip rather than oblanceolate with an acute to blunt tip, and they are also membranous (indurate to papery) at maturity, with multiple striae, and the outer paleae bend through 90° to cup the developing achenes.

Thus, while related to *Melanthera*, *Echinocephalum* is clearly distinct at generic level and should be reinstated. It is usually considered to be monotypic, although some authors (including Gardner 1848), have recognised two or three species, all from South America.

Generic circumscription of *Lipotriche*

Lipotriche brownii DC. (= *Lipotriche scandens* (Schum. & Thonn.) Orchard subsp. *scandens*, type of *Lipotriche*) is a perennial herb to 1 m tall, sometimes scandent to 4 m. It has large, deltate to ovate leaves and yellow, radiate capitula on long peduncles. The involucre of two or three series is green and herbaceous. Ray florets are pistillate (styles present), with yellow corollas; disc florets bisexual, fertile, with yellow corollas and black anther thecae. The paleae are yellow, linear, acuminate, indurate, with a distinct midrib and numerous striae, sparsely and shortly scabrous distally, lacking both an abaxial crest and marginal lobes. Achenes are yellow-brown, compressed, 2-angled, truncate, shortly hairy only on apex, ±smooth, with no elaiosomes; pappus of up to ten, short, erect, antrorsely barbed awns that are caducous, being shed at the slightest touch, no scales or pappus hairs. (Figure 9A–E)

Psathurochaeta dregei DC. (= *Lipotriche scandens* subsp. *dregei* (DC.) Orchard, type of *Psathurochaeta*) is similar in almost all respects, differing only in having paleae acute and somewhat shorter, and leaves cuneate, not subcordate at the base. (Figure 9F–O)

Wuerschmittia abyssinica Sch.Bip. ex Walp. (= *Lipotriche abyssinica* (Sch.Bip. ex Walp.) Orchard, type of *Wuerschmittia*) is also similar to *L. brownii* in most respects. It differs in having acute rather than acuminate paleae, with two small, lateral lobes near the tip. The achenes are rounded apically rather than abruptly truncate, and glabrous, although the ovaries of both the ray and disc florets are truncate, only becoming rounded as the achenes mature. The pappus is identical to that in *Lipotriche*, with short, erect, caducous awns. The ray florets are neuter (lacking a style). (Figure 10A–N)

All of these taxa, and about 12 others in Africa, have been included in a broadly defined *Melanthera* by Bentham (Bentham & Hooker 1873), Wild (1965) and Beentje and Hind (2005). If *Melanthera* is restricted to the core group of about six discoid taxa with white corollas from the Caribbean basin and the Andes as proposed in this paper, then the earliest available generic name for the African taxa is *Lipotriche* (syn. *Psathurochaeta* DC., *Wuerschmittia* Sch.Bip. ex Hochst.). The characteristics defining this genus are: involucre green, herbaceous; capitula radiate with yellow to orange corollas; ray florets pistillate or neuter; disc florets bisexual and fertile, with black anther thecae. The paleae

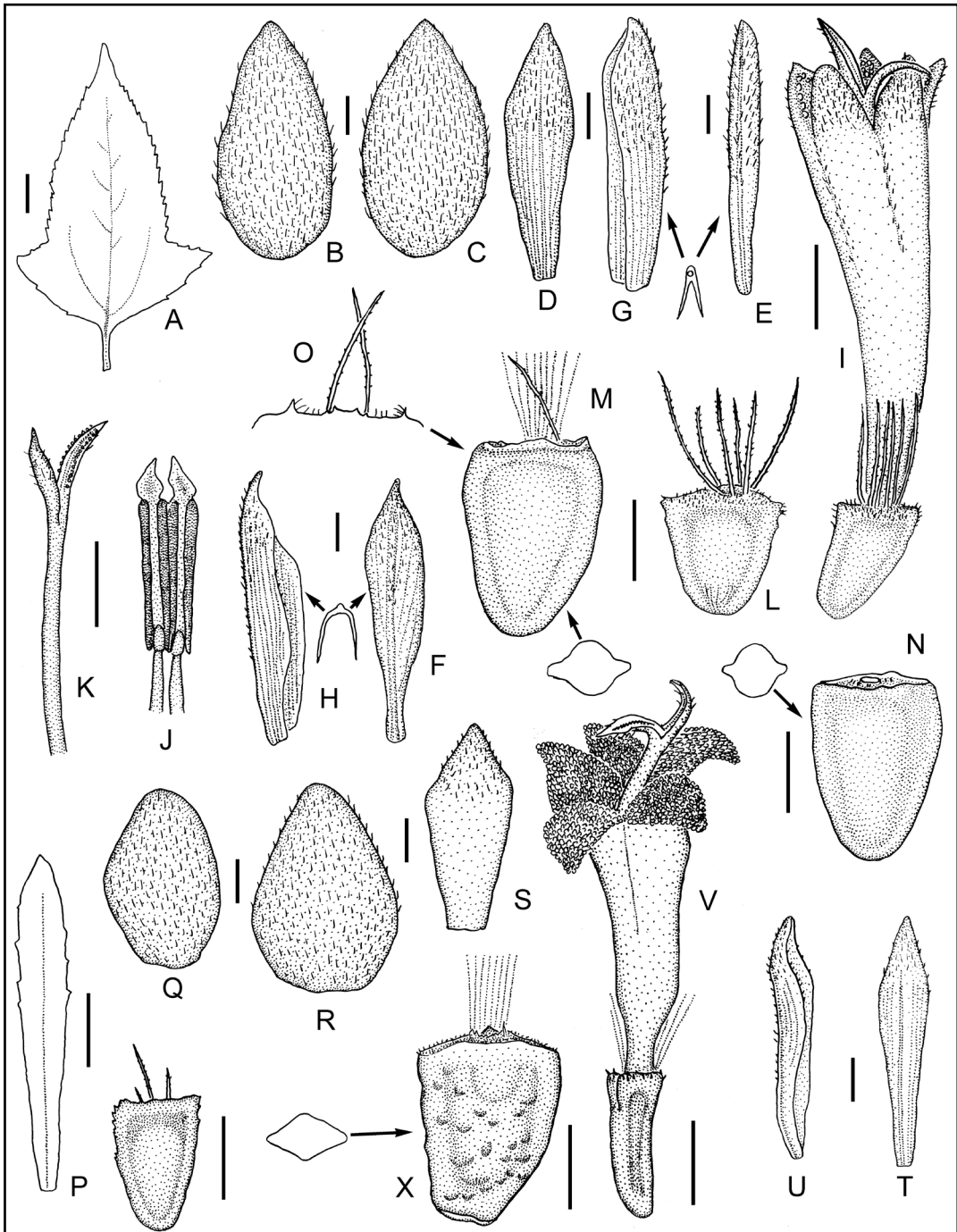


Figure 7. *Melanthera* species. A–O. *M. nivea*. A – leaf; B – outer involucre bract; C – mid-involucre bract; D – innermost involucre bract, transitional to palea; E, F – palea, dorsal view; G, H – palea, lateral view; I – floret; J – anthers; K – style; L – young developing achene; M, N – mature achene; O – diagrammatic transverse section of top of achene. P–X. *M. angustifolia*. P – leaf; Q – outer involucre bract; R – inner involucre bract; S – innermost involucre bract, transitional to palea; T – palea, dorsal view; U – palea, lateral view; V – floret; W – young achene; X – mature achene. (A–O based on F.R. Fosberg 56095 (K); P–W based on E.L. Ekman H13323 (K); X based on E.P. Killip 43939 (K)). Scale bars: A, P = 1 cm; B–O, Q–X = 1 mm. Del. A.E. Orchard.

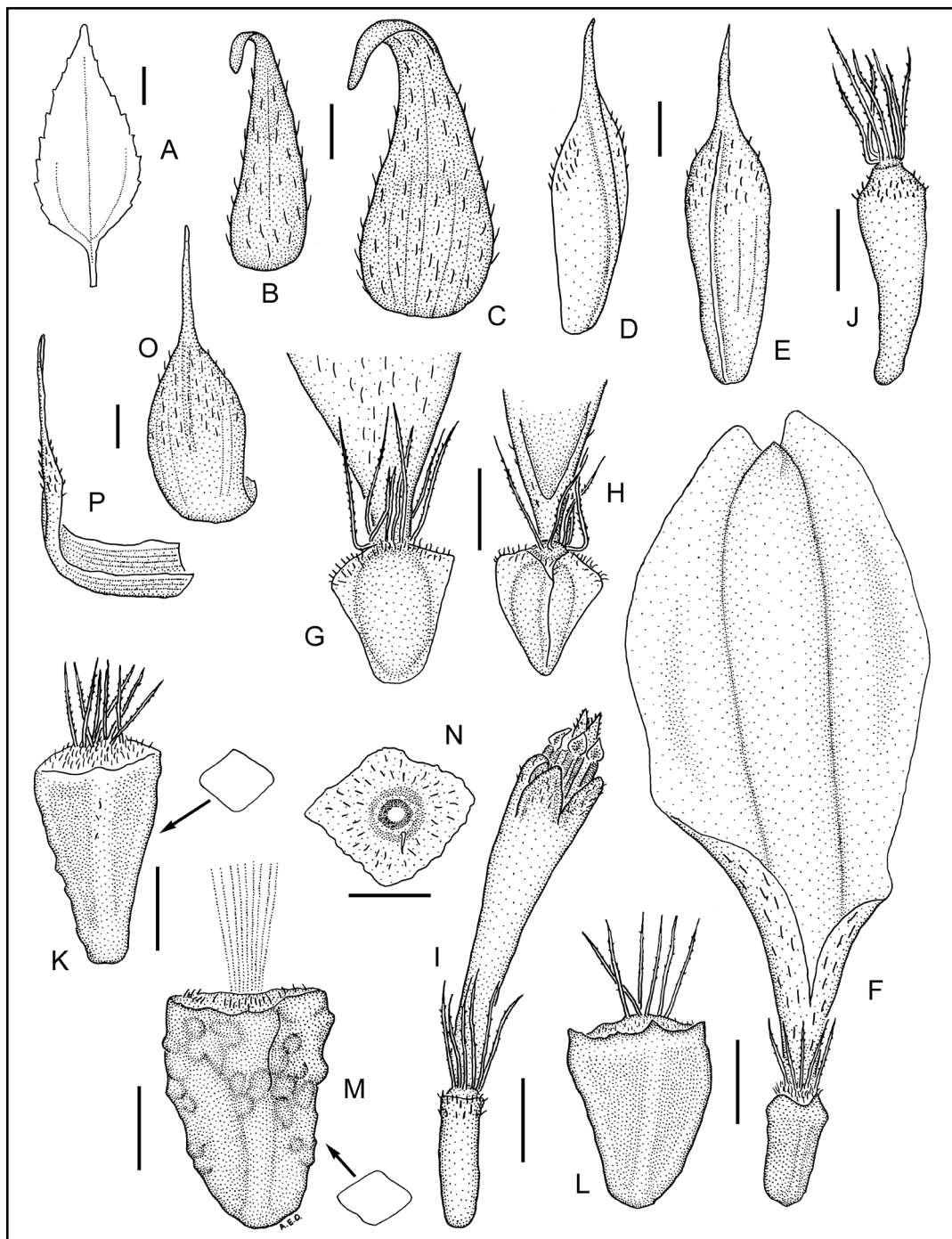


Figure 8. *Echinocephalum latifolium*. A – leaf; B – outer involucre bract; C – inner involucre bract; D – innermost involucre bract, transitional to palea; E – palea; F – ray floret; G – ray floret, detail of ovary, abaxial; H – ray floret, detail of ovary, adaxial; I – disk floret; J – disc floret, detail of ovary; K, L – young developing achene; M – mature achene, awns shed; N – apical view of achene; O – outer fruiting palea, dorsal view; P – outer fruiting palea, lateral view. (A–E, G, H, J, K, O, P based on *J.E.R. Collares & L. Dutra* 191 (K); F, I, M, N based on *E. Zardini & P. Aquino* 29887 (K); L based on *M.S. Bona Nascimento* 416 (K)). Scale bars: A = 1 cm; B–P = 1 mm. Del. A.E. Orchard.

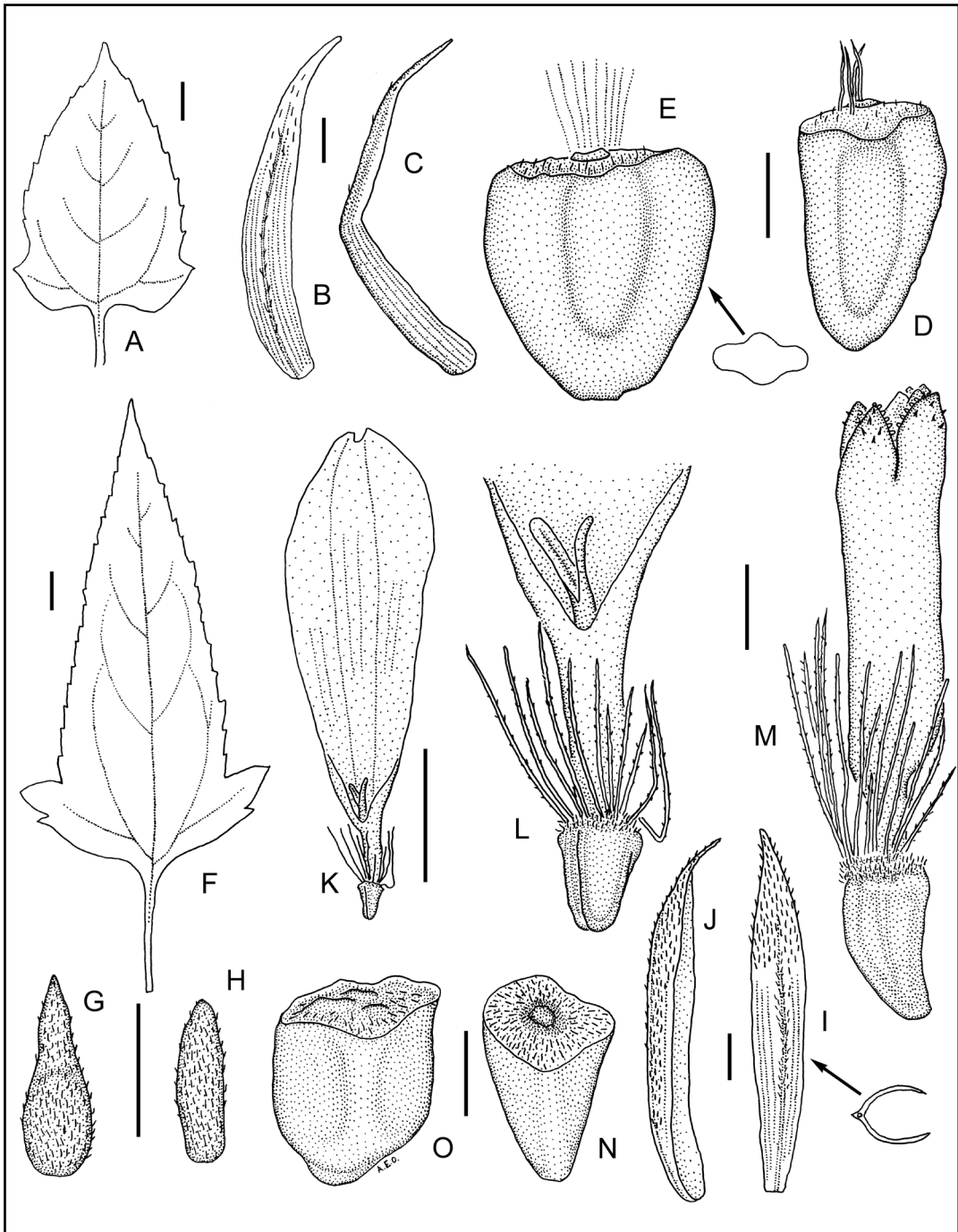


Figure 9. *Lipotriche* species. A–E. *Lipotriche scandens* subsp. *scandens*. A – leaf; B – palea, dorsal view; C – palea, lateral view; D – immature achene with a few residual awns; E – mature achene, awns shed. F–O. *Lipotriche scandens* subsp. *dregei*. F – leaf; G – outer involucre bract; H – inner involucre bract; I – palea, dorsal view; J – palea, lateral view; K – ray floret; L – ray floret, detail of ovary and awns; M – disc floret; N, O – mature achenes, awns shed. (A–E based on *P. Compère* 239 (K); F–N based on *A. Pegler* 420 (K); O based on *J.M. Wood* 348 (K)). Scale bars: A, F = 1 cm; G, H = 5 mm; B–E, I–O = 1 mm. Del. A.E. Orchard.

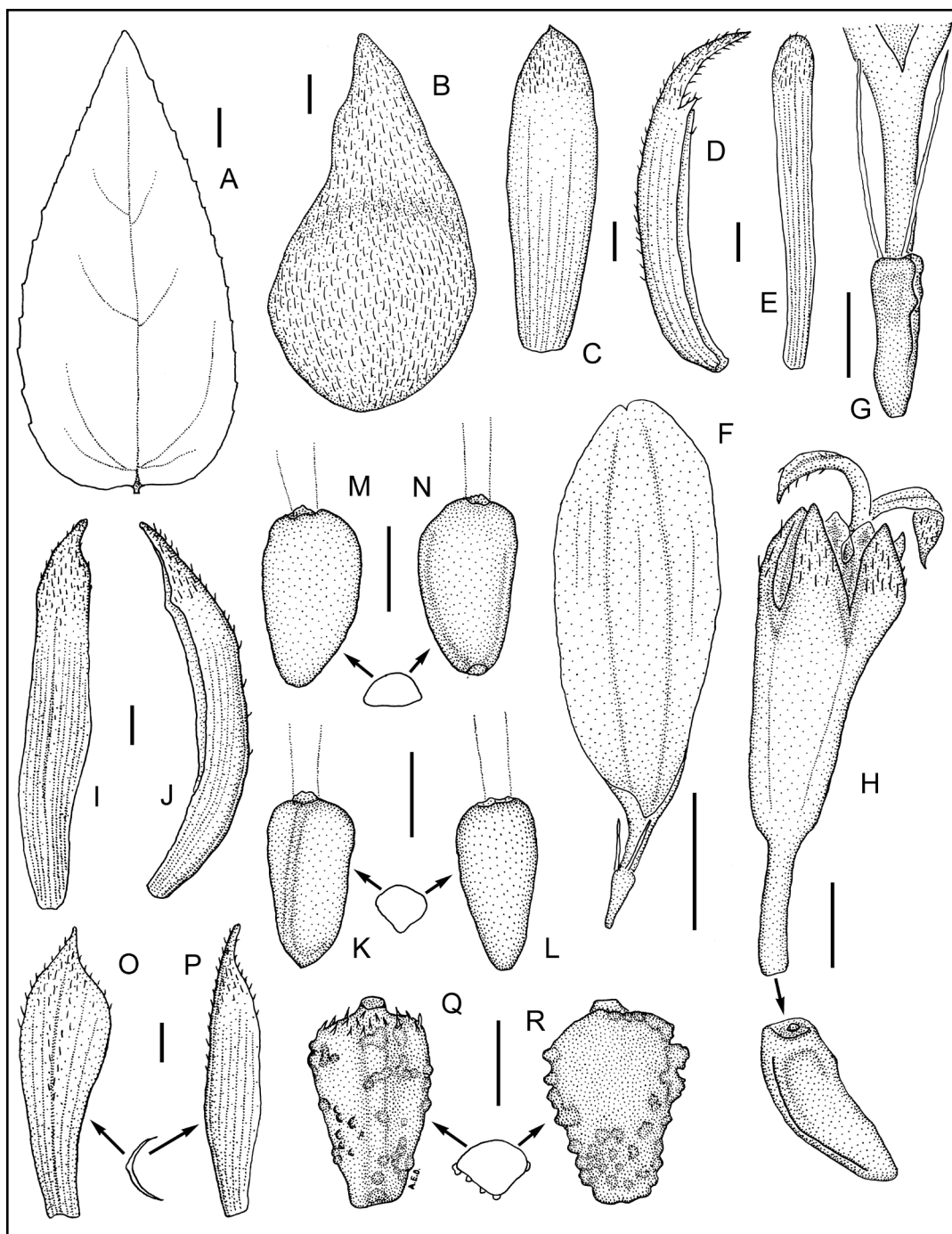


Figure 10. *Lipotriche* species. A–N. *Lipotriche abyssinica*. A – leaf; B – outer involucral bract; C – inner involucral bract, transitional to paleae; D – floret palea, dorsal view; E – floret palea, lateral view; F – ray floret; G – ray floret, detail of ovary and awns; H – disc floret, corolla separated from ovary; I – fruiting palea, dorsal view; J – fruiting palea, lateral view; K, L – ray achenes, adaxial and abaxial views; M, N – disc achenes, adaxial and abaxial views. O–R. *Lipotriche triternata*. O – palea, dorsal view; P – palea, lateral view; Q, R – ray achenes, adaxial and abaxial views. (A–J based on G. Aylmer 180 (K); K–N based on J.B. Gillett 14486a (K); O–R based on Leistner et al. 279 (K)). Scale bars: A = 1 cm; F = 5 mm; B–E, G–R = 1 mm. Del. A.E. Orchard.

are usually coloured (yellowish), linear to oblanceolate, acute to acuminate, without a differentiated apical appendage, with or without short lateral lobes near the tip, subhyaline to opaque, indurate, conduplicate, with a well-defined midrib and numerous striae, shortly scabrous distally. The outer paleae are often bent through 90° in fruit to cradle the achenes. Achenes are small, usually to 2 mm long, varying in colour from brown to purplish black, compressed, 2-, 3-, or 4-angled, truncate or rounded apically, with hairs only at apex, or glabrous, smooth to rugose, lacking elaiosomes; the pappus is of up to ten short, erect, antrorsely barbed or smooth awns that are caducous, being shed at the slightest touch, no scales or pappus hairs.

Species with rounded apices to their achenes include *L. pungens* (Oliv. & Hiern) Orchard (Figure 11Q, R), *L. gambica* (Hutch. & Dalziel) Orchard (Figure 11L–P), and *L. triternata* (Klatt) Orchard (Figure 10O–R). The last has achenes with raised rugose tubercles. Species with truncate achenes include *L. scandens* (Figures 9D, E, N, O, 11K) and *L. abyssinica* (Figure 10K–N).

Combinations in *Lipotriche* are not available for most taxa. As I have only examined limited material, I refrain from making new combinations here, apart from those required to discuss the taxa above. Further combinations should only be made as part of a revision of the genus to resolve the obvious species-level taxonomic problems mentioned by Wild (1965) and confirmed by Beentje and Hind (2005), among others.

Generic circumscription of *Wollastonia*

Wollastonia DC. ex Decne. was described (Decaisne 1834; Candolle 1836) with 15 species, although with later synonymy and transfers the genus was soon reduced to its type, *W. biflora*. Bentham (Bentham & Hooker 1873), included *Wollastonia* within a broad *Wedelia*, as *Wedelia* sect. *Wollastonia*. Wild (1965) transferred the genus to *Melanthera*. Subsequent authors have variously treated it as *Wollastonia*, *Melanthera* or *Wedelia* (see summary in ‘History of generic circumscription’ above), usually as a single species (*Wollastonia biflora*, *Melanthera biflora* or *Wedelia biflora*). With redefinition of the limits of *Wedelia* and *Melanthera* as above, it is clear that this species must be placed in a distinct genus, *Wollastonia*.

Wollastonia biflora (L.) DC. (Figures 12, 13B) is a straggling perennial herb or scandent subshrub to 3 m tall, and usually found as a strand plant in countries of the Indian Ocean, in Malesia, south-east and east Asia, and the south-western Pacific Ocean. It has small to large, ovate leaves, and radiate capitula on rather short peduncles. The involucre bracts are in two series, green, and herbaceous. Ray florets are pistillate and fertile with yellow corollas. Disc florets are bisexual and fertile, with a yellow, 5-lobed corolla and black (rarely dark brown) anther thecae. Paleae are oblanceolate to subspathulate, membranous (indurate), opaque, striate basally, with a well-defined midrib, the apex green, blunt, abaxially shortly scabrous, and usually hooded. The achenes are 3.5–4.5 mm long, at least the outer ones corky, 2- or 3-angled, truncate and shortly hairy apically, only weakly compressed, usually with a single (often oblique) antrorsely barbed awn that is deciduous (but not caducous). It is distinct from *Wedelia* in the characters of the paleae (texture, shape, indumentum) and of the pappus (no cup or rostrum, true awn present). From *Melanthera s. str.* it differs in having yellow corollas, a radiate capitulum, and a pappus consisting of a single, deciduous, oblique awn (rather than multiple, caducous, erect awns). From *Lipotriche* it differs less, but is distinguished by having a pappus of a single, oblique, deciduous awn (instead of multiple, erect, caducous awns), and paleae that are thicker, blunt and hooded beyond the developing achenes, and green rather than yellow. [Note: In this paper, caducous awns are defined as those which are extremely flimsily attached, ±soft, and usually shed before the achene matures. Deciduous awns are more substantial, stiffer, and usually persist until maturity,

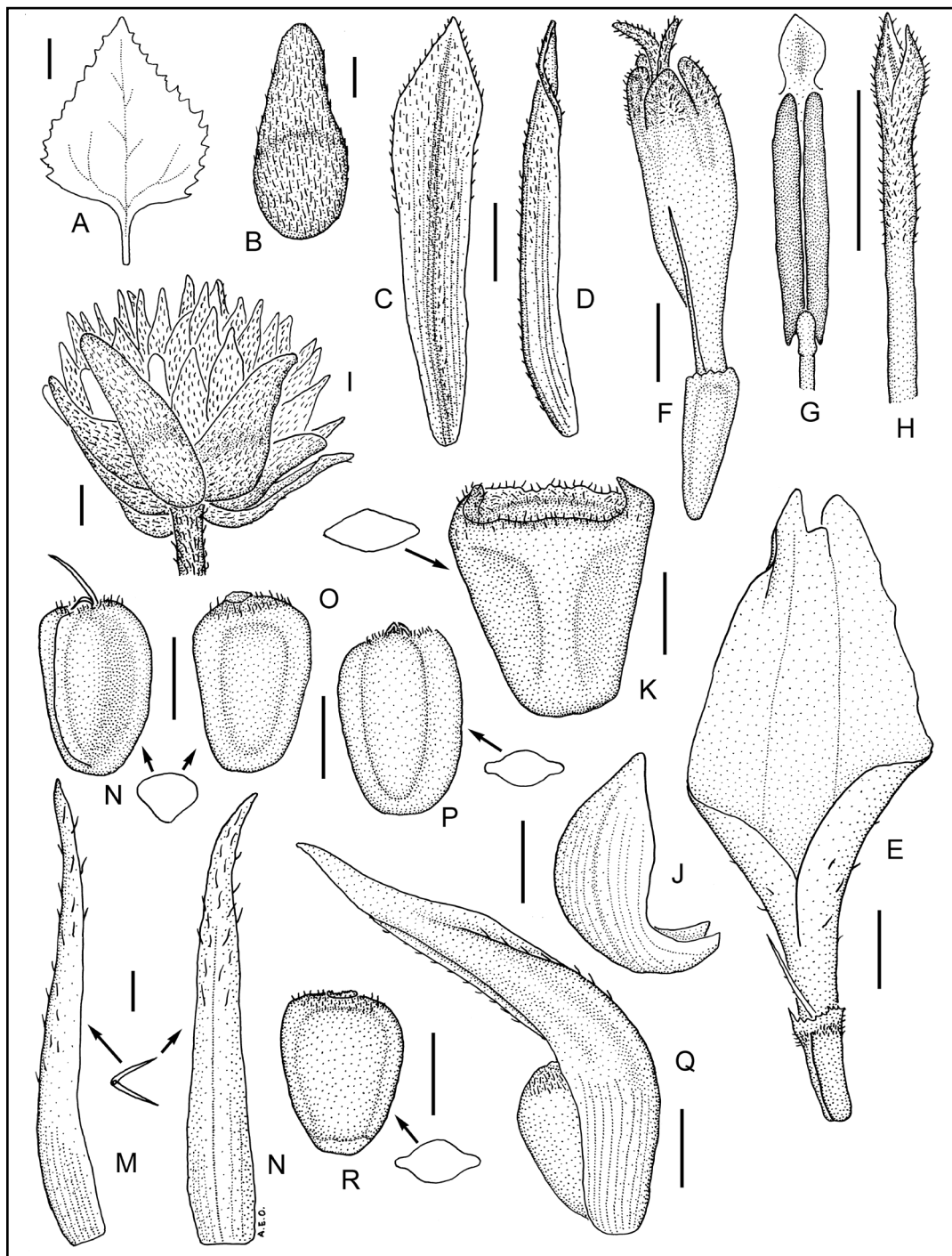


Figure 11. *Lipotriche* species. A– K. *Lipotriche scandens* subsp. *subsimplificifolia*. A – leaf; B – involucre bract; C – palea, dorsal view; D – palea, lateral view; E – ray floret; F – disc floret; G – stamen; H – style from disc floret; I – capitulum in bud; J – outer fruiting palea; K – achene. L–P. *L. gambica*. L – palea, dorsal view; M – palea, lateral view; N, O – ray achene, adaxial and abaxial view; P – disc achene. Q, R. *L. pungens*. Q – achene enclosed in palea; R – achene. (A–I based on *B. de Winter* 3953 (CANB); J, K based on *A. Leonard* 1455 (K); L–P based on *J.P. Ruxton* 50 (K); Q, R based on *F.W. Andrews* A1447 (K)). Scale bars: A = 1 cm; B–R = 1 mm. Del. A.E. Orchard.

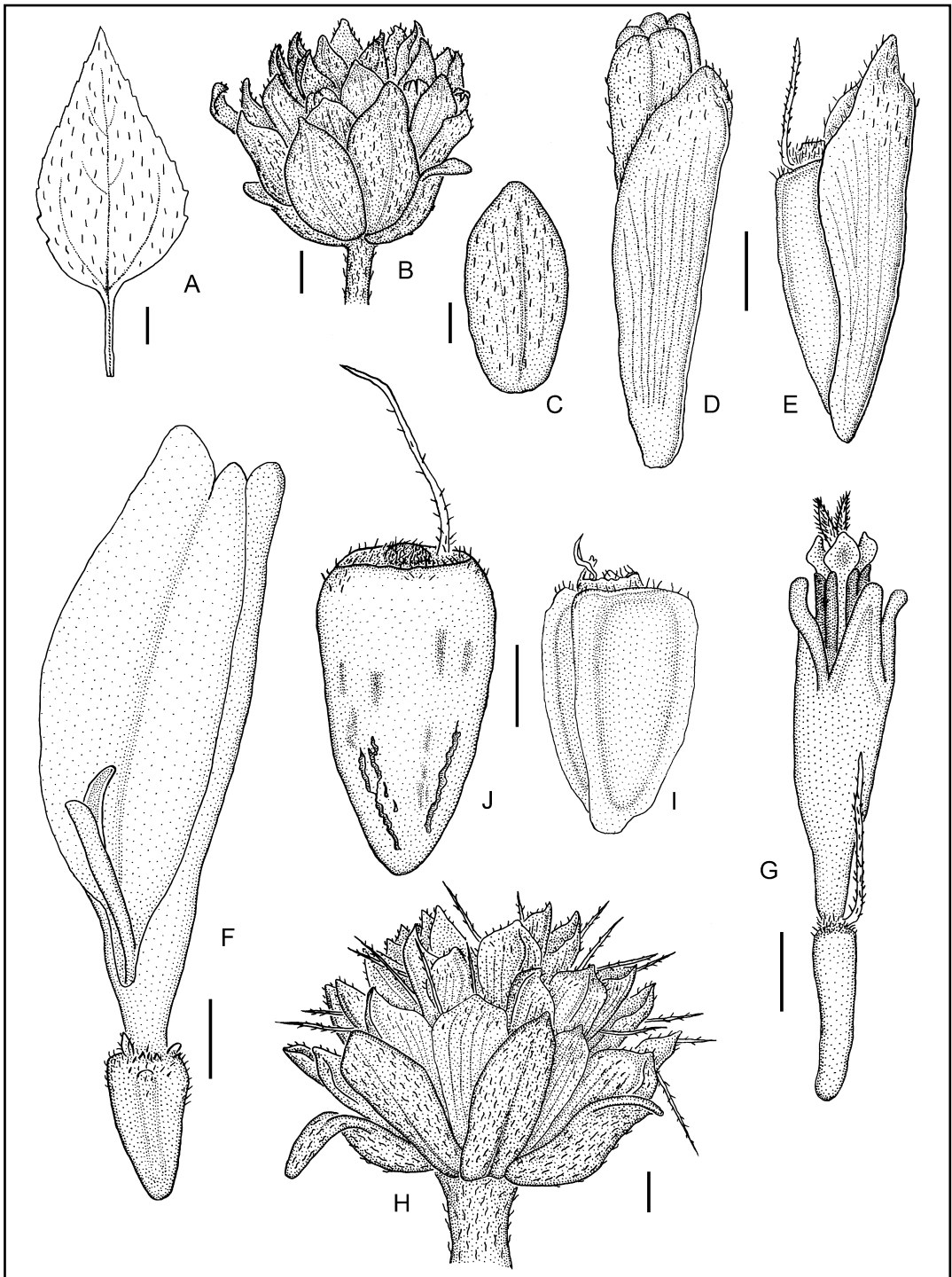


Figure 12. *Wollastonia biflora* var. *biflora*. A – leaf; B – capitulum in flower (bud); C – involucral bract; D – palea and disc floret in bud; E – palea with young achene; F – ray floret; G – disc floret; H – capitulum in fruit; I – slightly immature 3-angled achene; J – mature achene with corky outer layer, weakly 4-angled. (All based on *M.J.R. Barritt 1779* (DNA)). Scale bars: A = 1 cm; B–J = 1 mm. Del. A.E. Orchard.

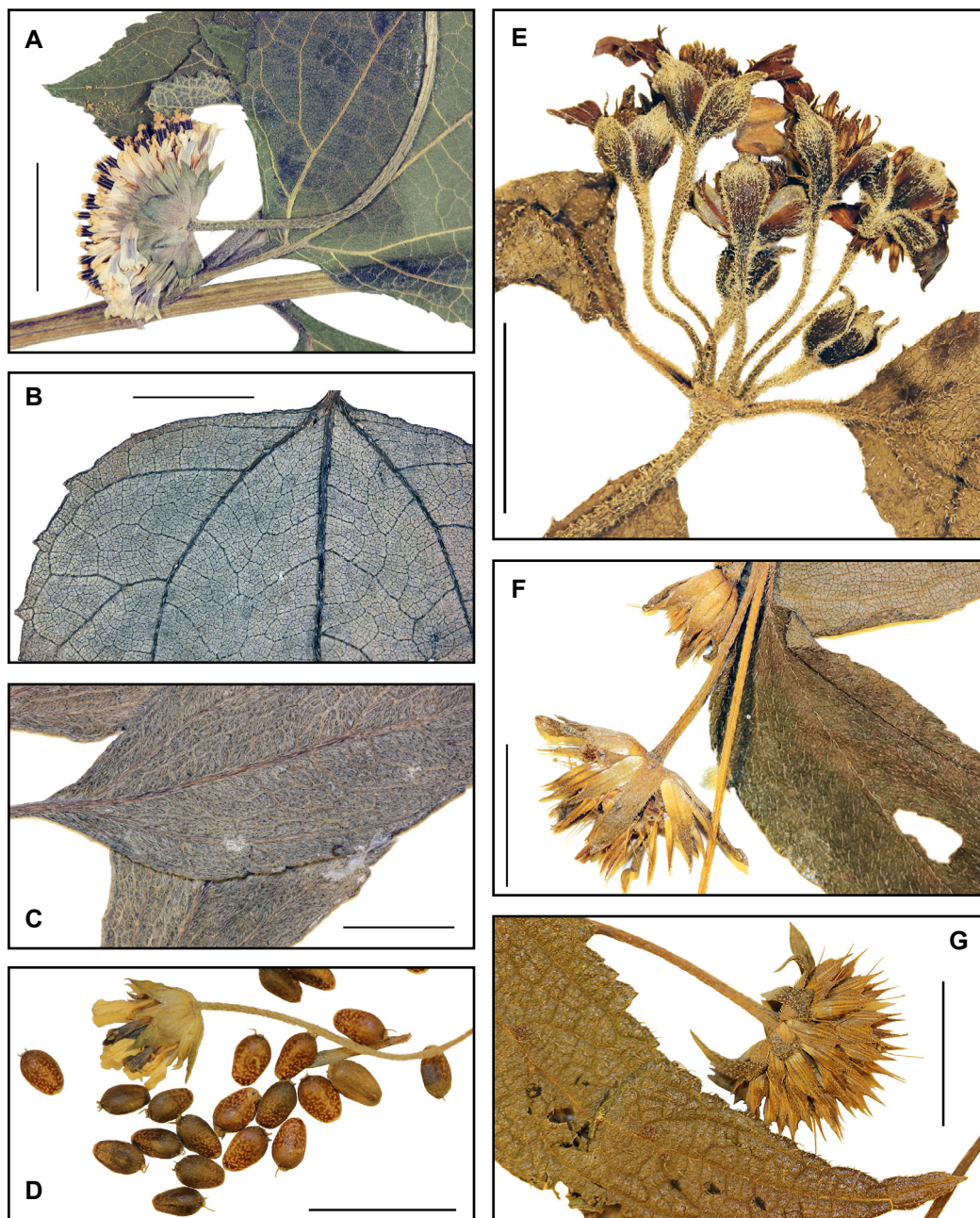


Figure 13. A – *Melanthera nivea*, flowering capitulum; B – *Wollastonia biflora* var. *biflora*, abaxial (under-) surface of leaf; C – *Wollastonia uniflora*, abaxial (under-) surface of leaf; D – *Indocypraea montana*, achenes and flowering capitulum; E – *Quadribractea moluccana*, dichasium of capitula; F – *Lipoblepharis urticifolia* subsp. *urticifolia*, fruiting capitulum; G – *Lipoblepharis asperima*, fruiting capitulum. (A from *J. Pruski & R. Ortiz* 4100 (K); B from *Korthals s.n.*, (L 2839 - type of *W. serrulata*); C from *E. Soakai* 782 (K); D from *L.F.G. Kerr* 2290 (K); E from *J. v. BorssumWaalkes* 3103 (L); F from [*H.*] *Zollinger* 296 (K); G from *J. Elbert* 1492 (L)). All scale bars = 1 cm. Photos A.E. Orchard.

but are readily dislodged through mechanical damage.] Panero *et al.* (1999) found that on chloroplast DNA data, *Wollastonia biflora* was well separated from core American *Wedelia*. *Wollastonia* has a chromosome number of $n = 15$, while *Wedelia* has numbers of $n = 11, 12, 13, 23$ (Strother 1991).

Examination of Australian collections revealed that there are two species of *Wollastonia* in Australia, *W. biflora* along the north coast, and matching other collections from the Indian Ocean, Malesia and the south-western Pacific, and another species (Figures 13C, 14), with usually narrower leaves, cuneate or rounded at the base (larger leaves in *W. biflora* are often subcordate), with dense, erect hairs on the abaxial surface (and to a lesser extent on the adaxial surface). Leaf hairs in *W. biflora* are sparser (to almost absent) and usually appressed (Figure 13B). This second species is found on the north-eastern (Pacific) coast of Australia, on Norfolk and Lord Howe Islands, and sporadically on south-western Pacific islands such as New Caledonia, Vanuatu and Guam. This taxon was described as *Buphthalmum uniflorum* by Willdenow (1803), based on a Forster collection from Norfolk Island, and was later transferred to *Wedelia* by Oliver and Hiern in Oliver (1917). Other collections from the Mariannas were described by Gaudichaud (1829) as *Verbesina canescens* and *V. argentea*. One of Gaudichaud's taxa was transferred to *Wollastonia* (as *W. canescens*) by Candolle (1836), and both were transferred to *Wedelia* by Merrill (1914). *Wedelia uniflora* (or one of its many illegitimate synonyms) has been treated as a synonym of *W. biflora* by most authors, but one of Gaudichaud's names (*V. canescens*) was taken up as a variety of *Wedelia biflora* by Fosberg (1955). As no combination in *Wollastonia* is available for *B. uniflorum* at present, it is made below.

Koyama (1995a) described *Wedelia biflora* var. *ryukyuensis* H.Koyama from Japan (Kyushu and Ryukyu islands). It differed from *W. biflora* var. *biflora* in having larger capitula with more ray and disc florets, larger leaves, and longer petioles. He reported (Koyama 1995b) that this variety was a triploid ($2n = 45$) as opposed to the diploid ($2n = 30$) *W. biflora* var. *biflora*. This variety has also been recorded for Taiwan by Peng *et al.* (1998) and, in view of its triploid chromosome number and distinctive morphology, and despite the fact that Wagner and Robinson (2002) did not recognise infraspecific taxa in this taxon (which they called *Melanthera biflora*), does seem worthy of recognition, but under *Wollastonia*.

Koyama (1995b) also recognised within *Wedelia* sect. *Wollastonia* the species *Wedelia prostrata* Hemsl., with two varieties, *W. prostrata* var. *prostrata* and var. *robusta* Makino. This species was also recognised (and illustrated) for Taiwan by Peng *et al.* (1995). It resembles *Wollastonia biflora* in most respects, differing in having creeping stems that root at the nodes, smaller leaves with fewer teeth, and a slightly larger achene, strigose, with one or two (rarely to four) weak awns. *Wedelia prostrata* var. *robusta* has larger leaves that resemble those of *W. biflora*. Chen and Hind (2011) treated this species as *Melanthera prostrata*. *Wedelia prostrata* var. *robusta* is thought by some authors (Peng *et al.* 1998; Wagner & Robinson 2002; Ohashi & Ohashi 2010) to be a hybrid between *Wollastonia biflora* and *Melanthera prostrata*. If this is so, it provides additional reason (beyond morphology) to include *Melanthera prostrata* in *Wollastonia*, and this is done below, where *M. prostrata* is treated as *W. dentata* (H.Lév. & Vaniot) Orchard (*non Wollastonia prostrata* (Hook. & Arn.) Hook. & Arn.). It has achenes in which the tiny scales of the pappus are sometimes elongated into up to five 'awns' (Figure 15).

Chen and Hind (2011) recognised two species of *Wollastonia* from China, *W. biflora* and *W. montana* (Blume) DC. The second is based on *Verbesina montana* Blume (1826), described from the mountains of Java. Chen and Hind gave China (widespread), Bhutan, India, Burma, Nepal and Thailand as the distribution of this species, about which they stated 'Two taxa are represented among the material cited by Candolle under *Wollastonia montana* [i.e. among specimens sent to Candolle by Blume].

That representing Blume's concept of *Verbesina montana* certainly does not belong in *Melanthera*. I concur with this statement, but exclude it from *Wollastonia* as well. '*Wollastonia montana*' has large, mottled achenes 5 mm long with a pappus of a short sessile crown of fused scales, and paleae that are subglabrous, not thickened and green at the tip, and have lateral lobes or teeth. It is allocated to a new genus *Indocypraea* Orchard below.

Lipochaeta lifuana was described from New Caledonia by Hochreutiner (1910), who noted that it was very similar to *Wedelia* and to *Lipochaeta integrifolia*. It was transferred to *Wedelia* by Guillaumin (1937). Fosberg (1993) noted its similarity to *Wollastonia*, and moved it to that genus. Wagner and Robinson (2002) again transferred it, to *Melanthera*, when they subsumed all of *Wollastonia* in *Melanthera*. It is a plant of rocky shores, just above high water, in this respect resembling other species of *Wollastonia* discussed above. It also has dense, appressed hairs on stems, leaves and involucre bracts, as in *W. uniflora*, and the paleae are blunt (subacute) and somewhat hooded. The pappus is of thick white hairs, the scales present in other species of *Wollastonia* being absent. The achene is tiny, about 1.5 mm long, and closely resembles that of *W. integrifolia* from Hawai'i (Figure 16). It cannot, with those characteristics, be placed in *Melanthera* or *Wedelia*, but fits comfortably into *Wollastonia*.

Finally, the c. 16 species of *Lipochaeta* sect. *Aphanopappus* must be considered. It has been suggested on morphological, chromosome number and flavonoid chemistry grounds (Gardner 1976), and experimental hybridisation evidence (Rabakonandrianina, 1980; Rabakonandrianina & Carr 1981), that *L.* sect. *Aphanopappus* was originally established in Hawai'i from a *Wollastonia biflora*-like ancestor (and that *L.* sect. *Lipochaeta* probably had its origin in an ancient hybridisation event involving a *W. biflora* ancestor and an unknown wedelioid species). Old specimens of both *W. biflora* (*Macrae s.n.*, K) and *W. uniflora* (*Anderson s.n.*, GB – type of *L. ovata*) are known from Hawai'i, and it is not inconceivable that both species have at various times found their way to those islands, but not persisted. Wagner and Robinson (2002) transferred the species of *L.* sect. *Aphanopappus* to *Melanthera*, but a placement in *Wollastonia* seems more appropriate.

The species of *Lipochaeta* sect. *Aphanopappus* all have the distinctive *Wollastonia*-like paleae, membranous, stramineous and striate basally, green, abaxially scabrid, ±blunt and hooded at the tip, and have fertile pistillate ray florets, differing in all of these characters from *Melanthera s. str.* The achenes are usually truncate with a pappus of short hairs and/or scales, and 1–several 'awns'. The 'awns' are flattened and sparsely marginally ciliate, being obviously elongated scales rather than true terete awns as in *Melanthera*. There is no rostrum and no pappus of a short fimbriate cup as in *Wedelia s. str.* Most achenes are angled, and the angles are sometimes shortly and irregularly winged. The body of the achene is often rugose or verrucose. (Figures 17, 18). In all of these aspects, *L.* sect. *Aphanopappus* fits comfortably within *Wollastonia*. Given the presumed origin of *Lipochaeta* from a *W. biflora*-like ancestor, and the demonstrated (limited) interfertility between *Lipochaeta* and *W. biflora* demonstrated in crossing experiments by Rabakonandrianina (1980) and Rabakonandrianina and Carr (1981), it is appropriate to transfer at least *L.* sect. *Aphanopappus* to *Wollastonia*, as already suggested by Fosberg and Sachet (1980a, 1980b), among others. This is done below. As the same experimental crosses (and discovery of a natural sterile intersectional hybrid by Sherff (1933)) showed major fertility barriers between the sections of *Lipochaeta*, and congruent morphological (disc floret lobe number) and phytochemical (flavonoids) evidence (Gardner 1976) also showed differences between the sections, it is appropriate to maintain *L.* sect. *Lipochaeta* as a distinct genus.

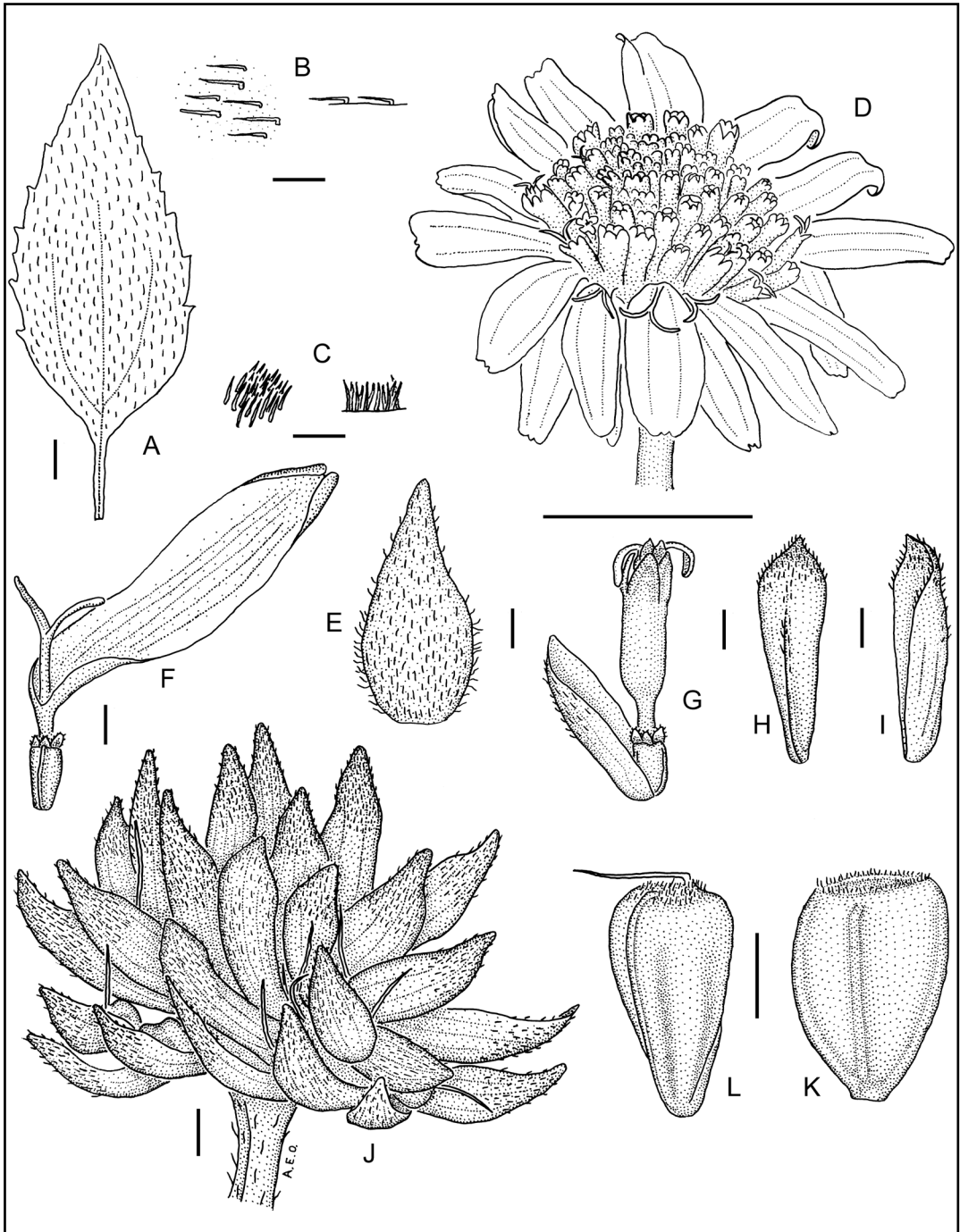


Figure 14. *Wollastonia uniflora*. A – leaf; B – hairs on upper leaf surface; C – hairs on lower leaf surface; D – capitulum in flower; E – involucre bract; F – ray floret; G – disc floret within palea; H – palea, dorsal view; I – palea, lateral view; J – capitulum in fruit; K – 3-angled ray achene; L – 4-angled disc achene. (All based on *G.N. Batianoff* 981060 & *J. Hacker* (CANB)). Scale bars: A, D = 1 cm; B, C, E–K = 1 mm. Del. A.E. Orchard.

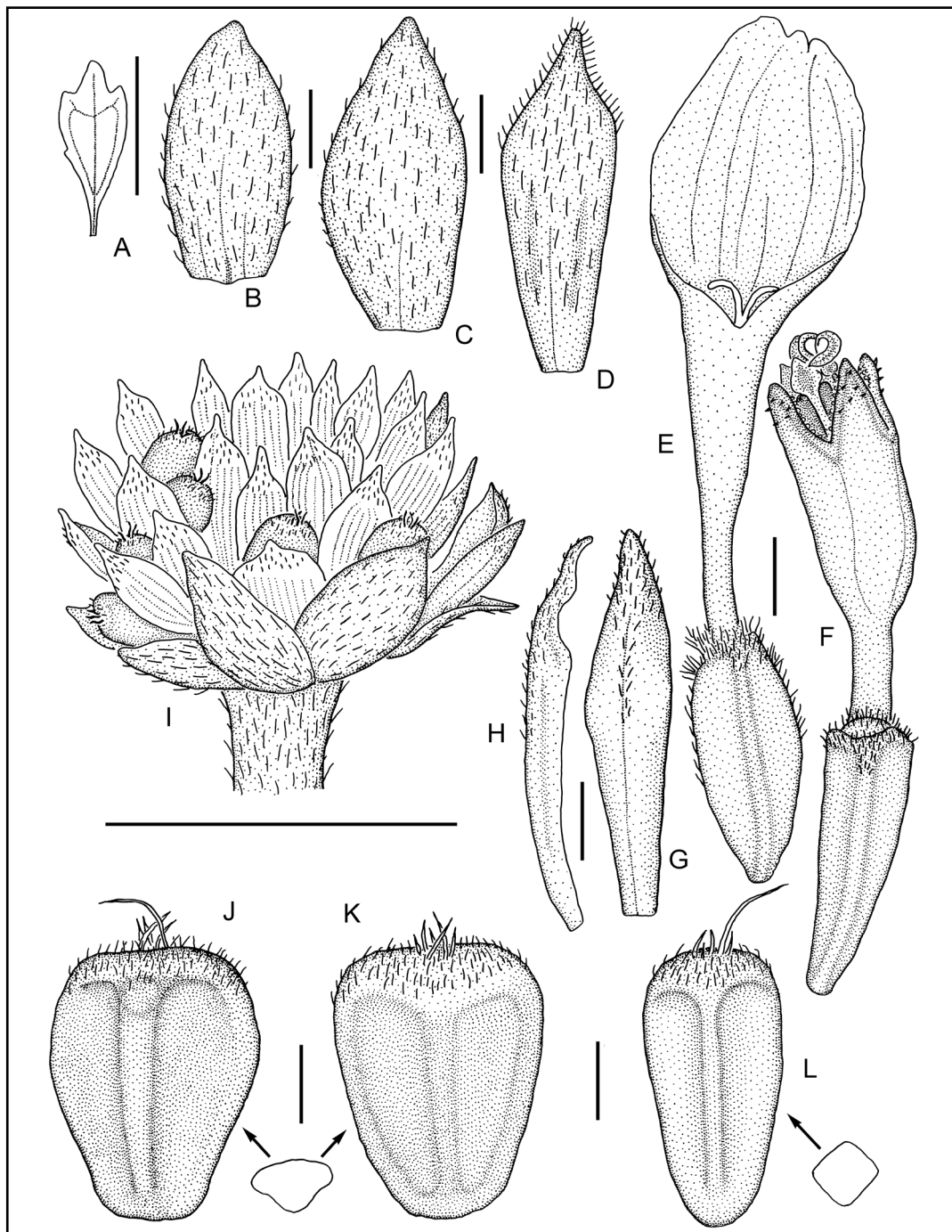


Figure 15. *Wollastonia dentata*. A – leaf; B – outer involucre bract; C – mid-involucre bract; D – inner involucre bract; E – ray floret; F – disc floret; G – palea, dorsal view; H – palea, lateral view; I – fruiting capitulum; J – ray achene, adaxial view; K – ray achene, abaxial view; L – disc achene. (A–H based on *J. & M.S. Clemens* 3077 (K); I–L based on *G. Murata* 19609 (G)). Scale bars: A, I = 1 cm; B–H, J–L = 1 mm. Del. A.E. Orchard.

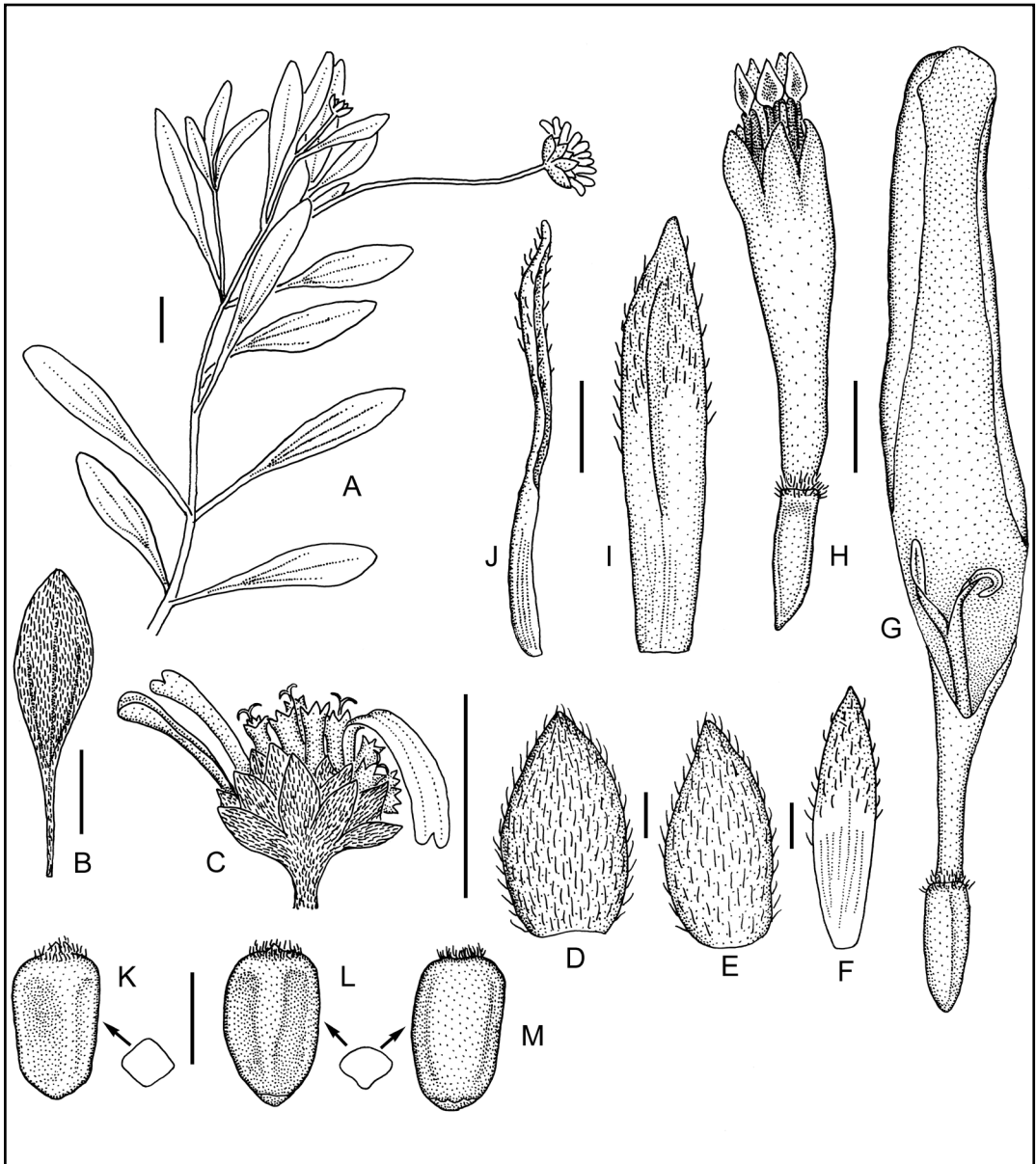


Figure 16. *Wollastonia lifuana*. A – habit; B – leaf; C – flowering capitulum (some ray florets removed); D – outer involucre bract; E – mid-involucre bract; F – innermost involucre bract, transitional to palea; G – ray floret; H – disc floret; I – palea, dorsal view; J – palea, lateral view; K – disc achene; L – ray achene, adaxial view; M – ray achene, abaxial view. (A–J based on P.S. Green RSNH1326 (K); K–M based on Deplanche (Veillard 799, type) (K)). Scale bars: A–C = 1 cm; D–M = 1 mm. Del. A.E. Orchard.

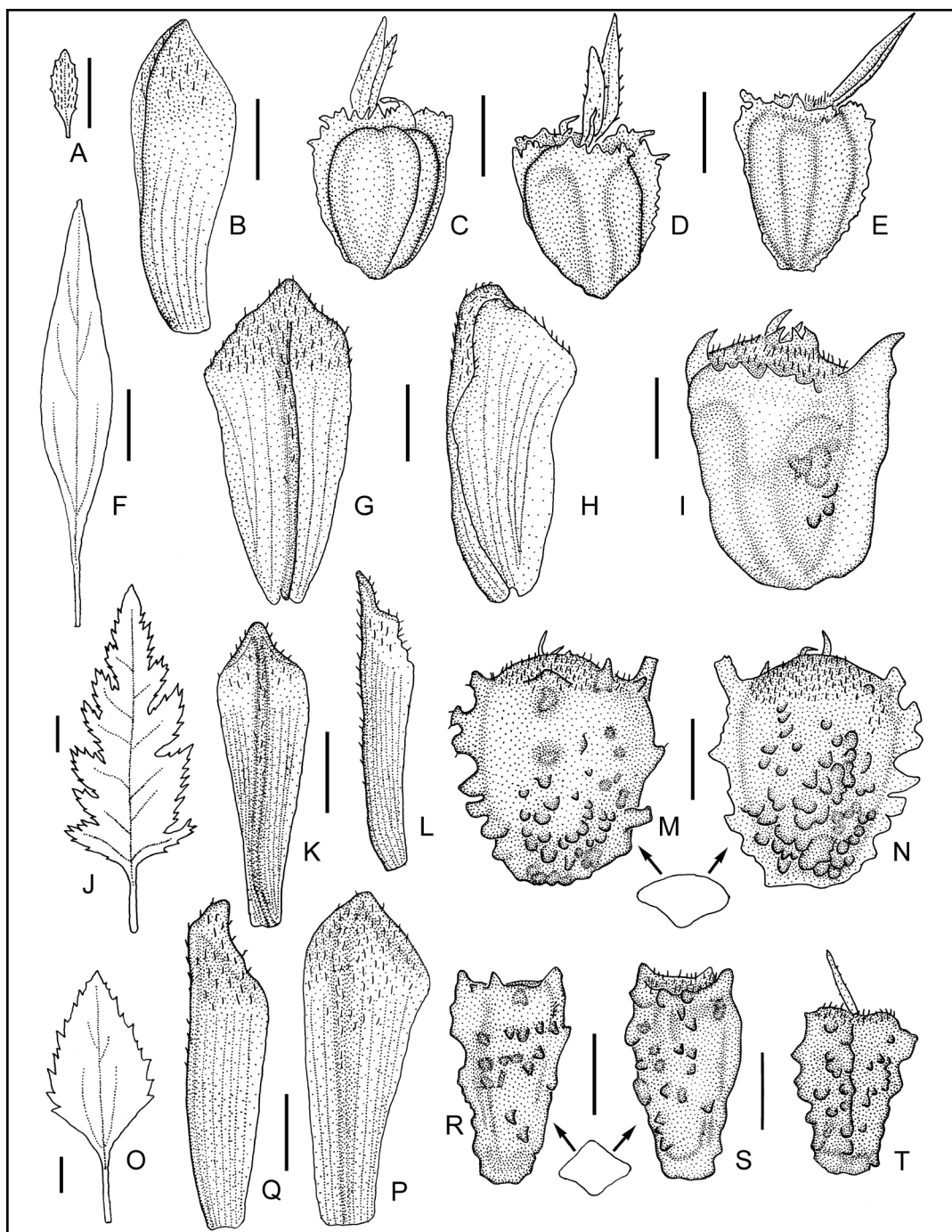


Figure 17. Hawai'ian *Wollastonia*. A–E. *Wollastonia integrifolia*. A – leaf; B – palea; C – ray achene, adaxial view; D – ray achene, abaxial view; E – disc achene. F–I. *Wollastonia lavarum*. F – leaf; G – palea, dorsal view; H – palea, ventral (adaxial) view; I – achene (pappus shed). J–N. *Wollastonia micrantha* subsp. *micrantha*. J – leaf; K – palea, dorsal view; L – palea, lateral view; M – ray achene, adaxial view (pappus mainly shed); N – ray achene, abaxial view. O–T. *Wollastonia remyi*. O – leaf; P – palea, dorsal view; Q – palea, lateral view; R – ray achene (pappus mainly shed); S, T disc achene (pappus shed). (A–E based on O. & I. Degener 33603 (CANB); F–I based on H. St. John 18821 *et al.* (CANB); J–N based on J.F. Rock *s.n.* (BISH 725607); O–S based on O. & I. Degener 24061 (BISH); T based on F.R. Fosberg 12859 (BISH)). Scale bars: A, F, J, O = 1 cm; B–E, G–I, K–N, P–T = 1 mm. Del. A.E. Orchard.

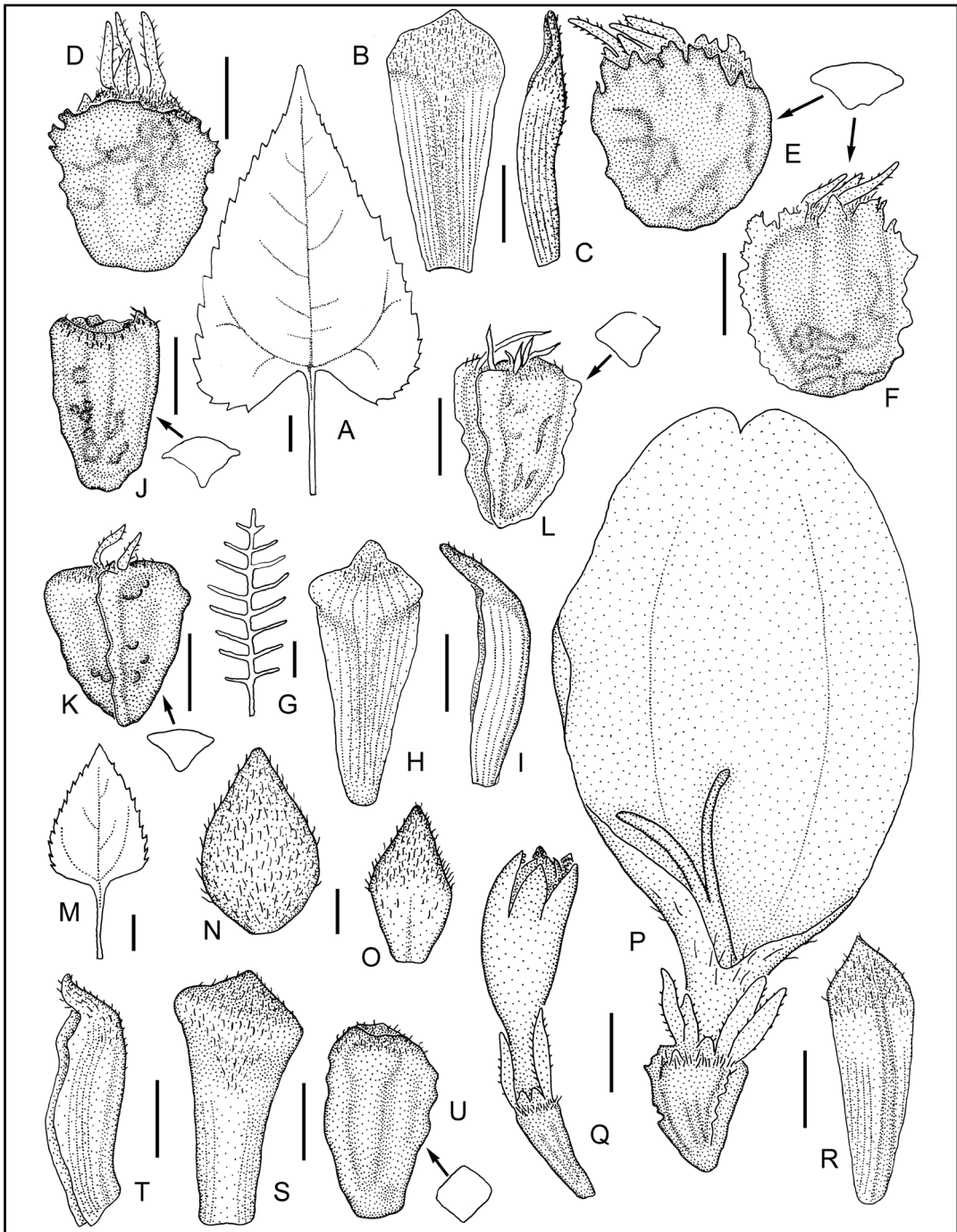


Figure 18. Hawaiian *Wollastonia*. A–F. *Wollastonia subcordata*. A – leaf; B – palea, dorsal view; C – palea, lateral view; D – achene, abaxial view; E – achene, abaxial view; F – achene, adaxial view. G–L. *Wollastonia tenuifolia*. G – leaf; H – palea, dorsal view; I – palea, lateral view; J–L achene. M–U. *Wollastonia venosa*. M – leaf; N – outer involucre bract; O – inner involucre bract; P – ray floret; Q – disc floret; R – floret palea, dorsal view; S – fruit palea, dorsal view; T – fruit palea, lateral view; U – achene. (A–F based on *H. Kennedy & S. Ishikawa* 3909 (BISH); G, J based on *W. Takeuchi et al.* Waianae 5 (BISH); H, I, K, L based on *J. Obata s.n.* (BISH); M, S–U based on *K. Nagata et al.* 2028 (BISH); N–R based on *S.J. Anderson* 505 (BISH)). Scale bars: A, G, M = 1 cm; B–F, H–L, N–U = 1 mm. Del. A.E. Orchard.

Generic circumscription of *Apowollastonia*

Mueller (1866) described *Wedelia spilanthoides* from ‘tropical Australia’. Bentham (1867) included this species plus five others in a broadly conceived *Wedelia* (including *Wollastonia*) from northern, central and eastern Australia. In this he was anticipating his concept of *Wedelia* published six years later in Bentham and Hooker (1873). This treatment of the Australian species was unfortunate, and has led to considerable confusion. Four of his six species were misplaced or based on misapplied names:

1: As already shown, *Wedelia biflora* should be placed in *Wollastonia*.

2: *Wedelia calendulacea sensu* Bentham was the name given to a Cunningham collection from the north-east coast of Australia. *Wedelia calendulacea* (L.) Less. is correctly now *Sphagneticola calendulacea* (L.) Pruski, and is an Asian/Malesian species. It does not occur in Australia, although it is known from Indonesia. Bentham’s plant has been located (E.C.T. [= East Coast Tropics], [*A. Cunningham s.n.*], ex herb. Hooker, printed label for *Flora Australiensis*, and mss *Wedelia calendulacea*, K) and is what is here called *Apowollastonia longipes*.

3: *Wedelia urticifolia sensu* Bentham was based on collections by Allan Cunningham and Robert Brown from Goulburn Island and the Gulf of Carpentaria respectively. These collections are *Blainvillea cunninghamii* (DC.) Orchard (the Cunningham collections being type specimens of that species). *Wedelia urticifolia* (Blume) DC. is a name applied rather loosely in the past, but strictly belongs to a species extending from Indonesia to south-east Asia, and here included in *Lipoblepharis*. It does not occur in Australia.

4: *Wedelia asperrima sensu* Bentham was also misapplied. The Mueller specimens he cited (both in K) are what is here called *Apowollastonia cylindrica* Orchard. *Wedelia asperrima* (DC. ex Decne.) Benth. in the sense of its type, is endemic to Indonesia, and is correctly *Lipoblepharis asperrima* (DC. ex Decne.) Orchard. It does not occur in Australia.

There are now seven Australian and one New Guinean species included in ‘*Wedelia*’ that cannot be placed in that genus. They lack the wedelioid paleae (hyaline, keeled, membranous, with a distinct terminal appendage and lateral lobes), having instead indurate, greenish, thickened, opaque paleae with entire margins, that are acute to blunt at the tip but never with an appendage, and are densely and shortly scabrous distally. They also differ in their pappus, which is never a fimbriate/lacinate cup seated on a rostrum, but instead consists of tiny scales and hairs \pm fused into a short, sessile crown, and sometimes with one or two short, persistent awns (pappus absent in *A. cylindrica* Orchard). Superficially they come closer to *Lipotriche*, but differ in their green, harsher paleae, and in their pappus. From *Melanthera* they differ in their pappus, and in their yellow, radiate capitula. Finally, they differ from all other taxa discussed in this paper in having yellow anther thecae. These eight species are therefore here described as a distinct genus, *Apowollastonia* Orchard, reflecting the fact that they come closest to *Wollastonia* in most characteristics, although differing in having paleae which are acute to almost acuminate instead of blunt, and yellow anther thecae. In addition to the above characters, *Apowollastonia* is characterised by yellow, radiate capitula in which the ray florets are pistillate and fertile, the disc florets have a 5-lobed corolla, are bisexual and fertile, and the achenes vary in length from 2–6 mm long, are variously cylindrical to cuneate or winged, shortly hairy only apically, or glabrous, and in habit are either small woody subshrubs or perennial herbs with a small, woody caudex and annual stems (*A. cylindrica* is an annual species). All are rather dry, harshly scabrous plants, adapted to dry habitats. (Figures 19–28)

Generic circumscription of *Acunniana*

Among Australian species often included in the *Wedelia* group is the anomalous plant described as *Wollastonia procumbens* DC. (Candolle 1836) but transferred to *Moonia* by Bentham (1866). It later became *Chrysogonum procumbens* (DC.) F.Muell. (Mueller 1882). It was excluded from both *Moonia* and *Chrysogonum* by Stuessy (1975, 1977). It has never been transferred to *Wedelia*, as the combination is pre-occupied by *Wedelia procumbens* (Baker) B.L.Turner from South America.

This species superficially resembles *Apowollastonia*, with the same habit, coarsely serrate leaves, and rather coarse indumentum. It differs in having black anther thecae, disc florets that are functionally staminate (never producing mature achenes), and ray floret achenes which are relatively massive, ovoid, 4.0–4.5 mm long, and sparsely hairy apically, with a pappus of a few small scales, semi-connate, seated on a short rostrum. The involucre also sets it apart from *Apowollastonia*. The outer involucre bracts are softly herbaceous and exceed the inner bracts and the disc florets in length. In *Apowollastonia* the involucre bracts are stiffer, subequal and are shorter than or equal to the disc florets in length. While the pappus somewhat resembles that in *Wedelia/Aspilia*, this is superficial only, and the paleae are of the *Wollastonia/Lipotriche* type. This taxon is here recognised as a distinct monotypic genus, *Acunniana* Orchard (Figure 29).

Generic circumscription of *Quadribractea*

In Malesia there is a plant that has also at times been included in *Moonia*, and is currently placed in *Wedelia*, as *W. moluccana* (Blume) Borl. It is a shrub 1–2 m tall, erect or scrambling, with large ovate leaves and radiate capitula with white corollas. The capitula have four decussate, broadly obovate to almost orbicular involucre bracts, each subtending a ray floret. Ray florets are four, pistillate and fertile with white corollas; disc florets are functionally staminate, with style branches fused, with corollas white, 5-lobed, and densely hairy at top of ovary/base of corolla; anther thecae black. The corolla of the disc florets is lost after anthesis, but the ovaries with a dense terminal tuft of hairs are persistent, forming a distinctive ‘tassel’ in the centre of the developing infructescence. The paleae are narrowly linear, flat, hyaline with a distinct midrib, sparsely hairy on margins and distally, lacking an abaxial crest and marginal lobes. Achenes are four, dull black, obovoid, ±compressed, 2-angled, rounded apically, glabrous, smooth, lacking elaiosomes; the pappus is a short rim of membranous callus tissue, slightly lobed, bearing three or four short pappus hairs. This genus with its single species seems to be somewhat isolated within the *Wedelia/Melanthera* complex. It differs from almost all other taxa in its white corollas, involucre bracts and ray florets consistently four, functionally staminate disc florets, the ovaries of which are persistent as pilose pseudopaleae, its narrow, flat, non-clasping paleae, and (among Australasian species) its relatively massive achenes, with a much reduced pappus. The large achenes are similar to those in *Acunniana procumbens* (DC.) Orchard and *Indocypraea montana* (Blume) Orchard, and the persistent functionally staminate disc florets have a parallel in *Acunniana* where the disc florets are also functionally staminate, although in the latter the florets are shed, leaving the paleae as a central tuft in the developing infructescence. This taxon is here recognised as a monotypic genus, *Quadribractea* (Figures 30, 13E).

Generic circumscription of *Indocypraea*

Verbesina montana was described from the mountains of Java by Blume (1826), and transferred to *Wollastonia* by Candolle (1836). Boerlage (1891) transferred it to *Wedelia*. It was later found to extend through Thailand and Burma as far west as India, and north to China. It is an erect or scandent perennial herb or subshrub 1–2(–6) m tall. It has large, ovate leaves with sparse to moderately dense, fine, soft hairs, and yellow, radiate capitula on moderately long peduncles. The involucre, in about two series, is soft, green and herbaceous, the outer bracts exceeding the inner ones and the disc florets. Ray florets are pale yellow, pistillate and fertile; disc florets are yellow, bisexual and fertile, with 5-lobed corolla, and brown to black anther thecae. The paleae are straw-coloured, strongly conduplicate, lanceolate (ovate if flattened out), with a shortly caudate tip, shortly lobed or toothed in the distal part, indurate to papery, with a distinct midrib and sometimes faint striae, shortly scabrous on midrib only, lacking an abaxial crest. Achenes are usually yellow to yellow-brown and mottled with red, sometimes greyish, strongly compressed, 2- or 3-angled, oblong to obovoid, rounded and shortly hairy at the apex, smooth, lacking elaiosomes; pappus a very short crown of semi-fused, shortly ciliate scales, of which two are frequently elongated into short, soft, awn-like or claw-like projections. Usually only about 6–8 achenes mature in each capitulum, randomly divided between ray and disc types.

This genus, here recognised as the monotypic *Indocypraea* Orchard, has frequently been confused with *Lipoblepharis* (*Wedelia*) *urticifolia*, but is distinct in a number of characteristics: in having long outer involucre bracts, straw-coloured paleae which are not striate or only obscurely so, and much larger oblong to obovoid achenes, frequently mottled red and yellow, with usually two short claw-like ‘awns’ (Figures 31, 13D).

Generic circumscription of *Lipoblepharis*

In Java and Sumatra, and in other parts of Malesia and south-east Asia, numerous names in *Wedelia* and *Verbesina* have been proposed for a suite of species with a perennial or annual herb lifeform, generally ovate to lanceolate leaves with soft or harsh, sparse or dense indumentum, yellow, radiate capitula, with an involucre of \pm equisized, green, herbaceous to greenish, indurate bracts in about two series, that do not exceed the disc florets. The ray florets are yellow, pistillate and fertile; disc florets with yellow, 5-lobed corollas and black anther thecae. The paleae are often coloured reddish or brown, linear-lanceolate to lanceolate, acute to subacuminate, entire or with very short lobes distally, subhyaline and striate, with a distinct midrib, membranous to papery, with a thickened tip, shortly scabrous on midrib and tip, lacking an abaxial crest. Achenes are grey to black, usually obcuneate, not noticeably compressed, 3- or 4-angled, truncate with a flat or sunken apex, hairy only apically, often rugose, and with no elaiosomes; pappus of short, \pm free, fimbriate scales and one or two often oblique awns, that are fragile but often persist. The achenes are small, usually only 3–4.5 mm long (excluding awns).

These species are here transferred to *Lipoblepharis* Orchard. Of the five species recognised in this paper, the best known name is *L. urticifolia*, which as *Wedelia urticifolia* has been misapplied to a wide range of taxa in Australia, Malesia and Asia. True *L. urticifolia* (Figures 32, 13F) is a widespread species, extending from Indonesia to India, China and Japan, and superficially resembles *Indocypraea montana*, but is distinguished by having involucre bracts of \pm equal size, striate, membranous paleae, and achenes which are grey to black, cuneate and truncate, and only 1–2 mm long. It does not occur in Australia, despite earlier misleading reports. The other species in the genus are similar, differing mainly in leaf shape and size, indumentum and achene size (Figures 33–35).

Key to the genera *Wedelia*, *Melanthera*, *Echinocephalum*, *Lipotriche*, *Acunniana*, *Quadribractea*, *Wollastonia*, *Indocypraea*, *Lipoblepharis*, *Apowollastonia* and *Lipochaeta*

1. Pappus a lacinate or fimbriate cup borne on a short rostrum;
achenes with basal elaiosomes **1. *Wedelia* (including *Aspilia*)**
- 1: Pappus absent, or reduced to a ring of very short hairs or a few scales,
sometimes with additional awns, or awns alone; achenes lacking basal elaiosomes
2. Capitula discoid; corollas white **2. *Melanthera***
- 2: Capitula radiate; corollas yellow or white
3. Corollas white; involucre bracts and ray florets always 4 per capitulum;
disc florets functionally staminate **8. *Quadribractea***
- 3: Corollas yellow; involucre bracts and ray florets variable in number but usually
more than 4; disc florets bisexual and fertile (functionally staminate in *Acunniana*)
4. Pappus of numerous (usually 10–20) caducous awns
5. Paleae ovate, with a long, terete-caudate tip and entire margins,
yellow-green becoming stramineous **3. *Echinocephalum***
- 5: Paleae linear, with a tip differentiated into an appendage,
but not terete-caudate, margins with lobes or teeth near apex,
often yellow **4. *Lipotriche***
- 4: Pappus of 1 or 2 fragile but not caducous awns, or awns absent
6. Disc corollas 4-lobed **11. *Lipochaeta***
- 6: Disc corollas 5-lobed
7. Disc florets functionally staminate; outer involucre bracts longer than inner
ones and exceeding disc florets **7. *Acunniana***
- 7: Disc florets bisexual, forming achenes; outer involucre bracts \pm equalling inner
bracts and disc florets (longer in *Indocypraea*)
8. Anther thecae yellow (rarely very light brown) **6. *Apowollastonia***
- 8: Anther thecae black
9. Achenes mottled yellow and red; pappus awns none or short
and soft, comprising elongated scales; outer involucre bracts
exceeding inner ones **9. *Indocypraea***
- 9: Achenes grey to black; pappus awns none or terete and stiff,
i.e. bristle-like; outer involucre bracts \pm equalling inner ones
10. Inner paleae blunt with tips inflexed and \pm hooded over achene;
pappus 'awns' elongated scales, flat, \pm soft, marginally ciliate
(occasionally bristle-like in *W. uniflora* & *W. biflora*) **5. *Wollastonia***
- 10: Inner paleae acute to acuminate and erect; pappus awns terete,
stiff, bristle-like **10. *Lipoblepharis***

Taxonomic treatments

1. *Wedelia* Jacq., *Enum. Syst. Pl.* 28 (1760), *nom. cons.*, & *Select. Stirp. Amer. Hist.* 1: 217, pl 130 (1763).

Type: W. fruticosa Jacq.

Aspilia Thouars, *Gen. Nov. Madagasc.* 12 (1806).

Type: A. thouarsii DC.

Seruneum Kuntze, *Rev. Gen. Pl.* 1: 364 (1891), *nom. illeg. superfl. (p.p.)*.

Based on the pre-Linnean *Seruneum aquatilis* Rumphius (1747), and used by Kuntze as a replacement name for *Wedelia*.

Erect or prostrate annual or perennial *herbs* or *shrubs* (0.1–)1–2.5 m tall. *Leaves* opposite, simple, variously lanceolate to ovate, sometimes 3-lobed, 1–15 cm long, to 8 cm wide, triplinerved, entire or serrate, obtuse to acute, petiolate (rarely sessile), variously hairy. *Capitula* radiate, on short to long peduncles, with 2 or 3 (or 4) series of bracts; *outer bracts* green at tip, chartaceous basally; *inner bracts* more chartaceous, abaxially scabrous, inner bracts often ciliate. *Ray florets* female and fertile or neuter; *corollas* white, yellow, orange, purple, red or pink. *Disc florets* bisexual and fertile; *corollas* yellow to orange, 5-lobed; *anther thecae* black. *Paleae* linear to lanceolate, conduplicate, membranous, hyaline, often tinted purplish red, with a well-developed crest or wing abaxially, no striae, with tip differentiated into a short, coloured appendage and margins shortly lobed distally, almost glabrous (sparse tiny hairs on appendage). *Achenes* usually brown, often 4–5 mm long, compressed, 2-angled, oblong to ovoid, usually rounded apically, hairs throughout, with usually prominent yellow swelling(s) at base (elaiosomes); *pappus* a lobed laciniate and/or fimbriate cup seated on a rostrum, usually lacking awns (up to 3 if present, derived by extensions of the pappus cup). $n = 11, 12, 13, ?23$ (Strother 1991).

A genus of perhaps 100 species, extending from the southern part of continental North America through the Caribbean and Central America to South America (*c.* 75 spp.), and in Africa/Madagascar (*c.* 25 spp.). Some authors (e.g. Adams 1963; Wild 1966; Beentje & Hind 2005) prefer to keep *Aspilia* distinct from *Wedelia*. Consideration of this is beyond the scope of this paper. For convenience they are treated here under *Wedelia* (except where only combinations in *Aspilia* are available). Records of *Wedelia* from the Indo-Pacific region (including Asia and Australasia) are erroneous; these taxa are treated below as *Wollastonia*, *Apowollastonia*, *Lipoblepharis*, *Indocypraea*, *Quadribractea* and *Acunniana*.

For keys and descriptions of continental North American species see Strother (1991), for keys and descriptions of African taxa (as *Aspilia*) see Wild (1966), for keys and diagnoses of tropical west African species (as *Aspilia*) see Adams (1963), and for tropical east African species (as *Aspilia*) see Beentje and Hind (2005). Only a selection of taxa, required to discuss illustrations etc., are cited below, and synonymy is restricted to homotypic names and heterotypic names of which type specimens have (in general) been examined.

Wedelia acapulcensis var. **hispid**a (Kunth) Strother, *Syst. Bot. Monogr.* 33: 62 (1991); *Wedelia hispid*a Kunth, in F.W.H.A. von Humboldt, A.J.A. Bonpland & C.S. Kunth, *Nov. Gen. Sp.* 4: 169, pl. 371 (1818); *Zexmenia hispid*a (Kunth) A.Gray, *Proc. Amer. Acad. Arts* 19: 10 (1883); *Seruneum hispidum* (Kunth) Kuntze, *Revis. Gen. Pl.* 1: 365 (1891). *Type citation*: ‘Crescit in convalli Tenochtitlensi, alt. 1200 hex. [Mexico]’ (*holo*: H. Mexici, *s. dat.*, M.A. Bonpland 4017, P 710018 photo!).

Lipochaeta texana Torrey & A.Gray, *Fl. N. Amer.* 2: 357 (1842); *Zexmenia texana* (Torrey & A.Gray) A.Gray, *Smithsonian Contrib. Knowl.* 3(5): 112 (1852); *Wirtgenia texana* (Torrey & A.Gray) Sch.Bip., in B. Seemann, *Bot. Voy. Herald* 304 (1856). *Type citation*: ‘Texas [USA], Riddell s.n.’ (*holo*: GH n.v.).

Illustrations. J.C. Parks, *Fl. N. America N. Mexico* 21: 124 (2006); Figure 3A–K herein.

Specimen examined. UNITED STATES OF AMERICA: along Yeager Creek Rd (Blanco Co. Rd. 202), Texas, 13 Aug. 2005, M.A. Vincent 12605 (CANB).

Conservation status. Unknown.

Note. The name ‘*Wedelia texana*’ has been applied to this species, and appears on some herbarium sheets, but this combination has never been validly made (Strother 2006).

Wedelia cylindrocephala H.Rob., *Phytologia* 56: 266 (1984). *Type citation*: ‘Brazil, Minas Gerais, Serra do Cabral, immediately E. of Joaquim Felício...6 March 1970, H.S. Irwin, S.F. da Fonsêca, R. Souza, R. Reis dos Santos, J. Ramos 27007’ (*holo*: UB n.v.; *iso*: C 10001531, K 487645, RB 389002, US 385797, all photo!).

Illustration. Figure 5L–Q herein.

Specimen examined. BRAZIL: Minas Gerais, Serra do Cabral, 14 Apr. 1996, G. Hatschbach, A. Schinini & J.M. Silva 64713 (CANB).

Conservation status. Unknown.

Wedelia fructicosa Jacq., *Enum. Syst. Pl.* 28 (1760) & *Select. Stirp. Amer. Hist.* 1: 217, pl. 130 (1763), as *Wedelia frutescens*. *Type citation*: ‘In Insulis Caribaesis vicinaque Americae continente’ (*holo*: n.v.).

Illustrations. N.J. Jacquin, *Select. Stirp. Amer. Hist.* 1: pl. 130 (1763), as *Wedelia frutescens*; USDA, *The PLANTS database*, <http://plants.usda.gov/> (accessed 16 August 2012); Figure 1 herein.

Specimens examined. PUERTORICO: Humacao, 29 Sep. 1886, I. Urban 5196 (K). VIRGIN ISLANDS: St. Croix, 24 July 1949, I. Véléz 3038 (K). ANTIGUA: Boggy Peak, Shekerley Mountains, 2 Apr. 1956, A.C. Smith 10400 (K). MONTSERRAT: Center Hills, Duck Pond, 9 Nov. 2005, M.A. Hamilton et al. 169 (K). DOMINICA: Mome Bruee, 1903, F.E. Lloyd 737 (K). MARTINIQUE: Vallée de St. Pierre, 1870, L. Hahn 166 (K); Martinique, *s. dat.*, J. Gay 201 (K). ST. LUCIA: St. Lucia, June 1879, H.B. Murray s.n. (K). BARBADOS: Barbados, Feb. 1896, Waby 66 (K). GRENADA: Lowther Wood, St. Georges, 25 June 1906, W.E. Broadway 3741 (K). TRINIDAD & TOBAGO: Tobago Cays, Petit Batteau, 17 Mar. 1956, A.C. Smith 20151 (K). LESSER ANTILLES: Ins. Saba, 1906, I. Boldingh 2315 (K); Aruba, St. Eustatius, 3 July 1953, A.L. Stoffers 3515 (K).

Conservation status. Probably not threatened in most countries.

Taxonomic note. The species *W. calycina* Rich. is sometimes segregated from this taxon, sometimes included within it.

Wedelia latifolia DC., *Prodr.* 5: 542 (1836). *Type citation:* ‘In Amer. austr. Terrâ firmâ legit cl. Bertero’ (*holo?*: am. mer., Balb., 1822, *Bertero s.n.*, G!).

Illustration. Figure 6 herein.

Specimen examined. PERU: San Ignacio Province, Cajamarca, 6 Jan. 1997, *J. Campos & P. Diaz* 3267 (CANB).

Conservation status. Unknown.

Wedelia montevidensis (Spreng.) B.L.Turner, *Phytologia* 72: 393 (1992); *Verbesina montevidensis* Spreng., *Syst. Veg.* ed. 16, 3: 578 (1826); *Aspilia montevidensis* (Spreng.) Kuntze, *Revis. Gen. Pl.* 3(3): 129 (1898). *Type citation:* ‘Monte Video [Uruguay], Sello’ (*holo: n.v.*).

Illustration. Figure 4 herein.

Specimen examined. ARGENTINA: Misiones, Elev. Ruta 204, camino a Profundidad, 5–10 km S de Ruta 12, 8 Aug. 1993, *M.M. Arbo, M.S. Ferrucci, V. Solla Neffa & S. Blanco* 5977 (CANB).

Conservation status. Unknown.

Aspilia pluriseta Schweinf., in v. Hoenel, *Zum Rudolf-See und Stephanie-See* 862 (1892). *Type citation:* ‘Massaihochland, Ndoro [Kenya], v. Hoehnel 66’ (*holo:* B, destroyed). *Neotype, fide* H. Wild, *Kirkia* 5: 210 (1966): Ukamba, Kenya, *s. dat.*, *Hildebrandt* 2712 (*neo:* K *n.v.*; *isoneo:* BM, M, both *n.v.*). [The combination in *Wedelia* has never been made.]

Illustration. Figure 2I–Q herein.

Specimen examined. RWANDA: Kibungu, P.N.K. colline Tuntu, 31 Jan. 1958, *G. Troupin* 5872 (CANB).

Conservation status. ‘Least concern (LC)’, *fide* Beentje and Hind (2005).

Wedelia silphoides (Hook. & Arn.) B.L.Turner, *Phytologia* 72: 394 (1992); *Leighia silphoides* Hook. & Arn., *J. Bot.* 3: 314 (1841). *Type citation:* ‘Buenos Aires [Argentina]; Tweedie; Mr Gillies’ (*syn:* Buenos Ayres, May & June 1820, *Dr Gillies*, K 487714, herb. Hooker!).

Illustration. Figure 3L–U herein.

Specimen examined. ARGENTINA: Chaco, Isla del Cerrito, confluencia de los rios Paraguay y Parana, 18 Jan. 1993, *A. Schinini* 27532 (CANB).

Conservation status. Unknown.

Nomenclatural note. The combination in *Aspilia* was implied, but not actually made, in Bentham and Hooker (1873).

Wedelia subpetiolata (Baker) B.L. Turner, *Phytologia* 72: 395 (1992); *Aspilia subpetiolata* Baker, in C.F.P. von Martius, *Fl. Bras.* 6: 203 (1884). *Type citation:* ‘Habitat in Sierra Moeda: Sello!’ (*syn:* K? n.v., US 385762 (fragment) photo!).

Illustration. Figure 5A–K herein.

Specimen examined. BRAZIL: Rod. MG-259, 3–5 km L da divisa com Datas, Minas Gerais, 21 Nov. 1997, G. Hatschbach, M. Hatschbach & E. Barbosa 67372 (CANB).

Conservation status. Unknown.

Wedelia thouarsii (DC.) H. Rob., *Phytologia* 72: 145 (1992); *Aspilia thouarsii* DC., *Prodr.* 5: 561 (1836). *Type citation:* ‘in ins. Madagascar, versimiliter prope Foulpointe, [Petit Thouars]’ (*syn:* [Madagascar], Herbier du Petit-Thouars, P 442915 photo!; Madag., Herbier du Petit-Thouars, P 442914 photo!).

Illustration. Figure 2A–H herein.

Specimen examined. MADAGASCAR: Tamatava, s. dat., H.-J. Schleiben 8006 (K).

Conservation status. Unknown.

2. *Melanthera* Rohr, *Skrift. Nat. Selsk. Kobenh.* 2: 213 (1792).

Type: *M. aspera* (Jacq.) Spreng. (= *M. nivea* (L.) Small) [but see also Strother (1970) and Nicholson (1981)].

Amellus P. Browne, *Civ. Nat. Hist. Jamaica* 317 (1756), *nom. rej., non Amellus* L.

Type: *Santolina amellus* L. (= *Melanthera nivea* (L.) Small).

Melanthera Michx., *Flora Bor.-Amer.* 2: 106 (1803).

Type: *M. hastata* Michx., *nom. illeg. superfl.* [included *Bidens nivea* L.] (≡ *M. nivea* (L.) Small).

Erect or sprawling perennial *herbs* or *subshrubs* 0.2–2.2 m tall. *Leaves* opposite, simple, broadly ovate to lanceolate, sometimes lobed basally, (1.5–)8–12 cm long, (0.5–)1–8 cm wide, triplinerved, crenate to serrate, usually acute, petiolate, glabrescent to hispid. *Capitula* discoid, on elongate peduncles, with 2 subequal series of bracts; *outer bracts* green; *inner bracts* more chartaceous, abaxially minutely scabrous, somewhat grading into paleae. *Ray florets* absent. *Disc florets* bisexual and fertile; *corollas* white, 5-lobed; *anther thecae* black. *Paleae* oblanceolate, conduplicate, subhyaline to opaque, greenish to stramineous, lacking an abaxial crest, striate, with tip acute, not differentiated into an apical appendage and lateral lobes, abaxially minutely scabrous distally. *Achenes* brown to grey, usually 2–3 mm long, compressed, 3- or 4-angled, obcuneate, truncate or slightly sunken, shortly hairy only on apex, lacking elaiosomes; *pappus* of several to c. 20 delicate, barbed awns 1–2 mm long, which are caducous at the slightest touch and rarely retained until achene maturity. *n* = 15 (Parks 1973).

A genus of three to five species, extending from the southern United States of America, through Central America and the Caribbean, to higher elevations in northern South America. Radiate species from South America previously included in *Melanthera* are here included in *Echinocephalum*, and those from Africa (except *M. biflora*) in *Lipotriche*. *Melanthera biflora* is treated as *Wollastonia biflora*. Records of *Melanthera* from Asia, Malesia, Australasia and the Indo-Pacific are here included in *Wollastonia*, *Lipoblepharis*, *Indocypraea* and *Quadribractea*.

For descriptions and keys to *Melanthera s. str.* see Parks (1973). Note that many authors now recognise fewer species than Parks. In particular, the type *M. aspera* is now often included in a broadly defined *M. nivea* (see, for example, Parks 2006). Only a selection of taxa required to discuss illustrations etc, are cited below, and only an incomplete synonymy, restricted to homotypic names and type specimens seen. For a more complete synonymy see Parks (1973, 2006).

Melanthera angustifolia A.Rich., in R. de la Sagra, *Hist. Fis. Cuba* 11: 54 (1850). *Type citation*: ‘Crescit in Insula Pinorum (Isla de Pinos) [Cuba]’ (*lecto, fide* J.C. Parks, *Rhodora* 75: 198 (1973): In isla de Pinos (Cuba), Ramon de la Sagra, P 2140219, ex herb. Richard, photo!).

Illustrations. J.C. Parks, *Rhodora* 75: 197, Figure 6 (1973); Figure 7P–X herein.

Specimens examined. MEXICO: Estapilla, 27 June 1939, *E. Matuda* 3502 (K). CUBA: Isle of Pines, road to Santa Isabel, 12 Apr. 1954, *E.P. Killip* 43939 (K). HAITI: Montagnes du Trou d’Eau, 27 Oct. 1924 (K). DOMINICAN REPUBLIC: Santo Domingo, Llano Costero, 12 Aug. 1929, *E.L. Eckman* H13323 (K). GUATEMALA: La Libertad and vicinity, Aug.–Nov. 1933, *H. Mercedes Aguilar* 4 (K).

Conservation status. Unknown, probably not threatened in most countries.

Melanthera nivea (L.) Small, *Fl. S.E. U.S.* 1340 (1903); *Bidens nivea* L., *Sp. Pl.* 2: 833 (1753). *Type citation*: ‘Habitat in Carolina [based largely on J.J. Dillenius, *Hort. Eltham.* t. 47 (1732)]’ (*lecto, fide* J.C. Parks, *Rhodora* 75: 184 (1973): ‘*Bidens scabra flore niveo, folio trilobato*’ in J.J. Dillenius, *Hort. Eltham.* 1: 55, t. 47, f. 55 (1732)).

Calea aspera Jacq., *Collectanea* 2: 290 (1788); *Melanthera aspera* (Jacq.) Spreng., *Neue Entd.* 3: 40 (1822), as *Melanthera aspera*. *Type*: not cited [*Jacquin*] (*holo*: BM n.v., *fide* J.C. Parks, *op. cit.*).

Melanthera molliuscula O.E.Schulz, in I. Urban, *Symb. Antill.* 7: 127 (1911). *Type*: not cited (*lecto, fide* J.C. Parks, *Rhodora* 75: 192 (1973): Santo Domingo, *s. dat.*, *H. von Türckheim* 3199, NY n.v.; *isolecto*: BM 1009678 photo!, BR 5334513 photo!, K 373255!, M 29989 photo!).

Melanthera brevifolia O.E.Schulz, in I. Urban, *Symb. Antill.* 7: 123 (1911). *Type*: Seven collections cited, USA to Caribbean (*lecto, fide* J.C. Parks, *Rhodora* 75: 194 (1973): Elliot’s Key, Florida, *s. dat.*, *Curtiss* 1415, US n.v.; *isolecto*: BR 5334841 photo!). *Syn*: Mantanza [Cuba], 1848, *F. Rugel* 24 (K!); Key West, Florida, *s. dat.*, *J.L. Blodgett* (NY 126603 photo!); Mexico, *s. dat.*, *Wawra* 74 (F 15268 photo!).

Melanthera hastata var. [β] *cubensis* O.E.Schulz, in I. Urban, *Symb. Antill.* 7: 125 (1911). *Type*: Eight specimens cited from Cuba and Puerto Rico (*lecto, fide* J.C. Parks, *Rhodora* 75: 192 (1973): prope Habana, Cuba, *s. dat.*, *C. Wright* 3608, NY 126610 & 126611 photo!; *isolecto*: GH 10094 photo!, US 125265 photo!). *Isosyn*: Vento, Cuba, 11 Jan. 1905, *A.H. Curtiss* 597 (K 373251!, M 29988 photo!).

Melanthera crenata O.E.Schulz, in I. Urban, *Symb. Antill.* 7: 123 (1911). *Type*: Five specimens from Bahamas cited (*lecto, fide* J.C. Parks, *Rhodora* 75: 194 (1973): New Providence, Nassau, Bahamas, Jan. 1890, *J. & A. Northrop* 58, NY 126609 photo!; *isolecto*: K 373250!).

Elephantopus cuneifolius Fourn., *Bull. Soc. Bot. France* 30: 186 (1883). *Type citation*: ‘Vulgaris. Cordoba [Mexico], Aug. [Kerber]’ (*holo*: P 2140216 photo!; *iso*: Cordoba (Vera Cruz), Mexico, Aug. 1882, *E. Kerber* 44, GOET 1454 photo!, JE 4591 photo!, K 497378!, M 29495 photo!, P 2140217 & 2140218 photo!).

Amellus asper var. [β] *glabriusculus* Kuntze, *Rev. Gen. Pl.* 1: 306 (1891); *Melanthera aspera* var. *glabriuscula* (Kuntze) Parks, *Rhodora* 75: 194 (1973). *Type citation*: ‘Colon [Panama]’ (*lecto, fide* J.C. Parks, *Rhodora* 75: 194 (1973): Colon, Panama, *s. dat.*, *O. Kuntze*, NY *n.v.*; *isolecto*: Colon, 4 June 1874, *Herb. O. Kuntze* 1834, K 373247!).

Amellus asper var. [γ] *canescens* Kuntze, *Rev. Gen. Pl.* 1: 306 (1891). *Type citation*: ‘Portorico: Cayey; St. Thomas’ (*syn*: Portorico, 11 Mar. 1874, *Herb. O. Kuntze* 336, K 373249!).

Illustrations. N.J. Jacquin, *Icon. Pl. Rar.* t. 583 (1789), as *Calea aspera*; J.C. Parks, *Rhodora* 75: 185, Figure 2 (1973), as *M. nivea*; J.C. Parks, *op. cit.* 191, Figure 4, as *M. aspera* var. *aspera*; J.C. Parks, *op. cit.*, 195, Figure 5, as *M. aspera* var. *glabriuscula*; J.C. Parks, *Fl. N. America N. Mexico* 21: 124 (2006); Figures 7A–O, 13A herein.

Other specimens examined (selection). UNITED STATES OF AMERICA: Cape Florida, Florida, 14 Mar. 1892, *J.H. Simpson* 538 (K). HAITI: Bords de la Riviere froide, Port-au-princa, 30 Apr. 1827, *V. Jacquemont s.n.* (K, ex herb. Gay). DOMINICAN REPUBLIC: road between Jarabacoa and Parque Duarte, 5 July 2006, *T.B. Croat* 97687 (K); Boca de Cumayasa, 6 July 2006, *J. Pruski & R. Ortiz* 4100 (K). PUERTO RICO: Arecibo, Rio Arriba, 28 July 1994, *F. Axelrod & B. Axelrod* 8123 (K). VIRGIN ISLANDS: Tortola, 1919, *W.C. Fishlock s.n.* (K). JAMAICA: Ocho Rios, 24 Jan. 1850, *A. Prior s.n.* (K). PANAMA: Continental Divide 1 mile [c. 1.5 km] west of Las Cumbres, 28 Feb. 1976, *F.R. Fosberg* 56095 (K). GUATEMALA: c. 5 km SE of Villa Canales, 8 Nov. 2008, *J. Pruski & A.-L. MacVean* 4499 (K). NICARAGUA: Greytown, 1867–8, *R. Tate s.n.* (K). COSTA RICA: San Jose, Faja Costeña del Valle de Parrita, 26 Mar. 1995, *J.F. Morales* 3749 & *V. Ureña* (K); TOBAGO: Little Rockly Bay, 2 June 1975, *D. Philcox & A. Raynal* 7838 (K). BRAZIL: Amazonas, Rio Solimões, 24 July 1973, *G.T. Prance et al.* 16768 (K).

Conservation status. Not threatened in most countries.

Nomenclatural note. The authority for the combination *Melanthera aspera* is usually given as *M. aspera* (Jacq.) Small, *Bull. Torrey Bot. Club* 36: 164 (1909). However, Sprengel, *Neue Entd.* 3: 40 (1822) made the combination ‘M[elanthera]. aspera Rich.’, which is an indirect reference to Michaux, *Fl. Bor.-Amer.* 2: 107 (1803), the text of which was at the time credited to L.C.M. Richard, and where *Calea aspera* Jacq. is cited (see *Taxonomic Literature* 2nd edn, Vol. 3: 459 (1981) for discussion). The name should therefore be cited as *Melanthera aspera* (Jacq.) Spreng.

3. *Echinocephalum* Gardner, *London J. Bot.* 7: 294 (1848).

Type: E. latifolium Gardner.

Sprawling *subshrub* (0.3–)0.8–1.5(–3.0) m tall. *Leaves* opposite, simple, ovate, 10–11 cm long, 8–9.5 cm wide (becoming linear-lanceolate above), triplinerved, serrate, acuminate, petiolate, sparsely pilose on both surfaces. *Capitula* radiate, on peduncles to 10 cm long, with 2 series of bracts; all *bracts* green, herbaceous (inner bracts sometimes straw-coloured). *Ray florets* neuter; corollas yellow to orange; *disc florets* bisexual and fertile; *corollas* 5-lobed, yellow to orange; *anther thecae* black. *Paleae* narrowly ovate and caudate in flower, conduplicate, membranous, subhyaline to opaque, yellow-green (becoming stramineous, ovate and terete-caudate in fruit, indurate to papery), with a distinct midrib and numerous striae, lacking an abaxial crest and marginal lobes, shortly scabrous distally. Outer paleae bend through 90° to cup developing achenes. *Achenes* dark grey, 2–3 mm long, slightly compressed, 4-angled, truncate, hairs only on apex, rugose, lacking elaiosomes; *pappus* of several to 20 short, erect, antrorsely barbed caducous awns, which are shed at the slightest touch, with no scales or pappus hairs.

A genus of one species, found in Paraguay, and central, eastern and southern Brazil, growing in open damp savannas.

Echinocephalum latifolium Gardner, *Lond. J. Bot.* 7: 294 (1848); *Melanthera latifolia* (Gardner) Cabrera, *Darwiniana* 16: 411 (1970). *Type citation*: ‘In cane fields near Crato, Province of Ceará [Brazil], Oct., 1838 ([Gardner] 1728); and in similar situations near Arrayas, Province of Goyaz, March, 1840 ([Gardner] 3848)’ (*syn: Gardner* 1728, BM? *n.v.*, GH 10095, NY 168294 & 168295, P 2140228–2140230, US 125269 (fragment), all photo!; *Gardner* 3848, BM? *n.v.*, NY 168296 & 168297, P 2140226 & 2140227, all photo!).

Echinocephalum lanceolatum Gardner, *Lond. J. Bot.* 7: 295 (1848). *Type citation*: ‘Near Aracaty, Province of Ceará [Brazil]. Aug. 1838 [Gardner 1729]’ (*holo: BM? n.v.; iso: US 125268* (fragment) photo!).

Echinocephalum angustifolium Gardner, *Lond. J. Bot.* 7: 295 (1848). *Type citation*: ‘Near Sapê, Province of Goyaz [Brazil]. Feb. 1840 [Gardner 3848 (bis)]’ (*holo: BM? n.v., iso: P 2140214 & 2140225, US 125263, all photo!*).

Illustration. Figure 8 herein.

Specimens examined. BRAZIL: Mato Grosso, Barra do Garças, Fazenda Brasil, 26 Mar. 1997, *G.F. Árbocz* 3634 *et al.* (K); Piauí, São João do Piauí, 2 Mar. 1994, *M.S. Bona Nascimento* 416 (K); Ceará, est. Aiuaba, Antonina do Norte, 7 June 1984, *J.E.R. Collares & L. Dutra* 191 (K); Rio Paraguai, Ladário, 15 Aug. 1981, *C. de Almeida* 1043 (K); Est. Paraná, Rio Paraná, Guaira, 17 Nov. 1966, *J.C. Lindeman & J.H. de Haas* 3289 (K). PARAGUAY: Acahay Massif, 20 Jan. 1992, *E. Zardini & P. Aquino* 29887 (K); Sargento Jose E. Lopez, 11 May 2000, *E.M. Zardini & M. Vera* 54448 (K).

Conservation status. Probably not threatened in most countries.

4. *Lipotriche* R.Br., *Obs. Compositae* 118 (1817).

Type: *L. brownii* DC., as ‘*brownei*’.

Psathurochaeta DC., *Prodr.* 5: 609 (1836).

Type: *P. dregei* DC.

Wuerschmittia Sch.Bip., in C.F. Hochstetter, *Flora* 24: *Intell.* 2: 27 (1841), *nom. inval.*, *nom. nud.*;
Wuerschmittia Sch.Bip. ex Walp., *Repert.* 6: 161 (1846).

Type: *W. abyssinica* Sch.Bip. ex Walp.

Trigonothea Sch.Bip., *Flora* 27: 672 (1844), *nom. inval. pro syn.*

[*Melanthera auct. non* Rohr: G. Bentham & J.D. Hooker, *Gen. Pl.* 2(1): 377 (1873), *p.p. Afric.*;
D. Oliver & W.P. Hiern, in D. Oliver, *Fl. Trop. Afr.* 3: 381–383 (1877); C.D. Adams, in F.N. Hepper
(ed.), *Fl. W Trop. Afr.* 2nd edn, 2: 240–241 (1963); H. Wild, *Kirkia* 5: 1–17 (1965); W.L. Wagner &
H. Robinson, *Brittonia* 53: 539–561 (2002), *p.p. Afric.*; H. Beentje & D.J.N. Hind, *Fl. Trop. E. Afr.*,
Compositae (Part 3) 737–744 (2005); *et auct. al. mult. Afric.*].

Annual or perennial *herbs*, sometimes scandent or climbing. *Leaves* opposite, simple, oblong, lanceolate or ovate, sometimes lobed basally, 1.5–14 cm long, (0.6–)1–6(–7.5) cm wide, triplinerved, entire or serrate, obtuse to acuminate, sessile or petiolate, usually scabrid. *Capitula* radiate, on peduncles 3–5(–10) cm long, with 2 or 3 series of bracts; *outer bracts* green, pilose throughout; *inner bracts* becoming chartaceous, scabrous apically. *Ray florets* pistillate or neuter; corollas yellow. *Disc florets* bisexual and fertile; *corollas* yellow, 5-lobed; *anther thecae* black. *Paleae* linear to oblanceolate, conduplicate, membranous, subhyaline to opaque, sometimes coloured yellow towards tip, lacking an abaxial crest, with or without a well-defined midrib, usually multiple striae present; tip entire or with very small lateral lobes. *Achenes* yellow-brown, purplish brown or grey, 2–3 mm long, slightly compressed or not, sometimes 2- or 3-angled, or cylindrical, often obtuse and truncate (sometimes sunken apically), otherwise ovoid, very shortly hairy apically only, lacking elaiosomes; *pappus* of several or up to 20 delicate, antrorsely barbed awns 1–2 mm long, that are caducous at the slightest touch and rarely retained until achene maturity.

A genus of about 14 species found throughout Africa, including Zanzibar, but not Madagascar, mostly in tropical areas. Until now usually treated as part of a broadly defined *Melanthera*.

Only a selection of taxa required to discuss illustrations etc., are cited below, and only an incomplete synonymy is given, restricted to homotypic names and type material seen. For a more complete synonymy, keys, and descriptions see Adams (1963), Wild (1965) and Beentje and Hind (2005), all as *Melanthera*.

Nomenclatural note. Bentham and Hooker (1873) reduced *Lipotriche* R.Br., *Trigonothea* Sch.Bip., *Psathurochaeta* DC., *Wuerschmittia* Sch.Bip. ex Walp., and *Echinocephalum* Gardn. to synonymy under *Melanthera* Rohr. However, they did not make, but only implied, the corresponding species combinations, contrary to citations in later (and some current) literature. The earliest valid combinations in *Melanthera* for the types of *Lipotriche* and *Wuerschmittia* seem to be in Oliver (1877). The corresponding

combination for *Psathurochaeta dregei* in *Melanthera* has apparently never been made (it is usually now considered a subspecies of the widespread *Lipotriche (Melanthera) scandens*; see Wild (1965)).

Lipotriche abyssinica (Sch.Bip. ex Walp.) Orchard, *comb. nov.*

Wuerschmittia abyssinica Sch.Bip., in C.F. Hochstetter, *Flora* 24: *Intell.* 2: 27 (1841), *nom. inval.*, *nom. nud.*; *Wuerschmittia abyssinica* Sch.Bip. ex Walp., *Repert.* 6: 162 (1846); *Melanthera abyssinica* (Sch.Bip. ex Walp.) Oliver & Hiern, *Fl. Trop. Africa* 3: 382 (1877). *Type citation*: ‘In declivibus australibus regionis mediae montis Abyssinia Scholoda [Ethiopia], [Schimper]’ (*syn.*: Adoense, in declivibus australibus regionis mediae montis Scholoda, Abyssinia [Ethiopia], 3 Oct. 1837, *Schimper* 334, BR 8876812 & 8362797 photo!; *idem* GOET 1821 photo!; *idem* STU 306 photo!; *idem* HBG 504884 photo!; *idem* K 410453, ex herb. Hooker!; *idem* K 410454, ex herb. Bentham!; *idem* TUB 5508 photo!).

Illustration. Figure 10A–N herein.

Specimens examined. SUDAN: Ercowie, Red Sea hills, 1 Mar. 1932, *G. Aylmer* 180 (K). KENYA: Kenya-Ethiopia Boundary Commission, 30 Nov. 1952, *J.B. Gillett* 14486a (K).

Conservation status. ‘Least concern (LC)’, *vide* Beentje and Hind (2005).

Lipotriche gambica (Hutch. & Dalziel) Orchard, *comb. nov.*

Melanthera gambica Hutch. & Dalziel, *Fl. W. Trop. Afr.* 2: 146 (1931). *Type citation*: ‘Gambia, Hayes 586’ (*holo.*: Gambia, 1928, *T.R. Hayes* 586, K 410457!).

Illustration. Figure 11L–P herein.

Specimens examined. GAMBIA, Kuntaur, 1948, *J.P. Ruxton* 50 (K). SENEGAL: Niokolo, Oct. 1958, *J.G. Adam* 15546 (K).

Conservation status. Unknown.

Lipotriche pungens (Oliver & Hiern) Orchard, *comb. nov.*

Melanthera pungens Oliver & Hiern, in D. Oliver, *Fl. Trop. Afr.* 3: 382 (1877). *Type citation*: ‘Nile Land. Djur-land, *Schweinfurth!*’ (*syn.*: im Lande der Djur, bei Seriba Ghattas, [Sudan], 28 June 1867, *G. Schweinfurth* 1990, BM 924413 photo!; K 410451 & 410452!; *idem* M 105203 photo!; *idem* P 73056 & 73057 photo!).

Illustration. Figure 11Q, R herein.

Specimens examined. SUDAN: bank of River Iasu, 24 May 1939, *F.W. Andrews* A1447 (K); Lado, Yei River, 10 Nov. 1919, *F. Sillitoe* 195 (K).

Conservation status. ‘Least concern (LC)’, *vide* Beentje and Hind (2005).

Lipotriche scandens (Schum. & Thonn.) Orchard, *comb. nov.*

Buphthalmum scandens Schum. & Thonn., *Beskr. Guin. Pl.* 392 (1827); *Melanthera scandens* (Schum. & Thonn.) Roberty, in *Bull. I.F.A.N.* 16: 68 (1968). *Type citation*: not cited ('Almindelig, blomstret i den fructbare Aarstid [Guinea?]) (*syn.*: *Buphthalmum scandens* Th. *Collectan: Guin., s. dat., Dr Th.* 52, C 10003432 photo!; *Buphthalmum, e Guinea, s. dat., Dom Thonning s.n., C 10003431 photo!*).

Illustration. H. Beentje & D.J.N. Hind, *Fl. Trop. E. Africa Compositae (Part 3)* p. 739, Figure 155 (2005), as *Melanthera scandens*.

Lipotriche scandens (Schum. & Thonn.) Orchard subsp. **scandens**

Lipotriche brownii DC., *Prodr.* 5: 544 (1836), as '*L. brownii*'; *Melanthera brownii* (DC.) Sch. Bip., *Flora* 27: 673 (1844), *nom. inval., pro syn.*; *Trigonotheca natalensis* Sch. Bip., *Flora* 27: 672 (1844), *nom. inval., pro syn.*; *Melanthera brownii* (DC.) Oliver & Hiern, *Fl. Trop. Afr.* 382 (1877), as '*M. brownii*'. *Type citation*: 'In Africâ aequin. ad ripas fluminis Congo legit infeliciss. Chr. Smith' (*holo*: G-DC?, *n.v.*; *iso*: Congo, *s. dat., Chr. Smith s.n., K 410455, ex herb. Hooker, ex herb. Brown!*; *idem* P 73153, *ex herb. K, ex herb. Brown photo!*).

Illustration. Figure 9A–E herein.

Specimens examined. DEMOCRATIC REPUBLIC OF THE CONGO: Seke Banza, route Kinzso Vuente, 7 Sep. 1959, *P. Compère* 239 (K); Matadi, 1932, *Dacremont* 279 (K).

Conservation status. Unknown, probably not threatened in most countries.

Lipotriche scandens subsp. **subsimplicifolia** (Wild) Orchard, *comb. nov.*

Melanthera scandens subsp. *subsimplicifolia* Wild, *Kirkia* 5: 6 (1965). *Type citation*: 'Cameroons, Likomba, Dec. 1928, Milbraed 10752 (K)' (*holo*: K, *n.v.*).

Illustrations. H. Beentje & D.J.N. Hind, *Fl. Trop. E. Africa Compositae (Part 3)*: p. 739, Figure 155 (2005), as *Melanthera scandens*; Figure 11A–K herein.

Specimen examined. DEMOCRATIC REPUBLIC OF THE CONGO: Yangambi, 2 Sep. 1958, *A. Leonard* 1455 (K); BOTSWANA: Okavango, 8.4 m. [c. 14 km] E of Kuringkuru, *B. de Winter* 3953 (CANB).

Conservation status. 'Least concern (LC)', *fide* Beentje and Hind (2005).

Lipotriche scandens subsp. **dregei** (DC.) Orchard, *comb. nov.*

Psathurochaeta dregei DC., *Prodr.* 5: 609 (1836); *Melanthera scandens* subsp. *dregei* (DC.) Wild, *Kirkia* 5: 8 (1965). *Type citation*: 'in Africâ australi ad Omsamcoubo [Natal], ferè ad maris altitudinem, detexit cl. Drege' (*holo*: G-DC? *n.v.*; *iso*: zum gebift bei Omsamwubo, 14 Dec. 1832, [*Drege*], P 73162 photo!).

Psathurochaeta dregei var. [α] *latifolia* DC., *Prodr.* 5: 609 (1836). *Type*: not cited [*Drege*] (*holo*: G-DC?, *n.v.*; *iso*: *Psathurochaeta dregei* α *latifolia* Candolle, *s. dat.*, [*Drege*] 5121, P 73161 photo!; *Psathurochaeta Dregei* α *latifolia* DC., *Drege* (donated 1844), P 73163, ex herb. Cosson, ex herb. Sch.Bip. photo!).

Psathurochaeta dregei var. [β] *reticulata* DC., *Prodr.* 5: 610 (1836). *Type*: not cited [*Drege*] (*holo*: G-DC? *n.v.*; *iso*: *Psathurochaeta Dregei* β *reticulata* DC., *s. dat.*, *J. Drege*, HAL 111906 photo!; *Psathurochaeta Dregei* β *reticulata* DC., *s. dat.*, [*Drege*], HBG 504883 photo!; *Psathurochaeta Dregei* β *reticulata*, Cape, *s. dat.*, *Drege s.n.*, K 410428, ex herb. Hooker!; *Psathurochaeta Dregei* β *reticulata*, Afr. austr., 1837, *Drege s.n.*, K 410426, ex herb. Bentham!; *Psathurochaeta Dregei* β *reticulata* DC., Cap de Bon Espérance, *s. dat.*, *Drege s.n.*, P 73165 photo!; *Psathurochaeta Dregei* β *reticulata* DC., zwischen Omtendo und Omsamculo, 200', 25 Feb. 1832, [*Drege*], P 73164 photo!; *Psammatrochaeta [sic] Dregei* B. *reticulata*, [*Drege*], *s. dat.*, P 73166 ex herb. Sch.Bip. photo!; *Psathurochaeta Dregei* β *reticulata* DC., *s. dat.*, [*Drege*], S 07-16911 photo!).

Illustration. Figure 9F–O herein.

Specimens examined. SOUTH AFRICA: Port Natal, 1840, *Krauss s.n.* (K 410430 & 410432); Transvaal, pre-1884, *C. Mudd s.n.* (K 410429); Kentani district, Jan. 1909, *A. Pegler* 420 (K); Pondoland, pr. Manundu's Kraal, Dec. 1885, *H. Tyson* 2819 (K); Inanda, Natal, June 1879, *J.M. Wood* 348 (K); Transvaal, Crocodile River, Dec., *Zeyher* 1042 (K).

Conservation status. Unknown, but probably not threatened.

Lipotriche triternata* (Klatt) Orchard, *comb. nov.

Wedelia triternata Klatt, *Bull. Herb. Boiss.* 4: 839 (1896). *Melanthera triternata* (Klatt) Wild, *Kirkia* 5: 9 (1965). *Type citation*: 'Sambesigebiet: Nhaondue, Menyhart [Mozambique], Juli 1891, No. 735' (*holo*: GH *n.v.*).

Melanthera marlothiana O.Hoffm., *Bot. Jahrb.* 10: 277 (1889). *Type citation*: 'Namibia: Hereroland, Okahandja, in fruticetis, alt. 1200 m. (*Marloth* no. 1332), Majo 1886' (*holo*: B, destroyed).

Illustrations. Figure 10O–R herein.

Specimen examined. NAMIBIA: Kunene River, Otjombapa area, 20 July 1976, *Leistner, Oliver, Steenkamp & Vorster* 279 (K).

Conservation status. Unknown.

5. Wollastonia DC. ex Decne., *Nouv. Ann. Mus. Hist. Nat.* 3: 414 (1834).

Wedelia sect. *Wollastonia* (DC. ex Decne.) Benth. & Hook.f., *Gen. Pl.* 2: 371 (1873).

Type: not designated (*lecto, fide* F.R. Fosberg & M.-H. Sachet, *Smithsonian Contrib. Bot.* 45: 32 (1980): *Wollastonia scabriuscula* DC. ex Decne., *nom. illeg. superfl.* [= *Wollastonia biflora* (L.) DC. ex Decne.]).

Aphanopappus Endl., *Gen. Pl. Suppl.* 2: 43 (1842); *Schizophyllum* Nutt., *Trans. Amer. Philos. Soc.* (n.s.) 7: 452 (1841), *nom. illeg., non* E.M. Fries (1821); *Lipochaeta* sect. *Aphanopappus* (Endl.) Benth. & Hook.f., *Gen. Pl.* 2: 372 (1873).

Type: *Aphanopappus nuttallii* Walpers, *nom. illeg.* [based on *Schizophyllum micranthum* Nutt., = *Wollastonia micrantha* (Nutt.) Orchard].

Niebuhrria Neck., *Elem. Bot.* 1: 30 (1790), *nom. inval.* (p.p., as to *N. biflora*).

Seruneum Kuntze, *Rev. Gen. Pl.* 1: 364 (1891), *nom. illeg. superfl.* (p.p., as to *S. biflorum*, *S. insulare* & their synonyms).

Niebuhrria Britten, *J. Bot.* 39: 68 (1901), *nom. illeg., non* *Niebuhrria* Scop. (1777), *nec* *Niebuhrria* DC. (1824).

Perennial *herbs* or low *shrubs*, sometimes scandent or prostrate and rooting at nodes, rarely annual. *Leaves* opposite, usually petiolate; lamina lanceolate to ovate, rarely ternately compound, pinnatisect or pinnatifid, triplinerved, usually dentate. *Capitula* terminal, solitary or few, in open dichasial cymes, often on long peduncles, radiate. Involucres hemispherical to campanulate; involucral *bracts* in 2 series. *Receptacles* convex, paleate. *Paleae* oblong, membranous and strongly striate basally; tips thickened, green, blunt or almost so, inner ones inflexed and \pm hooded over the maturing achenes, abaxially densely scabrous. *Ray florets* pistillate and fertile; *corollas* yellow; lamina shortly 2- (3-) lobed. *Disc florets* bisexual; *corollas* yellow or greenish yellow, 5-lobed, without fibres embedding the vascular strands; *anther thecae* black (rarely dark brown); anther appendages yellow. *Ray achenes* cuneiform, 3-angled, with truncate shortly hairy apices, sometimes shortly winged on angles. *Disc achenes* similar, but 4-angled. Elaiosomes absent. *Pappus* usually \pm absent (represented sometimes by a ring of very short hairs or tiny scales), sometimes with 1–6 weak, fragile awns.

Nomenclatural note. For discussion of the generic names *Niebuhrria* Britten and *Seruneum* Kuntze, see 'History of generic circumscription', above.

A genus of about 20 species, extending from the east African coast across the Indian Ocean to the Indian subcontinent, Malesia, northern and eastern Australia, and north to China and Japan, and across the southern Pacific to Fiji. A group of 16 species are endemic to Hawai'i. One species, *W. biflora*, is a strand plant found almost throughout the range of the genus (absent from most of eastern Australia, and from Hawai'i).

Key to the species of *Wollastonia* (adapted and expanded from Wagner *et al.* 1999)

1. Leaves ternately compound; leaflets sessile, pinnatifid, appearing to be 6 leaves per node..... **W. tenuifolia**
- 1: Leaves simple, entire or lobed to pinnatifid, never appearing to be 6 per node
2. Rays 2.3–6 mm long
3. Leaves thick, fleshy, (0.4–)0.8–3.0 cm long; achenes nearly smooth..... **W. integrifolia**
- 3: Leaves thin, herbaceous, (1.2–)2.1–16 cm long; achenes usually tuberculate, sometimes smooth
4. Leaves linear to narrowly elliptic, 0.5–0.8 cm wide, margins almost entire..... **W. waimeaensis**
- 4: Leaves deltate to ovate or lanceolate, (0.8–)1.5–10.0 cm wide; margins usually serrate to dissected, rarely entire
5. Leaves deeply dissected
6. Plants herbaceous annuals; petioles usually (0.6–)2.0–4.0 cm long **W. remyi**
- 6: Plants woody perennials; petioles 0.6–2.5(–3.0) cm long
7. Disc florets 5–9 per capitulum; stems decumbent; ray florets 4 or 5 per capitulum **W. micrantha**
- 7: Disc florets (11–)20–45 per capitulum; stems erect to arcuate-spreading; ray florets 4–8 per capitulum..... **W. venosa**
- 5: Leaves entire or shortly serrate..... **W. subcordata**
- 2: Rays 7–15 mm long
8. Leaves pinnately lobed to pinnatifid **W. kamolensis**
- 8: Leaves entire or serrate, sometimes with 2 basal lobes
9. Leaves thick, leathery; pappus of several elongate scales or absent; prostrate plant of seashores, stems rooting at nodes **W. dentata**
- 9: Leaves thin, herbaceous; pappus of (0–)1–several deciduous awns; erect or arcuate-spreading plants, not rooting at nodes, and (apart from *W. biflora*, *W. uniflora* and *W. lifuana*), not usually found on seashores
10. Ray florets 16–51 per capitulum; leaves densely grey-tomentose..... **W. lifuana**
- 10: Ray florets 4–12 (–15) per capitulum; leaves green
11. Leaves usually oblong, rarely oblong-lanceolate; ray florets 4 or 5 per capitulum; petioles 4–10 mm long **W. bryanii**
- 11: Leaves usually deltate to ovate or lanceolate, sometimes linear; ray florets (5–)6–12 (–15) per capitulum; petioles 4–35(–70) mm long
- 12: Leaf base rounded to truncate or cordate
13. Disc florets 1–20(–45) per capitulum; rays (3–)4–6(–7) mm long
14. Leaves deltoid, biserrate, occasionally with 2 basal lobes; achenes tuberculate, ray achenes narrowly winged, achenes never corky **W. populifolia**
- 14: Leaves ovate, margins entire to very shortly serrate; achenes all smooth, not winged, at least some with corky pericarp when fully mature..... **W. biflora**
- 13: Disc florets 30–80 per capitulum: rays 7–13 mm long

15. Leaves 7–13 cm long..... **W. fauriei**
- 15: Leaves 1.2–4.4 cm long
16. Stems decumbent; ray florets 8–12 per capitulum, 8.3–12 mm long;
 achenes without a fringe of scales on the distal outer rim;
 disc florets 50–60 per capitulum **W. tenuis**
- 16: Stems erect or arcuate-spreading; ray florets 5–8(–9) per head,
 3–9 mm long; achenes with a fringe of scales on the distal outer rim;
 disc florets *c.* 80 per capitulum **W. perdita**
- 12: Leaf base cuneate to attenuate
17. Achenes lacking wings **W. uniflora**
- 17: Achenes with narrow (0.2–0.5 mm wide) wings
18. Stems decumbent; achenes tuberculate, without a fringe
 of scales on the distal outer rim..... **W. tenuis**
- 18: Stems erect; achenes nearly smooth, with a fringe
 of scales on the distal outer rim..... **W. lavarum**

Australian species of *Wollastonia*

Key to the Australian species of *Wollastonia*

1. Abaxial surface of leaves subglabrous or moderately hairy with hairs appressed..... **1. W. biflora**
- 1: Abaxial surface of leaves densely hairy, with hairs erect (or semi-appressed) **2. W. uniflora**

1. *Wollastonia biflora* (L.) DC., *Prodr.* 5: 546 (1836).

Verbesina biflora L., *Sp. Pl.* 2nd edn, 2: 1272 (1763); *Acmella biflora* (L.) Spreng., *Syst. Veg.* 16th edn, 3: 591 (1826); *Wedelia biflora* (L.) DC. ex Wight, *Contr. Fl. India* 18 (1834); *Stemmodontia biflora* (L.) W. Wight, *Contr. U.S. Natl. Herb.* 9: 377 (1905); *Melanthera biflora* (L.) Wild, *Kirkia* 5: 4 (1965).
Type citation: ‘Habitat in India’ (*lecto, fide* H. Wild, *Kirkia* 5: 4 (1965): India, *s. dat.*, LINN 1021.4 photo!; *isolecto?*: *Verbesina biflora* Herb. Linn., ex Sir J.E. Smith, K, ex herb. Hooker!).

Buphthalmum australe Biehler, *Pl. Nov. Herb. Spreng.* 38 (1807), replacement name for *Buphthalmum helianthoides sensu* J.G.A. Forster, *Fl. Ins. Austr.* 57, no. 304 (1786), *non* C. Linnaeus, *Sp. Pl.* 2: 904 (1753). *Type citation* (by Forster): ‘Passim intra tropicos’ (*lecto*, chosen here: ‘*Buphthalmum helianthoides* Forst., *Fl. Ins. Austr.* p. 57’. Printed label – The Forster Herbarium. Presented by The Corporation of Liverpool, August, 1885, K!). *Excluded syn*: *Insula maris pacifici, s. dat.*, J.R. & G. Forster *s.n.*, BM!). See *Nomenclatural notes* below.

Verbesina scandens Roxb., *Hort. Bengal.* 62 (1814), *nom. inval.*, *nom. nud.*; *Verbesina scandens* Roxb., *Fl. Ind. ed. 1832* 3: 441 (1832). *Type citation*: ‘native of hedges, uncultivated places about Calcutta [Roxburgh]’ (*holo*: East India, *s. dat.*, *Dr Roxburgh s.n.*, K, ex herb. Bentham, ex herb. Forsyth!; *iso?*: E. Ind., *s. dat.*, [*W. Roxburgh*], LINN 1367.6 photo!).

Verbesina strigulosa Gaudich., *Voy. Uranie* 463 (1829); *Wollastonia strigulosa* (Gaudich.) DC. ex Decne., *Nouv. Ann. Mus. Hist. Nat.* 3: 414 (1834). *Type citation*: ‘in insulis Moluccis (Rawak, Waigiou, Pisang, Timor &c.) [Indonesia]’ (*syn*: Timor, *s. dat.*, *C. Gaudichaud s.n.*, P 3060202 photo!; Rawak, *s. dat.*, *C. Gaudichaud s.n.*, P 3060201 photo!).

Wollastonia scabriuscula DC. ex Decne., *Nouv. Ann. Mus. Hist. Nat.* 3: 414 (1834), *nom. illeg. superfl.*

Wollastonia insularis DC., *Prodr.* 5: 548 (1836). *Type citation*: ‘in sterilibus saxosis insularum ad oram borealem Australasiae ap. flor. legit cl. A. Cunningham’ (*holo*: *Wedelia* sp.? barren stony spots on the Islands of the North Coast of Australia, April 1818, *Mr A. Cunningham* [58], G-DC!; *iso*: barren stony spots on the islands of the North Coast, Australia, So. Goulburn Isld, 1st Voy., Apr. 1818, *A. Cunningham* [304], K!; Goulburn Island, 1st Voyage of Mermaid, *A. Cunningham* [304], BM!). See *Nomenclatural notes* below.

Wollastonia glabrata DC., *Prodr.* 5: 548 (1836); *Wedelia glabrata* (DC.) Boerl., *Handl. Fl. Ned. Ind.* 2: 242 (1891). *Type citation*: ‘In insula Timor leger. bot. Baudinianae exped. (v.s. comm. à Mus. reg. Par.)’ (*holo*: Timor, voy. de Baudin, P 270137 photo!; *iso*: *Verbesina biflora*?, Timor, Museum de Paris 1821, G-DC!; Timor, *m. du Caisne* 1834. nov. n. 1, G-DC!; Timor, *m. du Caisne* 1834. nov. n. 2, G-DC!).

Wollastonia zanzibarensis DC., *Prodr.* 5: 547 (1836). *Type citation*: ‘in ins. Zanzibar legit cl. Bojer’ (*holo*: G-DC? *n.v.*; *iso*: Hab. in insula Zanzibar ad marginem sylvarum, *s. dat.*, [*Bojer*], K, herb. Hooker!).

Spilanthes peregrina Blanco, *Fl. Filip.* 622 (1837). *Type citation*: ‘La vi en Bauang en un sitio llamado Gasang [Philippines], [*Blanco*]’ (*holo*: not preserved? – see TL-2). *Neotype*, *fide* E.D. Merrill, *Sp. Blancoan.* 380 (1918): Taytay, Palawan, May 1913, *Merrill Species Blancoanae* No. 528 (*neo*: PNH?; *isoneo*: BM!, K!, L 281741!).

Wollastonia serrulata Miq., *Fl. Ned. Ind.* 2: 74 (1864). *Type citation*: ‘Sumatra [Indonesia], (Korthals)’ (*holo*: Sumatra, *s. dat.*, *Korthals s.n.*, L 2839!; *iso*: Sumatra, *s. dat.*, [*Korthals s.n.*], U 1362 photo!).

Straggling perennial *herb*, or scandent *subshrub* (0.8–)1.0–3.0(–4.0) m tall; *stems* decumbent or scrambling over adjacent plants, not rooting at nodes, glabrous (sparsely hairy at nodes). *Leaves* ovate, petiolate, aromatic; lamina triplinerved, 6–11(–24) cm long, 3–6(–12) cm wide, often succulent, dark glossy green; base rounded to truncate; tip usually attenuate; both surfaces subglabrous or sparsely appressed pubescent, with hairs fine, 0.5 mm long, separated by at least their own length; margins entire or very finely or coarsely serrate; petiole 25–35(–70) mm long. *Capitula* 1–3, 1.5–3.0 cm diam., on peduncles 1.5–3.0 cm long. *Involucral bracts* in 2 series, lanceolate to ovate, 3.5–4.5 mm long, appressed hairy. *Paleae* oblanceolate to subspathulate, 5 mm long, 2 mm wide, conduplicate and clasping floret, membranous, striate and glabrous basally, ±hooded, green and abaxially scabrous apically, very shortly apiculate, persistent. *Ray florets* 8–12(–15); *corollas* yellow; ray 3-lobed, with several longitudinal veins, sparsely pilose abaxially. *Disc florets* c. 20–35(–70); *corolla* yellow, 5-lobed; lobes very shortly scabrous abaxially, densely and shortly bearded adaxially. *Anther thecae* black (or dark brown); *anther appendages* yellow. *Achenes* grey-black (white when immature), corky, obovoid, 3.5–4.5 mm long, 2.0–2.7 mm wide, 3-angled (ray), 4-angled (disc), apically truncate and shortly hairy; *pappus* of usually 1 erect, antrorsely barbed, deciduous awn c. 2 mm long.

A variable taxon. Two varieties have been recognised, distinguished as follows:

Key to the varieties of *Wollastonia biflora*

1. Capitula 1.5 cm diam.; ray florets 8–12; disc florets 20–35
(diploid, $2n = 30$)..... **1a. *W. biflora* var. *biflora***
- 1: Capitula 2.5–3.0 cm diam.; ray florets 14 or 15; disc florets 45–70
(triploid, $2n = 45$)..... **1b. *W. biflora* var. *ryukyuensis***

1a. *Wollastonia biflora* var. *biflora*

Illustrations. Y. Ling, Y.-L. Chen, C. Shih, F.-H. Chen, C.-C. Chang, Y.-Q. Tseng, C.-M. Hu & X.-L. Huang, *Fl. Repub. Pop. Sinicae* 75: 355, pl. 60 (1–6) (1979), as *Wedelia biflora*; A.C. Smith, *Fl. Vitiensis Nova* 5: 272, Figure 31 (1991), as *Wollastonia biflora*; H.J. Chowdhery, *Fl. India* 12: 423, Figure 121 (1995), as *Wedelia biflora*; G.D. Pike & G.J. Leach, *Handbk Vasc. Pl. Ashmore & Cartier Is.* p. 57 (1997), as *Melanthera biflora*; C.-I. Peng, K.-F. Chung & H.-L. Li, *Fl. Taiwan* 2nd edn 4: 188, photo 498 (1998), as *Wedelia biflora*; H. Beentje & D.J.N. Hind, *Fl. Trop. E. Africa Compositae (part 3)*, p. 743, Figure 156 (2005), as *Melanthera biflora*; Figures 12, 13B herein.

A diploid taxon, with *capitula* c. 1.5 cm diam., containing c. 8–12 *ray florets* and 20–35 *disc florets*. $n = 15$ (Rabakonandrianina & Carr 1981; see also under *Taxonomic notes* below). (Figures 12, 13B)

Selected Australian specimens examined. COCOS (KEELING) ISLAND: West Island, 29 Apr. 1983, A.S. George 16255 (CANB, PERTH); West Island, 2 May 1985, I.R. Telford 10000 & C. Howard (CANB, K, MEL); Home Island, 10 May 1985, I.R. Telford 10069 & C. Howard (CANB, K); West Island, 4 Mar. 1986, D.G. Williams 12 (CANB). CHRISTMAS ISLAND: The Ravine, S of Dolly Beach, 8 July 1984, B.A. Mitchell 137 (CANB, K). ASHMORE REEF: West Isle, W. tip, 23 May 1990, D. Pike s.n. (DNA, MEL). NORTHERN TERRITORY: Twin Eagle Pt, Cape Arnhem, 8 Mar. 1995, M.J.A. Barritt 1779 (DNA, MEL); Buroga Island, 29 Aug. 1996, I. Cowie 6741 (DNA, MEL); Bomby Islands, 3 May 1996, I. Cowie 6912 (DNA, MEL); Wunya Beach, Aurari Bay, 6 June 1988, A.A. Munir 6150 (AD, CANB, DNA); Yirrkala, 14 Aug. 1948, R.L. Specht 892 (AD, BRI, CANB, MEL, PERTH); Nhulunbuy, E. Woody Island, 11 Feb. 1988, G.M. Wightman 4136 (AD, BRI, CANB, MEL). QUEENSLAND: Saibai Island, 21 Oct. 1981, J.R. Clarkson 3879 (BRI, CANB); Lake Patricia, Weipa, 3 Mar. 1990, P.I. Forster 6474 & M.R. O'Reilly (BRI, QRS); Murray Island, 26 July 1970, M. Lawrie 14 (BRI); 13.5 km NNW of Weipa Mission, 6 Dec. 1974, R.L. Specht W81 & R.B. Salt (BRI); Saibai, 15 July 1975, G.C. Stocker 1335 (BRI, QRS); Macdonald River, 8 Mar. 2008, B.M. Waterhouse 7629 (BRI, CANB).

Selected extra-Australian specimens examined. KENYA: Watamu, 11 Sep. 2009, J.M. Kimeu et al. KEFRI 640 (K). TANZANIA: Kaole near Bagamoyo, 24 Feb. 1968, S.J. Harris 1400 (K). ZANZIBAR: Chuaka, 22 June 1961, H. Faulkner 2835 (K). MOZAMBIQUE: Mapuo, Ponta do Ouro, 18 Nov. 1944, F.A. Mendonça 2910 (K). SOUTH AFRICA: Natal, Kosi estuary, 8 May 1965, Vahrmeijer & Toelken 887 (K). ALDABRA: Cinq Cases dunes, 18 Jan. 1968, F.R. Fosberg 48902 (K). INDIA: Orissa, Jambu, Mahanadi Delta, 7 June 1949, H.F. Mooney 3405 (L). SRI LANKA: Blue Lagoon, 12 miles [19 km] N of Trincomalee, 22 Feb. 1969, A. Grierson 1032 (CANB). MALDIVE ISLANDS: Gan I., Addu Atoll, 3 July 1964, D.C. Sigeo 2 (K). THAILAND: Ban Ka Pong Ba Ruu, 20 Aug. 1988, C. Niyomdham & W. Ueachirakan 1893 (K). MALAYSIA: Johore, Pulau Pisang, 7 July 1956, H.M. Burkill & Kiah 654 (K, L). SINGAPORE: Ula Pandan Nature Reserve, 9 Dec. 1964, Hardial 122 (K, L). INDONESIA: N. Moluccas, Obi Island, Jikodolong, 22 Nov. 1974, E.F. de Vogel 4207 (CANB, K, L); SE Celebes, Konkiang Ria, Buton Island, 11 Nov. 1909, J. Elbert 2827(6859) (CANB, K, L); W. Papua, Masni-

coast, Gondopi-Aroei, 2 Mar. 1961, *C. Koster* BW11071 (CANB, K, L). SOLOMON ISLANDS: Luesaleba, Santa Cruz Is., 4 June 1980, *P. Bakolo* 75 (CANB). PAPUA NEW GUINEA: Markham River valley, 35 miles [56 km] W of Lae, 9 Feb. 1962, *T.G. Hartley* 9879 (CANB, K); Bolu Bolu, Goodenough Is., 1 Oct. 1953, *L.G. Brass* 24458 (CANB, K). CHINA: Hong Kong, Shatin, 26 Nov. 1968, *S.-Y. Hu* 6250 (K); Hainan, Naam Shan Leng, 17 July 1932, *S.K. Lau* 280 (K). JAPAN: Yaku Island, between Hinokuchi and Hirano, 10 Apr. 1984, *T. Yahara et al.* 9110 (K). Ryukyu Is., Uehara, Taketomi Cho, 17 July 2002, *K. Yasuda* 783 (K). VIETNAM: Tonkin, Haiphong, 25 Aug. 1889, *B. Balansa* 895 (K). MARSHALL ISLANDS: Ebon Is., 9 Sep. 1946, *H. St John & R.S. Cowan* 22113 (CANB). MARIANAS ISLANDS: Guam, Tumon Bay, 30 June 1965, *M. Evans* 221 (K). CAROLINE ISLANDS: Palau, Kayangel Atoll, 9 Apr. 1983, *F. Pollitt* 37 (L). PHILIPPINES: Red Beach, Tacloban, Leyte, 24 Feb. 1957, *G.M. Frohne* PNH35092 (CANB, K). NEW CALEDONIA: south side of Mt Dore, 17 Sep. 1947, *J.T. Buchholz* 1053 (K). KIRIBATI: Abaiang, May 1968, *F. Adair s.n.* (K). VANUATU: Santo, Big Bay (Malao), 27 Aug. 1971, *H.S. McKee* RSNH24120 (K). FIJI: Tavenui, near Mua, 8 Sep. 1958, *J.W. Parham* 11512 (K). TONGA: Tongatubu Island, July 1874, *Moseley* (Challenger Exped.) (K). SAMOA: Tau, Luma, 2 Aug. 1921, *D.W. Garber* 547 (K). COOK ISLANDS: Rarotonga, July 1899, *T.F. Cheeseman* 590 (K). AUSTRAL ISLANDS: Rurutu, Tea, 31 Aug. 1934, *F.R. Fosberg* 12017 (K). HAWAII: Byron's Bay, Owhyhae [=Hilo], *Macrae s.n.* (K, herb. Hooker).

Distribution and habitat. Recorded from the east coast of Africa across the Indian Ocean to the Indian subcontinent, Malesia, northern Australia, east Asia (China, Japan), and eastwards across the south Pacific, at least as far as the Austral Islands as far east as 'Rapa' (Rapa Iti) (Fosberg & Sacht 1980a). Two old collections are reputed to come from Hawai'i. In Australia, found in coastal regions and off-shore islands of the Northern Territory, to the western coast of Cape York Peninsula (Queensland) and Torres Strait (Dauan Island, Murray Island) (Figure 36, Map 1). It is also recorded from the Australian Indian Ocean Territories of Christmas Island, Cocos (Keeling) Island and Ashmore Reef. Typically a sprawling shrub with long, arcuate stems, on beaches just above high water mark, or scrambling over other shrubs, on a range of soils from sand to laterite, sometimes associated with mangroves. In Papua New Guinea and Indonesia, sometimes found in inland sites in disturbed forest to 1,400 m.

Phenology. Flowering and fruiting occurs year-round, particularly February–August.

Conservation status. Not threatened.

Local names. MOZAMBIQUE: 'Tolomba' (*F.A. Mendonça* 2910, K). SRI LANKA: 'Moodu-gam-palu' (Singhalese) (Dassanayake 1980). COCOS (KEELING) ISLANDS: 'Pokok dilam' (*H. St. John* 26409, K). ASHMORE & CARTIER ISLANDS: 'Rumput sagara', 'Lamtoro' or 'Rumput mambar' (Indonesian), 'Nau mambari' (Rotinese), and 'Beach sunflower' (English) (Pike & Leach 1997). TORRES STRAIT: 'Gauri' (Dauan Is., *M. Lawrie s.n.*, BRI); 'Wasao' (Murray Is., *M. Lawrie* 14, BRI); 'Ton-dronganama' (Mapoon, *J.F. Baileys s.n.*, BRI). INDONESIA: 'Geletang' & 'Lahunai' (Java, *Noorudin* NBF6261, K, L); 'Darunu' (Sangi & Talaud Is., *H.J. Lam* 3394, K); 'Nampong' (Krakatau Is., *J. van Borssum Waalkes* 1040, K). MALAYSIA: 'Sarunei, Serenah, Sunai Laut' (Malay Peninsula) (Ridley 1923); and Brunei, *Noorudin* NBF6261, K, L). PAPUA NEW GUINEA: 'Kukaru' (Garumaia & Kulumo languages, New Britain, *W.R. Barker & A. Vinas* LAE66522 & 66720, K, L); 'Ambiama' (Samu Kundi language, Abelam, PNG, *vide J. Wiakabu & A.M.C.*, LAE73550, K); 'Kavis' (Kurte language, Manus Island, *vide M.J.S. Sands et al.* 2641, K). 'Mopia' or 'Bopia' (Mohai Oru Konua dialect, Bougainville Is.), & 'Ngoboro' (New Georgia, *J.H.L. Waterhouse* 644-B, K); 'Hugpo' (Bougainville Is., *J.H.L. Waterhouse* 294-B, K); 'Viakono' (Koara Va Teop dialect, Bougainville Is., *J.H.L. Waterhouse* 682-B, K); 'La ka karo' (W. Nakanai, *A. Floyd* 3527, K). SOLOMON ISLANDS: 'Kokoi' (Kwara'ae language, *I.H. Gafui et al.* BSIP14821 (K)); 'Fitoitoi' (Kwara'ae language, *T.C. Whitmore* BSIP2169,

K); ‘Nonigla’ (Graciosa Bay, *D.E. Yan* BSIP19935). PHILIPPINES: ‘K‘Hagonoy’ (Merrill, *Sp. Blancoan*. 380 (1918)). MARSHALL ISLANDS: ‘Marijetch’ (Tabal Islet, *H. St. John* 21396, K). VANUATU: ‘Novolyamsong’ (Sie language, *P. Curry* 598, K); ‘Navenu’ (Lelepa language, *P. Curry* 47, K); ‘Kokofe’ (Aniwa language, *P. Curry* 1421, K). COOK ISLANDS (NUIE): ‘Matakula’ (Sykes 1970). SAMOA: ‘Ateate’ (Parham 1972) TONGA: ‘Ate’ (Yuncker 1959). FIJI: ‘Lawati’ (*A.C. Smith* 5, K). See also Fosberg and Sacht (1980b) for 91 different local names for this taxon in Micronesia.

Nomenclatural notes. *Wollastonia scabriuscula* DC. ex Decne. is illegitimate, as ‘*Verbesina biflora* Blume’ was included in the synonymy. Blume in fact attributed *V. biflora* to Linnaeus. The taxonomic (as well as nomenclatural) equivalence of *W. scabriuscula* and *W. biflora* is confirmed by specimens in G-DC under the former name, cited in Candolle (1836), all of which are *W. biflora* (Penang & Singapore, *Wallich s.n.*; Rangoon, *Wallich s.n.*; Timor ex *Decaisne* - an isotype of *W. glabrata*).

The holotype of *W. insularis* bears the number 58, and an annotation ‘Mr A. Cunningham, 1836’. Both of these annotations relate to a consignment list of material sent by Cunningham to Candolle in 1836, and do not constitute collection dates or numbers. The isotype of *W. insularis* in K is annotated (Heward label) ‘barren stony spots on the Islands of the North Coast, Australia, Apr. 1818, A. Cunningham s.n.’ It is also annotated in pencil by Cunningham ‘1st V. Disc.’ [First Voyage of Discovery, with P.P. King] and separately, in ink, possibly also by Cunningham, ‘So. Goulburn Isld, 304, 1st Voy.’ The BM isotype bears the number 304. This number is also a consignment list number, on specimens sent from Cunningham to Banks and Aiton in 1818. The discrepancy in numbers between the K/BM and G-DC specimens is therefore not significant, and all specimens are from the same collection. The numbering and disposition of Cunningham collections will be the subject of separate papers (see Orchard & Orchard (2013) for further discussion of Cunningham’s numbers).

Forster (1786) listed *Buphthalmum helianthoides* for the Pacific. This name has been cited at times as *B. helianthoides* Forst., which would be an illegitimate later homonym of *B. helianthoides* L. (now *Heliopsis helianthoides* (L.) Sweet, a North American species). However, Forster clearly ascribed the name to Murray, *Systema Vegetabilium*, and as such it is a misapplication, not a homonym. Biehler (reprinted in Sprengel 1807) later coined the name *Buphthalmum australe* for the plant in Forster’s sense. Fosberg (1993) apparently did not find the Forster specimen that was the basis of these two names, but suggested they were synonyms of a broadly defined *Wollastonia biflora* (including *W. uniflora*). In BM there is a specimen labelled (on the reverse) ‘Insula [blank] maris pacifici, J.R. & G. Forster.’ There is a second specimen in K from the Forster Herbarium, ‘Presented by The Corporation of Liverpool, August 1885’, annotated ‘Probable isotype of *Buphthalmum australe* Sprengel’ by P. Garnock-Jones in 1985. Unfortunately, while the BM specimen fits the current circumscription of *W. uniflora*, that in K is *W. biflora*. Neither the Forster description of the leaves, nor that of Biehler, (‘foliis ovatis’), is sufficient to decide whether Forster considered his concept of *B. helianthoides* was one or the other of these species. However, separately Forster recognised *B. uniflorum* from Norfolk Island, and Biehler described *B. australe* (based on *B. helianthoides sensu* Forster) as ‘corymbis...multifloris’. On this basis it seems most logical to equate Forster’s ‘*B. helianthoides*’ with *W. biflora*, and the K specimen is therefore chosen above as lectotype, that in BM being an excluded syntype.

Taxonomic notes. The presence of an awn on the achenes is intermittent. Sometimes it is lacking on ray achenes but present on disc achenes in the same capitulum. Sometimes some achenes have an awn, others in the same capitulum lack one. In all cases the awn is fragile and easily dislodged.

Some specimens from Micronesia and Polynesia approach *W. uniflora* in leaf indumentum, and it is likely that there is a degree of introgression between the two species in this region (see, for example:

Guam, *M. Evans* 221, K; Tonga, *Lawrence* 18, K [mixed with true *W. uniflora*]). Both are strand plants and their achenes seem capable of sea transport.

A specimen from the Chagos Archipelago (N. Indian Ocean) has unusually long slender involucre bracts that significantly exceed the paleae in length (Eclipse Point, 23 Mar, 1971, *A.M. Hutson* 11, K).

Vouchers for meiotic chromosome counts, $n = 15$, by B.L. Turner, 1963, have been seen. [Thailand, *R.M. King* 5555, 5556 & 5557, K].

Notes. The leaves are used to flavour food in earth ovens (Dauan Island, *M. Lawrie s.n.*, BRI), and the wood is used for spears (Mapoon, *J.F. Bailey s.n.*, BRI). An extract of the plant is used against earache in West Papua (*P. van Royen* 3110, L), and the plant is used as a condiment and salad in Sabah (*Noorudin* NBF6261, K, L). In New Britain the juice is mixed with water and used for fevers and sores (*A. Floyd* 3527, K). In Vanuatu the young leaves are eaten baked in an earth oven with fish (*P. Curry* 598, K; *S.F. Kajewski* 196, K) or cooked in a banana leaf on a fire (*P. Curry* 1421, K). In the Solomon Islands the young green fruits are eaten for stomach ache (*B. Sirute'e* BSIP18143, K). Fosberg and Sachet (1980b) describe use of this plant in Micronesia for a wide range of activities, including medicinal remedies, garlands, magic rituals, and as cattle feed and compost.

1b. *Wollastonia biflora* var. *ryukyuensis* (H.Koyama) Orchard, *comb. nov.*

Wedelia biflora var. *ryukyuensis* H.Koyama, *Acta Phytotax. Geobot.* 33: 245 (1982); *Melanthera biflora* var. *ryukyuensis* (H.Koyama) K. Ohashi & H. Ohashi, *J. Jap. Bot.* 85: 59 (2010). *Type citation:* ‘Japan, Ryukyu: Isl. Iriomote, *Koyama et al.* 177’ (*holo:* KYO *n.v.*; *iso:* TNS *n.v.*).

A triploid taxon, with *capitula* 2.5–3.0 cm diam., containing *c.* 14 or 15 *ray florets* and 45–70 *disc florets*.

Specimens examined. No specimens were examined for the present study.

Distribution and habitat. Confined to Kyushu and Ryukyu in Japan, and Taiwan. Reported to be from seashores.

Phenology. Flowers April–May.

Conservation status. Unknown.

Local name. Ō-kidachi-hamaguruma (Japan) (Koyama 1995).

Taxonomic notes. Koyama (1995) reported that this taxon had a triploid chromosome number, $2n = 45$, whereas var. *biflora* had a diploid number of $2n = 30$. Shimabuku (1997) recorded $2n = 30$, 50, and 75 for var. *biflora*. Despite this apparent disparity, var. *ryukyuensis* was recognised by Peng *et al.* (1998) and by Ohashi and Ohashi (2010), and is maintained here on their authority.

2. *Wollastonia uniflora* (Willd.) Orchard, *comb. nov.*

Bupthalmum uniflorum G.Forst., *Fl. Ins. Austr.* 91 (1786), *nom. nud.*; *Bupthalmum uniflorum* Willd., *Sp. Pl.* 3(3): 2235 (1803); *Bupthalmum uniflorum* Spreng., *Syst. Veg.* 16th edn, 3: 605 (1826), *isonym*;

Wedelia forsteriana Endl., *Prodr. Fl. Norfolk*. 51 (1833) *nom. illeg. superfl.*; *Wollastonia forsteriana* (Endl.) DC., *Prodr.* 5: 548 (1836), *nom. illeg. superfl.*; *Wedelia uniflora* (Willd.) W.R.B.Oliv., *Trans. Proc. New Zealand Inst.* 49: 155 (1917). *Type citation*: ‘Norfolk Island’ (*holo*: Habitat in insula Norfolk [sic], *s. dat.*, specimen 16422, Herb. B-Willd., ex herb. Sprengel, IDC microfiche!; *iso*: Norfolk Island, Oceani Pacifici, *s. dat.*, *J.A. & G. Forster s.n.*, BM 820296!; *possible iso*: *Buphthalmum uniflorum*, *s. loc.*, *s. dat.*, *Forst. s.n.*, P 698454, ex herb. Sprengel (no. 1673), ex herb. Schultz Bip., ex herb. Cosson, photo!).

Buphthalmum procumbens G.Forst., *Fl. Ins. Austr.* 91 (1786), *nom. inval.*, *nom. nud.* *Citation*: ‘Amicorum insulae’ (Based on: Habitat in Tongataboo, Printed label – The Forster Herbarium. Presented by the Corporation of Liverpool, August 1885, K!).

Verbesina canescens Gaudich., *Voy. Uranie* (part 11) 463 (1829); *Wollastonia canescens* (Gaudich.) DC., *Prodr.* 5: 547 (1836); *Stemmodontia canescens* (Gaudich.) W.Wight, *Contr. U.S. Natl. Herb.* 9: 377 (1905); *Wedelia canescens* (Gaudich.) Merr., *Philipp. J. Sci., C.* 9: 155 (1914); *Wedelia biflora* var. *canescens* (Gaudich.) Fosberg, *Phytologia* 5: 291 (1955). *Type citation*: ‘In insulis Mariannis’ (*holo*: Iles Mariannes, *s. dat.*, *C. Gaudichaud s.n.*, P 710001 photo!).

Verbesina argentea Gaudich., *Voy. Uranie* (part 11) 463 (1829); *Wedelia argentea* (Gaudich.) Merr., *Philipp. J. Sci., C.* 9: 155 (1914). *Type citation*: ‘In insulis Mariannis’ (*holo*: Iles Mariannes, *s. dat.*, *C. Gaudichaud s.n.*, P 123244 photo!).

Wedelia chamissonis Less., *Linnaea* 6: 161 (1831), *nom. illeg. superfl.* [*Verbesina canescens* Gaudich. in synonymy]. *Type citation*: ‘Ill. Chamisso in Guahan [?Guam]’ (*holo*: ?LE, *n.v.*).

Lipochaeta ovata R.C.Gardner, *Rhodora* 81: 321–3 (1979). *Type citation*: ‘Hawai‘i, Honolulu, 1852, *N.J. Anderson s.n.*’ [? actually south-eastern Polynesia, see Wagner & Robinson (2001: 551)] (*holo*: GB (photo OS) *n.v.*).

Illustrations. W.E. Safford, *Contr. U.S. Natl. Herb.* 9: inter 376 & 377, pl. LXV (1905); R.C. Gardner, *Rhodora* 81: 322, Figure 10 (1979) as *Lipochaeta ovata*; T.D. Stanley, *Fl. SE Queensland* 2: 562, Figure 78B (1986), as *Wedelia biflora*; P.S. Green, *Fl. Australia* 49: 284, Figure 65 & 389, Figure 89B (1994), as *Wollastonia biflora*; L. Murray, *Fl. New South Wales* 3: 276 (1992) as *Melanthera biflora*; Figures 13C, 14 herein.

Straggling perennial *herb*, or scandent *subshrub* 0.5–1.0(–3.0) m tall; *stems* decumbent, rooting at nodes, rarely erect, sparsely appressed pilose. *Leaves* ovate to lanceolate or elliptic, petiolate, not noted as aromatic; lamina triplinerved, 2–10(–12) cm long, 1.5–6.5 cm wide, grey-green to yellow green, often thickened (exposed sites); base usually rounded; tip acute to obtuse, sometimes attenuate; adaxial surface with sparse to moderately dense, appressed, coarse hairs; abaxial surface with dense, ±erect or semi-appressed, long, coarse hairs; margins usually serrate, rarely almost entire; petiole 2–3(–4) cm long. *Capitula* 1–3(–5) on peduncles 1–6(–12) cm long, 2.0–2.5 cm diam. *Involucral bracts* in 2 series, ovate, 5 mm long, densely appressed pilose. *Paleae* oblanceolate to oblong, 5 mm long, 2 mm wide, keeled, folded and clasping floret, stramineous, membranous, striate and glabrous basally, ±hooded, green, abaxially scabrous apically; tip blunt to subacute; persistent. *Ray florets* (12–)14–16; corollas yellow; ray shortly 2- or 3-lobed, with several longitudinal veins, sparsely pilose abaxially. *Disc florets* c. 50; corollas yellow, 5-lobed; lobes sparsely pilose on margins, densely pilose adaxially. *Anther thecae* light to dark brown; *anther appendages* yellow. *Achenes* dark grey to black, not corky,

obovoid, (2.2–)2.5–3.0 mm long, 1.5–2.0 mm wide, apically truncate, shortly and densely pilose apically, otherwise glabrous. *Pappus* 1 usually oblique (rarely erect) ±glabrous deciduous awn *c.* 2 mm long, or, often, awn absent. (Figures 13C, 14)

Selection of Australian specimens examined. QUEENSLAND: Wilson Island, 12 km N of Heron Island, 19 Oct. 1998, *G.N. Batianoff* 981060 & J. Hacker (CANB); North West Island National Park, 23 May 2000, *G.N. Batianoff* 205027 (BRI, CANB); 2.5 km N of mouth of McIvor River, 3 Feb. 1984, *J.R. Clarkson* 5218 (DNA, K, NSW, PERTH, QRS); mouth of Kolan River Conservation Park, about 3 km N of Moore Park, 7 Jan. 2001, *J. Hodgson* 481 (BRI). NEW SOUTH WALES: Bogangar, 15 km S of Tweed Heads, 28 Apr. 1976, *G.N. Batianoff* 20 (BRI); 2 miles [3.2 km] S of New Brighton, 1 Sep. 1972, *R. Coveny* 4390 (BRI); Yamba Beach, 23 Nov. 1987, *C.J. Dunn* 134 *et al.* (BRI, CANB, K, MEL); Norries Head, 2 Dec. 1977, *L. Haegi* 1519 (AD, BRI); Wallabi Point, Taree, 25 May 1958, *M. Wilkes s.n.* (NE 34549); Manly Beach near Sydney, *s. dat.*, *W. Woolls s.n.* (MEL 2166669); Paramatta, *s. dat.*, *W. Woolls s.n.* (MEL 2166667). LORD HOWE ISLAND: Lagoon Beach, 4 Mar. 2000, *G.N. Batianoff* 200336 (BRI); The Clear Place, 20 Oct. 1978, *M.D. Crisp* 4480 & *I.R. Telford* (CANB); North Beach, 21 Oct. 1978, *M.D. Crisp* 4491 & *I.R. Telford* (CANB); Middle Beach, 27 Oct. 1963, *R.D. Hoogland* 8653 (CANB); Middle Beach, 1 Feb. 1992, *Swarbrick* 10468 (BRI). NORFOLK ISLAND: Norfolk & Philip Islands, 14 & 15 June 1986, *B.D. Duncan* 86066n (MEL); Anson Bay, 16 Feb. 1989, *P. Gilmour* 7035 (CANB); Ball Bay Reserve, 30 Oct. 1967, *R.D. Hoogland* 11230 (CANB); Duncombe Bay, 1 Feb. 1975, *M. Lazarides* 8067 (CANB, K); Emily Bay, 31 Oct. 1978, *I.R. Telford* 7206 (CANB).

Selection of extra-Australian specimens examined. MARIANAS ISLANDS: Guam Experiment Stn, *J.B. Thompson* 351 (K). VANUATU: Erromango, 14 July 1930, *L.C. Cheeseman* 21 (K). TONGA: Tongatabu, south coast, Mar. 1880, *Graeffe* 1436 (K); Tongatapu, 4 June 1958, *E. Lawrence* 18 (K), *p.p.*; Tongatapu, Niutatoua Beach, 25 Apr. 1958, *E. Lawrence* 22 (K).

Distribution and habitat. In Australia *Wollastonia uniflora* extends from the islands of Torres Strait south along the east coast of Queensland to the north coast of New South Wales. Old collections are known from around Sydney (Figure 36, Map 2). It is also known from Norfolk and Lord Howe Islands in the Tasman Sea. The type specimens of Gaudichaud's names came from the Marianas Islands, and Fosberg and Sachet (1980a) recorded it (as *Wollastonia biflora* var. *canescens*) from the Marianas and Caroline Islands, with possible collections from Bonin Island and Rarotonga (Cook Islands). They later (Fosberg & Sachet 1980b) gave a more a detailed distribution for Micronesia. True *W. uniflora* is known from Tonga, Vanuatu and Guam, and scattered specimens intermediate between *W. biflora* and *W. uniflora* are known throughout Micronesia. The type specimen of *Lipochaeta ovata* is reputed to come from Hawai'i, but the species has not been found there recently. Frequent on coastal sand, coral rubble and dunes, often a sand-binder rooting at the nodes, with *Spinifex*, *Ipomoea* and *Triumfetta*, but also recorded in coastal heaths and on rocky headlands. It is particularly common on the shores of islands in Torres Strait and the Great Barrier Reef.

Phenology. Flowering and fruiting in most months.

Conservation status. Not threatened.

Local names. Mile-a-Minute (Norfolk Island; Green (1994)); masiksik (Pagan), akangkang tasi (Guam), masigsic (and minor variations, Guam); masigsic chunge (Guam) and ngesil (Palau), all cited in Fosberg and Sachet (1980b).

Nomenclatural notes. In validly publishing the name *Buphthalmum uniflorum*, Willdenow (1803) explicitly based it on Forster's *nomen nudum* of 1786, and cited no other material. The type must therefore be the Forster material from Norfolk Island cited above. Green (1994) erroneously listed the type of this name as a Bauer specimen, collected in 1804–1805, which is after publication of Willdenow's description.

In describing *Wedelia chamissonis* Less., to accommodate a Chamisso collection from Guahan [?Guam] Lessing included the name *Verbesina canescens* Gaudich. in synonymy, making his name superfluous. The Chamisso specimen has not been located during this study, but the holotype of *V. canescens* is filed under the Lessing name in P.

The name *Verbesina biflora* has been misapplied to this taxon by Safford (1905), the name *Wedelia biflora* has been misapplied to this taxon by several authors, among them Bentham (1866, *p.p.*) and Stanley (1986), the name *Wollastonia biflora* has been misapplied by Green (1994), and the name *Melanthera biflora* has been misapplied by Murray (1992). This is not an exhaustive list. Many other authors, referring to a broad *Wedelia biflora* (or its synonyms) have misapplied the name in part, particularly in the context of Australian taxa.

Oliver (1917) based his combination *Wedelia uniflora* on *Buphthalmum uniflorum* Spreng., *Syst. Veg.* 16th edn, 3: 605 (1826), overlooking (as have most other authors, except Hiepko (1969) and Green (1994)), the earlier valid combination *Buphthalmum uniflorum* Willd., *Sp. Pl.* 3(3): 2235 (1803). Both names were based on the invalid (*nom. nud.*) *Buphthalmum uniflorum* G.Forst., making *B. uniflorum* Spreng. an isonym of *B. uniflorum* Willd.

Gardner (1979) described *Lipochaeta ovata* from Hawai'i, based on an 1852 specimen collected by N.J. Anderson, allegedly from Honolulu. It was known only from the type, and was presumed extinct. Wagner *et al.* (1999) accepted this taxon as described, but Wagner and Robinson (2001) placed the name in the synonymy of *Melanthera biflora*, noting that the localities on many Anderson collections were in error, and that this specimen probably came from south-eastern Polynesia. From the description and Gardner's illustration it seems that the specimen, which has a densely strigose abaxial surface to the leaf, is *Wollastonia uniflora* not *W. biflora*. It is possible that the Anderson locality is correct. Occasional old collections of *W. biflora* (e.g. *Macrae s.n.*, K) are also reputed to come from Hawai'i, although that species does not occur there now.

Taxonomic notes. This is a very variable species, particularly in leaf size and shape. Many Australian specimens lack awns on the achenes. If awns are present, they are usually oblique to subappressed apically on the achene.

Notes. The earliest Australian collection seems to be one by Banks and Solander, 1770, without exact locality [East Coast] (MEL 2166672).

Although this species is not noted as a poison plant, in feeding trials 1 kg dry weight killed a sheep (*P. Oelrichs s.n.*, 24 June 1980, Indooroopilly, BRI 255218).

Wollastonia uniflora is sometimes used medicinally in Guam, where the roots and leaves are boiled and drunk for tuberculosis (Fosberg & Sachet 1980b, under the name *W. biflora* var. *canescens*).

Other species of *Wollastonia*

In the summary below only limited synonyms are cited, usually only those isotypic with the accepted name, or those taxonomic synonyms for which type material has been sighted for this study. For full descriptions of Hawai'ian taxa, see Gardner (1979) and Wagner *et al.* (1999). For full synonymy (including taxonomic synonyms) and typification of Hawai'ian taxa, see Wagner *et al.* (1999) and Wagner and Robinson (2001). For description of the New Caledonian/Vanuatu taxon (*W. lifuana*), see Hochreutiner (1910). For descriptions and synonymy of Asian species, see Peng *et al.* (1998), Koyama (1995b), and Chen and Hind (2011).

Hybrid: *Wollastonia* × *Lipochaeta*

× *Lipochaeta procumbens* O.Deg. & Sherff, *Bot. Gaz.* 95: 94 (1933). *Type citation*: 'Otto Degener, K.K. Park and *W. Hirai* (Degener distrib. no.) 4178, ... Kaena Point, Isl. Oahu, Hawai'ian Isls., Mar. 21, 1931' (*holo*: F *n.v.*; *iso*: K! & M *n.v.*).

A natural hybrid (sterile) between *Lipochaeta lobata* and *Wollastonia integrifolia*. See under 'History of generic circumscription – *Lipochaeta*', above, for discussion.

Wollastonia bryanii (Sherff) Orchard, *comb. nov.*

Lipochaeta bryanii Sherff, *Bot. Gaz.* 95: 97 (1933); *Melanthera bryanii* (Sherff) W.L. Wagner & H. Rob., *Brittonia* 53: 552 (2001). *Type citation*: 'Hawai'ian Islands, Kaho'olawe, 300 m., 16 Feb. 1931, E.H. Bryan Jr. 736' (*holo*: BISH 501028 (photo F) *n.v.*; *iso* BISH *n.v.*, *fide* Wagner & Robinson 2001).

Distribution. Hawai'i. Known only from the type.

Conservation status. Thought to be extinct.

Phenology. Flowering February.

Wollastonia dentata (H.Lév. & Vaniot) Orchard, *comb. nov.*

Eclipta dentata H.Lév. & Vaniot, *Bull. Acad. Int. Géogr. Bot.* 20: 11 (1910), *non E. dentata* B. Heyne ex Wall., *J. Numer. List* 3211 (1831), *nom. nud.* *Type citation*: 'Corée, Quaelpaert, sables du rivage à l'est, 10 Sept. 1908, Taquet 1038' (*holo*: E 414253 photo!).

Verbesina prostrata Hook. & Arn., *Bot. Beechey Voy.* 195 (1837), *nom. illeg.*, *non V. prostrata* L. (1753) [= *Eclipta prostrata*]; *Wollastonia prostrata* (Hook. & Arn.) Hook. & Arn., *Bot. Beechey Voy.* 238 (1837), *nom. illeg.*, *non Wollastonia prostrata* DC. (1836) [= *Eclipta elliptica*]; *Wedelia prostrata* Hemsl., *J. Linn. Soc. Bot.* 23: 434 (1888), *nom. nov.*; *Melanthera prostrata* (Hemsl.) W.L. Wagner & H. Rob., *Brittonia* 53: 557 (2002). *Type citation*: 'Macao, Apr. 1827, Lay & Collie *s.n.*; Macao and adjacent islands, C. Millett *s.n.*; Canton, G.H. Vachell 208' (*syn*: K? *n.v.*).

Wedelia prostrata var. *robusta* Makino, *J. Jap. Bot.* 1: 23, Figure 2 (1917); *Wedelia robusta* (Makino) Kitam., *Mem. Coll. Sci. Kyoto Univ.* ser. B. 16: 258 (1942); *Melanthera robusta* (Makino) K. Ohashi & H. Ohashi, *J. Jap. Bot.* 85: 59 (2010). *Type citation*: 'Japan, Tosa, Kashi-wa-jima in Hata-gôri, Sept.

1881, Oct. 1885, *T. Makino s.n.*' (*lecto, fide* K. Ohashi & H. Ohashi, *J. Jap. Bot.* 85: 59 (2010): MAK 242001 photo!; *syn*: MAK 104746 photo!, 241999, 242000 & 242001, last three *n.v.*).

Illustrations. T. Makino, *J. Jap. Bot.* 1: 24, Figure 2 (1917), as *Wedelia prostrata* var. *robusta*; T. Makino, *Makino's New Illustr. Fl. Japan* p. 640, no. 2560, as *Wedelia robusta* & p. 641, no. 2561 (1975), as *Wedelia prostrata*; A.C. Smith, *Fl. Vitiensis Nova* 5: 272, Figure 31 (1991); H.J. Chowdery, in *Fl. India* 12: 423, Figure 121 (1995), as *Wedelia biflora*; C.-I. Peng, K.-F. Chung & H.L. Li, *Fl. Taiwan* 4: 1096, pl. 523, & p. 1188, photo 500 (1998), as *Wedelia prostrata* var. *prostrata*; K. Ohashi & H. Ohashi, *J. Jap. Bot.* 85: 60–62, Figures 1–4 (2010), as *Wedelia robusta*; Figure 15 herein.

Specimens examined. CHINA: Ngai District, Sam Ah Kaai, Hainan, 15 Sep. 1932, *S.K. Lau* 504 (G); Lantao Island, Tungchung and vicinity, Hong Kong, 12 Sep. 1940, *Y.W. Taam* 1690 (G). JAPAN: Shirahama in Awa, Honshu, 29 Oct. 1957, *N. Maruyama* & *K. Okamoto* TNS1604 (G); Hakoishi, Kumihama-cho, Kumano-gun, Honshu, 30 July 1965, *G. Murata* 19609 (G). VIETNAM: Tourane and vicinity, Annam, May–July 1927, *J. & M.S. Clemens* 3077 (G, K); prov. Ba Ria, 6 July 1866, *L. Pierre s.n.* (G, K). THAILAND: Lam Pa, P[h]uket, 9 Mar. 1929, *A.F.G. Kerr* 17389 (K). PHILIPPINES: Manila and vicinity, Feb.–Apr. 1911, *E.D. Merrill* 7549 (K).

Distribution and habitat. China, Taiwan, Japan, Korea, Thailand, Vietnam and Philippines. Locally common on beach dunes.

Phenology. Flowering March–October; fruiting July–September.

Conservation status. Unknown, probably not threatened in most countries.

Nomenclatural notes. 'Verbesina prostrata' as described by Hooker and Arnott (1837) from Macao was not the plant earlier described as *V. prostrata* L., which is now *Eclipta prostrata*. Hooker and Arnott's name was therefore an illegitimate later homonym. Later in the same publication Hooker and Arnott transferred their species to *Wollastonia*, but this combination was also illegitimate, postdating by a year *Wollastonia prostrata* DC. from Brazil (which is now *Eclipta elliptica*). Hemsley finally validated Hooker and Arnott's name, as *Wedelia prostrata* Hemsley, in Forbes and Hemsley (1888). This plant was recently transferred to *Melanthera* as *M. prostrata* (Hemsl.) W.L. Wagner & H. Rob. (Wagner & Robinson 2002), and accepted under that name for China by Chen and Hind (2011). However, the ovaries and achenes of this species lack the multiple caducous awns of true *Melanthera*, as well as having radiate capitula, excluding it from *Melanthera* as accepted here. The paleae of the capitula are blunt and slightly hooded, and the pappus consists of several small scales, some of which are somewhat elongated, standing above the dense short indumentum on the apex of the achenes, and resembling soft short 'awns' (Figure 15). In all of these characteristics, as well as in its habitat preference for sandy seashores, it closely agrees with *Wollastonia*, and is therefore transferred to that genus. The combination *Wollastonia prostrata* is preoccupied by Candolle's name. However, Lévêillé and Vaniot in Lévêillé (1910) described the same plant as *Eclipta dentata* H.Lév. & Vaniot, and this name is available as basionym for this species, as *Wollastonia dentata*.

Taxonomic note. The taxon *Wedelia prostrata* var. *robusta* (or *Wedelia robusta*), recorded from Japan and Taiwan, is thought to be a hybrid between *Wollastonia dentata* (*Wedelia prostrata*) and *Wollastonia biflora*, although this is still to be proven. Although recognised as a named taxon by Koyama (1995b), Peng *et al.* (1998), and Ohashi and Ohashi (2010), it was not recognised by Wagner and Robinson (2001) or Chen and Hind (2011). As no specimens were available for the present study, I refrain from making a combination in *Wollastonia* for this infraspecific taxon.

Wollastonia fauriei* (H.Lév.) Orchard, *comb. nov.

Lipochaeta fauriei H.Lév., *Repert. Spec. Nov. Regni Veg.* 10: 122 (1911); *Melanthera fauriei* (H.Lév.) W.L. Wagner & H. Rob., *Brittonia* 53: 552 (2001). *Type citation*: ‘Hawai‘ian Islands, Kaua‘i, Holokele [Olokele], Mar. 1910, *U. Faurie* 1012’ (*holo*: P (photo F) *n.v.*; *iso*: BM *n.v.*, *fide* Wagner & Robinson 2001).

Illustration. H. St. John, *Pacific Sci.* 26: 292, Figure 9 (1972), as *Lipochaeta deltoidea*.

Distribution. Hawai‘i. Kaua‘i.

Phenology. Flowering March.

Conservation status. Rare, and federally (USA) listed as endangered, *fide* Wagner and Robinson (2002).

Wollastonia integrifolia* (Nutt.) Orchard, *comb. nov.

Microchaeta integrifolia Nutt., *Trans. Amer. Philos. Soc.* II, 7: 451 (1841); *Lipochaeta integrifolia* (Nutt.) A. Gray, *Proc. Amer. Acad. Arts* 5: 130 (1861); *Melanthera integrifolia* (Nutt.) W.L. Wagner & H. Rob., *Brittonia* 53: 552 (2001). *Type citation*: ‘Hawai‘ian Islands, Kaua‘i [‘Atooi’], 4–26 Jan–Mar. 1835, *T. Nuttall s.n.*’ (*holo*: BM, *fide* Wagner & Robinson (2002), *n.v.*).

Lipochaeta integrifolia var. *argentea* Sherff, *Bot. Gaz.* 95: 84 (1933). *Type citation*: ‘on sandy isthmus, Isl. Maui [Hawai‘ian Islands], *H. Mann & W.T. Brigham* 371’ (*holo*: F 276879 *n.v.*; *iso*: K, herb. Hooker!, & BISH, F, G, GH, MO, NY, US, all *n.v.*).

Lipochaeta integrifolia var. *major* Sherff, *Bot. Gaz.* 95: 85 (1933). *Type citation*: ‘on the old lava flow back of Diamond Head, Isl. Oahu [Hawai‘ian Islands], Apr. 8, 1895, *A.A. Heller* 2092’ (*holo*: GH *n.v.*; *iso*: K 2 sheets!, & A, MO, NY, US, all *n.v.*).

Lipochaeta porophila O. Deg. & I. Deg., *Flora Hawaiiensis Fam. 344. Lipochaeta porophila* (1970). *Type citation*: ‘Hawai‘i, Kau, between Lunaluu and Kamehame Hill, near coast, 7 Jun. 1969, *O. Degener, I. Degener & Mr & Mrs Picco* 31985’ (*holo*: NY *n.v.*; *iso*: K!, & MO, US, both *n.v.*).

Illustrations. O. Degener, *Fl. Hawaiiensis* (20 Aug. 1956), as *Lipochaeta integrifolia* var. *major*; W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai‘i* 335, pl. 30 (1999), as *Lipochaeta integrifolia*; Figure 17A–E herein.

Specimens examined. HAWAI‘I: Punaluu coast, Kau, 19 Jan. 1976, *O. Degener* 33603 & I. Degener (CANB); Ninole, Kau, 16 May 1983, *O. & I. Degener* 35799 (BISH); between Waiohunu & Kaalualu, Kau, 16 Feb. 1976, *O. Degener* 36563 & I. Degener (CANB); Poaiwa, Lanai, 22 Feb. 1975, *R. Gardner* 388 (BISH); 12 mi [c. 19 km] from Camp Maluhia, West Maui, 3 Dec. 1973, *S. Ishikawa* 354 (BISH); Kure Atoll, Green Island, 15 Aug. 1964, *C.H. Lamoureux* 2798 (CANB); Makapua Point, Kaohikaipu Islet, Oahu, 10 Aug. 1967, *C.H. Lamoureux* 4076 *et al.* (CANB); Paneluu, Kau District, 25 Dec. 1931, *H. St. John* 11317 *et al.* (CANB); Halawa, Molokai, 27 Dec. 1932, *H. St. John* 12725 *et al.* (CANB); Paopao Point, Paoma, Lanai, 13 Apr. 1938, *H. St. John* 18833 & *E.Y. Hosaka* (CANB).

Distribution. Hawai‘i, along the shores of Kure Atoll and all of the main islands.

Phenology. Flowering throughout the year.

Conservation status. Not threatened.

Taxonomic note. $n = 15$ (Rabakonandrianina 1980; Rabakonandrianina & Carr 1981).

Wollastonia kamolensis (O.Deg. & Sherff) Orchard, *comb. nov.*

Lipochaeta kamolensis O.Deg. & Sherff, in E.E.Sherff, *Amer. J. Bot.* 38: 63 (1951); *Melanthera kamolensis* (O.Deg. & Sherff) W.L. Wagner & H. Rob., *Brittonia* 53: 552 (2001). *Type citation:* ‘Maui, Kamole Gulch [Hawai‘ian Islands], 21 Dec. 1948, O. Degener, H.F. Clay, R. Bertram 19288’ (*holo:* F *n.v.*; *iso:* K!, US 214286 photo!, & B, BISH, BM, CM, CU, F, G, GH, LA, M, MO, NY, P, PH, all *n.v.*)

Distribution. Hawai‘i, two small sites on Maui, now reduced to one population of fewer than 1000 individuals.

Phenology. Flowering December–February.

Conservation status. Listed federally (USA) as endangered, *fide* Wagner and Robinson (2002).

Wollastonia lavarum (Gaudich.) Orchard, *comb. nov.*

Verbesina lavarum Gaudich., *Voy. Uranie* 464 (1829); *Lipochaeta lavarum* (Gaudich.) DC., *Prodr.* 5: 611 (1836); *Microchaeta lavarum* (Gaudich.) Nutt., *Trans. Amer. Philos. Soc.* II, 7: 451 (1841); *Melanthera lavarum* (Gaudich.) W.L. Wagner & H. Rob., *Brittonia* 53: 553 (2001). *Type citation:* ‘In insulis Sandwicensibus [Hawai‘ian Islands], (Alt. 350–400 hex.)’ (*holo:* Iles Sandwich, *s. dat.*, [C.] Gaudichaud *s.n.*, P 123042, ex herb. Richard, ex herb. E. Drake, photo!; *iso:* B, photo F, presumably destroyed).

Lipochaeta lavarum var. *conferta* Sherff, *Field Mus. Nat. Hist. Bot. Ser.* 17: 582 (1939). *Type citation:* ‘Lana‘i, s.l. [Hawai‘ian Islands], H. Mann & W.T. Brigham 358’ (*holo:* F 276873 *n.v.*; *iso:* K, herb. Hooker!, & BISH, GH, MO, NY, US, all *n.v.*)

Lipochaeta lavarum var. *ovata* Sherff, *Bot. Gaz.* 95: 88 (1933). *Type citation:* ‘Maui, below the crater at Kahikinui, Isl. Maui [Hawai‘ian Islands], November 1910, J.F. Rock 8674’ (*holo:* GH *n.v.*; *iso:* K!, & BISH, CAS, F, NY, UC, all *n.v.*)

Illustrations. O. Degener, *Fl. Hawaiiensis* (27 Dec. 1957), as *Lipochaeta lavarum*; O. Degener, *Fl. Hawaiiensis* (7 Apr. 1958), as *Lipochaeta lavarum* var. *hillebrandiana*; W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai‘i* p. 335, pl. 30 (1999), as *Lipochaeta lavarum*; W. Wagner & H. Robinson, *Brittonia* 53: 548, Figure 1K–O (2001), as *Melanthera lavarum*; Figure 17F–I herein.

Specimens examined. HAWAI‘I: Maunalei, Maunalei Gulch, 12 Apr. 1938, *H. St. John* 18816, A.J. Eames & E. Hosaka (CANB, BISH, K), & *loc. cit.*, *H. St. John* 18813 *et al.* (CANB); Koele–Keomoku road, Mohana, 12 Apr. 1938, *H. St. John* 18821 *et al.* (CANB); Puu Nohonaohae-iki, 12 Aug. 1981, L.W. Cuddihy & S. Anderson 857 (BISH); W coast of Kamohio Bay, 22 Apr. 1980, G. Clarke & C. Corn 391 (BISH); E. Maui, Lualihua Hills, 26 Dec. 1951, *H. St. John* 24739 (BISH); Maui, Papawai Point, 29 Dec. 1951, *H. St. John* 24761 (BISH, K); Lanai, Manele Bay, 13 June 1974, D. Herbst 4054 (BISH).

Distribution and habitat. Hawai‘i, in mainly coastal but also inland situations on Moloka‘i, Lana‘i, Maui, Kaho‘olawe and north-western Hawai‘i, usually in dry exposed areas along the margins of old lava flows.

Phenology. Flowering throughout the year.

Conservation status. Not threatened.

Taxonomic note. $n = 15$ (Rabakonandrianina 1980; Rabakonandrianina & Carr 1981).

Wollastonia lifuana (Hochr.) Fosb., *Allertonia* 7: 80 (1993).

Lipochaeta lifuana Hochr., *Bull. New York Bot. Gard.* 6: 297 (1910); *Wedelia lifuana* (Hochr.) Hochr. ex Guillaum., *Bull. Soc. Bot. France* 84: 59 (1937); *Melanthera lifuana* (Hochr.) W.L. Wagner & H. Rob., *Brittonia* 53: 553 (2001). *Type citation:* ‘New Caledonia, Lifou, 1861–1867, E. Viellard 799’ (*holo:* NY 214295 photo!; *iso:* K!, GH photo!, NY 214296 & 214297 photo!).

Illustration. Figure 16 herein.

Specimens examined. NEW CALEDONIA: Ause Nata, 5 Aug. 1950, M.G. Baumann-Bodenheim 5114 & 5120 (G); Kūto, 27 May 1951, M.G. Baumann-Bodenheim 13580 (G); Wé, Lifu, 24 Dec 1927, C. Bergeret 65 (G); Kunié, paeninsula Oro, Ile de Pins, 17 July 1965, L. Bernardi 9691 (G); Anse Vata beach, Noumea, 23 Mar. 1948, J.T. Buchholz 1783 (K); Noumea, 15 Apr. 1917, Franc 2113 (G); Observatory Point, Isle of Pines, Sep. 1853, J. MacGillivray 781 (K); Observatory Sound, Isle of Pines, Oct. 1853, Milne 103 (K); without locality, M. Paucher 345 (K); Lifu, on the sandy beach on the E side of the island, Loyalty Islands, 1863–1877, S.J. Whitmee 62 (CANB). VANUATU: Ipota, Erromango, 10 Aug. 1971, P.S. Green RSNH1326 (K); côte S entre Pointe Narabo et Baie François, Efate, 30 June 1971, J. Raynal RSNH16004 (K).

Distribution and habitat. New Caledonia (Loyalty Islands, Ile des Pins, Grande Terre), and Vanuatu (Erromanga, Efate, Anatom). Grows with *Messerschmidia* Hebenstr. on coastal coral sand and rocks just above high water, adjacent to *Araucaria–Pandanus* woodland.

Phenology. Flowering March–December, fruiting April–December.

Conservation status. Unknown, probably not threatened.

Local name. Sesinaya (Lifu, Viellard 799, K).

Taxonomic note. *Wollastonia lifuana* has frequently been misidentified as *W. uniflora*, which has much larger leaves, usually 5 cm or more long, and the indumentum, particularly on the adaxial surface, is widely spaced, allowing the underlying epidermis to be clearly visible. Achenes in *W. uniflora* are 2.2–3.0 mm long, and often have an oblique awn. In *W. lifuana* the leaves rarely exceed 2–3 cm in length, and are densely silvery pubescent on both surfaces, the hairs hiding the epidermis. The achenes are c. 1.5 mm long and lack awns.

Wollastonia micrantha (Nutt.) Orchard, *comb. nov.*

Schizophyllum micranthum Nutt., *Trans. Amer. Philos. Soc.* II, 7: 453 (1841); *Aphanopappus nuttallii* Walp., *Repert. Bot. Syst.* 2: 620 (1843), *nom. illeg.*; *Lipochaeta micrantha* (Nutt.) A.Gray, *Proc. Amer. Acad. Arts* 5: 131 (1861); *Aphanopappus micranthus* (Nutt.) A.Heller, *Minnesota Bot. Stud.* 1: 915 (1897). *Type citation*: ‘The island of Atooi, in shady woods, near Kolao, [Kaua‘i, Koloa, [Hawai‘ian Islands] 1835, T. Nuttall s.n.]’ (*holo*: BM n.v.; *iso*: Atooi, s. dat., [T.] Nuttall s.n., K, herb. Hooker!).

Two subspecies are recognised:

Wollastonia micrantha (Nutt.) Orchard subsp. **micrantha**

Lipochaeta micrantha var. *micrantha*, *sensu* Gardner (1979) and Wagner *et al.* (1999).

Illustrations. O. Degener, *Fl. Hawaiiensis* (28 Dec. 1959), as *Lipochaeta micrantha*; W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai‘i* p. 339, pl. 31 (1999), as *Lipochaeta micrantha* var. *micrantha*; Figure 17J–N.

Specimens examined. HAWAI‘I: Olokele Canyon, Kaua‘i, 3 July 1926, O. Degener 2143 (K); Hanapepe and Wahiawa watershed, Kaua‘i, 25 June 1895, A.A. Heller 2409 (K); District of Waimea, Koai‘e Stream, Kaua‘i, 29 Mar. 1986, J. Lau 2202 (BISH); Kaua‘i, 1916, J.F. Rock s.n. (BISH 725607).

Distribution and habitat. Hawai‘i, two valleys on Kaua‘i, on moist, shady or sunny banks in forested areas.

Phenology. Flowering June–October.

Conservation status. Listed federally (USA) as endangered, *fide* Wagner and Robinson (2002).

Wollastonia micrantha subsp. **exigua** (O.Deg. & Sherff) Orchard, *comb. nov.*

Lipochaeta exigua O.Deg. & Sherff, in E.E. Sherff, *Amer. J. Bot.* 28: 30 (1941); *Lipochaeta micrantha* var. *exigua* (O.Deg. & Sherff) R.C.Gardner, *Rhodora* 81: 325 (1979); *Melanthera micrantha* subsp. *exigua* (O.Deg. & Sherff) W.L.Wagner & H.Rob., *Brittonia* 53: 554 (2001). *Type citation*: ‘Hawai‘i, Kaua‘i, grassy shrubby summit ridge, 0.71 mi SW of Hokunui, Nawiliwili, 8 Jan. 1940, O. Degener & E. Ordoñez 12610’ (*lecto, fide* C.A. Gardner, *Rhodora* 81: 326 (1979): F 1014051 n.v.; *isolecto*: B, BISH, F, G, GH, MO, UC, US, all n.v., NY 214271–214275 photos!).

Illustration. O. Degener, *Fl. Hawaiiensis* (16 July 1962), as *Lipochaeta exigua*.

Distribution and habitat. Hawai‘i, Kaua‘i, in grassy and shrubby areas.

Phenology. Flowering January–July.

Conservation status. Listed federally (USA) as endangered, *fide* Wagner and Robinson (2002).

Taxonomic note. *n* = 15 (Rabakonandrianina 1980; Rabakonandrianina & Carr 1981).

Wollastonia perdita (Sherff) Orchard, *comb. nov.*

Lipochaeta perdita Sherff, *Bot. Gaz.* 95: 99 (1933); *Melanthera perdita* (Sherff) W.L. Wagner & H. Rob., *Brittonia* 53: 554 (2001). *Type citation*: ‘David Nelson, Hawai‘ian Isls., 1778–1779’ [Hawai‘i, probably Ni‘ihau, 26–29 Jan. 1779] (*holo*: BM (photo F) *n.v.*).

Lipochaeta kawaihoaensis H. St. John, *Pacific Sci.* 13: 181 (1959). *Type citation*: ‘Niihau, Kawaihoa Point, [Hawai‘i], 300 ft. alt. in dry tuff, head of steep gully, erect, much branched shrubs, rays yellow, disk dark yellow, March 31, 1949, *H. St. John* 23,611’ (*holo*: BISH *n.v.*; *iso*: K 518009! & K unnumbered!).

Illustration. H. St. John, *Pacific Sci.* 13: 183, Figure 9 (1959), as *Lipochaeta kawaihoaensis*.

Distribution and habitat. Hawai‘i, Ni‘ihau.

Phenology. Flowering March.

Conservation status. Listed federally (USA) as extremely rare and possibly extinct, *vide* Wagner and Robinson (2002).

Wollastonia populifolia (Sherff) Orchard, *comb. nov.*

Lipochaeta subcordata var. *populifolia* Sherff, *Bot. Gaz.* 95: 91 (1933); *Lipochaeta populifolia* (Sherff) R.C. Gardner, *Rhodora* 81: 328 (1979); *Melanthera populifolia* (Sherff) W.L. Wagner & H. Rob., *Brittonia* 53: 554 (2001). *Type citation*: ‘G.C. Munro 670, Maunalei Valley, Isl. Lanai, [Hawai‘ian Islands], June 18, 1918’ (*holo*: F 75168 photo!; *iso*: BISH *n.v.*, US 466263 & 125305 photo!).

Distribution and habitat. Hawai‘ian Islands, known only from the type.

Phenology. Flowering June.

Conservation status. Almost certainly extinct.

Note. This taxon was recognised as distinct at species level (*Lipochaeta populifolia*) by Gardner (1979), included within *L. subcordata* by Wagner *et al.* (1999), and recognised as distinct (*Melanthera populifolia*) by Wagner and Robinson (2001). It is almost certainly extinct.

Wollastonia remyi (A. Gray) Orchard, *comb. nov.*

Lipochaeta remyi A. Gray, *Proc. Amer. Acad. Arts* 5: 131 (1861); *Melanthera remyi* (A. Gray) W.L. Wagner & H. Rob., *Brittonia* 53: 554 (2001). *Type citation*: ‘Hawai‘ian Islands, O‘ahu, 1851–1855, *J. Rémy* 260’ (*holo*: GH (fragment at BISH, photo F) *n.v.*).

Illustrations. O. Degener, *Fl. Hawaiiensis* (15 Sep. 1946), as *Lipochaeta remyi*; W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai‘i* p. 339, pl. 31 (1999), as *Lipochaeta remyi*; Figure 170–T herein.

Specimens examined. HAWAI‘I: E of Kaena Point, Oahu, 10 Apr. 1956, *O. & I. Degener* 24069 (BISH, K); hills E of Kawaihapai, Oahu, Dec. 1930, *O. Degener & K.K. Park* 4186 & 4187 (K); Kealia,

Waianae Mountains, 2 Feb. 1936, *F.R. Fosberg* 12859 (BISH); Manini Pali area, Waialua District, 25 Apr. 1976, *D. Herbst* 5842 (BISH); Kaala Mountains, Oahu, *s. dat.*, *H. Mann & W.T. Brigham* 533 (K); Kaena Point, Oahu, 29 Jan. 1956, *G. Pearsall & H. St. John* 84 (K).

Distribution and habitat. Hawai‘ian Islands, on O‘ahu, in the Waianae Range, in moist areas in hillside forest understoreys.

Phenology. Flowering December–June.

Conservation status. Unknown, probably not threatened.

Taxonomic note. *n* = 15 (Rabakonandrianina 1980; Rabakonandrianina & Carr 1981).

Wollastonia subcordata (A.Gray) Orchard, *comb. nov.*

Lipochaeta subcordata A.Gray, *Proc. Amer. Acad. Arts* 5: 130 (1861); *Melanthera subcordata* (A.Gray) W.L.Wagner & H.Rob., *Brittonia* 53: 554 (2001). *Type citation:* ‘[Hawai‘ian Islands, Hawai‘i], 1840, U.S. Exploring Expedition *s.n.*’ (*holo*: US 57067 *n.v.*).

Illustrations. O. Degener, *Fl. Hawaiiensis* (15 Aug. 1950), as *Lipochaeta flexuosa*; W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai‘i* p. 342, pl. 32 (1999), as *Lipochaeta subcordata*; Figure 18A–F herein.

Specimens examined. HAWAI‘I: Pohakuloa Training Area, 7 June 1980, *J. Davis* 299 (BISH); between Puuwaawaa and Huehue, 22 Aug. 1926, *O. Degener* 4189 (K); between Honuapo & Hilea, 17 Feb. 1939, *O. Degener* 4302 (K); Huehue, Kona, 11 Feb. 1952, *O. Degener* 21816 (K); Kona Coast, along Mamalaho Hwy 190, Hualalai Ranch, 4 Mar. 1979, *H. Kennedy & S. Ishikawa* 3909 (BISH); Upper Malepiula paddock, Puawaawaa, 20 Aug. 1971, *S.L. Montgomery s.n.* (BISH 455175); Kealakehe, North Kona, 14 July 1991, [*K.*] *Nagata* 4218 (BISH); crater of Pulehua, Land of Keauhou 2, 25 Jan. 1992, *K. Nagata* 4235 (BISH); Kaupulehu, 20 May 1989, *W. Takeuchi & C. Shimabukuro* 5802 (BISH).

Distribution and habitat. Hawai‘ian Islands, Hawai‘i, mainly in the North Kona district, in dry forest and grassland.

Phenology. Flowering throughout the year.

Conservation status. Unknown, probably not threatened.

Taxonomic note. *n* = 15 (Rabakonandrianina 1980).

Wollastonia tenuifolia (A.Gray) Orchard, *comb. nov.*

Lipochaeta tenuifolia A.Gray, *Proc. Amer. Acad. Arts* 5: 131 (1861); *Melanthera tenuifolia* (A.Gray) W.L.Wagner & H.Rob., *Brittonia* 53: 554 (2001). *Type citation:* ‘[Hawai‘ian Islands, O‘ahu, Ka‘ala Mountains], 1840, U.S. Exploring Expedition *s.n.*’ (*lecto, fide* E.E. Sherff, *Bernice P. Bishop Mus. Bull.* 135: p.? [cited in Wagner and Robinson (2002)] (1935): GH *n.v.*; *isolecto*: NY *n.v.*, US 214707 photo!). *Syn:* *Rémy* 276 (GH, P, both *n.v.*).

Illustrations. O. Degener, *Fl. Hawaiiensis* (15 Aug. 1950), as *Lipochaeta tenuifolia*; W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai'i* p. 342, pl. 32 (1999), as *Lipochaeta tenuifolia*; Figure 18G–L herein.

Specimens examined. HAWAI'I: Upper Makua Valley, Oahu, 10 May 1931, *O. Degener, K.K. Park & W. Bush* 4174 (BISH, K); Wainae Mountains, Oahu, 17 Feb. 1974, *W.G. Goghé* 692 *et al.* (CANB); Kaala Mountains, Oahu, 1869, *W. Hillebrand s.n.* (K); Kaala Mountains, Oahu, Nov. 1866, *H. Mann & W.T. Brigham* 534 (K); Waianae Kai, Oahu, 13 July 1980, *J. Obata s.n.* (BISH 475106); side ridge from Kamaileu crestline, Oahu, 2 Oct. 1983, *W. Takeuchi et al.* Wainanae 5 (BISH).

Distribution and habitat. Hawai'ian Islands, Wai'anae Mountains, O'ahu, on dry talus slopes with grasses and low shrubs.

Phenology. Flowering May.

Conservation status. Unknown, probably not threatened.

Wollastonia tenuis (O.Deg. & Sherff) Orchard, *comb. nov.*

Lipochaeta tenuis O.Deg. & Sherff, *Bot. Gaz.* 95: 102 (1933); *Melanthera tenuis* (O.Deg. & Sherff) W.L.Wagner & H.Rob., *Brittonia* 53: 555 (2001). *Type citation:* 'Otto Degener, Wai'anae Valley up toward Mt. Kaala, Isl. O'ahu, [Hawai'ian Islands], Apr. 24, 1932' (*lecto, fide* R.C. Gardner, *Rhodora* 81: 320 (1979): *O. Degener, K.K. Park & W. Bush* 4258, F 666542 *n.v.*; *isolecto:* K!, & F, MO, NY, all *n.v.*).

Illustration. O. Degener, *Fl. Hawaiiensis* (15 Sep. 1946), as *Lipochaeta tenuis* var. *sellingii*.

Specimens examined. HAWAI'I: NE ridge of Puu Hapapa, 7 May 1939, *O. Degener, E. Ordovas & J. Foster* 12332 (K).

Distribution. Hawai'ian Islands, central Wai'anae Mountains, O'ahu, among grasses.

Phenology. Flowering April–September.

Conservation status. Unknown.

Taxonomic note. *n* = 15 (Rabakonandrianina 1980).

Wollastonia venosa (Sherff) Orchard, *comb. nov.*

Lipochaeta venosa Sherff, *Bot. Gaz.* 95: 100 (1933); *Melanthera venosa* (Sherff) W.L.Wagner & H.Rob., *Brittonia* 53: 555 (2001). *Type citation:* 'J.F. Rock 8349, Nohonaohae Crater, Waimea, Isl. Hawai'i, June, 1910' (*holo:* F 659409 *n.v.*; *iso:* K!, US 214710 photo!, & BISH, GH, UC, all *n.v.*).

Illustrations. W.L. Wagner, D.R. Herbst & S.H. Sohmer, *Man. Fl. Pl. Hawai'i* p. 342, pl. 32 (1999), as *Lipochaeta venosa*; Figure 18M–U herein.

Specimens examined. HAWAI'I: Holoholoku cone, 5 Apr. 1982, *S.J. Anderson* 502 (BISH); NE of Nohonaohae cinder cone, 5 Apr. 1982, *S.J. Anderson* 505 (BISH); Puu Holoholoku Paddock, Waimea, 25 May 1938, *E.Y. Hosaka* 2114 (K); Puu Nohonaohae, lower slopes of Puu, 13 Jan. 1980, *K. Nagata, W. Teraoka & C. Corn* 2028 (BISH).

Distribution. Hawai'ian Islands, South Kohala District, Hawai'i.

Phenology. Flowering May–June.

Conservation status. Federally (USA) listed as endangered, *fide* Wagner and Robinson (2002).

Taxonomic note. *n* = 15 (Rabakonandrianina 1980).

Wollastonia waimeaensis (H.St.John) Orchard, *comb. nov.*

Lipochaeta waimeaensis H.St.John, *Pacific Sci.* 26: 293 (1972); *Melanthera waimeaensis* (H.St.John) W.L.Wagner & H.Rob., *Brittonia* 53: 555 (2001). *Type citation:* 'Hawai'ian Islands, Kaua'i, Waimea Canyon, upper slope of W side, 1200 ft, 17 Apr. 1967, *R.W. Hobdy* 101' (*holo:* BISH 501058 *n.v.*; *iso:* K!, & BISH, GH, US, all *n.v.*).

Illustration. H. St. John, *Pacific Sci.* 26: 294, Figure 10 (1972).

Distribution and habitat. Hawai'ian Islands, Waimea Canyon, Kaua'i, only known from the type locality.

Phenology. Flowering April.

Conservation status. Federally (USA) listed as endangered, *fide* Wagner and Robinson (2002).

Taxonomic note. *n* = 15 (Rabakonandrianina 1980).

6. Apowollastonia Orchard, *gen. nov.*

Type: *Apowollastonia spilanthoides* (F.Muell.) Orchard

Niebuhr Neck., *Elem. Bot.* 1: 30 (1790), *nom. inval.*

Seruneum Kuntze, *Rev. Gen. Pl.* 1: 364 (1891), *nom. illeg. superfl., p.p.*, as to *S. spilanthoides*.

Niebuhr Britten, *J. Bot.* 39: 68 (1901), *nom. illeg. superfl., p.p.*, as to *N. spilanthoides*, *non Niebuhr* Scop., *Intr. Hist. Nat.* 134 (1777), *nom. illeg. superfl., et nec Niebuhr* DC., *Prodr.* 1: 242 (1824), *nom. illeg.*

[*Wedelia auct. non* Jacq.: G. Bentham, *Fl. Austral.* 3: 537–539 (1866), *p.p.* (excl. *W. biflora* & *W. urticifolia*); & most subsequent Australian authors.]

Subshrubs, or perennial or annual *herbs* with a woody caudex and annual stems, usually coarsely

scabrous throughout. *Leaves* opposite, simple, ovate to lanceolate or linear, usually serrate, rarely entire, 3-veined at base. *Capitula* terminal, solitary or in dichasial groups of up to 5, on short or long peduncles, radiate; usually hemispherical in flower, becoming subglobose in fruit; receptacle almost flat in flower, becoming hemispherical in fruit; *involucral bracts* in c. 2 whorls, (linear-) lanceolate to ovate, green, usually coriaceous, scabrous; paleae lanceolate (rarely linear or ovate), green and slightly thickened at tip, often striate and submembranous basally, tip rigidly erect, more or less acute to acuminate, scabrous on abaxial surface, usually entire. *Ray florets* in 1 whorl, c. 8–12(–18), pistillate and fertile; *corollas* yellow, 2- or 3-lobed, often striate, sometimes shortly pilose abaxially. *Disc florets* numerous, bisexual and fertile; *corollas* yellow to yellow-orange, 5-lobed, with papillae on adaxial surface of lobes, usually shortly scabrous externally at least on lobes; *anther thecae* yellow to pale yellow-brown (?rarely black in some specimens of *A. major* Orchard - see *Taxonomic notes* below); *anther appendages* cream; anther tails very short and rounded; *filament collars* swollen or not. *Achenes* oblong to obovoid, usually black or dark grey, ray achenes 3-angled, not or hardly compressed, disc achenes 2-angled, compressed or not, the angles sometimes obscure (*A. cylindrica*) or expanded into corky or membranous wings; *pappus* rarely entirely absent, usually a ring of tiny hairs and/or scales, sometimes with 1–3 weak and usually deciduous fragile awns.

Distribution and habitat. A genus of eight species with its main centre of diversity (seven species) in northern and central Australia, and one species in New Guinea and Indonesia. Three Australasian species are perennial herbs, with a compact buried woody caudex from which annual stems arise, bearing usually rather dry, scabrous leaves and sparse, terminal, radiate capitula, with yellow corollas, four species are shrubs with perennial woody stems, and one is an annual herb; all mostly found in grassland or grassy woodland.

Nomenclatural note. For discussion of the generic names *Niebuhrria* Neck., *Niebuhrria* Britten and *Seruneum* Kuntze, see under ‘History of generic circumscription – *Apowollastonia*’, above.

Taxonomic notes. All *Apowollastonia* species differ from *Wollastonia* in having paleae that are acute or almost so, often acuminate, with rigidly erect, ±fleshy, dorsally scabrous tips, and anther thecae that are yellow, sometimes pale yellow-brown (a few specimens of *A. major* appear to have black or dark brown anther thecae, but this may be an artefact of collecting practices). The species of *Apowollastonia* fall into three subgroups: 1. shrubs with perennial woody stems, achenes usually winged (*A. verbesinoides* (Benth.) Orchard, *A. hibernica* Orchard, *A. stirlingii* (Tate) Orchard and *A. hamersleyensis* Orchard); 2. annual herbs, achenes not angled (or only extremely weakly veined) nor winged (*A. cylindrica*); and 3. perennial herbs with a small woody caudex and annual herbaceous stems, achenes 2–3.5(–4) mm long, mostly angled or winged (*A. major*, *A. longipes* (Klatt) Orchard, *A. spilanthoides*). Occasional intermediate specimens are found within these groupings, but not between them, suggesting that these are natural lineages.

Notes. *Apowollastonia* appears to be a relatively recent, rapidly evolving group. The species are generally similar in gross morphology: rather dry, usually linear to lanceolate or ovate, serrate, simple leaves, coarsely scabrous, usually shrubs or sprawling perennial herbs, rather generalised capitula with coriaceous, green involucral bracts, a single whorl of pistillate, fertile ray florets and numerous bisexual, fertile disc florets, both with yellow(–orange) corollas, yellow anther thecae, and paleae with acute to acuminate, erect, stiff tips that are abaxially scabrous. Achenes are usually 2- or 3-angled, often winged on the angles. The group (under the name *Wedelia*) has a reputation in Australia for being difficult taxonomically. This stems from a number of factors: the individual species, while varying widely in habit, leaf shape and size, and achene morphology, and thus possessing a range of potentially diagnostic characteristics, tend to be environmentally plastic; there is some evidence of

intermediates and intergradation within the main habit groups; there is a general paucity of preserved mature fruiting specimens that might provide definitive evidence of species limits. Most existing collections have been made when the plants are in conspicuous flower. Collection of better fruiting specimens in future should allow fine tuning of the classification presented below.

Etymology. From the Greek *apo-* (in the sense of ‘away from’) plus *Wollastonia*, an allusion to the suspicion that this is a recently evolved sister group to *Wollastonia*.

Key to species of *Apowollastonia*

1. Annual herbs, or perennial herbs with a short, buried, woody caudex and annual stems
 2. Perennial herbs; disc achenes 2-angled, ray achenes 3-angled, often with angles produced into thick, corky wings; pappus of tiny scales
 3. Annual stems 1–2 mm diam. at base
 4. Leaf lamina narrowly linear to narrowly lanceolate 1. **A. spilanthoides**
 - 4: Leaf lamina ovate to suborbiculate 2. **A. longipes**
 - 3: Annual stems 2–4 mm diam. at base 3. **A. major**
 - 2: Annual herbs; achenes all cylindrical, sometimes with 1 or 2 longitudinal veins but not angled; pappus often \pm absent 8. **A. cylindrica**
- 1: Subshrubs with perennial woody stems
 5. Capitula on peduncles 1.5–2.5(–3.0) cm long
 6. Achenes *c.* 3 mm long; leaf lamina ovate to suborbiculate 4. **A. verbessinoides**
 - 6: Achenes *c.* 5–6 mm long; leaf lamina lanceolate 5. **A. hibernica**
 - 5: Capitula on peduncles 6–12(–18) cm long
 7. Leaves serrate to subpinnatisect 6. **A. stirlingii**
 - 7: Leaves entire 7. **A. hamersleyensis**

1. *Apowollastonia spilanthoides* (F.Muell.) Orchard, *comb. nov.*

Wedelia spilanthoides F.Muell., *Fragm.* 5: 64 (1866); *Seruneum spilanthoides* (F.Muell.) Kuntze, *Rev. Gen. Pl.* 1: 365 (1891); *Niebuhrnia spilanthoides* Britten, *J. Bot.* 39: 69 (1901), *nom. superfl.* *Type citation:* ‘Per magnam Australiae tropicae partem diffusa’ (*lecto*, chosen here: Warwick, *s. dat.*, [*Anon. s.n.*, herb. Mueller], MEL 2166644!). Residual *syntypes*: see *Nomenclatural notes* below.

Illustration. J. Britten (ed.), J. Banks & D. Solander, *Illustr. Bot. Capt. Cook’s Voy.* pl. 159 (1901), as *Niebuhrnia spilanthoides*.

Perennial *herb* 0.2–0.5 m tall; stems 1–2 mm diam., sprawling or prostrate, not rooting at nodes, stiff, striate, densely semi-appressed scabrous. *Leaves* sessile or subsessile, very variable in shape, narrowly linear to narrowly lanceolate, 30–50(–90) mm long, 2–5(–10) mm wide, dark green and coarsely scabrous both surfaces, cuneate basally, acute, usually coarsely serrate with spreading teeth, the 2 basal teeth often larger and shortly lobe-like (occasionally some leaves almost entire). *Capitula* in groups of 1–3, often solitary, on peduncles 10–15(–25) cm long; outer and inner *involucral bracts* lanceolate, 4–5 mm long, subacute, shorter than disc florets, densely scabrous abaxially. *Capitulum* in fruit 9 mm long, 10–12 mm

diam. *Ray florets* 8–11(–18); lamina 12–20(–25) mm long, 2- or 3-lobed, weakly veined, glabrous or very sparsely pilose abaxially. *Disc florets* 26–35; corolla yellow, ±glabrous externally; anther thecae yellow. *Paleae* lanceolate, 4–5 mm long in flower, yellow-green, with midrib prominent, outer paleae almost flat, inner ones ±conduplicate, coarsely scabrous on margins and midrib. *Achenes* dark grey-black, obovoid, 2.5–3.0(–3.5) mm long, 1.0–1.2 mm wide, weakly and bluntly 2- or 4-angled (disc) or 3-angled (ray), not winged, and sometimes lacking angles, very sparsely and shortly (0.05–0.1 mm) hairy apically, smooth. *Pappus* a few sparse minute scales, on a short rostrum, with no awns. (Figure 19)

Specimens examined (selection). QUEENSLAND: Goodicum State Forest, SE of Kalpowar, 10 June 1996, *A.R. Bean* 10403 (BRI); Palmgrove National Park, NW of Taroom, Bigge Ra., 4 Nov. 1998, *P.I. Forster* 23704 & *R. Booth* (BRI); 25 miles [40.2 km] W of Bauhinia Downs, 18 Mar. 1968, *W.T. Jones* 3736 (CANB); Mt Surprise–40 Mile Scrub National Park, 24 Jan. 2001, *K.R. McDonald* 705 (BRI). NEW SOUTH WALES: Timbarra, Dec., *Anon.* 121 (MEL); MacLeay River, Dec. 1896, *F. Brown s.n.* (AD); Manning River, Dec. 1899, *E. Cheel s.n.* (MEL 2169046; NSW 380186); Liverpool Ra., *s. dat.*, *J.E. Tenison-Woods s.n.* (MEL 2169052); Bellangry, 14 Jan. 1981, *T. & J. Whaite* 3723 (NSW); Clarence River, *s. dat.*, *W. Woolls s.n.* (MEL 2169048).

Distribution and habitat. Extends from southern Cape York Peninsula in northern Queensland to north-eastern New South Wales (Figure 36, Map 3). Usually found in the relatively dry grassy understorey of open woodlands of *Eucalyptus*, *Corymbia* and *Angophora*, on a range of soils (basalts, sandstones, loams, granitic sand), at altitudes of about 120–650 m.

Phenology. Flowers and fruits recorded in most months, with a peak in mid-year.

Conservation status. Not threatened.

Nomenclatural notes. Mueller's type statement is very vague, but indicates that he considered the species to be widespread in tropical Australia. In MEL there are at least 14 specimens annotated by Mueller with this name, some with dates and collectors, most without. The collectors were probably mostly Bowman and Dallachy, although this is rarely stated. Most of these specimens must be considered syntype material. They vary from some clearly within current concepts of this species, to others somewhat intermediate with *A. longipes* (see discussion below). From among these I have chosen a collection from Warwick as the lectotype because it is the best specimen (many are scrappy), represents a median in the range of (leaf) variation exhibited by the syntypes, is in agreement with the protologue and maintains current usage. Probable duplicates of some of these specimens are also in K and NSW. The following are specimens which should be considered additional syntypes, divided into two groups: Group 1, those falling comfortably within the circumscription of *A. spilantheidoides*; and Group 2, those somewhat intermediate with *A. longipes*.

Group 1: Burdekin, *s. dat.*, *Anon. s.n.* (MEL 2166648); Rockingham Bay, *s. dat.*, *Anon. s.n.* (MEL 2166645); Burnett River, *s. dat.*, *Anon. s.n.* (MEL 2166654); McLeay River, *s. dat.*, *Anon. s.n.*, (MEL 2169050); Rockhampton, *s. dat.*, *Anon.* 2 (MEL 2166655); Queensland, *s. dat.*, *Bowman s.n.* (MEL 2166652, 2166649 & 2166646); Fitzroy's River, *s. dat.*, *Bowman* 5 (MEL 2166653).

Group 2: Queensland, *s. dat.*, *Anon. s.n.* (MEL 2166656); Rockhampton, *s. dat.*, *Anon. s.n.* (MEL 2166647); Rockingham Bay, *s. dat.*, *Anon. s.n.* (MEL 604840, ex herb. Sonder); Rockhampton, 20 Dec. 1862, *Anon.* [*Dallachy?*] 54 (MEL 2166651); Rockhampton, *s. dat.*, *Dallachy s.n.* (K, MEL 60484); Queensland, *s. dat.*, *D[allachy] s.n.* (MEL 2166650).

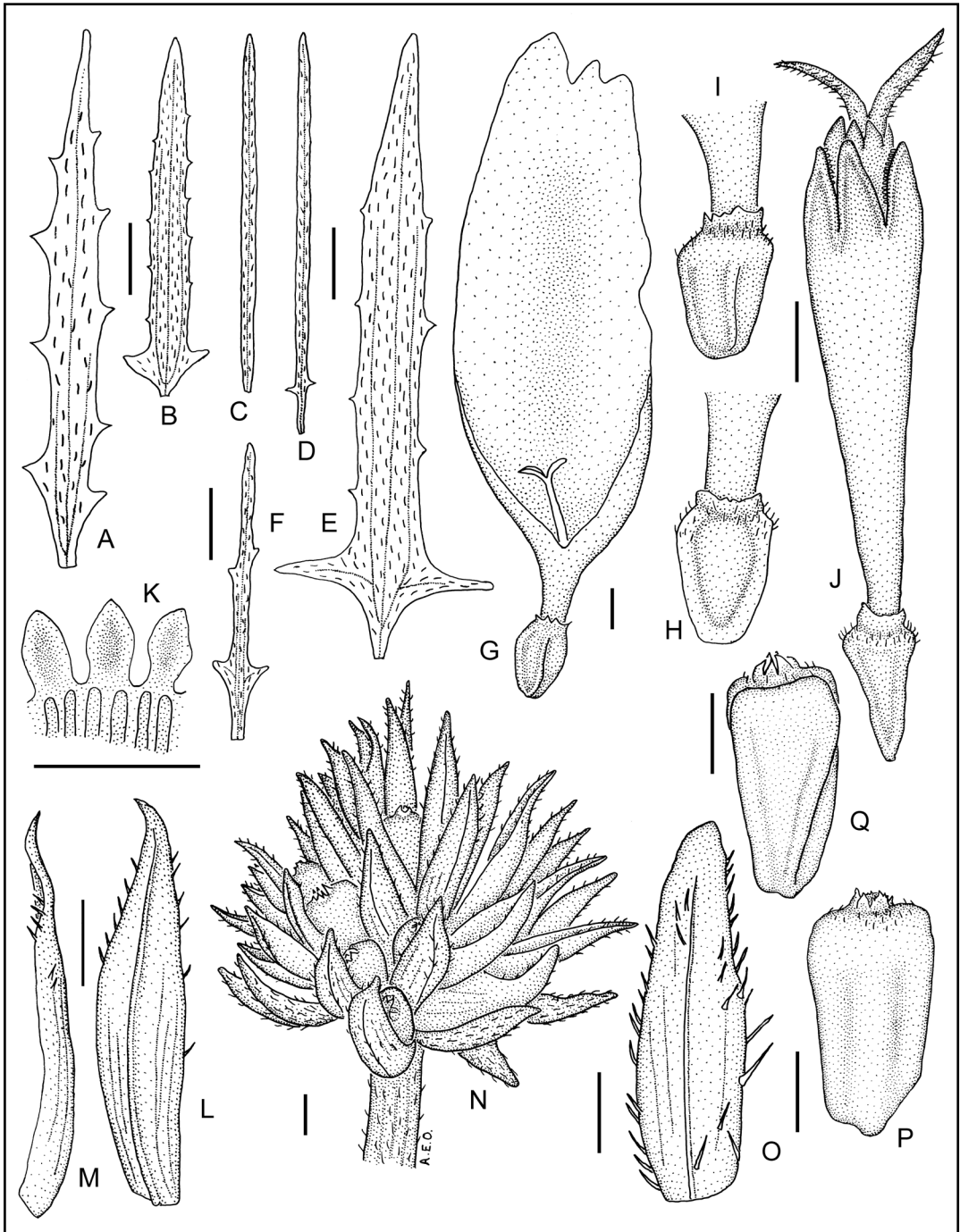


Figure 19. *Apowollastonia spilanthoides*. A–F – leaves; G – ray floret; H – ray floret detail of ovary (abaxial); I – ray floret, detail of ovary (adaxial); J – disc floret; K – detail of anther appendages; L – palea (floret), dorsal view; M – palea (floret), lateral view; N – capitulum in fruit; O – involucral bract (fruit); P – mature 4-angled disc achene; Q – mature 3-angled ray achene. (A based on *P.I. Forster* 9472 (BRI); B based on *A.R. Bean* 10403 (BRI); C, D based on *P.I. Forster* 23704 & *R. Booth* (BRI); E based on *K.P. McDonald* 705 (BRI); F–M, O–Q based on *W.T. Jones* 3736 (CANB)). Scale bars: A–F = 1 cm; G–Q = 1 mm. Del. A.E. Orchard.

Taxonomic notes. *Apowollastonia spilanthisoides* is very variable, particularly in leaf shape. Most specimens have leaves that are linear to oblong or narrowly lanceolate, about 10 mm wide, with relatively even moderate serrations. In the southern part of its range (mainly south-eastern Queensland and north-eastern New South Wales) the leaves may become extremely narrow (1–2 mm wide), and almost entire, while in the northern part they become wider with coarser teeth, approaching those of *A. longipes* in shape. Leaf length also varies considerably, further complicating descriptions of overall shape. These variations, while broadly clinal north (broad) to south (narrow) are not consistently so, and also appear in populations apparently randomly. Variation in leaf shape is particularly marked in the vicinity of Rockhampton, and north to about Cairns, and is apparent in the syntypes that came from this region. This trend in leaf shape is carried further in the related *A. longipes*, found mainly in northernmost Cape York Peninsula. *Apowollastonia longipes* differs in having ovate to subrotund, coarsely serrate leaves, but with a similar long-pedunculate capitulum, and also differs in achene shape: strongly angled, with the disc achenes distinctly compressed vs. obovoid and scarcely angled in *A. spilanthisoides*. Differentiation of *A. spilanthisoides* from *A. longipes* in the central east coast region of Queensland can be problematic, especially as collections, although relatively numerous, are largely inadequate for identification, lacking basal parts (mature leaves) and achenes. It is possible that additional taxa (at least at infraspecific level) could be distinguished in this complex, but recognition of these, plus definition of a firmer boundary between *A. longipes* and *A. spilanthisoides*, must await detailed field studies and collection of a suite of more adequate specimens. In this treatment, specimens lacking achenes, but with leaves of linear to lanceolate order are assigned to *A. spilanthisoides*, while those with broader leaves approaching ovate shapes, are assigned to *A. longipes*. This is not entirely satisfactory, but does recognise the distinctiveness from *A. spilanthisoides* of the far-northern *A. longipes* with its large, rotund leaves. The illustration of ‘*Niebhria spilanthisoides*’ in Britten’s publication of the illustrations from Cook’s voyage (cited above) is indicative of the ambiguity in this group. The illustration is of a broad-leafed form of *A. spilanthisoides*, approaching *A. longipes*, but maintained in *A. spilanthisoides* in this treatment. A Banks and Solander collection in MEL (2169054) is not a good match with this illustration. It has even broader leaves and more closely approaches *A. longipes*.

Notes. *Apowollastonia spilanthisoides* has been suspected of causing stock poisonings. However, a letter attached to *P.J. Allen s.n.*, Millaroo (BRI 131008) describes feeding trials with yearling Shorthorn cattle, that failed to demonstrate any adverse effects.

2. *Apowollastonia longipes* (Klatt) Orchard, *comb. nov.*

Wedelia longipes Klatt, *Ann. K. K. Naturhist. Hofmus.* 68 (1896). *Type citation:* ‘Cape York, leg. Daemel, Herb. Mus. Palat. Vindob. Nr. 38386’ (*holo:* W 38386 photo!; *iso:* Cape York, *s. dat.*, Daemel, BM!; Cape York, Australia, Mar. 1868, *Mr Daemel*, K!).

Perennial *herb* (0.3–)0.6–1.0(–1.2) m tall; *stems* 1–2 mm diam., erect or scrambling, not rooting at nodes, stiff, striate, moderately appressed scabrous. *Leaves* shortly petiolate to sessile; petiole 5–10 mm long; lamina ovate to suborbiculate, becoming narrower (lanceolate) above, 40–75(–140) mm long, 20–60(–105) mm wide, often grey-green, densely and coarsely scabrous (hairs erect to semi-appressed) on both surfaces, especially on prominent veins abaxially, broadly cuneate basally, acute to obtuse, shortly serrate. *Capitula* in terminal groups of 1–3, on peduncles 10–12 cm long (often with a median pair of small leafy bracts); outer and inner *involucral bracts* ovate to lanceolate, 5–6 mm long, subacute, *c.* as long as disc florets, densely appressed-scabrous abaxially. *Capitulum* in fruit 7–8 mm long, 10–12 mm diam. *Ray florets* 10–12(–16); *corolla* lamina 9–12 mm long, 2- (or 3-)lobed, weakly veined, glabrous or sparsely pilose abaxially. *Disc florets* 10–20; *corolla* yellow or orange-yellow, shortly scabrous externally; *anther thecae* yellow-brown. *Paleae* linear-lanceolate,

5.5 mm long in flower, yellowish, with midrib prominent plus multiple fine striae basally, conduplicate, coarsely scabrous on midrib, margins and abaxial surface of tip. *Achenes* grey-black, sometimes mottled, obovoid, 2.5–3.0(–4.0) mm long, 1.5–2.0 mm wide, 2-angled and compressed (disc) or 3-angled (ray), the angles sometimes with narrow, corky wings, shortly scabrous apically and on wing margins, smooth or slightly rugose. *Pappus* a ring of tiny, lacinate scales, with 1 or 2 sometimes elongated into soft ‘awns’ to 0.5 mm long. (Figure 20)

Specimens examined. QUEENSLAND: Lockerbie, 26 Apr. 1948, *L.J. Brass* 18435 (BRI, CANB, K); 2.7 km WSW of Beagles North Camp, 27 May 1982, *J.R. Clarkson* 4347 (BRI, HO, K, NT, QRS); 4.6 km S of Batavia Downs on Peninsula Development Road, 19 Apr. 1990, *J.R. Clarkson* 8245 & *V.J. Neldner* (BRI, DNA, QRS); SE of Mareeba on Tinaroo Creek Road, 27 May 1983, *B.J. Conn* & *J. De Campo* 1188 (BRI, CANB, MEL); head of Garraway Creek, Cape Weymouth, 16 Apr. 1988, *P.I. Forster* 4224 & *D.J. Liddle* (BRI, K); Bakers Blue Mountain, Font Hills, 11 Apr. 1995, *B. Hyland* 15286, 15290 (QRS); Tinaroo State Forest, June 1970, *V.K. Moriarty* 305 & 324 (BRI, CANB); Mt Archer near Rockhampton, 18 Feb. 1980, *T. Stanley* 584 (BRI); Horn Island, 29 May 2002, *B.M. Waterhouse* 6439 (CANB).

Distribution and habitat. Confined to north-eastern Queensland, on Cape York Peninsula, mainly north of 13° S, with outliers near Mareeba and Rockhampton provisionally included (see discussion under *A. spilanthoides*, *Taxonomic notes*) (Figure 36, Map 4). Found in usually sandy soils in grasslands, on beaches, in grassy understorey of *Eucalyptus/Corymbia* woodland, and understorey of monsoon forest/vine thicket, at altitudes from sealevel to 650(–1,000) m.

Phenology. Collected in flower January–August, in fruit January–July.

Conservation status. Not threatened.

Notes. This species is clearly allied to *A. spilanthoides*, sharing the long-pedunculate capitula of that species, and differing mainly in its large, ovate to suborbiculate leaves (linear to lanceolate in *A. spilanthoides*), and strongly angled achenes. It differs from most other *Apowollastonia* species in its strongly compressed disc achenes. For further discussion see under *A. spilanthoides*.

3. *Apowollastonia major* Orchard, *sp. nov.*

Type: c. 1 km inland from Gona along Popondetta track, Papua New Guinea, 27 July 1953, *R.D. Hoogland* 3449 & *G. Macdonald* (*holo:* CANB 40866!; *iso* BM!, K!, & *ex sched.* A, BRI, L, LAE, US, all *n.v.*).

[*Wedelia spilanthoides* *auct. non* F.Muell.: J.G. Boerlage, *Handl. Fl. Ned. Ind.* 2: 242 (1891); C. Lauterbach, in H.A. Lorentz, *Nova Guinea* 8: 866 (1912); J. Matfeld, *Bot. Jahrb.* 62: 436 (1929); J.T. Koster, *Blumea* 25: 270–271 (1979), and other New Guinean authors.]

Perennial *herb* 0.7–1.0(–2.0) m tall; *stems* 2–4 mm diam., erect or ascending, stiff, striate, appressed hairy. *Leaves* shortly petiolate; petioles 5–10 mm long; lamina ovate to lanceolate, 70–110 mm long, (20–)35–45 mm wide, becoming narrower above, green and discolorous, moderately densely appressed-scabrous both surfaces, cuneate to rounded basally, acute to subobtuse apically, serrate with even-sized short teeth (1–2 mm). *Capitula* usually in groups of 1–3, on peduncles 5–7 cm long; outer *involucral bracts* ovate, 4–5 mm long, obtuse, shorter than disc florets, densely appressed-scabrous abaxially.

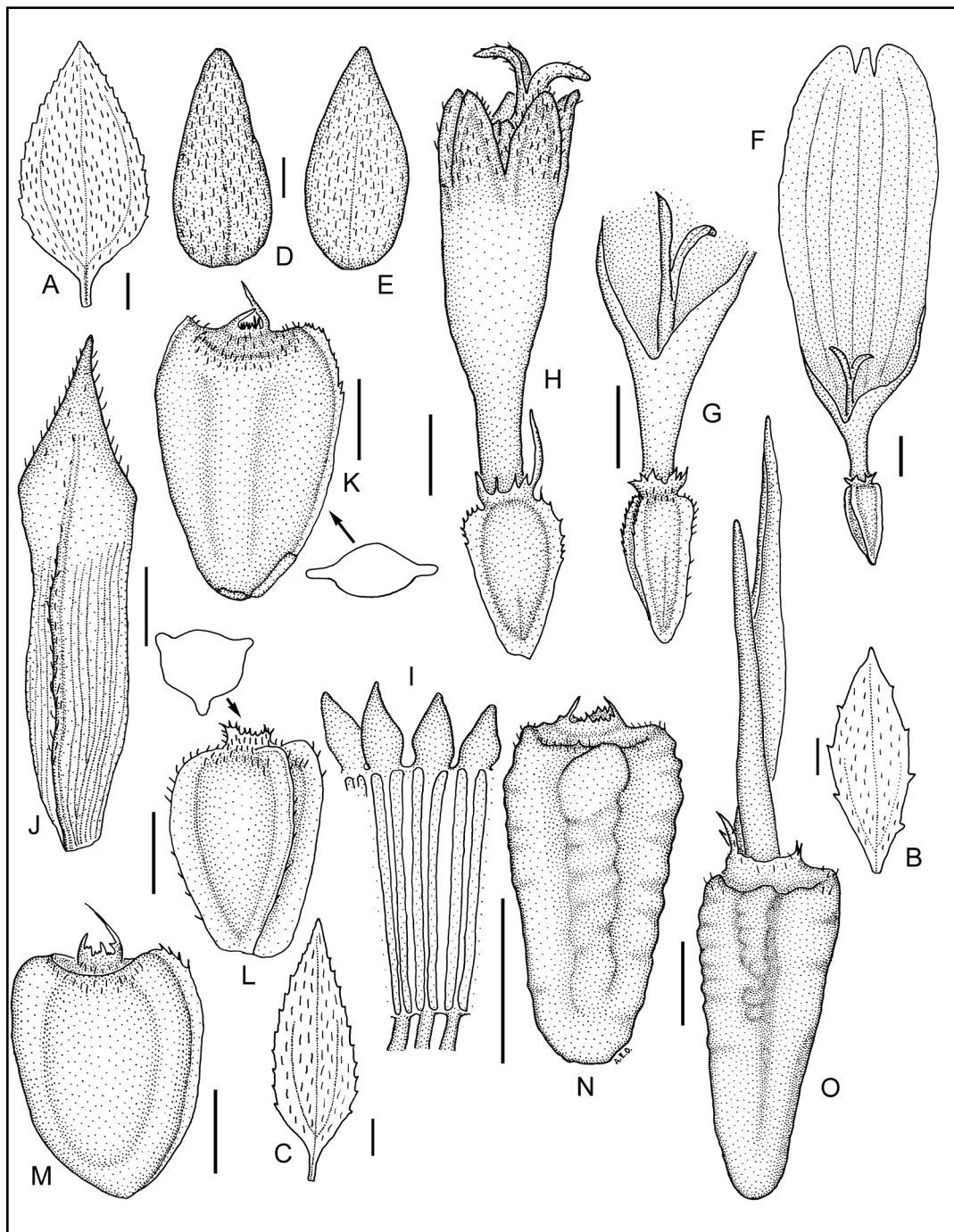


Figure 20. *Apowollastonia longipes*. A–C – leaves; D – outer involucre bract; E – inner involucre bract; F – ray floret; G – detail of ray floret ovary; H – disc floret; I – stamens; J – palea; K, M – disc achene; L – ray achene; N, O – anomalous achenes (elongate, with some pappus scales elongated). (A, D–L based on *J.R. Clarkson 8245 & V.J. Neldner* (BRI); C, M based on *J.R. Clarkson 8245 & V.J. Neldner* (QRS); B, N, O based on *B.M. Waterhouse 6439* (CANB)). Scale bars: A–C = 1 cm; D–O = 1 mm. Del. A.E. Orchard.

Capitulum in fruit 6 mm long, 8 mm diam. *Ray florets* 8 or 9; *corolla* lamina c. 6 mm long, 2- (rarely 3-)lobed, with 2 main veins and c. 9 lesser ones, shortly and sparsely hairy on main veins abaxially. *Disc florets* c. 25; *corolla* yellow, shortly hairy on exterior of lobes; *anther thecae* usually yellow, rarely yellow-brown (and perhaps black - see *Notes* below). *Paleae* obcuneate to obovate, outer ones sometimes with 2 apical teeth, 4 mm long in flower, green, midrib faint but longitudinal striae present basally, conduplicate, coarsely scabrous abaxially. *Achenes* dark brown to black, obloid to obovoid, 2–3 mm long, 1.5–2.0 mm wide, bluntly 2- or 3-angled but not winged, minute hairs apically, smooth. *Pappus* a ring of very short hairs and tiny, laciniate scales. (Figure 21)

Specimens examined. INDONESIA: Roga, Flores, 8 Feb. 1910, *J. Elbert* 4343 (CANB, L); Manokwari, West Papua, 1 Aug. 1848, *A. Kostermans* 2912 (L). PAPUA NEW GUINEA: G. Pisero, 1903, *Atasrip* 232 (BO); Koitari, 9 May 1935, *C.E. Carr* 12233 (BM, CANB, K); Lake Wanum, E shore, 8 May 1976, *S.E. Garrett-Jones* ANU21139 (CANB); BGD Cattle Property, Leron, 4 Jan. 1963, *E.E. Henty* 14864 (CANB, K); Leron plain near gorge, Lae, 8 Jan. 1968, *E.E. Henty & M.J.E. Coode* NGF29177 (CANB); 8 km from Sialum, 28 May 1975, *E.E. Henty & F. Katik* NGF49795 (K); Kgeloopeberge, Oosttelling, 16 June 1911, *K. Gjellerup* 496 (BO); 29 km ESE of Dreikikir, 18 July 1966, *P.C. Heyligers* 1412 (CANB); Finschhafen, 1889–1891, *Lauterbach* 1276 (BO); near Tarengi, Wewak–Maprik road, 22 Aug. 1959, *R.G. Robbins* 2224 (CANB); N of Simboro Strait, Sentani Lake, W of Hollandia, Feb. 1945, *R.S. Sigafos* 14 (BO); Port Moresby, *s. dat.*, *C.T. White s.n.* (K); W side of Kupiano High School, 30 June 1977, *J. Wiakabu et al.* LAE70423 (CANB, K).

Distribution and habitat. Indonesia, on the island of Flores and in West Papua; Papua New Guinea. In tall grasslands dominated by *Themeda*, *Imperata* and *Ophiuros*, at altitudes of at least 15–450 m.

Phenology. Flowers present January–August, achenes May–July.

Conservation status. Unknown, probably not threatened.

Taxonomic notes. Previous accounts of this species have usually equated it with *Apowollastonia spilanthoides* (as *Wedelia spilanthoides*). It differs from *A. spilanthoides* in its much more robust habit, with stems frequently 4 mm in diameter (less than 2 mm in most Australian collections), and large, lanceolate leaves 70–110 × (20–)35–45 mm (30–70(–90) × 3–10 mm in *A. spilanthoides*). Despite its robust habit and large leaves, *A. major* has smaller capitula and achenes than *A. spilanthoides*.

Notes. One of the characteristics distinguishing species of *Apowollastonia* from those of *Wollastonia* are their yellow anther thecae. Most collections of *A. major* have yellow thecae, but in a few specimens they appear black. It is possible that these black specimens are the result of alcohol pretreatment and/or excessive heat applied during drying. Field notes on this character are not available.

Etymology. The epithet *major* (Latin, ‘greater’) is adopted as this is the most robust of all *Apowollastonia* species.

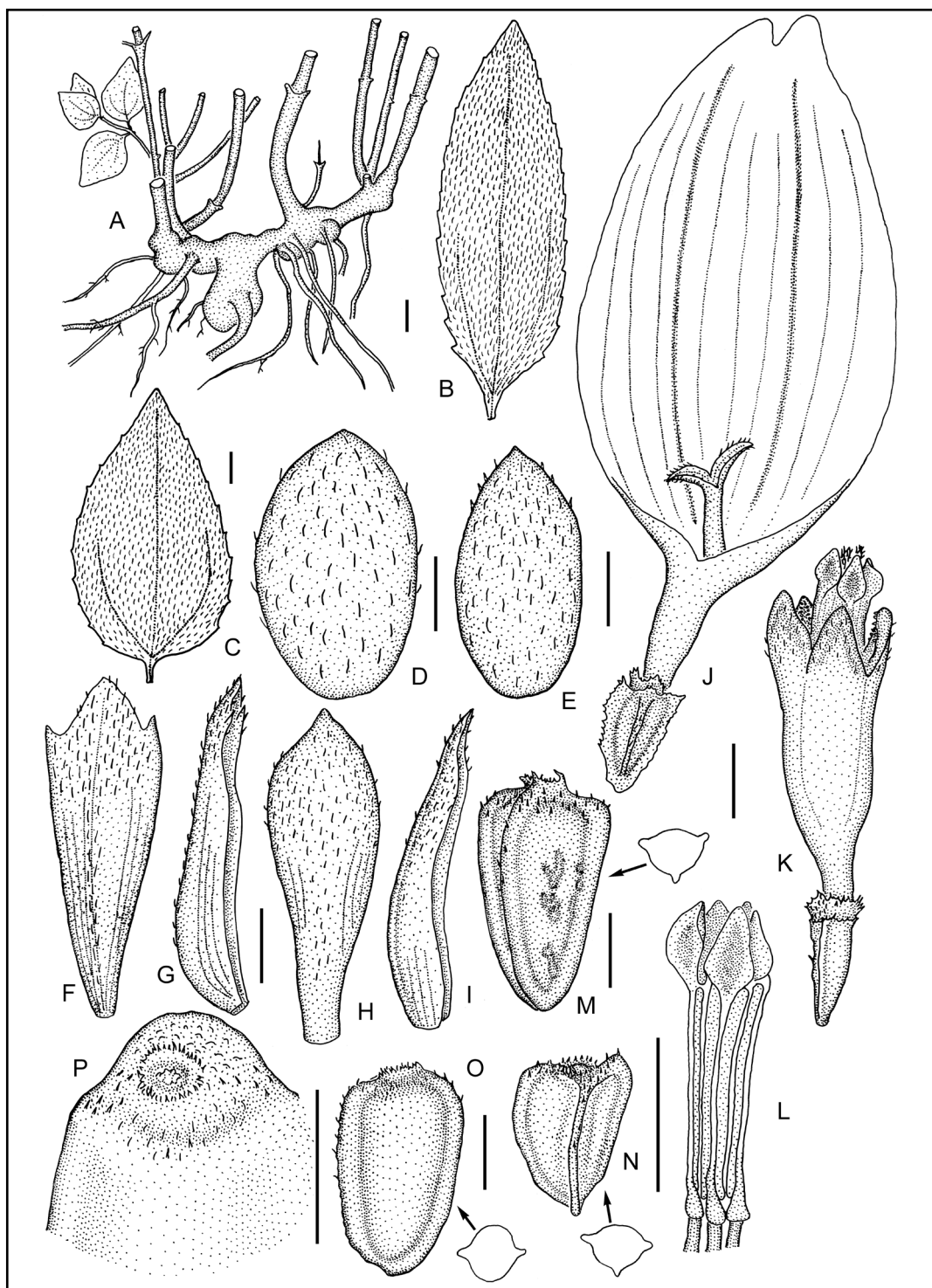


Figure 21. *Apowollastonia major*. A – rootstock; B, C – leaf; D – outer involucre bract; E – inner involucre bract; F – innermost involucre bract, transitional to palea, dorsal view; G – innermost involucre bract, lateral view; H – palea, dorsal view; I – palea, lateral view; J – ray floret; K – disc floret; L – stamens; M, N – ray achenes; O – disc achene; P – disc achene, detail of pappus. (A, C based on *S.E. Garrett-Jones* ANU21139 (CANB)); B, D–L, N–P based on *R.D. Hoogland* 3449 & *G. Macdonald* (CANB); M based on *J. Wiakabu et al.* LAE70423 (CANB)). Scale bars: A–C = 1 cm; D–P = 1 mm. Del. A.E. Orchard.

4. *Apowollastonia verbesinoides* (Benth.) Orchard, *comb. nov.*

Wedelia verbesinoides Benth., *Fl. Austral.* 3: 538 (1867); *Seruneum verbesinoides* (Benth.) Kuntze, *Revis. Gen. Pl.* 1: 365 (1891). *Type citation*: ‘N. Australia, F. Mueller; Arnhem S. Bay, R. Brown; Finke river, McDouall Stuart’s Expedition’ (*lecto*, chosen here: Buphthalmum, Arnhem South Bay, Point U1, adlat: coll: granitic, 6 Feb. 1803, R. Brown [Bennett no. 2115], BM 1053448 photo!; *isoleccto*: Caledon Bay (Arnhem South Bay), Mt Caledon (point U1), 6 Feb. 1803, R. Brown s.n. [‘Buphthalmum strigosum, North Coast’], CANB 279200!; Caledon Bay (Arnhem South Bay), Mt Caledon (point U1), 6 Feb. 1803, R. Brown s.n., MEL 537475!, NSW!; ‘East Coast’ (sphalm.), herb. R. Brown, K!; *syn*: Trop. Austral., *s. dat.*, [F. Mueller s.n.], MEL 2258044 photo!; Trop. Australia, *s. dat.*, Dr. M[ueller], K, herb. Hooker!; Finke River, McDouall Stuart’s Expedition, K, herb. Hooker!). *Excluded syn*: Finke R., *s. dat.*, J.M. Stuart s.n. (AD 97643097A (fragment)!, ex herb. J.M. Black ‘lent by Vict. Natl. Herbarium Apr. 1934’), = *Apowollastonia stirlingii* subsp. *stirlingii*.

Wedelia sp. B *sensu* A.J.G. Wilson, in J.R. Wheeler (ed.), B.L. Rye, B.L. Koch & A.J.G. Wilson, *Fl. Kimberley Reg.* 961 (1992).

Illustrations. J.R. Wheeler (ed.), B.L. Rye, B.L. Koch & A.J.G. Wilson, *Fl. Kimberley Reg.* p. 952, Figure 289S (1992), as *Wedelia* sp. B; Figures 22, 23 herein.

Subshrub 0.6–1.0(–2.0) m tall; young *stems* erect, branching, moderately densely scabrous with spreading hairs; older stems glabrous with pale, ± corky bark. *Leaves* shortly petiolate; petioles 10 mm long; lamina ovate to suborbicular, 45–80 mm long, (20–)35–40 mm wide, shiny, discoloured, finely appressed hairy adaxially, more densely scabrous abaxially especially on the prominent veins, cuneate basally, blunt apically, shortly serrate. *Capitula* in clusters of 3–5, on peduncles 15–25 mm long; outer bracts lanceolate, 4 mm long, acute, *c.* as long as disc florets, appressed-scabrous, especially on margins; inner bracts similar, paler, strongly striate. *Capitulum* in fruit 8 mm long, 10 mm diam. *Ray florets* *c.* 12; *corolla* lamina 6–7 mm long, 2-lobed, weakly veined, sparsely pilose abaxially. *Disc florets* *c.* 24; *corolla* yellow, sparsely scabrous externally towards apex; *anther thecae* yellow. *Paleae* linear-lanceolate, 5.5 mm long in flower, green, with midrib and lateral longitudinal striae, conduplicate, scabrous abaxially. *Achenes* dark brown to black, usually narrowly obovoid, sometimes obcuneate, 2.5–3 mm long, 1.5 mm wide (both excluding wings), 2-angled (disc) or 3-angled (ray) variously winged on angles (wings thick and corky), short hairs apically, body of achene usually rugose. *Pappus* a ring of very short irregular scales, sometimes with a single fragile awn 1.5–2.0 mm long. (Figures 22, 23)

Specimens examined (selection). WESTERN AUSTRALIA: [localities withheld for conservation reasons] 23 June 1976, A.C. Beaglehole 53643 (CANB, PERTH); 7 Feb. 1979, K.F. Kenneally 7070 (CANB); 21 July 1959, M. Lazarides 6380 (AD, BRI, CANB, DNA, K, MEL, NSW); 1887, C.W. Nyulasy s.n. (MEL 1609756). NORTHERN TERRITORY: Settlement Creek, June 1922, L. Brass 159 (BRI, CANB, K); Mataranka, Elsey National Park, 16 Feb. 1999, I. Cowie 4586 & J. Egan (DNA, MEL); Mataranka, Elsey National Park, 17 Feb. 1994, J. Egan 3213 & C. Dunlop (BRI, CANB); 42 km SE Oenpelli, 14 June 1978, P.K. Latz 7778 (NT); South West Island, 28 May 1977, D. McKay 136 (DNA).

Distribution and habitat. Almost entirely confined to the Northern Territory, from Arnhem Land around the Gulf of Carpentaria almost to the Queensland border, with a few collections from the vicinity of Bedford Downs, and Mitchell River, Kimberleys, Western Australia (Figure 36, Map 5). Usually found in well-drained sandy soils in open situations or in the grassy understorey of woodlands, on a range of substrates (sandstone, limestone, calcrete, granite).

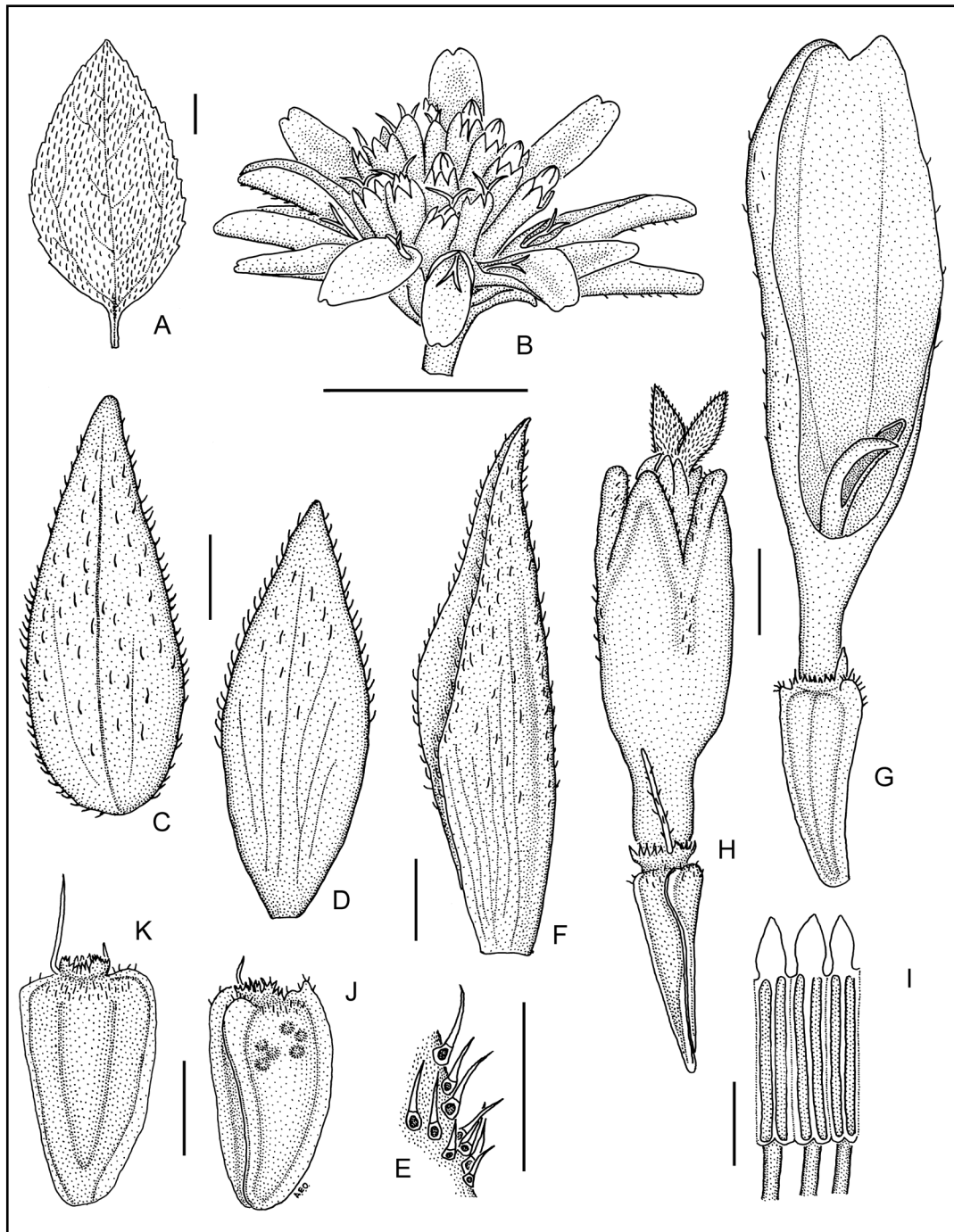


Figure 22. *Apowollastonia verbesinoides*. A – leaf; B – flowering capitulum; C – outer involucre bract; D – inner involucre bract; E – detail of hairs on margin of involucre bract; F – palea; G – ray floret; H – disc floret; I – stamens; J – ray achene; K – disc achene. (All based on *J. Egan* 3213 & *C. Dunlop* (CANB)). Scale bars: A, B = 1 cm; C–K = 1 mm. Del. A.E. Orchard.

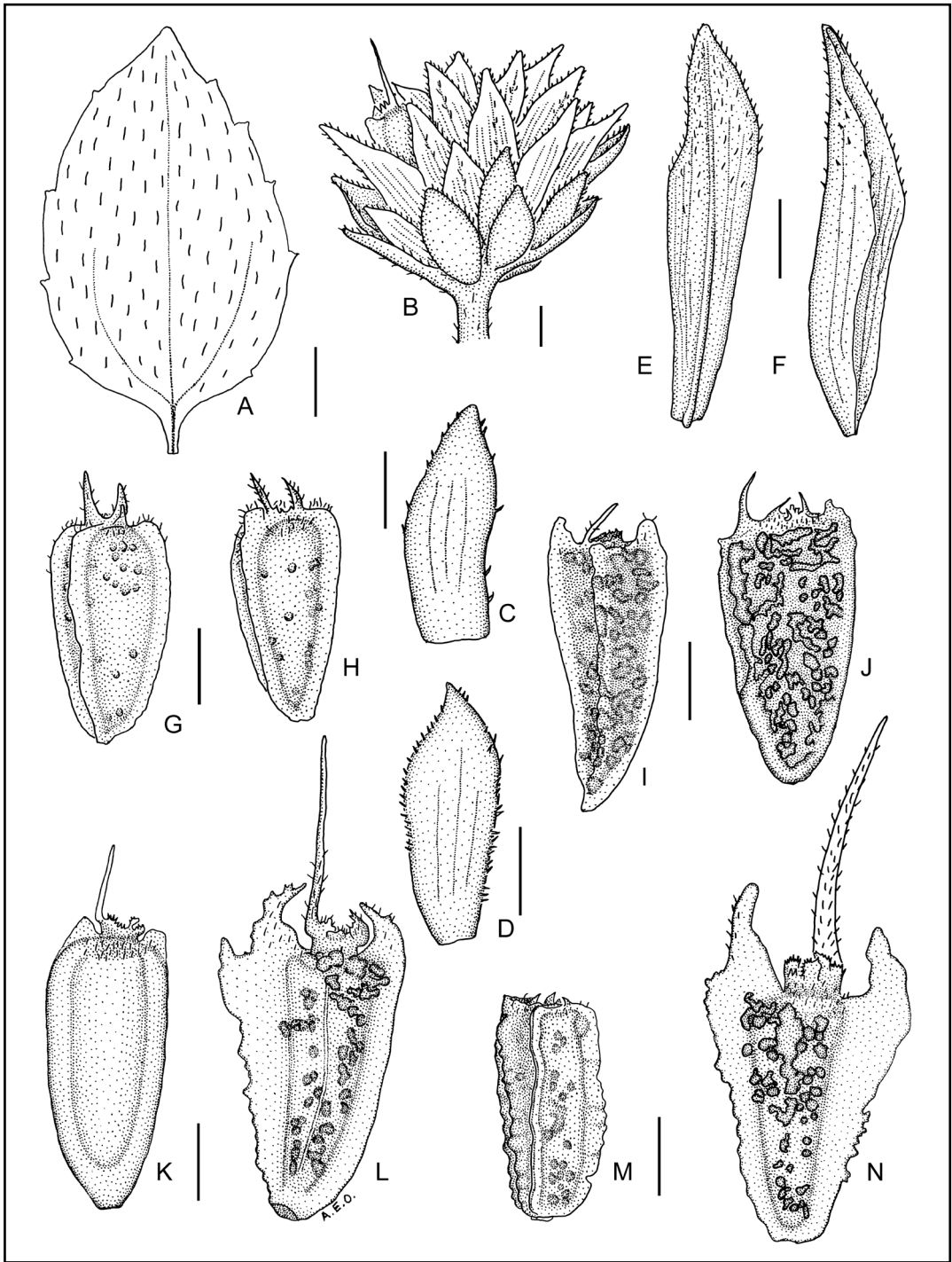


Figure 23. *Apowollastonia verbesinoides* (cont.). A – leaf; B – fruiting capitulum; C – outer involucre bract; D – inner involucre bract; E – palea, dorsal view; F – palea, lateral view; G–N – achenes (K is immature). (A–H based on *M. Lazarides* 6380 (BRI); I, J based on *M. Lazarides* 6380 (MEL); K, L based on *C.W. Nyulasy s.n.* (MEL); M based on *P.K. Latz* 7778 (NT); N based on *L.J. Brass* 159 (CANB)). Scale bars: A = 1 cm; B–N = 1 mm. Del. A.E. Orchard.

Phenology. Flowers collected January–July, fruits February–July(–September).

Conservation status. Listed by Smith (2012) as Priority One under the Department of Environment and Conservation's (DEC; now the Department of Parks and Wildlife) Conservation Codes for Western Australian Flora, as *Wedelia verbesinoides*. Elsewhere, probably not threatened.

Taxonomic notes. The shape of achenes in this species is very variable, from oblong with narrow wings, to rather broadly cuneate-winged. It is clearly closely allied to *A. hamersleyensis*, *A. stirlingii* and *A. hibernica*, and there are suggestions of introgression with *A. stirlingii* in the southern part of the range of *A. verbesinoides*, and with *A. hibernica* to the south-west. However, the species are usually easily distinguished on leaf shape and size, and in the case of *A. verbesinoides* vs. *A. hibernica*, achene size. *Apowollastonia verbesinoides* is further distinguished from *A. stirlingii* and *A. hamersleyensis* by its relatively short peduncles.

The collection *M. Lazarides* 6380 from near Bedford Downs, Kimberley, Western Australia, has been tentatively separated in the past as '*Wedelia* sp. B', and the Kimberley populations are apparently disjunct from those of the Northern Territory. The achenes of *M. Lazarides* 6380 in MEL are undoubtedly fairly distinct from those of Northern Territory collections (see Figure 23I, J), but those on the duplicate specimen in BRI are well within the range of Northern Territory collections (Figure 23G, H). The Kimberley populations otherwise match *A. verbesinoides* fairly well, and given the small number of Kimberley collections, the variation observed elsewhere, and the variation within this one sample, the Kimberley plants are not formally recognised as distinct at this time.

The specimen from the Bungle Bungles which was the basis of '*Wedelia* sp. A' (Wilson, *loc. cit.*) has not been located for this study. From the description (which was based on a flowering specimen only) it seems likely that this taxon is *Pentalepis trichodesmoides* subsp. *incana* Orchard.

Notes. One collector noted that the plant had a strong odour when picked. The innermost disc florets apparently do not always set fertile achenes.

5. *Apowollastonia hibernica* Orchard, *sp. nov.*

Type: Killarney Stn, site K3, Northern Territory, 6 October 2002, *J.A. Risler & D.J. Milne* 1927 (*holo:* DNA 157104).

Subshrub 0.8–1.5 m tall; young *stems* erect, branched, appressed hairy; older stems glabrous with pale, ±corky bark. *Leaves* shortly petiolate; petioles 5–7(–20) mm long; lamina lanceolate, 40–60(–100) mm long, 10–12(–30) mm wide, discolorous, coarsely appressed-scabrous on both surfaces especially on prominent veins abaxially, rounded to cuneate basally, acute to acuminate, shortly serrate. *Capitula* in clusters of 1–3, on peduncles 15–20(–30) mm long; *outer bracts* linear to lanceolate or narrowly ovate, 6(–10) mm long, acute, *c.* equalling disc florets, appressed-scabrous abaxially; *inner bracts* similar but narrower with hairs more apical. *Capitulum* in fruit 7–10 mm long, 8–10 mm diam. *Ray florets* 6–10; *corolla* lamina 8 mm long, 2-lobed, weakly veined, sparsely pilose abaxially. *Disc florets* *c.* 20; *corolla* yellow to orange, pilose externally; *anther thecae* yellow. *Paleae* linear to lanceolate, 7–8 mm long in flower, green, with midrib and 2 or 3 lateral, longitudinal striae, conduplicate, abaxially densely hispid. *Achenes* narrowly obcuneate, 5–6 mm long, 2 mm wide, 3-angled with angles narrowly winged, and wing tips extended at apex into short, acute lobes; body of achene densely and minutely tuberculate. *Pappus* a ring of very short, irregular scales to 0.2 mm long. (Figure 24)

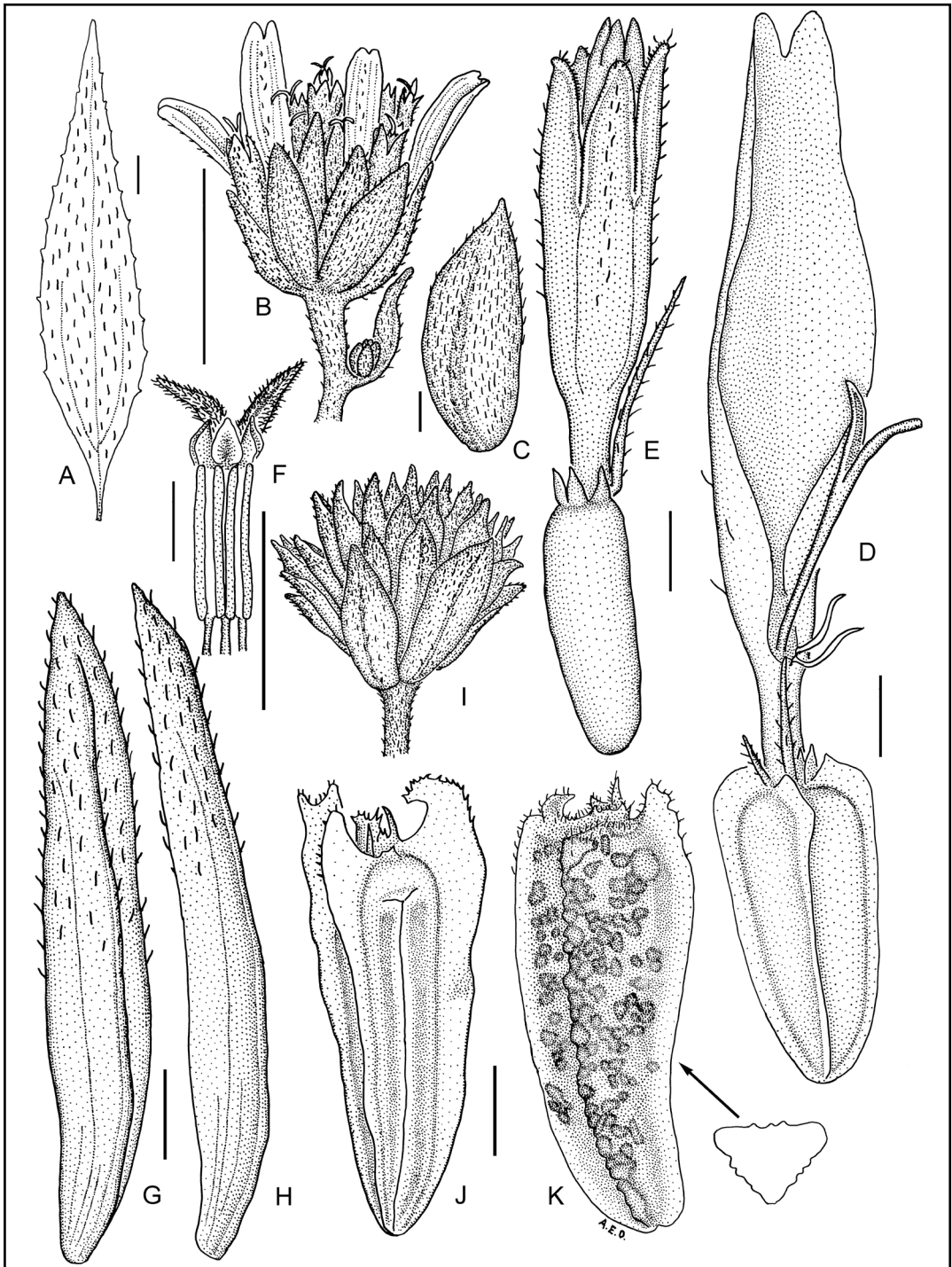


Figure 24. *Apowollastonia hibernica*. A – leaf; B – flowering capitulum; C – involucre bract; D – ray floret; E – disc floret; F – stamens and stigma; G – palea, dorsal view; H – palea, lateral view; I – fruiting capitulum; J – immature achene; K – mature achene. (A, B based on *T.S. Henshall* 45 (CANB); C, I, K based on *J.A. Risler & D.J. Milne* 1927 (DNA); D–H based on *J.A. Risler & A.J. Fisher* 1942 (DNA); L based on *K.G. Brennan* 4192 (DNA)). Scale bars: A, B, I = 1 cm; C–H, J, K = 1 mm. Del. A.E. Orchard.

Specimens examined. NORTHERN TERRITORY: Limestone Gorge, 19 July 1995, *R. Booth* 1268 (DNA); Killarney Stn, 21 May 1999, *K.G. Brennan* 4192 (DNA); Top Springs, 17 June 1953, *H.F. & M. Broadbent* 888 (CANB); Lennee Creek, Davenport Ranges, 11 Sep. 2003, *A. Duguid* 500 (DNA); Seigals Creek Outstation S of Calvert Hills, 30 May 1973, *N. Henry* 772 (BRI, CANB); 16 miles [c. 25 km] S Goyder River crossing, 16 June 1972, *P.K. Latz* 2798 (AD, BRI, CANB, MEL, PERTH); 48 km NE of Devils Marbles, 15 Apr. 1983, *P.K. Latz* 9714 (DNA, NT); Whistleduck Gorge, Davenport Ra., 23 Sep. 1983, *P.K. Latz* 9765 (DNA, NT); Killarney Stn, 24 May 1999, *C.R. Michell* 2706 (DNA); c. 21 km W of Wollogorang on road to Calvert Hills, 12 May 1974, *R. Pullen* 9218 (CANB, NSW); Killarney Stn, site 6, 12 Dec. 2002, *J.A. Risler & A.J. Fisher* 1942 (DNA); Killarney Stn track N from Monster Bore, 27 Apr. 2003, *J.A. Risler & D.L. Lewis* 3124 (DNA).

Distribution and habitat. Confined to the Northern Territory, in a broad area mainly south of Arnhem Land, to the Davenport Range, and from about the Victoria River to the Queensland border (c. (13°–)16–21° S, 130° 30'–137° 45' E) (Figure 36, Map 6). Found in open grasslands of *Enneapogon*, *Sorghum* and *Aristida* spp., or the understorey of *Eucalyptus/Corymbia* open grassy woodland, on a range of soils and substrates (limestone, granite, sandstone).

Phenology. Flowers and fruits collected April–December.

Conservation status. Probably not threatened.

Taxonomic notes. For distinguishing characteristics between this and related species, see under *A. verbesinoides*. *Apowollastonia stirlingii* subsp. *stirlingii* is almost contiguous with *A. hibernica* and appears similar in flower, but has much longer peduncles and smaller leaves.

Notes. The innermost disc flowers apparently do not set fruit. Most collectors describe this species as having 'yellow flowers', but *Pullen* 9218 describes it as having yellow rays and orange disc.

Etymology. This species has been frequently collected on Killarney Station, hence the epithet '*hibernica*'.

6. *Apowollastonia stirlingii* (Tate) Orchard, *comb. nov.*

Wedelia stirlingii Tate, *Trans. R. Soc. S. Aust.* 19: 81 (1895), *nom. nud.*; R. Tate, *Report Horn Exped. Central Austral.* 3: 167, 188 (1896). *Type citation:* 'Rocky and stony ground, Stokes Pass, slopes of Mereenie Bluff, Mount Francis and Mount Sonder, Finke Gorge and Stuart's Pass!' (*lecto*, chosen here: Red Bank, Upper Finke River, Horn Expedition, *s. dat.*, *S. Baldwin s.n.* [herb. Tate], AD 97632384!). *Syn:* Mereenie Bluff, 1894, *R. Tate s.n.* (K!); Mereenie Bluff, 1894 (AD 97643097B, herb. Tate, herb. J.M. Black (fragment)!); Mereenie Bluff, *R. Tate s.n.* (AD 97918148 photo!); Stokes Creek Gorge, *R. Tate s.n.* (AD 97918142 photo!); Central Australia, *R. Tate s.n.* (AD 97449202 photo!); Horn Expedition [no other data], NSW!).

Subshrub 0.3–0.75(–1.5) m tall (to 2 m diam.); young *stems* stiffly erect to spreading, weakly striate, coarsely and densely scabrous; older stems with white, ±corky bark. *Leaves* sessile to subsessile; lamina linear-lanceolate to lanceolate, (15–)25–60(–70) mm long, (5–)6–8(–20) mm wide (excluding teeth), grey-green, densely and coarsely appressed-scabrous on both surfaces, cuneate at base, acute, serrate (sometimes subentire) or pinnatisect. *Capitula* usually solitary, on stout peduncles 10–12(–18) cm long; *outer bracts* lanceolate, 4.0–4.5 mm long, acute, shorter than disc florets, densely and coarsely appressed-scabrous; *inner bracts* similar but broader. *Capitulum* in fruit 7–10 mm long, 8–15 mm

diam. *Ray florets* c. 15; *corolla* lamina 7–10 mm long, 2-lobed, veins obscure, sparsely pilose on veins abaxially. *Disc florets* c. 50–100; *corolla* yellow to orange, shortly scabrous on lobes externally; *anther thecae* yellow. *Paleae* linear, 6 mm long in flower, green, with distinct midrib and 2 main lateral, longitudinal striae, strongly conduplicate, scabrous on midrib and dorsally. *Achenes* brown with lighter wings, obcuneate to obovoid, 3.0–3.5(–5.0) mm long, 2.0 mm wide (excluding wing), 2-angled (disc) or 3-angled (ray), with angles bearing well-developed thick, subcorky or submembranous wings which are often extended above into auricles; very shortly hairy apically, body of achene smooth or with an indistinct longitudinal vein or minutely tuberculate. *Pappus* a ring of short, lacinate scales, sometimes shortly fused at base, occasionally 1(–3) extended into a short, fragile awn.

Notes. A variable species from central Australia, characterised by long, stout peduncles, grey-green, linear-lanceolate, coriaceous and densely scabrous leaves, and achenes with two or three submembranous, apically auriculate wings. It differs from other *Apowollastonia* species in having paleae that are acute rather than acute-acuminate. The paleae are shed shortly after the achenes (long-persistent in other species). However, in other characteristics it clearly belongs in this genus. Most collectors describe the corollas as yellow, but the label on *P.E. Conrick* 792, Mt Cuthbert, South Australia, describes the capitulum as having ‘orange yellow petals, orange centre’, and this is supported by the photograph displayed in *FloraBase* (Western Australian Herbarium 1998–; see below). Two subspecies can be distinguished as follows:

Key to the subspecies of *Apowollastonia stirlingii*

1. Leaves (20–)30–40(–60) mm long, lanceolate to linear-lanceolate;
lamina 4–5(–10) mm wide, almost entire or with deltate teeth
1–2(–3) mm long **6a.** subsp. **stirlingii**
- 1: Leaves 20 mm long, almost pinnatisect (c. ovate in outline);
rachis of lamina 1–1.5 mm wide, with long filiform spreading teeth
3–4(–8) mm long **6b.** subsp. **fontaliciana**

6a. *Apowollastonia stirlingii* (Tate) Orchard subsp. *stirlingii*

Illustrations. D.A. Cooke, in J.P. Jessop & H.R. Toelken, *Fl. S. Australia* 4th edn 3: 1441, Figure 650 (1986), as *Wedelia stirlingii*; Western Australian Herbarium, in *FloraBase*, <http://florabase.dec.wa.gov.au> [accessed 16 April 2012], as *Wedelia stirlingii*; Figure 25 herein.

Leaves (20–)30–40(–60) mm long, lanceolate to linear-lanceolate; *lamina* 4–5(–10) mm wide, almost entire or with deltate teeth 1–2(–3) mm long; fruiting *capitula* usually large, to 10 mm long, 15 mm diam.; *achenes* 3–5 mm long (excluding wings), with well-developed wings which are apically auriculate. (Figure 25)

Specimens examined (selection). WESTERN AUSTRALIA: [locality withheld for conservation reasons] 24 June 1989, *D.J. Pearson* 630 (PERTH). NORTHERN TERRITORY: Finke River, 3 miles [c. 5 km] S of Glen Helen HS, 4 Feb. 1955, *G. Chippendale s.n.* (NT); Mount Riddock Stn, 13 Sep. 1973, *N.M. Henry* 916 (BRI, CANB); Simpsons Gap, 18 Apr. 1974, *T.S. Henshall* 3 (CANB); Yuendumu, 19 Mar. 1980, *T.S. Henshall* 2866 (AD, MEL, NT); 13 km SW Todd River Downs HS, 16 Mar. 1995, *P.K. Latz* 14174 (DNA). SOUTH AUSTRALIA: sandy flats near Fregon, 18 May 1983, *R. Bates* 3013 (AD); Ernabella, 16 Apr. 1950, *E.C. Black s.n.* (AD); summit of Mt Morris, 7 Sep. 1963, *Hj. Eichler* 17360 (AD); Tomkinson Ra., 22 Sep. 1955, *W.S. Reid* 86 (AD); foot of Mt Harriet, 5 Sep.

1963, *D.J.E. Whibley* 944, (AD). QUEENSLAND: [locality withheld for conservation reasons] 10 July
1982, *R.W. Purdie* 2242 (BRI, CANB).

Distribution and habitat. Confined to the ranges of central Australia: widespread in the Northern Territory, from the Davenport Range south through the MacDonnell Ranges to the Musgrave and Tomkinson Ranges of South Australia, and west to the Warburton Range in Western Australia. One collection is known from the Toko Range in Queensland (see *Notes* below) (Figure 37, Map 7). Found in dry, rocky situations on sandstone or limestone, with spinifex (*Triodia* spp.) in open woodland dominated by *Eucalyptus*, *Acacia* and *Dodonaea*.

Phenology. Flowers have been collected year-round, fruits February–September.

Conservation status. Recently listed as Priority One under DEC Conservation Codes for Western Australian Flora, as *Wedelia stirlingii* (Western Australian Herbarium 1998–). In Northern Territory and South Australia: probably not threatened. In Queensland: poorly known, status unclear (see *Notes* below).

Nomenclatural notes. Tate cited at least six collections from the Horn Expedition when describing *Wedelia stirlingii*. These are now in three or more herbaria (AD, K, NSW), and all are rather scrappy. The Red Bank specimen in AD is chosen as lectotype because it is relatively large, and is from Tate's own herbarium, although he undoubtedly saw all of the syntypes.

Notes. The leaf lamina of this subspecies is relatively broad, usually 4–5 mm wide, with short teeth (some leaves on some plants almost entire). The species is only sparingly collected in Queensland, where one collection (*Purdie* 2242) is a good match with Northern Territory specimens. Other Queensland collections are variable, and only tentatively assigned to subsp. *stirlingii*: a collection from Cameron River, 15 Feb. 1998, *A. Fraser* 257 (CANB) has winged achenes, but pappus \pm absent; another from Mt Booka Booka, Elderslie, 29 Oct. 1935, *S.T. Blake* 10055 (AD) has achenes barely angled, and leaves linear, 70 mm long, coarsely toothed; a third from 20 miles [32 km] NW of Kihee, 11 Nov. 1949, *E. Riek & I. Common* 258 (CANB) has \pm entire leaves, but flowers only, no achenes. These last three collections need reconsideration when additional collections with mature fruit have been made from the Channel Country of south-western Queensland.

6b. *Apowollastonia stirlingii* subsp. *fontaliciana* Orchard, *subsp. nov.*

Type: Standley Chasm, Northern Territory, 17 November 1954, *G. Chippendale s.n.* (*holo:* NT 523; *iso:* AD 98672975, BRI 365709, CANB 33209, PERTH 525103).

Leaves 20 mm long, approximately ovate in outline, almost pinnatisect; rachis of *lamina* 1–1.5 mm wide, with long, filiform, spreading teeth 3–4(–8) mm long; fruiting *capitula* smaller, 7–8 mm long, 8 mm diam.; *achenes* 2.5–3.0 mm long, excluding the narrow wings, which are not markedly auriculate. (Figure 26)

Specimens examined (selection). NORTHERN TERRITORY: Spencer Gorge, Chewings Ra., 26 May 1977, *P.K. Latz* 7109 (NT); Hugh Gorge, Hamilton Downs Stn, 11 Aug. 1984, *W.A. Low* 189 (NT); Standley Chasm, 28 July 1979, *N. Ollerenshaw* 312 (CBG); Standley Chasm, 14 July 1968, *A.E. Orchard* 813 (AD, K, P); Standley Chasm, 4 Sep. 1955, *R.A. Perry* 5384 (AD, BRI, CANB (2 sheets), K, MEL, NSW, PERTH); 35.4 km from Hermannsburg Mission, 6 Oct. 1981, *L.D. Williams* 12122 (AD).

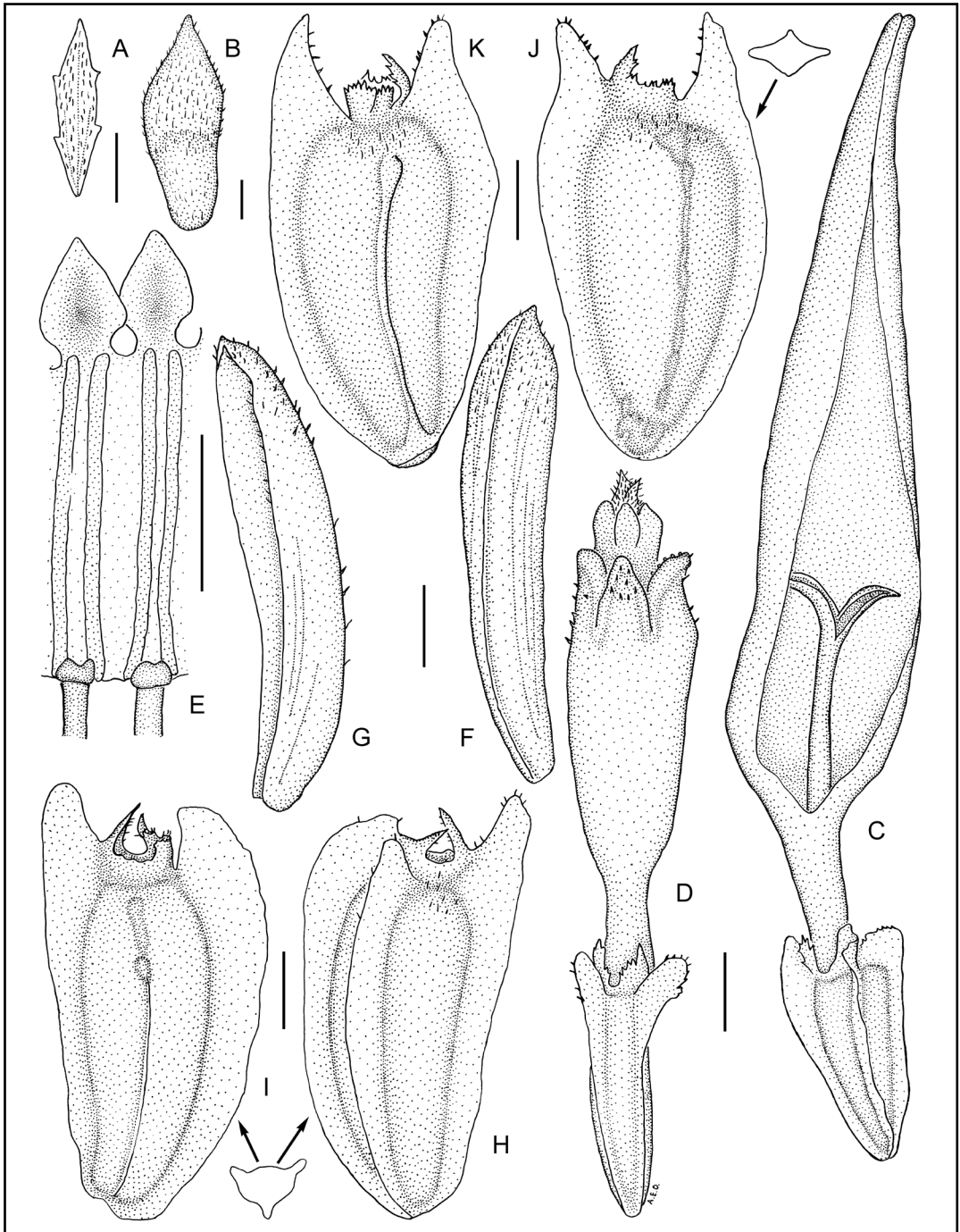


Figure 25. *Apowollastonia stirlingii* subsp. *stirlingii*. A – leaf; B – involucre bract; C – ray floret; D – disc floret; E – stamens; F – palea, dorsal view; G – palea, lateral view; H – ray achene, adaxial view; I – ray achene, abaxial view; J, K – disc achene, two sides. (All based on *E.C. Black s.n.* (AD 97637379)). Scale bars: A = 1 cm; B–K = 1 mm. Del. A.E. Orchard.

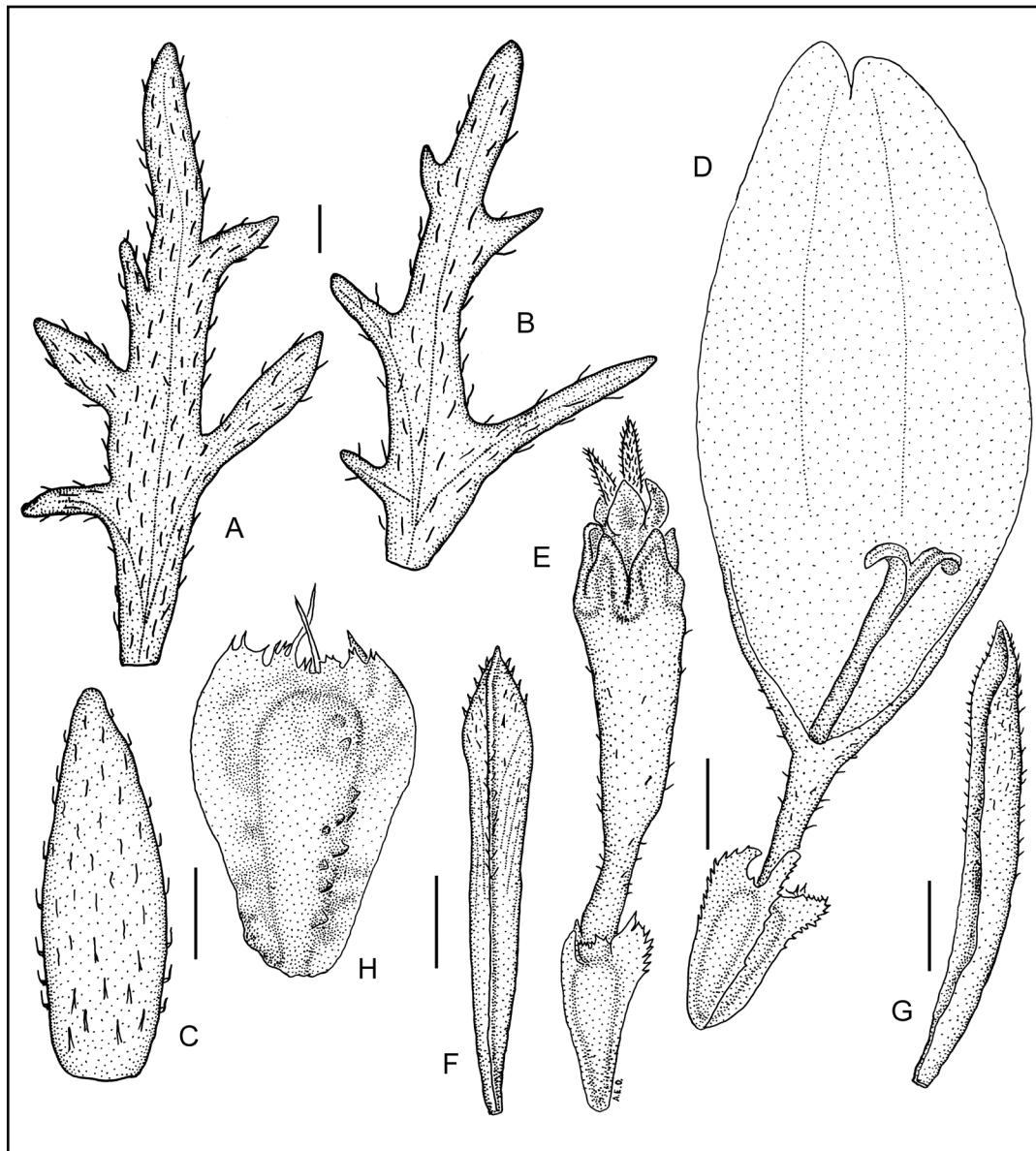


Figure 26. *Apowollastonia stirlingii* subsp. *fontaliciana*. A, B – leaves; C – involucre bract; D – ray floret; E – disc floret; F – palea, dorsal view; G – palea, lateral view; H – achene. (A–G based on *G. Chippendale s.n.* (NT 523); H based on *A.E. Orchard* 813 (AD)). Scale bars: A–H = 1 mm. Del. A.E. Orchard.

Distribution and habitat. Confined to the MacDonnell Ranges near Alice Springs, Northern Territory, and particularly well-collected from Standley Chasm and Spencer Gorge, with other specimens somewhat intermediate with subspecies *stirlingii* as far west as Ormiston Gorge (Figure 37, Map 8). Found in dry, rocky situations on the slopes of sandstone gorges and in river sand in the bed of dry creeks, with occasional *Eucalyptus* spp., *Acacia* spp. and *Dodonaea* spp.

Phenology. Collected in flower and fruit May–December.

Conservation status. Of restricted distribution in the Northern Territory, but probably not threatened.

Etymology. From the Latin *fons* (spring), *alicia* (latinisation of Alice), and *-ana* (place of origin).

7. *Apowollastonia hamersleyensis* Orchard, *sp. nov.*

Type: east of Paraburdoo, in major gully through Channar range, Western Australia, 26 Apr. 1985, E.M. Mattiske EMCH 1636 (*holo:* PERTH 6184294; *iso:* AD, BRI, CANB 684289, DNA, K, MEL, MO, NSW).

Wedelia sp. Hamersley (A.S. Weston 8444), *sensu* G. Paczkowska & A.R. Chapman, *West. Austral. Fl.: Descr. Cat.* 179 (2000).

Illustrations. Western Australian Herbarium, in *FloraBase*, <http://florabase.dec.wa.gov.au> [accessed 16 April 2012], as *Wedelia* sp. Hamersley (A.S. Weston 8444); Figure 27 herein.

Subshrub 0.4–1.0(–1.5) m tall, (0.6–1.0(–2.0) mm diam.); young *stems* stiffly erect to spreading, striate, moderately appressed-scabrous; older stems with white, ±corky bark. *Leaves* sessile; lamina linear, (15–)25–30(–80) mm long, (1–)2–5 mm wide, grey-green, coarsely appressed-scabrous on both surfaces, cuneate basally, bluntly acute, entire. *Capitula* 1–3, on stout peduncles 6–9 cm long; outer bracts ovate, 3–4 mm long, bluntly acute, shorter than disc florets, densely and coarsely appressed-scabrous abaxially; inner bracts similar but narrower. Capitulum in fruit 6–7 mm long, 7–8 mm diam. *Ray florets* 10–14; *corolla* lamina 6 mm long, 2-lobed, 2-nerved, sparsely and coarsely hairy on nerves abaxially. *Disc florets* 25–30; *corolla* yellow-orange, shortly scabrous externally on lobes; *anther thecae* yellow. *Paleae* linear to narrowly oblanceolate, 5.0–6.0 mm long in flower, green, with central midrib plus multiple fine, longitudinal striae basally, conduplicate, scabrous abaxially on tip only. *Achenes* black with paler marginal angles/wings; body of achenes obovoid, 4–5 mm long (excluding wings), 3-angled and winged (ray) or 2-angled and -winged (disc), often anisopterous, with wings truncate or shortly auriculate, submembranous; with sparse, short hairs apically and on distal wing margins. *Pappus* a ring of small, uneven, fimbriate scales, sometimes with 1 or 2 short awns. (Figure 27)

Specimens examined (selection). WESTERN AUSTRALIA: 30 km ESE Duck Creek Stn HS, 3 Aug. 1999, B. Backhouse et al. 229 (CANB); Yampire Gorge, Wittenoom, 2 June 1954, H.F. & M. Broadbent 1998 (BM, CANB); Hamersley Ra. National Park, between Mt Bruce and Joffre Falls, 17 July 1978, C. Dawe 052 (BRI, CANB, DNA, PERTH); 10.5 km SSW of Mt Truchanas, 10 Sep. 1996, S. van Leeuwen 2725 (DNA); Mt Barricade, Karijini National Park, 30 July 1998, S. van Leeuwen 3534 (PERTH); lower end of Bee Gorge, Hamersley Ra. National Park, 8 Aug. 1973, A.S. Weston 8444 (CANB, PERTH).

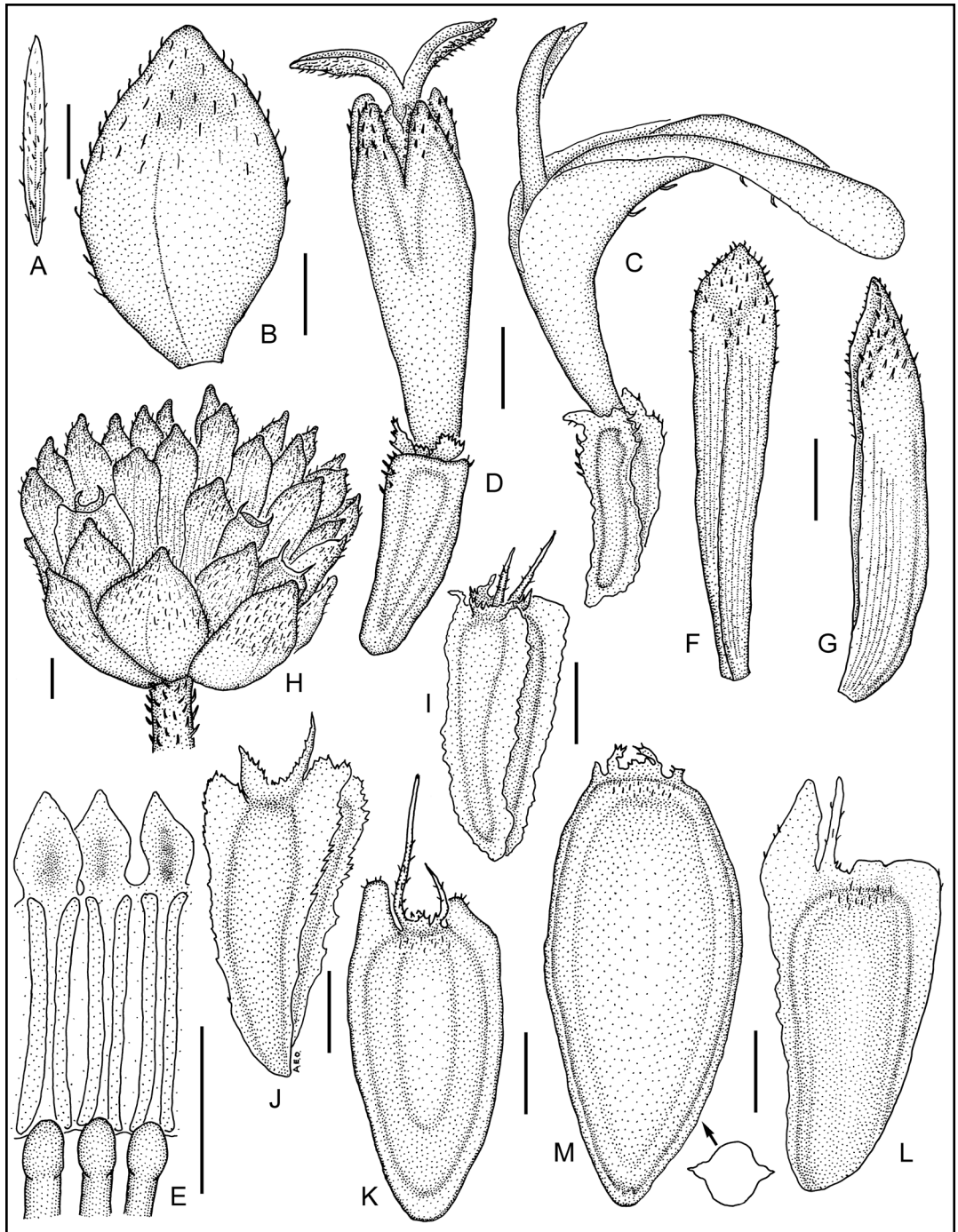


Figure 27. *Apowollastonia hamersleyensis*. A – leaf; B – involucre bract; C – ray floret; D – disc floret; E – stamens; F – palea, dorsal view; G – palea, lateral view; H – fruiting capitulum; I, J – immature ray achenes; K – immature disc achene; L – mature ray achene; M – mature disc achene. (A–H, M based on *C. Dawe* 052 (PERTH); I based on *A.S. Weston* 8444 (PERTH); J based on *M. Hughes s.n.* (PERTH 3634299); K based on *B. Backhouse et al.* 229 (CANB); L based on *M. Hughes s.n.* (PERTH 3634280)). Scale bars: A = 1 cm; B–M = 1 mm. Del. A.E. Orchard.

Distribution and habitat. Confined to the Pilbara region of Western Australia (Figure 37, Map 9). Found in dry, stony, well-drained sites, in loams, clays and skeletal red soils, on ironstones, basalts etc., among low shrubs and *Triodia* in open woodlands of mallee *Eucalyptus*, *Acacia*, *Callitris*, *Brachychiton* and other low trees, at altitudes up to at least 1,100 m.

Phenology. Flowers collected May–Sep., fruits June–Aug.

Conservation status. Not currently considered to be of conservation concern.

Etymology. Hamersley [Range], main distributional area, and Latin *-ensis* (place of origin).

8. *Apowollastonia cylindrica* Orchard, *sp. nov.*

Type: 38.7 miles [62 km] south-east of Ranken, Northern Territory, 20 June 1960, *G. Chippendale* NT 7250 (*holo:* CANB; *iso:* AD, NT).

Wedelia asperrima (Decne.) Benth., *sensu* G. Bentham, *Fl. Austral.* 3: 539 (1867), *sed excl. typus*; *sensu* F.M. Bailey, *Queensland Flora* 3: 862 (1900); *sensu* G. Paczkowska & A.R. Chapman, *West. Austral. Fl.: Descr. Cat.* 179 (2000).

Annual *herb*, (0.15–)0.3–1.0(–1.5) m tall; *stems* erect, striate, moderately densely appressed-strigose, all green. *Leaves* petiolate; petiole 5–7 mm long; lamina oblong to lanceolate or linear, (30–)40–65(–90) mm long, 10–20(–30) mm wide, grey-green from dense and fine semi-appressed-scabrous indumentum on both surfaces, cuneate basally, blunt to acute, finely serrate to almost entire. *Capitula* c. 5–11 on stout peduncles 10–15 cm long; *outer bracts* narrowly ovate, 6–8 mm long, with midrib and 2 lateral veins often purplish, acute, shorter than disc florets, densely appressed-scabrous abaxially and marginally fimbriate; *inner bracts* similar but narrower. Capitulum in fruit 10–12 mm long, 15–20 mm diam. *Ray florets* 9–12; *corolla* lamina 7–8 mm long, 2-lobed, lacking veins, pilose abaxially. *Disc florets* c. 50–60; *corolla* yellow, sometimes striped purple, sparsely and minutely scabrous externally on lobes; *anther thecae* yellow. *Paleae* linear, 6 mm long in flower, green with purple midrib, conduplicate, abaxially and marginally scabrous. *Achenes* black, paler apically, occasionally mottled, cylindrical, 4 mm long, sometimes very weakly 4-angled or with 2 weak, white, longitudinal veins, minutely rugulose apically, glabrous or with occasional short apical hairs. *Pappus* a circular, white callus, usually glabrous, sometimes with sparse, minute hairs, no awns. (Figure 28)

Specimens examined (selection). WESTERNAUSTRALIA: 47 km S of Forrest River crossing, Duncan Highway, 20 Apr. 1977, *Hj. Eichler* 22398 (CANB, MEL); corner of Weaber Road and Arawato Road, 20 km from Kununurra, 17 July 1992, *A.A. Mitchell* 2629 (DNA, PERTH); 18.5 km N of Warmum (Turkey Creek), 10 May 1999, *R.W. Purdie* 4860 (CANB, NSW, PERTH); 47.4 km S of Forrest Creek along Duncan Road, 14 Apr. 2004, *P.S. Short* 5180 (CANB, DNA, PERTH). NORTHERN TERRITORY: Anthony Lagoon, 16 May 1947, *S.T. Blake* 17801 (BRI, CANB, K, MEL); 27 miles [42 km] S Austral Downs, 12 Aug. 1955, *G. Chippendale s.n.* (BRI, CANB, NT); Kelly Stn, 24 May 1994, *J.L. Egan* 3940 (DNA); Wave Hill Stn, 29 Aug. 1994, *J.L. Egan* 4271 (DNA, MEL). QUEENSLAND: Iffley Stn, 20 Aug. 1936, *S.T. Blake* 12632 (BRI); near Maxwellton, 1 May 1954, *S.L. Everist* 5367 (DNA); Flinders Highway, 27 km E of Hughenden, 20 July 1989, *R.A. McKenzie* 17 (BRI); Corindi, Mar. 1946, *G.R. Moule s.n.* (BRI, CANB, K).

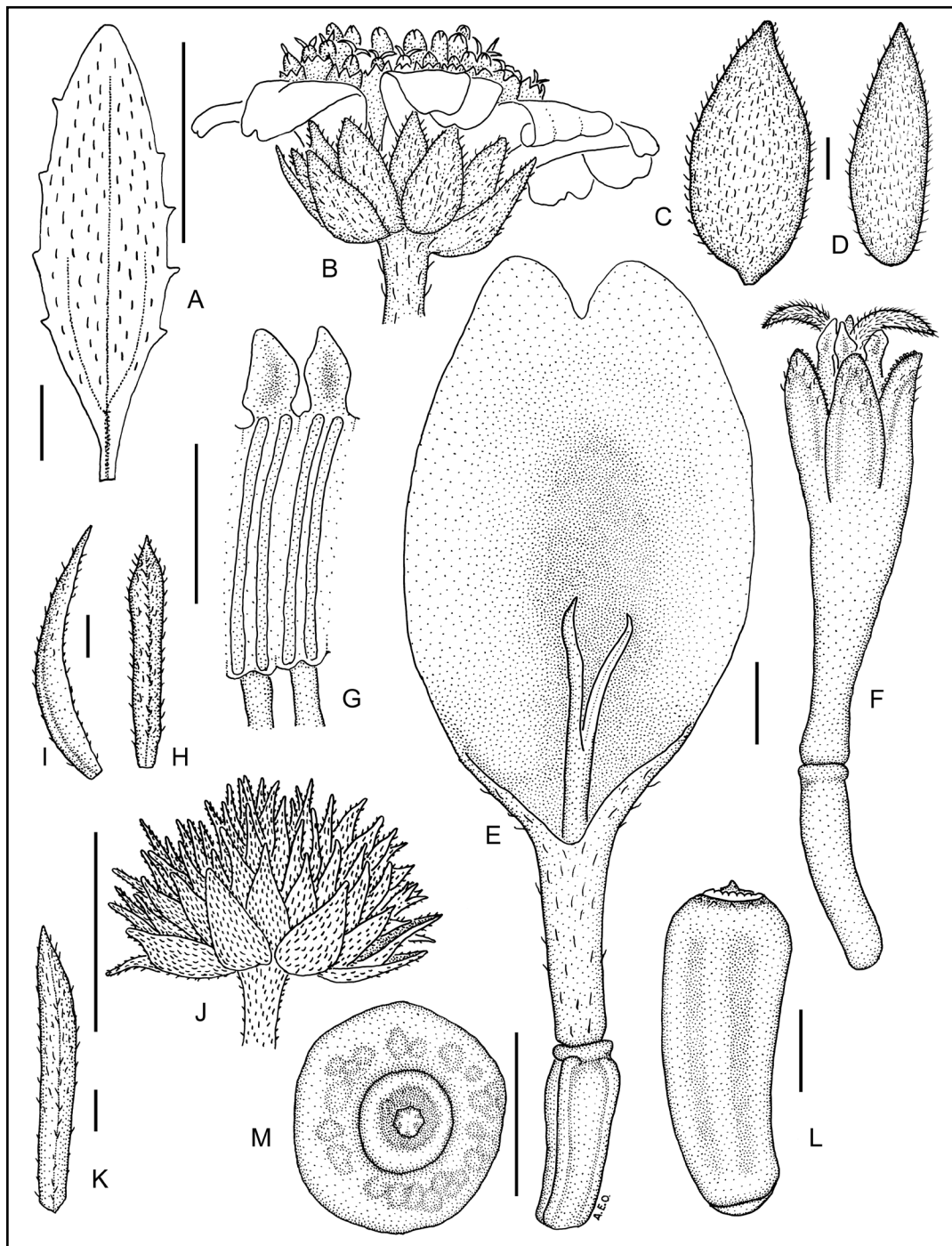


Figure 28. *Apowollastonia cylindrica*. A – leaf; B – flowering capitulum; C – outer involucral bract; D – inner involucral bract; E – ray floret; F – disc floret; G – stamens; H – palea, dorsal view; I – palea lateral view; J – fruiting capitulum; K – fruiting palea; L – achene; M – apical view of achene. (All based on *J.L. Egan* 4271 (DNA)). Scale bars: A, B, J, = 1 cm; C–I, K–M = 1 mm. Del. A.E. Orchard.

Distribution and habitat. Widespread in inland areas in the Kimberley region of Western Australia, across the northern part of the Northern Territory north of 20°S, and western Queensland south of the Gulf of Carpentaria. Isolated coastal records from the mouth of the Gascoyne River, Western Australia, and from Ayr, Queensland, probably represent recent introductions via long distance human-mediated dispersal (Figure 37, Map 10). Recorded mainly from damp soils and heavy clays, often associated with irrigation channels and creeks, on Mitchell grass (*Astrebla* spp.) plains, occasionally invading crops (e.g. chia – *Salvia hispanica* L.).

Phenology. Flowers have been collected February–August, fruits March–August.

Conservation status. Not threatened.

Nomenclatural notes. Bentham (1867), describing Australian plants, based *Wedelia asperrima* on Decaisne's *Wollastonia asperrima* from Timor, the type specimen of which is now in P (2515133). *Wollastonia asperrima* is now treated as *Lipoblepharis asperrima* (Decne.) Orchard, and is a creeping perennial herb, rooting at the nodes, with soft, lanceolate to ovate leaves, coarsely serrate, usually coarsely hairy, with solitary capitula on slender peduncles, and black anther thecae in the disc florets. The paleae are membranous, ±flat, ovate, with an acuminate tip, and the achenes are angled with a pappus of short, lacinate scales and, sometimes, one or more short awns. The Australian plants which have been treated under this name since Bentham's time are quite different, being erect annual plants, with oblong to lanceolate or linear leaves, that are rather dry, entire or finely serrate, and densely and finely scabrous. The capitula are in clusters of c. 5–11 on stout peduncles, and the anther thecae are yellow. The paleae are green, subfleshy, linear and conduplicate, with an acute, but not acuminate, tip. The achenes are cylindrical and lack a pappus (or almost so), and never bear awns. Bentham's description applies to the Australian plants, but the type specimen to the Indonesian plants.

Notes. The disc florets are apparently all fertile, but because of crowding only some develop into mature achenes.

This species has sometimes been considered poisonous to stock, but testing results have been ambiguous. According to notes attached to *A. Nisbett s.n.* (BRI 26793), a watery extract drenched to sheep caused death in c. 18 hours, yet *R. Hunter s.n.* (CANB 38872) reported that 'cattle raised in the area where the plant is abundant do not seem to be affected at any time even though they have been seen eating the weed. The same applies to horses.' *R.C. Cowley s.n.* (BRI 365721) reported that it is used to make a lotion for sore eyes.

Etymology. The epithet *cylindrica* refers to the shape of the achene.

7. **Acunniana** Orchard, *gen. nov.*

Type: *A. procumbens* (DC.) Orchard (≡ *Wollastonia procumbens* DC.)

Perennial *herb* 0.3–1.0 m tall. *Leaves* opposite, simple, ovate to lanceolate, 25–55 mm long, 10–35 mm wide, triplinerved, coarsely serrate with basal teeth often enlarged and lobe-like, acute, shortly petiolate, moderately densely appressed hairy. *Capitula* radiate on short to long peduncles, with 2 series of bracts; *outer bracts* green, herbaceous, exceeding inner bracts and disc florets; *inner bracts* green; all abaxially hairy. *Ray florets* pistillate, fertile; *corollas* yellow. *Disc florets* functionally staminate, not forming achenes; *corollas* yellow; anther thecae brown-black. *Paleae* lanceolate (inner

ones linear), conduplicate, stiff, coriaceous, opaque, green in flower, becoming stramineous, lacking an abaxial crest; midrib apparent plus several striae; tip slightly expanded or slightly lobed, abaxially shortly scabrous. *Achenes* only developed from ray florets, brown to grey, 4.0–4.5 mm long, slightly compressed, 3-angled, ovoid, rounded apically, with sparse, minute hairs apically, lacking elaiosomes; *pappus* absent or of *c.* 3 small scales fused basally into a shallow, 3-toothed cup.

Etymology. The generic name recognises its discoverer, the botanist Allan Cunningham (1791–1839), whose name as an author is abbreviated A.Cunn., plus the Latin suffix *-iana* (related to, belonging to).

A genus of a single species, confined to northern Australia. In habit *Acunniana* resembles the partly sympatric *Apowollastonia*, but differs in its large outer involucre bracts, dark anther thecae, its functionally staminate disc florets, and relatively large achenes. In its large outer involucre bracts, dark anther thecae, and relatively large achenes it resembles *Indocypraea montana*, and is perhaps most closely related to that monospecific genus, but it differs in its coarsely serrate leaves, in its functionally staminate disc florets, and short pappus scales that never become elongated into ‘awns’ or claws, and it lacks the distinctive red and yellow mottling found on the achenes of *I. montana*.

Acunniana procumbens (DC.) Orchard, *comb. nov.*

Wollastonia procumbens DC., *Prodr.* 5: 548 (1836); *Moonia procumbens* (DC.) Benth., *Fl. Austral.* 3: 540 (1867); *Chrysogonum procumbens* (DC.) F.Muell., *Syst. Census Austral. Pl.* 83 (1882), *non Wedelia procumbens* (Baker) B.L.Turner, *Phytologia* 72: 394 (1992). *Type citation:* ‘In littoribus insularum ad oram borealem Australasiae apr. flor. legit A. Cunningham’ (*holo:* *Wedelia* sp. A procumbent plant upon the Clifly shores of the Islands of the North coast of Australia, Apl. 1818, *A. Cunningham s.n.* [57- see *Nomenclatural notes* below], G–DC 135234!; *iso:* Palm Bay, Crocker’s Island, 1st Voyage of Mermaid, 1818, [*A. Cunningham*] 244, BM 820300!; *Verbesina radula*. A procumbent plant. Edges of Cliffs &c, Palm Bay, Crokers Island, 15 April 1818, *A. Cunningham s.n.* [244 - see *Nomenclatural notes* below], K!; *Verbesina radula*. Palm Bay, Croker’s Isl’d, N.C. [= North Coast of Australia], *s. dat.*, [*A. Cunningham s.n.*], K, herb. Hooker!).

Perennial *herb* 30–45(–100) cm tall; stems 1–2 mm diam., sprawling or prostrate, sometimes rooting at nodes, stiff, striate, appressed-softly hairy. *Leaves* shortly petiolate; petiole 2–5 mm long; lamina ovate to lanceolate, 25–55 mm long, 10–35 mm wide, discolorous, moderately appressed-hairy, rounded to cuneate basally, acute, coarsely serrate with 2 basal teeth often larger and shortly lobe-like. *Capitula* usually solitary, on peduncles 1.5–8 cm long; inner and outer *involucre bracts* lanceolate, 10–11 mm long, subacute, longer than disc florets, softly hairy abaxially or sometimes only at tip. *Capitulum* in fruit 8 mm long, 10–11 mm diam. *Ray florets* 5–12; *corolla* lamina (4–)7–9 mm long, 3-lobed, weakly nerved, glabrous. *Disc florets* (8–)10–12(–15); *corolla* cream-yellow, glabrous; *anther thecae* brown–black. Outer *paleae* (of ray florets) lanceolate, 8–9 mm long, stiff, erect, abaxially scabrous at tip; inner *paleae* (of disc florets) linear with a slightly expanded tip, 8 mm long, stiff, erect, abaxially scabrous at tip, all conduplicate. *Achenes* apparently only developing from ray florets, ovoid, weakly 3-angled, 4.0–4.5 mm long, not winged, with short, sparse hairs apically, smooth. *Pappus* absent or a short cup with 3 small teeth. (Figure 29)

Specimens examined (selection). NORTHERN TERRITORY: Bachelor Farm near Darwin, Jan. 1914, *C.E.F. Allen* 46 (K); Point Smith, Port Essington, [*J.J. Armstrong*] 586 (K); Tipperary Rd, Mary River area, 16 Mar. 1987, *M.J. Clark* 779 (BRI, CANB, DNA); Port Essington, Wangewanja Cove, 13 Apr. 1993, *I. Cowie* 3380 (CANB); Melville Island, near Pickertarramoor, 31 Mar. 1994, *I.D. Cowie*

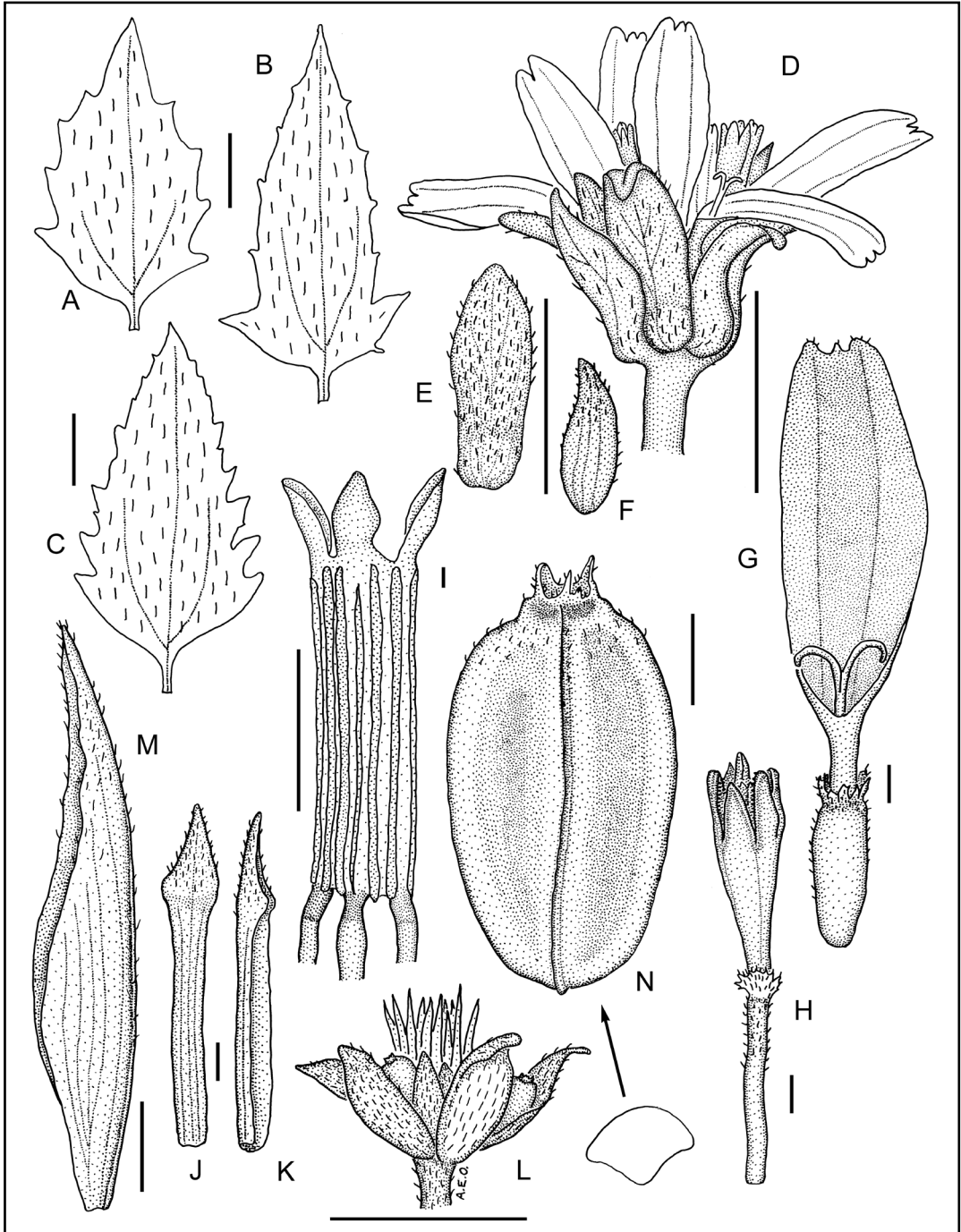


Figure 29. *Acunniana procumbens*. A–C – leaves; D – flowering capitulum; E – outer involucre bract; F – inner involucre bract; G – ray floret; H – disc floret; I – stamens; J – palea, dorsal view; K – palea, lateral view; L – fruiting capitulum; M – fruiting palea; N – achene. (All based on *I.D. Cowie* 4841 (CANB)). Scale bars: A–D, L = 1 cm; E–K, M, N = 1 mm. Del. A.E. Orchard.

4841 (CANB, MEL); Cobourg Peninsula, base of Danger Point Peninsula, 6 Feb. 2005, *I.D. Cowie & K.G. Brennan* 10449 (DNA); East Alligator River, 23 Feb. 1973, *C. Dunlop* 3330 (BRI, CANB); Victoria, Port Essington, Dec. 1840, [*J.J. Gilbert s.n.*] (K); Melville Island, Renell Beach to MacLear Creek road, 20 Jan. 1992, *G. Leach* 2937 & *I. Cowie* (DNA); 3–4 miles [c. 5 km] NNW El Sharana, 19 Jan. 1973, [*P.] Martenz & [R.] Schodde* AE441 (BRI, CANB); Gunn Point, 24 miles [c. 40 km] NE of Darwin, 18 Feb. 1973, *J. McKean* B954 (BRI, DNA). QUEENSLAND: S end of Temple Bay, 8 June 1978, *J.R. Clarkson* 2188 (BRI).

Distribution and habitat. Almost confined to the Northern Territory, in western and central Arnhem Land, with a possible outlier at Temple Bay, eastern Cape York Peninsula, Queensland. Found in damp spots in the grassy understorey of *Eucalyptus* and *Melaleuca* woodland.

Phenology. Flowers recorded December–June, fruits January–April.

Conservation status. Apparently not threatened.

Nomenclatural notes. The holotype (G-DC) bears a label in Cunningham's hand that has the date Apr. 1818 (the date of collection), and in another hand 'Mr A. Cunningham 1834' and '57'. The numbers appearing on Cunningham specimens are those of despatch lists, not collection numbers. In this case, 57 is the number of the specimen included in a despatch of material from Cunningham to Candolle, from London, in 1834, prior to Cunningham's return to New South Wales. Similarly, the number 244 appearing on one of the K isotypes and the BM isotype is that of the despatch list from Cunningham in New South Wales to Aiton and Banks in 1818. Despite the different numbers, these specimens are almost certainly part of the same collection, and are treated so here. Both K isotypes bear tickets in Cunningham's hand. The one with number 244 also bears a large label prepared by R. Heward (who inherited Cunningham's herbarium). For further explanation of the interpretation of Cunningham labels see Orchard and Orchard (2013).

Taxonomic notes. Many Northern Territory collections of *Acunniana procumbens* have in the past been misidentified as *Wedelia urticifolia*, a Malesian/Asian taxon not found in Australia, and here recognised as *Lipoblepharis urticifolia*.

The Queensland specimen is only tentatively assigned to this species. It has only flowers and old empty capitula, but its long involucre bracts and apparently sterile disc florets suggest that it is this species, rather than *Apowollastonia longipes*, which is vegetatively somewhat similar.

8. *Quadribractea* Orchard, *gen. nov.*

Type: *Q. moluccana* (Blume) Orchard (\equiv *Verbesina moluccana* Blume).

Erect or scrambling *shrubs* 1–2 m tall. *Leaves* opposite, simple, ovate, 3.5–8.0(–14.0) cm long, 2.0–6.0(–9.0) cm wide, triplinerved, shortly serrate to almost entire, obtuse to acute, petiolate, scabrous. *Capitula* radiate, on short, clustered peduncles, with 4 decussately arranged bracts; outer bracts green, herbaceous, abaxially hairy throughout; inner bracts similar but hairy only on midrib and margins. *Ray florets* pistillate, fertile; *corollas* white. *Disc florets* functionally staminate, with undivided, non-stigmatic styles; *corollas* green, 5-lobed; *anther thecae* black. *Paleae* narrowly linear, flat, membranous, hyaline, lacking an abaxial crest, with a well-defined midrib but no striae, tip acute-acuminate, shortly hairy on margins and abaxially near tip. *Achenes* dull black, 4 mm long, not or

scarcely compressed, 2-angled, developing only from ray florets, ovoid, rounded apically, glabrous, lacking elaiosomes; *pappus* almost absent, a very short cup formed from the fused bases of *c.* 3 tiny scales/hairs; awns absent.

A genus of a single species, found in eastern Indonesia and in East Timor.

Etymology. The generic name emphasises the distinctive capitulum involucre of four decussately arranged bracts, unique in the wedelioid taxa of Malesia.

Quadribractea moluccana (Blume) Orchard, *comb. nov.*

Verbesina moluccana Blume, *Bijdr. Fl. Ned. Ind.* 912 (1826); *Wollastonia moluccana* (Blume) DC., *Prodr.* 5: 547 (1836); *Wedelia moluccana* (Blume) Borl., *Fl. Ned. Ind.* 2: 242 (1899); *Moonia moluccana* (Blume) Koster, *Repert. Spec. Nov. Regni Veg.* 34: 17 (1933). *Type citation:* ‘Crescit: in Moluccanis insulis’ (*lecto*, chosen here: *Verbesina moluccana* Bl., Archipel. Molucc., *s. dat.*, [Blume], L 2159!; *isolecto:* *Verbesina moluccana* Bl., Archipel. Indie, *s. dat.*, [Blume], L 2160!).

Verbesina dichotoma Reinw. ex Miq., *Fl. Ned. Ind.* 2: 75 (1856), *nom. inval. pro syn., non V. dichotoma* Murr. (1779).

Wedelia quadribracteata Warb., *Bot. Jahrb. Syst.* 13: 449 (1891); *Moonia quadribracteata* (Warb.) Mattf., *Bot. Jahrb. Syst.* 62: 430 (1929). *Type citation:* ‘Die Pflanze ist sehr häufig auf der trockenen Rücken von Kl. Key, [New Guinea: Papua]’ (*holo:* B? *n.v.*).

Erect or scrambling *shrub* 1.0–2.0 m tall; young *stems* sparsely scabrous; older stems glabrous with white bark. *Leaves* opposite, simple, petiolate; petiole 10–25 mm long; lamina ovate, 35–80(–140) mm long, 20–60(–90) mm wide, triplinerved, with 10–20 small or minute teeth each side, obtuse to acute, rounded or very shortly cuneate basally, sparsely appressed-scabrous adaxially (hairs 0.3–0.4 mm long, on swollen bases), similar abaxially but mainly on prominent midrib and primary veins. *Capitula* in dichasial clusters of 3–5, on slender peduncles to 20 mm long. *Involucral bracts* 4, decussate; outer bracts obovate (rarely lanceolate to oblanceolate), 4–5 mm long, green, herbaceous, acute, densely pilose on both surfaces; inner bracts similar but broader, with the hairs confined to the tip, margins and midrib. *Ray florets* 4, pistillate, fertile; *corolla* white, with lamina *c.* 4 mm long, broadly 2-lobed, *c.* 6-striate, sparsely pilose abaxially on major veins. *Disc florets* numerous (*c.* 50), functionally staminate; *corolla* green, tubular, 5-lobed with gland-tipped hairs apically; *anther thecae* and appendages black; style arms fused; ovary filiform, topped by a tuft of long, crisped hairs. *Paleae* narrowly linear, 4 mm long, 0.2–0.4 mm wide, membranous, hyaline, flat (not conduplicate), with a well-defined midrib but no striae, margins and tip with short hairs. *Achenes* formed only from ray florets, dull black, obovoid, 4 mm long, not or only slightly compressed, 2-angled, glabrous. Disc floret corollas deciduous, but the filiform ovaries, topped with long, crisped hairs, persistent as pseudo-paleae in fruiting capitula. *Pappus* almost absent: a very short whitish cup or callus ring topped by about 3 tiny scales/hairs; never forming awns. (Figures 13E, 30)

Other specimens examined. INDONESIA: Kp. Bioba, W. slope of G. Timau, West Timor, 4 Mar. 1939, *S. Bloembergen* 3382 (K); Letwurung, Babar Island, 1 Mar. 1956, *J. van Borssum Waalkes* 3037 (K); Letwurung, Babar Island, 3 Mar. 1956, *J. van Borssum Waalkes* 3103 (K, L); Selaru, Namtabung, Tanimbar Island, 17 Mar. 1956, *J. van Borssum Waalkes* 3178 (K, L); Jamdena, Sifnana, Tanimbar Island, 11 Apr. 1956, *J. van Borssum Waalkes* 3339 (K); Umgebung d. Tihusees, Wetar Island, Feb.

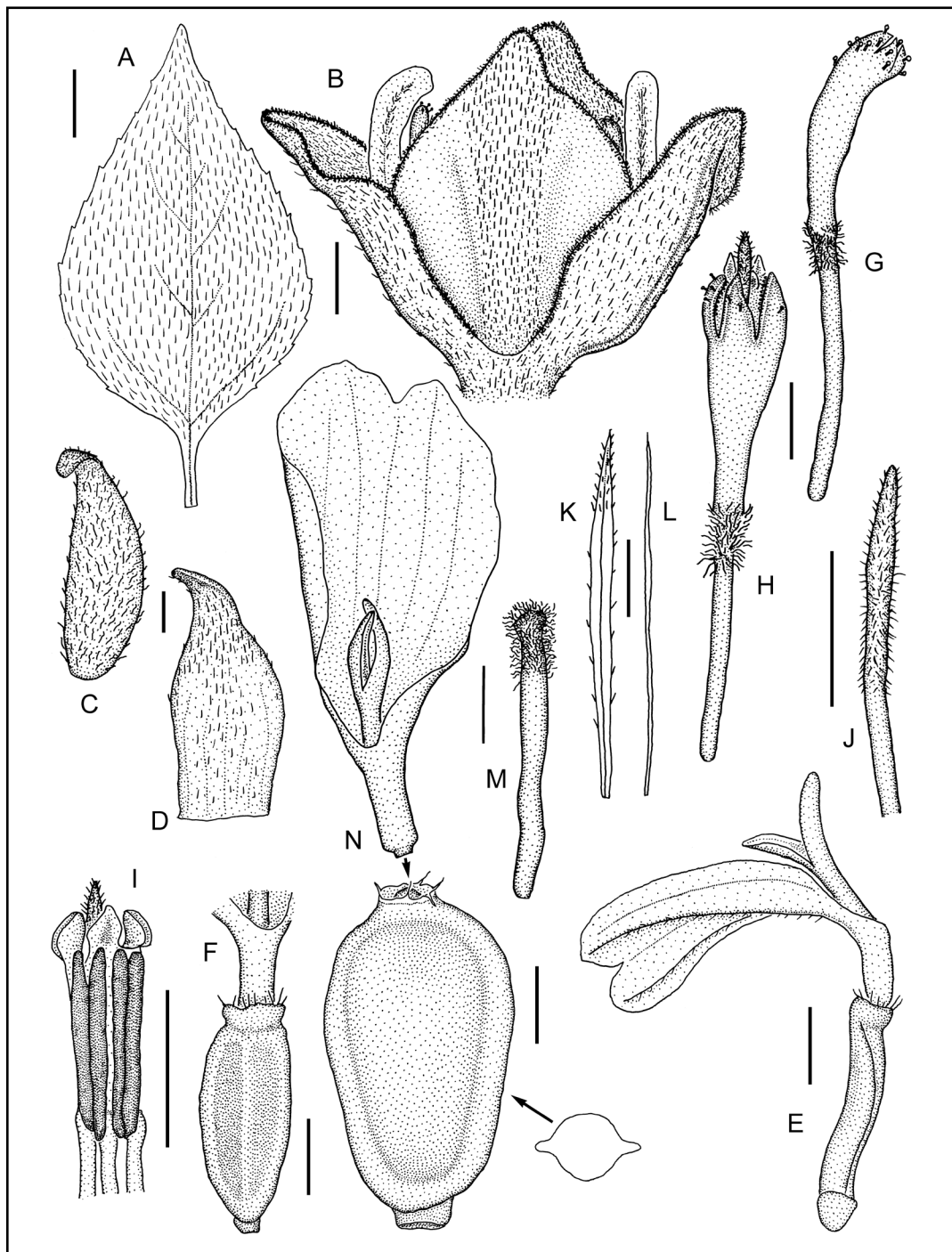


Figure 30. *Quadribractea moluccana*. A – leaf; B – capitulum in bud/early flower; C – outer involucre bract; D – inner involucre bract; E – young ray floret, lateral view; F – ray floret ovary, adaxial view; G – disc floret in bud; H – disc floret; I – stamens; J – disc floret style with fused stigma arms; K – palea, dorsal view; L – palea, lateral view; M – ovary of disc floret, persistent on receptacle in fruit; N – achene and deciduous ray corolla. (A, C, D, G–N based on *C.G.G.J. van Steenis* 18133 (CANB); B, E, F based on *C.R. Trainor* 64 (DNA)). Scale bars: A = 1 cm; B–N = 1 mm. Del. A.E. Orchard.

1910, *J. Elbert* 4539 (CANB, K); vicinity of Tikusus, Wetar Island, 16 June 1916, *Gründler (Elbert Exped.)* (K). EAST TIMOR: Ira Siquero River, Mehara area near Los Palos, 4 Oct. 2005, *I.D. Cowie & A.F. Xavier* 10770 (DNA); Plateau of Fuloro (Lautem), Muapitine, 19 Dec. 1953, *C.G.G.J. van Steenis* 18133 (CANB, K); Bauno area near Los Palos, 29 Aug. 2005, *C.R. Trainor* 64 (DNA).

Distribution and habitat. Found in East Timor, and in eastern Indonesia from Seram to Nusa Tenggara (Lesser Sunda Islands) and Kai (Kei) Islands. It may eventually be found also in New Guinea. Grows in *Eucalyptus* and other forest, swamp and grassland, from sealevel to 1,300 m, often on limestone, but also on alluvium, persisting in disturbed forests, including those converted to rough coconut plantations.

Phenology. Flowering February–October; fruiting December.

Conservation status. Unknown, widespread but sparingly collected.

Nomenclatural note. The two type sheets of *Verbesina moluccana* in L are almost certainly true duplicates. The sheet L 2159 is here chosen as lectotype as it is definitely attributed to Blume.

Taxonomic note. The specimen seen by Candolle (1836) is in G-DC: *Verbesina* [scripsit Blume?], Moluques, 1816, *M. Lambert*, G-DC!

9. *Indocypraea* Orchard, *gen. nov.*

Type: *Indocypraea montana* (Blume) Orchard (\equiv *Verbesina montana* Blume).

Perennial *herbs*, sometimes scandent, 0.3–1.0(–3.0) m tall. *Leaves* opposite, simple, ovate, (3–)4–7(–12) cm long, (2–)2.5–5(–7) cm wide, triplinerved, shortly serrate, acute to subacuminate, petiolate, finely and softly pilose on both surfaces. *Capitula* radiate, on short to long peduncles, with 2 series of bracts; *outer bracts* green, herbaceous, longer than inner bracts and disc florets, abaxially pilose; *inner bracts* cartilaginous to papery, pale green to stramineous, opaque, with a well-defined midrib but no or weak striae, glabrous or sparse, short hairs mainly on midrib. *Ray florets* pistillate, fertile; *corollas* yellow. *Disc florets* bisexual; *corollas* yellow; *anther thecae* black. *Paleae* lanceolate, conduplicate, stiff, coriaceous, opaque, stramineous, lacking an abaxial crest, with midrib apparent but no striae; margins erose towards apex; tip acute, sparsely scabrous mainly on midrib. *Achenes* usually mottled red and yellow, rarely (immature?) greyish, 4–5 mm long, slightly compressed, 3-angled (ray) or 2-angled (disc), ovoid to obovoid, rounded and sparsely and minutely hairy apically, lacking elaiosomes; *pappus* a ring of tiny scales (to 0.2 mm long) slightly fused basally, with 1 or 2 often elongated to 1 mm as awn-like projections.

A genus of a single species, found from Indonesia to India and China.

Etymology. The generic name is a compound of the Latin *Indo-* (from India, (East) Indies), and *Cypraea*, the Latin name for cowrie shells. The achene closely resembles the Tiger or Leopard Cowrie (*Cypraea tigris*), and the genus is largely confined to India, and the East Indies.

Note. The awns on the achenes of this genus are not true awns (i.e. terete), but are instead elongated, flattened scales. They differ in this respect from *Lipotriche*, *Lipoblepharis*, *Melanthera* and *Wollastonia*, all genera with which *Indocypraea* has in the past been confused. The large red and yellow achenes are most distinctive, and further serve to distinguish *Indocypraea* from these genera. *Indocypraea*

shares with *Acunniana* capitula in which the outer involucre bracts are elongated, exceeding the inner bracts and the disc florets, and both genera have rather large ovoid to obovoid achenes. *Indocypraea* differs from *Acunniana* in its colourful achenes, its fertile disc florets and its leaves, which are softer with finer serrations.

Indocypraea montana (Blume) Orchard, *comb. nov.*

Verbesina montana Blume, *Bijdr. Fl. Ned. Ind.* 911 (1826); *Wollastonia montana* (Blume) DC., *Prodr.* 5: 527 (1836); *Wedelia montana* (Blume) Boerl., *Handl. Fl. Ned. Ind.* 2: 242 (1891). *Type citation*: ‘[Java] in montanis’ (*lecto*, chosen here: Java, *s. dat.*, Bl[ume] *s.n.*, L 2836!; *isolecto*: Java, *s. dat.*, Blume *s.n.*, L 2835!; Java, ‘1836’, M[onsieur] Blume *s.n.*, P 2515127 photo!, see *Nomenclatural notes* below).

Wedelia wallichii Less., *Linnaea* 6: 162 (1831); *Wedelia urticifolia* var. *wallichii* (Less.) DC., in R. Wight, *Contr. Bot. Ind.* 18 (1834); *Wollastonia montana* var. *wallichii* (Less.) H.Koyama, *Acta Phytotax. Geobot.* 36(4–6): 168 (1985). *Type citation*: ‘Cel. Wallich in Nepaulia’ (*holo*: KW? *n.v.*; *syn*: Napaul, *s. dat.*, Mr Wallich *s.n.*, G-DC 148364!; Napaul, 1821, G-DC 136256!; Napolia, 1832, Wallich *s.n.*, K, herb. Bentham!).

Wedelia urticifolia var. *wightii* DC., in R. Wight, *Contr. Bot. India* 18 (1834), as β . *wightii*. *Type citation*: ‘In collibus Dindigul.–Wight. cat. n. 1449.–*Verbesina urticaefolia*, Wight! herb. olim.–*Verbesina biflora*, Wall.! cat. n. 3207, b et forte d.’ (*syn*: Dindigal Mount, *s. dat.*, Herb. R. Wight 1449, Presented 1871, K!; Peninsula Ind. orientalis, *s. dat.*, [R.] Wight 1449, P 2693189 photo!; [India], 1832, Dr Wallich Cat. no. 3207B/317B, G!).

Wollastonia horsfieldiana Miq., *Fl. Ned. Ind.* 2: 72 (1856). *Type citation*: ‘Java, in Soerakarta (Horsfield)’ (*holo*: Java, *s. dat.*, Horsfield *s.n.* U 1361 photo!; *iso*: [annotation on reverse of sheet] Java, Surokirto, *s. dat.*, Horsfield *s.n.*, BM!; *possible iso*: Comp. 61, *Wollastonia montana*, Herb. Javanicarum, *s. dat.*, Dr Horsfield *s.n.*, K!; Comp 62. *Wollastonia Horsfieldiana* Miq., Herb. Javanicum, *s. dat.*, Dr Horsfield *s.n.*, K! & K, herb. Hooker!).

Wedelia montana var. *pilosa* H.Koyama, *Acta Phytotax. Geobot.* 36: 170 (1985). *Type citation*: ‘Thailand, N. Chiang Mai: Doi Chiang Dao, Shimizu et al. T-21117’ (*holo*: BKF *n.v.*; *iso*: KYO *n.v.*).

Illustrations. H. Koyama, *Acta Phytotax. Geobot.* 36: 167, Figure 1 (1985), as *Wedelia montana* var. *wallichii*; K.M. Matthew, *Further Illustr. Fl. Tamilnadu Carnatic* 4: pl. 338 (1988), as *Wedelia urticifolia*; H.J. Chowdery, in *Fl. India* 12: 425, Figure 122 (1995), as *Wedelia montana* var. *wallichii*; Figures 13D, 31 herein.

Perennial *herbs*, sometimes scandent, 0.3–1.0(–3.0) m tall; *stems* erect to arcuate, not rooting at nodes. *Leaves* petiolate; lamina ovate, (3–)4–7(–12) cm long, (2–)2.5–5(–7) cm wide, green, discolorous, soft, shortly serrate, acute to subacuminate; indumentum on both surfaces moderate to sparse, of appressed fine soft hairs. *Capitula* in terminal dichasial groups of 1–3(–5); peduncles very slender, (1–)2–6(–12) cm long, pilose. *Outer bracts* green, lanceolate, 6–8 mm long, 2 mm wide, acute, sparsely appressed hairy, longer than inner involucre bracts and disc florets; *inner bracts* cartilaginous to papery, pale green to stramineous, lanceolate, 4–5 mm long, 1–1.5 mm wide, acute to shortly acuminate, obscurely midribbed and striate, often slightly erose or even shortly lobed towards tip, sometimes marginally ciliate, sparsely pilose abaxially. *Ray florets* (4–)6–8(–10), pistillate, fertile. *Disc florets* c. 10; *anther thecae* and *appendages* black. *Paleae* lanceolate, 4–5 mm long, 1.5–2 mm wide, strongly conduplicate

and clasping florets/achenes, acute, often erose or slightly lobed towards tip, weakly midribbed, opaque and usually lacking visible striae, with short hairs abaxially towards tip. *Achenes* c. 4–8 maturing per capitulum, when fully mature usually mottled red and yellow (or red and yellow-brown), ovoid to obovoid, 4–5 mm long, 2- or 3-angled, compressed, rounded and shortly and sparsely hairy at apex; *pappus* a very short cup of connate scales, of which 2 are often slightly elongated to form soft curved ‘awns’ or claws. (Figures 13D, 31)

Other specimens (selection). CHINA: Hainan, 1889, *A. Henry* 8138 (K); S-Guilin at Nauxi (South Creek) Hill, Guangxi, 15 Aug. 1988, *D.A. Link* XII/III (K). NEPAL: N of Hitaura, Rapti Valley, 24 Aug. 1967, *Williams & Stainton* 8269 (K). BHUTAN: Rinkimpung, July 1881, *J.S. Gamble* 9594 (K). INDIA: Dindigul, Tamilnadu, 13 Dec. 1986, *K.M. Matthew* RHT47943 (K); Bhaulpodar, Orissa, 12 July 1950, *H.F. Mooney* 3881 (K); Umbarthan, Maharashtra, 13 Aug. 1983, *P.L. Narabinatan* 165250 (K); Delei Valley, Assam, 14 Aug. 1923, *F.K. Ward* 8520 (K). BURMA: hills west of Paungdaw Power Station, Oct. 1961, *J. Keenan et al.* 1603 (K). THAILAND: Doi Sutip, 24 Dec. 1911, *A.F.G. Ker* 2290 (K). INDONESIA: Bukit Palelawan Natural Reserve, Sumatra, 10–14 Feb. 1983, *J.J. Afriastini* 791 (K); Tjibodas, Gergerbentang, W. Java, 25 May 1948, *D.R. Pleyte* 176 (BO); Pusung dowo, Pujon, Malang, Java, 23 Apr. 1981, *Rochadi Abdulhadi* 1627 (L).

Distribution and habitat. Found from Indonesia to Thailand, Burma, India, Nepal and China, often in damp, shaded forest areas and stream banks, in a range of soils from humus to stony ground, at (250–)600–1,400(–1,700) m.

Conservation status. Unknown, but probably not threatened in most countries.

Nomenclatural notes. The two type sheets of *Verbesina montana* in L and the one in P are almost certainly true replicates. The sheet L 2836 is chosen here as lectotype because it comprises the best material, including ripe fruit.

The date 1836 on the type sheet of *V. montana* in P is interpreted as a date of donation, rather than a date of collection.

Note. Both ray and disc florets are fertile and can produce achenes, which are 3- and 2-angled respectively, but only about 6–8 achenes per capitulum mature, apparently randomly.

10. *Lipoblepharis* Orchard, *gen. nov.*

Type: *L. urticifolia* (Blume) Orchard (\equiv *Verbesina urticifolia* Blume).

Perennial *herbs* or *shrubs*, 0.3–2.0 m tall. *Leaves* opposite, simple, usually lanceolate to ovate, rarely linear, (3.5–)4.5–6.0(–19) cm long, (1.5–)3.0–4.5(–6) cm wide, triplinerved, usually finely to coarsely serrate (rarely biserrate), rarely entire, acute to acuminate, petiolate, finely and softly pilose to coarsely scabrous on both surfaces. *Capitula* radiate, on short to long peduncles, with 2 or 3 series of bracts; *bracts* green, often coriaceous, subequal, abaxially hairy, not or obscurely striate. *Ray florets* pistillate, fertile; *corollas* cream to yellow. *Disc florets* bisexual, fertile; *corollas* cream to yellow; *anther thecae* black. *Paleae* linear to lanceolate, conduplicate, stiff, coriaceous to papery, opaque to semi-hyaline, green or stramineous to brown or reddish purple, lacking an abaxial crest, midrib well developed, striae absent to numerous, with tip often slightly lobed or laterally erose, acute, abaxially shortly scabrous. *Achenes* dark grey to black, 1.5–3.5(–4.5) mm long, compressed or not, often 3-angled (ray), 2- or

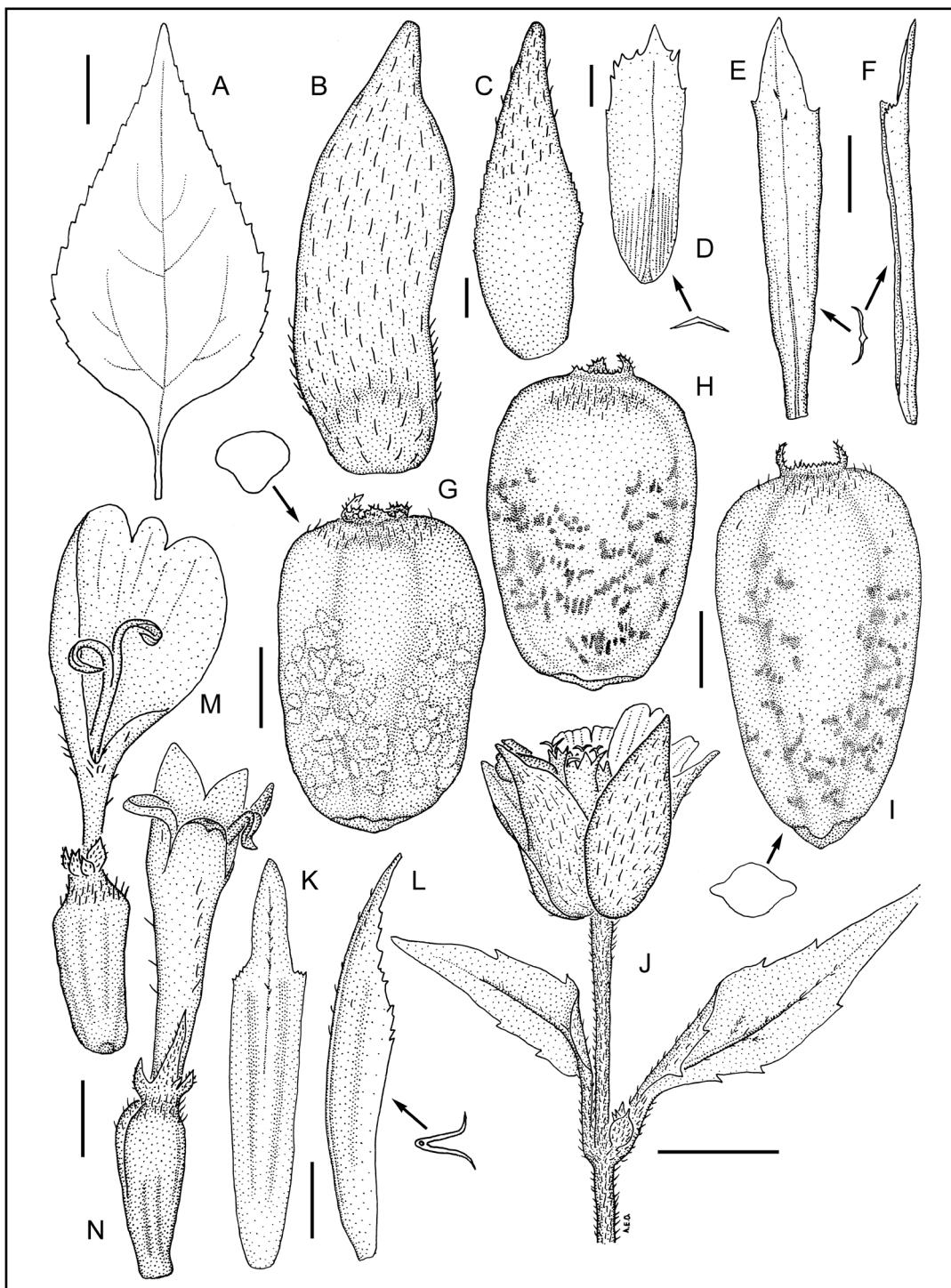


Figure 31. *Indocypraea montana*. A – leaf; B – outer involucre bract; C – inner involucre bract; D – innermost involucre bract, transitional to paleae; E – palea, dorsal view; F – palea, lateral view; G, H – ray achene, adaxial and abaxial views; I – disc achene; J – flowering capitulum; K – palea, dorsal view; L – palea, lateral view; M – ray floret; N – disc floret. (A–I based on lectotype, *C.L. Blume s.n.* (L 2836); J–N based on *S.J. van Oostroom* 13874 (L)). Scale bars: A = 1 cm; J = 5 mm, B–I, K–N = 1 mm. Del. A.E. Orchard.

4-angled (disc), ±obcuneate, usually truncate or subtruncate, shortly and often densely hairy apically, lacking elaiosomes; *pappus* a ring of very short, free scales, and usually with 1–3 short, fragile and often oblique, antrorsely barbed awns (awns always absent in *L. floribunda*).

A genus of five species, extending from Malesia to south, south-east and east Asia (Indonesia to China and Japan, and west to India), and east to Vanuatu.

Etymology. The name *Lipotriche* (from the Greek *leipo*, ‘abandon, leave’; and *thrix, trichos*, ‘hair’) was coined by Robert Brown for African species in which the pappus consisted of caducous hairs. When Candolle moved one of the original species to a new genus, he kept the sense of the original name by coining *Lipochaeta* (Greek *chaite*, ‘long hair’). The new genus erected here is related to both of these, and has fragile awns (although slightly more robust than *Lipotriche*), so the name *Lipoblepharis* seems appropriate (Greek *blepharis*, ‘eyelash’), eyelashes being more robust than hairs. The name is feminine.

Key to species of *Lipoblepharis*

1. Leaves ovate to lanceolate, 15–70 mm wide
 2. Achenes *c.* 3–4.5 mm long, leaves usually ovate, with sparse, soft, fine hairs
 3. Leaves acute but hardly acuminate; achenes bluntly angled, with angles not produced into peaks apically..... **1. *L. urticifolia***
 - 3: Leaves acuminate; achenes sharply angled, with angles produced into peaks apically..... **2. *L. thailandica***
 - 2: Achenes 2–3 mm long; leaves usually lanceolate to narrowly ovate, hairs coarse and stiff (or if soft and fine, inflorescence a group of *c.* 10–12 capitula on short peduncles)
 4. Leaf hairs coarse, stiff and usually dense, particularly on the major veins abaxially; capitula in groups of 1–3(–5), on simple or dichasially branching peduncles (30–)40–60 mm long (Indonesia & East Timor)..... **3. *L. asperima***
 - 4: Leaf hairs soft, fine; capitula in groups of 10–12, arranged on dichasially branching peduncles (10–)20–40 mm long (Vanuatu)..... **4. *L. floribunda***
- 1: Leaves linear, 3–7 mm wide..... **5. *L. stenophylla***

1. *Lipoblepharis urticifolia* (Blume) Orchard, *comb. nov.*

Verbesina urticifolia Blume, *Bidjdr. Ned. Ind.* 911 (1826), as ‘*urticaefolia*’; *Wedelia urticaefolia* (Blume) DC., in R. Wight, *Contr. Bot. India* 18 (1834); *Wollastonia urticaefolia* (Blume) Hassk., *Cat. Pl. Hort. Bog.* 99 (1844). *Type citation:* ‘in fruticetis montanis. [Java]’ (*lecto*, chosen here: *Wedelia* sp. nova, Java, *s. dat.*, [Blume] P 2515017 photo!). *Excluded syn:* Java, ‘1836’, *Mr Blume* (P 710050 photo!), see *Taxonomic notes* below.

Wedelia urticaefolia γ? *scaberrima* DC., in R. Wight, *Contr. Bot. India* 18 (1834), *nom. inval.*, et non *Wedelia scaberrima* Benth., *Ann. Nat. Hist.* 2: 110 (1838).

Shrub or perennial *herb* 0.3–1.5 m tall. *Leaves* green, usually ovate (rarely narrowly ovate), 45–60(–100) mm long, 30–45(–60) mm wide, coarsely serrate or biserrate, sparsely and shortly appressed-hairy on both surfaces, especially (and sometimes more densely) on abaxial veins. *Capitula* on peduncles

50–80 mm long; *involucral bracts* ovate (inner ones narrower), bluntly acute, appressed-hairy abaxially. *Ray floret corollas* cream to yellow; lamina linear to ovate, sparsely hairy abaxially. *Disc florets*, if present, with *corollas* yellow; *anther thecae* black. *Ovaries* of all florets narrowly obovoid, with a pappus of several small scales and up to 3 short, antrorsely barbed awns. *Paleae* stramineous, opaque, linear to lanceolate, acute, conduplicate, with a well defined midrib and usually several striae, shortly appressed-scabrous distally. *Achenes* grey-black, obcuneate, 3–4 mm long, 2.0–2.5 mm wide, somewhat compressed, weakly 3-angled (ray) or 4-angled (disc), with short hairs apically, weakly rugose; *pappus* of several short scales and, sometimes, 1–3 awns; achenes not formed in subsp. *hortorum*.

Taxonomic notes. The identity of this species has been obscure almost since it was described, and the name has thus been applied (or misapplied) to a range of taxa. The problem is twofold. Blume did not unequivocally cite the specimen(s) on which he based his description, and Candolle in Wight (1834), in transferring the species to *Wedelia*, described three varieties, two of which are here identified as *Indocypraea montana*. Only the last (*γ. scaberrima*) seems to agree with *Verbesina urticaefolia* in the sense of Blume. No specimen that can be unequivocally identified as a type of *V. urticifolia* has been discovered. No putative type specimen is held at L. There is a Blume specimen from Java in P(710050) which is annotated ‘*Wedelia urticaefolia*. *Verbesina* [urticaefolia] Bl. Java. Mr Blume 1836.’ Several other specimens in P have the information ‘Blume 1836’ which is interpreted here as the date of donation rather than of collection. If this is so, then P 710050 is a possible syntype. It is rather densely hairy with narrow leaves, and more closely resembles what is here identified as *L. asperrima* than *L. urticifolia*. There is another specimen in P (2515017, ex herb Schultz Bip., ex herb. Cosson) which bears a label ‘*Wedelia* sp. nova, Java’ in a hand which appears to be that of Blume. It has additional labels (perhaps in error) ‘ex prope Bandung, Java, Zollinger’. It is identified as *Wedelia urticifolia γ. scaberrima*. It is far less pilose than P 710050, with broader leaves, and agrees with the concept of *L. urticifolia* adopted here.

In describing *Wedelia urticaefolia γ. scaberrima* Candolle included the name *Verbesina urticaefolia* Blume as a synonym, thus fixing this as the type variety, and making ‘*scaberrima*’ invalid.

Blume’s description of the species is somewhat vague, with perhaps the most critical characteristics being ‘foliis...ovato-oblongis, acuminatis argute duplicato-serratis...pilosiusculis...’ (with leaves... ovate-oblong, acuminate, sharply doubly serrate...shortly (or sparsely?) pilose). This description matches P 2515017 better than P 710050, and the former is thus here chosen as lectotype. A further indication of Blume’s intention (that the name *V. urticifolia* should be applied to the broad-leafed rather than the narrow-leafed taxon in Java), can be obtained from an addendum to his description ‘*Variet.: foliis strigosis, flore pleno. Crescit: in hortis colitur.*’ This description of an unnamed ‘double’ form of the species, collected from cultivation, can be identified unequivocally. Specimens exist in G, L and NY, among other places. The plant is apparently widespread in cultivation in Asia and Malesia, and has only pistillate ray florets in multiple series. With no staminate or bisexual florets it is sterile. It is propagated by cuttings, and sometimes escapes from cultivation via its prostrate stems which freely root. The leaves of this plant are relatively broad with sparse, short hairs. Because this cultivated plant is so widespread, and identified with *L. urticifolia s. str.*, it is here redescribed and named.

Key to the subspecies of *L. urticifolia*

1. Capitula with both ray and disc florets; forming achenes..... **1a.** subsp. **urticifolia**
1: Capitula with (pistillate) ray florets only; not forming achenes **1b.** subsp. **hortorum**

1a. *Lipoblepharis urticifolia* (Blume) Orchard subsp. *urticifolia*

Wollastonia zollingeriana Sch.Bip. ex Miq., *Fl. Ned. Ind.* 2: 72 (1864). *Type citation*: ‘Java, op de rotsen van Batoe oeló in de province Poeger (Zoll.)’ (*holo*: ad rupes Bati uló pr. Poeger, *s. dat.*, [H.] Zollinger 2728, P 2515013, ex herb. Sch.Bip, ex herb. Cosson!; *iso*: Ad rupes prope Batu uló Prov. Puger, 25.II.45, [H.] Zollinger 2728, P 2515125 photo!; *H. Zollinger* 2728, K, ex herb. Hooker!; [H.] Zollinger 2728, P 2515014, 25015 & 2515128, all photo!).

Wedelia rhombifolia J.Kost., *Repert. Spec. Nov. Regni Veg.* 34: 19 (1933). *Type citation*: ‘Wetar: Umgebung des Tihu-sees, [Indonesia], 485–500 m. ([J. Elbert] n. 4550 bl.)’ (*holo*: L!; *iso*: K!).

Wollastonia javana Turcz., *Bull. Soc. Imp. Nat. Moscou* 24(2): 70 (1851). *Type citation*: ‘Java. Zoll. n. 2922’ (*holo*: KW? *n.v.*; *iso* [or *syn?* - see *Nomenclatural notes* below]: Java, Prope Kupang prov. Boesoki, *Zollinger* 2922 – 563D?, P2515035 herb. Drake photo!; In montosis siccis prope Kupang, Pro. Bondowoizo, iv.45, [Zollinger] 2922 = (563Z?), P 2515036, herb. Drake photo!; Java, *s. dat.*, *Zollinger* 2922, P 2515129 photo!).

Shrub or perennial *herb* 0.3–1.5 m tall; *stems* erect, scrambling or procumbent. *Leaf* lamina ovate, 45–60(–80) mm long, 30–45(–50) mm wide, serrate to biserrate, acute, shortly and sparsely appressed hairy. *Capitula* containing both pistillate *ray florets* and bisexual *disc florets*. *Ray corollas* cream to yellow. *Paleae* lanceolate, conduplicate, stramineous, with well-defined midrib and usually several lateral striae, acute, margin entire, shortly scabrous apically. *Achenes* obconate, 3–4 mm long; *pappus* of a few tiny scales and, sometimes, up to 3 short awns. (Figures 13F, 32)

Other specimens (selection). CHINA: Kwangtung Province, Aug. 1887, *C. Ford* 101 (K); Yunnan, *s. dat.*, *G. Forrest* 10919 (K); Yangtze valley, NW Yunnan, Oct. 1921, *G. Forrest* 20786 (K). JAPAN: China-choo Is., Kyuysu, 7 Dec. 1966, *M. Furuse* 44812 (K); Yonama Amagi-choo Is., Kyuysu, 22 June 1969, *M. Furuse* 47644 (K). INDIA: Pykana Falls, Nilgiris, Madras, June 1884, *J.S. Gamble* 14400 (K); Bailadila Peak, Bastar State, 16 Dec. 1938, *H.F. Mooney* 892 (K); Bhatodih, Orissa, Koonjhar State, 1 Oct. 1946, *H.F. Mooney* 2757 (K). BURMA: Maymyo Plateau, 19 June 1908, *J.H. Lace* 3254 (K). THAILAND: Ban Nai, Surat, Sep. 1927, *Yuang* 32 (K). INDONESIA: Magelang, Java, 8 Oct. 1941, *P. van der Meer* & *G. den Hoed* 1777 (L); Malang, Pujon, Coban Rondo, E.Java, 12 July 1980, *J.P. Moge* 2451 (BO); Bodu Gendru, Java, 1912, *J.P. Mousset* 89 (L); Letti [Leti] and Babar, *c.* 1883, *Reidel s.n.* (K); Gunung Guntur, Jarut, Feb. 1915, *H.N. Ridley s.n.* (BM, K); Prov. Preanger, prope Garut, Java, 11 Feb. 1894, *V. Schiffner* 2768 (L); Palembang, Banding Agoeng, Sumatra, 28 Oct. 1929, [*C.G.G.J.*] *van Steenis* 3330 (L); Ruteng, Flores, *J.A.J. Verheijen* 554 (L); Java, [H.] *Zollinger* 197 & 296 (K).

Distribution and habitat. Found from southern Indonesia to south-eastern Asia, India, China and Japan, growing on coasts and in savannah forest at altitudes to 1,200 m. Occasionally cultivated (e.g. Cult. in Hort. Bog. XVI, I, 16, 16 Oct. 1934, *C.G.G.J. van Steenis s.n.* (BO)).

Phenology. Flowering and fruiting August–December.

Conservation status. Unknown, but probably not threatened in most countries.

Nomenclatural notes. It is not clear whether all the ‘Zollinger 2922’ type specimens of *W. javana* in P represent one or multiple collections (i.e. whether they are isotypes or syntypes), but they are all conspecific.

Taxonomic notes. This plant can be confused with *Indocypraea montana*. The two are easily distinguished by their achenes, if present. If only in flower, *I. montana* is distinguished from *L. urticifolia* by its long outer involucre bracts, exceeding the inner bracts and disc florets.

1b. *Lipoblepharis urticifolia* subsp. *hortorum* Orchard, *subsp. nov.*

Type: Java, *s. dat.*, Blume *s.n.* (*holo:* Java, *s. dat.*, Blume, L 791046!; *probable iso:* in montanis Javae, 1831, herb. Blume, G 135220!; Java, *s. dat.*, Anon. [Blume?], L 791045!; Java, *s. dat.*, Blume, NY 274465 photo!).

Verbesina urticaefolia ‘Variet.: foliis strigosis, flore pleno’ *sensu* Blume, *Bijdr. Ned. Ind.* 912 (1826), *sine nom. val.*

Perennial herb 0.3 m tall; stems procumbent. Leaf lamina ovate, 60 mm long, 30–40 mm wide, coarsely serrate to biserrate, acute, shortly and sparsely appressed-hairy. Capitula containing only pistillate ray florets; corollas cream to yellow; ovary narrowly obovoid, shortly pilose apically; pappus of c. 3 short awns. Paleae lanceolate, conduplicate, stramineous, with well-defined midrib and several lateral striae, acute, with margin entire, shortly scabrous apically. Achenes not formed. (Figure 33A–G)

Other specimens: BURMA: Prome, culta, Comp. angl. des Indes, 1830, [Wallich] 318 (G 135221). VIETNAM: Chaudoc [Chau Phu], *s. dat.*, L. Pierre 1072 (K, P photo). THAILAND: Chieng Mai, 1 Nov. 1914, A.F.G. Kerr 3446 (K). MALAYSIA: Penang Gardens, Nov. 1884, C. Curtis 40 (K); Malacca, *s. dat.*, Dr Yvan *s.n.* (G, herb. Delessert). SINGAPORE: Singapore, Oct. 1861, [T.?] Anderson 51 (K, herb. Hooker). INDONESIA: cult. in Hort. Bogor, Java, *s. dat.*, Anon. *s.n.* (BO, K); Java, *s. dat.*, Anon. *s.n.* (K, herb. Hooker); between Solok and Datur, Sumatra[?], 1897, [C.] Curtis 471 (K); Java, *s. dat.*, Kollmann *s.n.* (G, herb. Boissier & Barbey-Boissier); Medan, 29 Sep. 1928, J.A. Lörzing 13967 (BO); Medan, 24 June 1915, J. Roesel 421 (BO).

Distribution and habitat. Widely cultivated as an ornamental species in south-east Asia and Malesia, from Vietnam and Burma to Indonesia, rarely escaping into the wild.

Phenology. Flowering October–November, never setting fruit.

Conservation status. Unknown, but probably not threatened in most countries.

Taxonomic notes. In describing his ‘Variet.’ Blume omitted to provide a valid epithet. Various later authors have adopted the last two words of his description ‘flore-pleno’ as an epithet, but this has no nomenclatural standing, except perhaps horticulturally. As the plant is a readily recognised, widely cultivated taxon, it is here given a formal name.

Local name. ‘Luntarkuning’ (Medan, J.A. Lörzing 13967, BO).

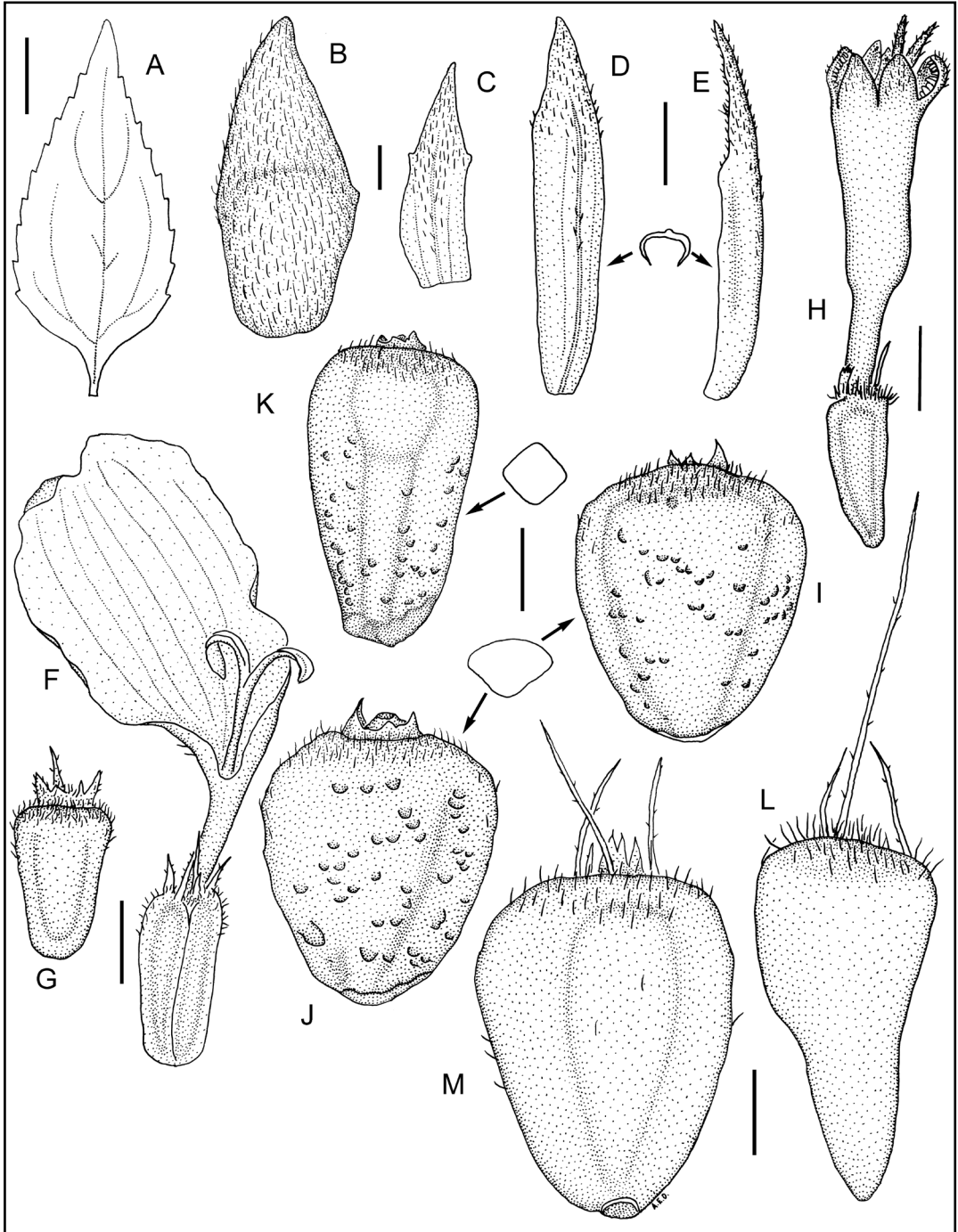


Figure 32. *Lipoblepharis urticifolia* subsp. *urticifolia*. A – leaf; B – outer involucre; C – inner involucre, transitional to paleae; D – palea, dorsal view; E – palea, lateral view; F – ray floret adaxial view; G – ray floret ovary, abaxial view; H – disc floret; I, J – ray achenes, adaxial and abaxial views, awns shed; K – disc achene, awns shed; L – immature achene with some residual awns; M – mature achene with some residual awns. (A–K based on *V. Schiffner* 2768 (L); L, M based on *C. G. G. J. van Steenis* 3330 (L)). Scale bars: A = 1 cm; B–M = 1 mm. Del. A.E. Orchard.

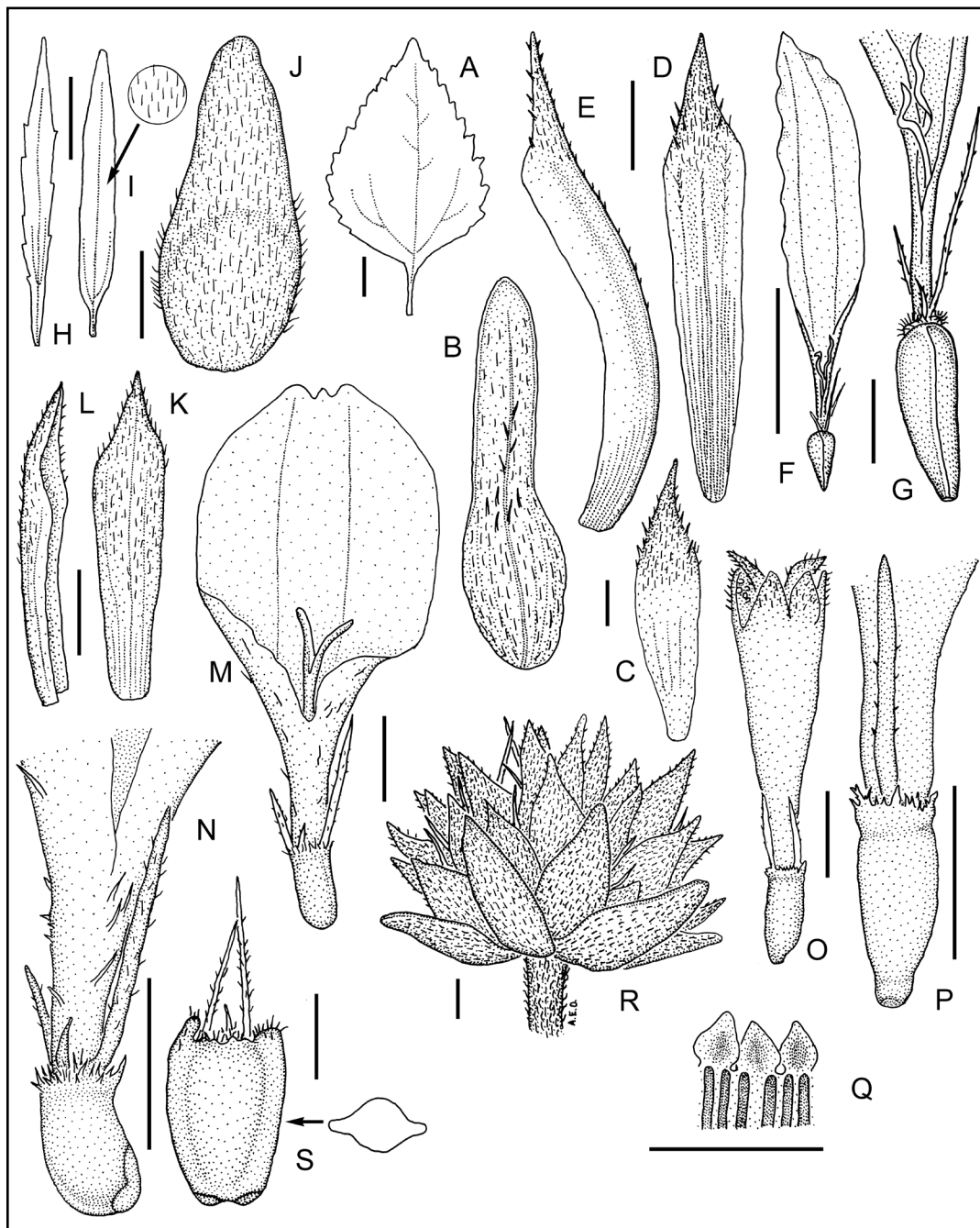


Figure 33. *Lipoblepharis* species. A–G. *Lipoblepharis urticifolia* subsp. *hortorum*. A – leaf; B – outer involucre bract; C – inner involucre bract; D – palea, dorsal view; E – palea, lateral view; F – floret; G – detail of ovary. H–S. *Lipoblepharis stenophylla*. H, I – leaves; J – involucre bract; K – palea, dorsal view; L – palea, lateral view; M – ray floret; N – ray floret, detail of ovary; O – disc floret; P – disc floret, detail of ovary; Q – anther appendages; R – fruiting capitulum; S – achene. (A–G based on *L. Pierre* 1072 (K); H–S based on *J. Elbert* 3464 (CANB)). Scale bars A = 1 cm; B–E, G–S = 1 mm, F = 5 mm. Del. A.E. Orchard.

2. *Lipoblepharis thailandica* (Koyama) Orchard, *comb. nov.*

Wedelia thailandica Koyama, *Acta Phytotax. Geobot.* 36: 168 (1985). *Type citation*: ‘Thailand, N Chiang Mai: Doi Khun Tan (Tagawa et al. T-9303 KYO-Holotype, BKF.)’ (all *n.v.*).

Illustrations. H. Koyama, *Acta Phytotax. Geobot.* 36: 167, Figure 1 & 169, Figure 2 (1985).

Perennial *herbs* 1.0–1.5 m tall. *Leaves* green, discolorous, ovate to narrowly ovate, 100–190 mm long, 30–60 mm wide, finely serrate to biserrate, scabrous, particularly on lower surface. *Capitula* on peduncles 15–40 mm long; involucrel *bracts* oblong-elliptical, acute, shortly pilose dorsally. *Ray florets* yellow, linear, sparsely pilose abaxially. *Disc florets* yellow; *anther thecae* black. *Paleae* not described. *Achenes* 3.5–4.5 mm long, *c.* 2 mm wide, sharply 3-angled with the angles produced into short peaks apically, strongly tuberculate; *pappus* a shallow, dentate cupule, with 1 or 2 short, setiform awns on at least the disc achenes.

Other material examined. THAILAND: Chiang Dao, 2 Nov. 1922, *A.F.C. Kerr* 6519 (K); Chang Mai, Mae Soi Ridge, near Ban Bab Cluay, 13 Aug. 1991, *J.F. Maxwell* 91-742 (P photo!); Chiang Mai, Doi Chiang Dao, 20 Dec. 1931, *A. Put* 4422 (K). ?‘EAST INDIES’: *V. Jacquemont* 476 (P 2693187 photo!); *V. Jacquemont* 777 (P 2693185 & 2693186 photo!).

Distribution and habitat. Endemic to Thailand. Reported to be from mountain slopes in scattered deciduous and/or evergreen forest with bamboo thicket and mixed forest, altitude 1,200–1,850 m. (Koyama 1985).

Phenology. Flowering August–December.

Conservation status. Unknown.

Taxonomic notes. The leaf lamina in this species is larger and proportionately narrower than in *L. urticifolia* subsp. *urticifolia*, and the tip is distinctly long-acuminate rather than acute. The type has not been examined during this study, but the original paper has a photograph of the type and an illustration of the achene. Other specimens from Thailand can be matched with the type, particularly in relation to its distinctive large leaves, but *L. urticifolia* specimens from, for example, Tibet and Java, have been seen in which the leaf shape approaches that of *L. thailandica*, although they are much smaller. Specimens examined for this study lacked fruit. The fruit illustrated by Koyama differs substantially in shape from that of *L. urticifolia*, and this has heavily influenced the decision to accept this species mainly on the basis of its description. As specimens agreeing with *L. urticifolia* are also known from Thailand, further studies of specimens from that country are required to establish whether there are one or two species involved.

3. *Lipoblepharis asperrima* (DC. ex Decne.) Orchard, *comb. nov.*

Wollastonia asperrima DC. ex Decne., *Nouv. Ann. Mus. Hist. Nat.* ser. 3, 3: 414 (1834) [*Herb. Tim. Desc.* 86 (1834)]; *Wedelia asperrima* (DC. ex Decne.) Benth., *Fl. Austral.* 3: 539 (1866), *descr. excl.*; *Wedelia urticaefolia* var. *asperrima* (DC. ex Decne.) Gagnep., in H. Lecomte, *Fl. Indo-Chine* 3: 602 (1924). *Type citation*: ‘Cette courte description a été faite d’après un exemplaire unique, conservé dans les herbiers du Muséum [Paris], [Timor]’ (*holo*: Timor, *s. dat.*, without collector, P 2515133 photo!).

?*Wollastonia junghuhniana* Miq., *Pl. Jungh.* 502 (1855–57); *Wollastonia scabriuscula* var. [β .] *junghuhniana* (Miq.) Miq., *Fl. Ned. Ind.* 2: 71 (1856). *Type citation*: Not specified [Java or Sumatra, *Junghuhn*] (*holo*: ?L n.v.). See *Nomenclatural notes* below.

Wedelia schultzi Miq., *Fl. Ned. Ind.* 2: 69 (1856). *Type citation*: ‘Eiland Bali in het gebergta van Saraja ([H.] Zollinger 729, Z)’ (*holo*: In montanis Saraja ins. Bali, *s. dat.*, *Zollinger 729Z*, P 4430431 photo!; *iso*: Java, *s. dat.*, [H.] *Zollinger 729Z*, P 2515018 photo!)

Wedelia acerba S.Moore, *J. Bot.* 64 (Suppl. 1): 146 (1926). *Type citation*: ‘Timor, [Forbes] 3567’ (*holo*: Timor, *s. dat.*, *H.O. Forbes 3567*, BM 945847!).

Shrub or perennial *herb* 0.3–1.0 m tall (*stems* sometimes creeping and rooting at nodes). *Leaves* green, usually narrowly ovate to lanceolate (rarely lower leaves ovate), (35–)65–100 mm long, (15–)25–35(–70) mm wide, finely to coarsely serrate, roughly scabrous on both surfaces, densely so on abaxial veins. *Capitula* on peduncles (30–)40–60 mm long; involucrel *bracts* lanceolate, outer slightly longer than inner, acute, appressed hairy abaxially. *Ray corollas* yellow, with an ovate to oblong lamina, sparsely pilose abaxially. *Disc corollas* yellow; *anther thecae* black. *Paleae* stramineous or red/yellow, lanceolate (becoming oblong to subovate in fruit), acute to subacuminate, conduplicate, with a well-defined midrib and several dark striae, shortly scabrous on midrib and abaxially near tip. *Achenes* grey to black, obcuneate, 2–3 mm long, 2.0–2.5 mm wide, slightly compressed, 3-angled (ray) or 4-angled (disc), with short hairs on truncate apex, weakly rugose; *pappus* of several tiny, free scales, plus 1 or 2, often oblique, fragile, antrorsely barbed, terete awns 2–3 mm long. (Figures 13G, 34)

Other specimens (selection). INDONESIA: 5 km S of Bima, Sumbawa, 20 Feb. 1939, *S. Bloembergen* 3143 (L); Nasimitan near Kapan, W. Timor, 17 Mar. 1939, *S. Bloembergen* 3507 & 3513 (BO, L); Rindjani Vulkangebirge, Pringabaya, Lombok, 8 June 1909, *J. Elbert* 1984 (L); Roga, Flores, 8 Feb. 1910, *J. Elbert* 4343 (CANB, L); Wono–Lodang, Celebes, 24 July 1937, *P.J. Eyma* 1248 (BO); Alor, Kalabahi nach Adang, 1 May 1938, *O. Jaag* 214 (BM, L); Simarang, Tilomojo, Java, 13 June 1897, *S.H. Koorders* 27695B (L); Manau near Ruteng, W. Flores, 25 Apr. 1965, *Kostermans & Wirawan* 641 (L); Sumatra, *Korthals s.n.* (L 791023); Batu Sangia peak, Kabaena, 3 Aug. 1993, *McDonald & Ismail* 4094 (CANB, K); Wayungan near Palu, Sulawesi, 19 May 1975, *Noerta & W. Meijer* 10220 (L); Tjisaroea, Tjibodas, Java, 20 July 1896, *H. Raap* 913 (L); Bali, Apr. 1939, *C.N.A. de Voogd s.n.* (BO); Penelokan along path to Lake Batur, Bali, 18 July 1970, *R.H. Willemse s.n.* (L 791034); Maumaru, Sumba, 24 June 1975, *H. Wiriadinata* 467 (L). EAST TIMOR: Desa Wala near Tilomar, 10 Mar. 2006, *A.A. Mitchell* 8517 (CANB, DNA).

Distribution and habitat. Apparently confined to the Indonesian archipelago: Sumatra and Java to Nusa Tenggara (Lesser Sunda Islands) and Sulawesi (Celebes), Indonesia; also in East Timor. Reported mainly from grassland and disturbed areas in heath forest, rainforest and secondary forest, on a range of soils including volcanic breccia, at altitudes of 150–1,500 m. Occasionally cultivated (e.g. Cult. in Hort. Bog. 15 June 1893, *Hallier* D180a, BO).

Phenology. Flowers present February–August, fruits (February–)April–October.

Conservation status. Unknown, but probably not threatened.

Nomenclatural notes. Bentham (1866) validly made the combination *Wedelia asperrima*, but misapplied the name to Australian plants, which are correctly referred to *Apowollastonia cylindrica*.

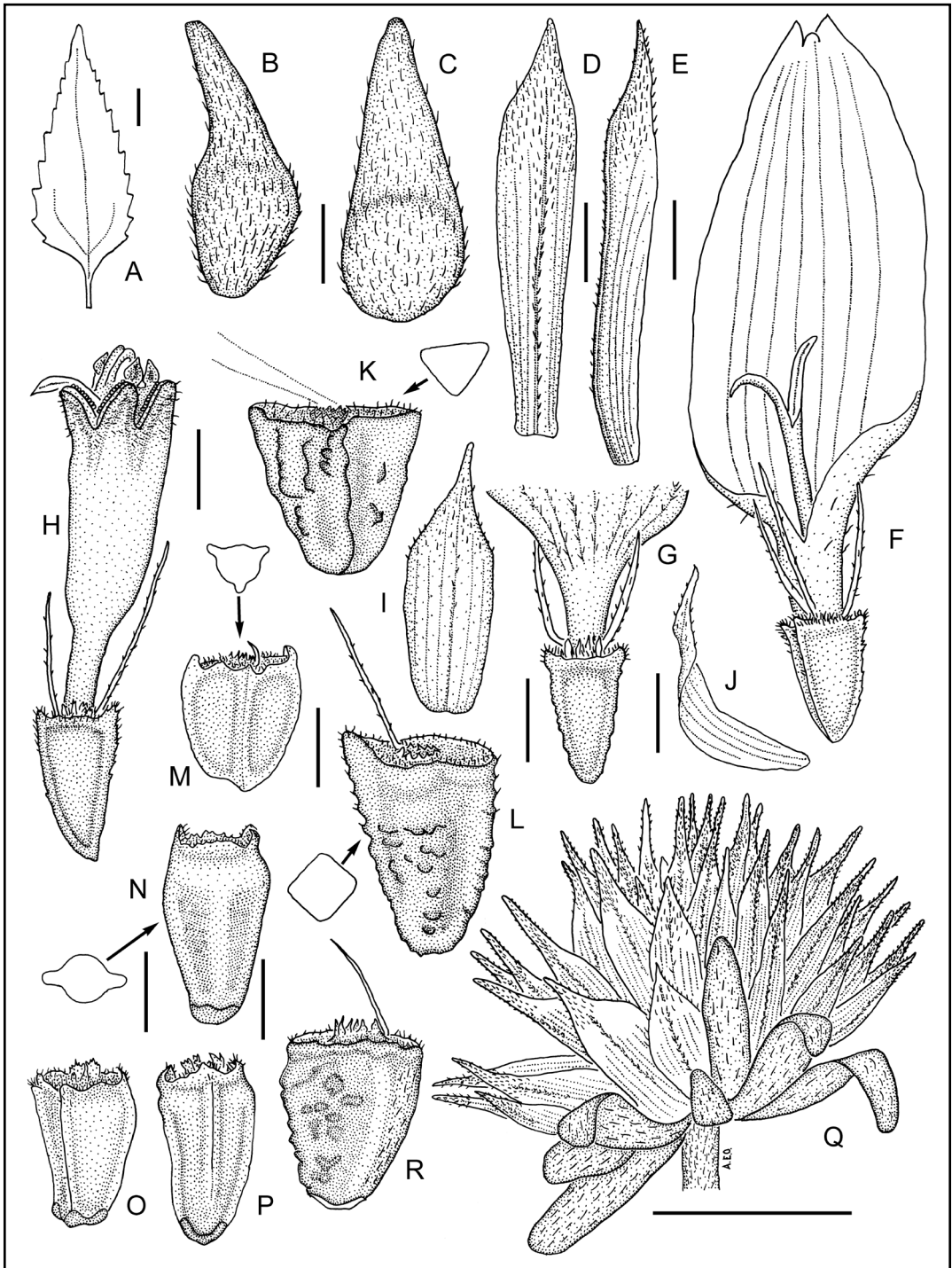


Figure 34. *Lipoblepharis asperrima*. A – leaf; B – outer involucral bract; C – inner involucral bract; D – palea, dorsal view; E – palea, lateral view; F – ray floret; G – ray floret, detail of ovary, abaxial view; H – disc floret; I, J – fruiting palea, dorsal and lateral views; K, M, O, R – ray achenes; L, N, P – disc achenes; Q – fruiting capitulum. (A–H, K, L based on *W. Meijer* 10220 (L); M, N based on *Kosterman & Wirawan* 641 (L); O, P based on *J. Elbert* 4343 (L); Q, R based on *J. Elbert* 4343 (CANB)). Scale bars: A = 1 cm; Q = 5 mm; B–P, R = 1 mm. Del. A.E. Orchard.

Miquel (1855–57) did not cite a specimen in his description of *W. junghuhniana*, although it was implied that it was a Junghuhn collection from Java or Sumatra. His description of *W. scabriuscula* var. [β .] *junghuhniana* (Miquel 1856) was not directly referenced, although as in both cases *W. scabriuscula* was mentioned, and the description is almost identical, it can be taken that the same taxon was meant, and that *W. scabriuscula* var. *junghuhniana* is the basionym of *W. junghuhniana* (or perhaps *vice versa*, the exact dates of publication being obscure). In the second publication a specimen ‘Java, Diënggebergte op heuvelachtige plaatsen, om de vlakke (Junghuhn)’ was cited, and this can be accepted as the type. It has not been located for this study, but is probably at L. From the description, it seems to agree with *L. asperrima*.

Taxonomic notes. *Lipoblepharis asperrima* is sympatric with *L. urticifolia* in Indonesia, and can easily be confused with that species. *Lipoblepharis asperrima* is distinguished by having proportionately narrower leaves (usually \pm lanceolate *vs.* ovate), with often coarser teeth, and coarser, more scabrous hairs. The achenes of *L. asperrima* are smaller (usually *c.* 2.0–2.5 mm long) than those of *L. urticifolia* (*c.* 3–4 mm long), and in fruit the outer paleae of *L. asperrima* are semi-transparent, membranous, with very distinct red-brown and yellow striae (Figure 13G), while those of *L. urticifolia* are stramineous, cartilaginous, with, at most, indistinct striae (Figure 13F).

Local names. Arangah (Alor, *O. Jaag* 214); Hau pune (W. Timor, *S. Bloembergen* 3507); Pula (Sumba, *H. Wiriadinata* 467).

4. *Lipoblepharis floribunda* Orchard, *sp. nov.*

Type: near Pic Fatmalapa, Efate, Vanuatu, 11 Nov. 1988, *D. Mueller-Dombois & J. Wheatley* 88111107 (*holo:* CANB 571665!; *iso:* BISH 628504 *n.v.*).

Shrub 1–2 m tall. *Leaves* greyish, discolorous, narrowly ovate to lanceolate, 60–110 mm long, 20–45 mm wide, very finely serrate, sparsely and shortly scabrous on both surfaces. *Capitula* in terminal dichasial cymes of 10–12, on peduncles (10–)20–40 mm long; involucrel *bracts* lanceolate, blunt, densely grey-hairy abaxially. *Ray corollas* yellow, with an oblong lamina, glabrous. *Disc corollas* yellow; *anther thecae* black, with paler anther appendages. *Paleae* greenish, sometimes with a purplish streak, opaque, oblanceolate, blunt to subacute, conduplicate, with obscure midrib and striae, densely and shortly scabrous abaxially. *Achenes* grey-black, obcuneate, 2 mm long, 1 mm wide, slightly compressed, 3-angled (ray) or 2-angled (disc), densely hairy on truncate apex, with very minute, transverse wrinkles but otherwise smooth; *pappus* of a few very small, free scales hidden in apical indumentum. (Figure 35)

Distribution and habitat. Known only from the type collection from Vanuatu. Collected from open *Miscanthus* grassland near a forest fragment, at 400 m elevation.

Phenology. Flowers and fruits present in November.

Conservation status. Unknown, but possibly vulnerable. Only known from the type.

Taxonomic notes. *Lipoblepharis floribunda* is notable for its large leaves which resemble those of *Apowollastonia major*, *Lipoblepharis asperrima* and *L. thailandica*, but differ from all these taxa in being distinctly greyish and of a rather thick texture. From other species of *Lipoblepharis* it differs also in its dense inflorescence of about 10–12 capitula in terminal dichasial cymes on rather short

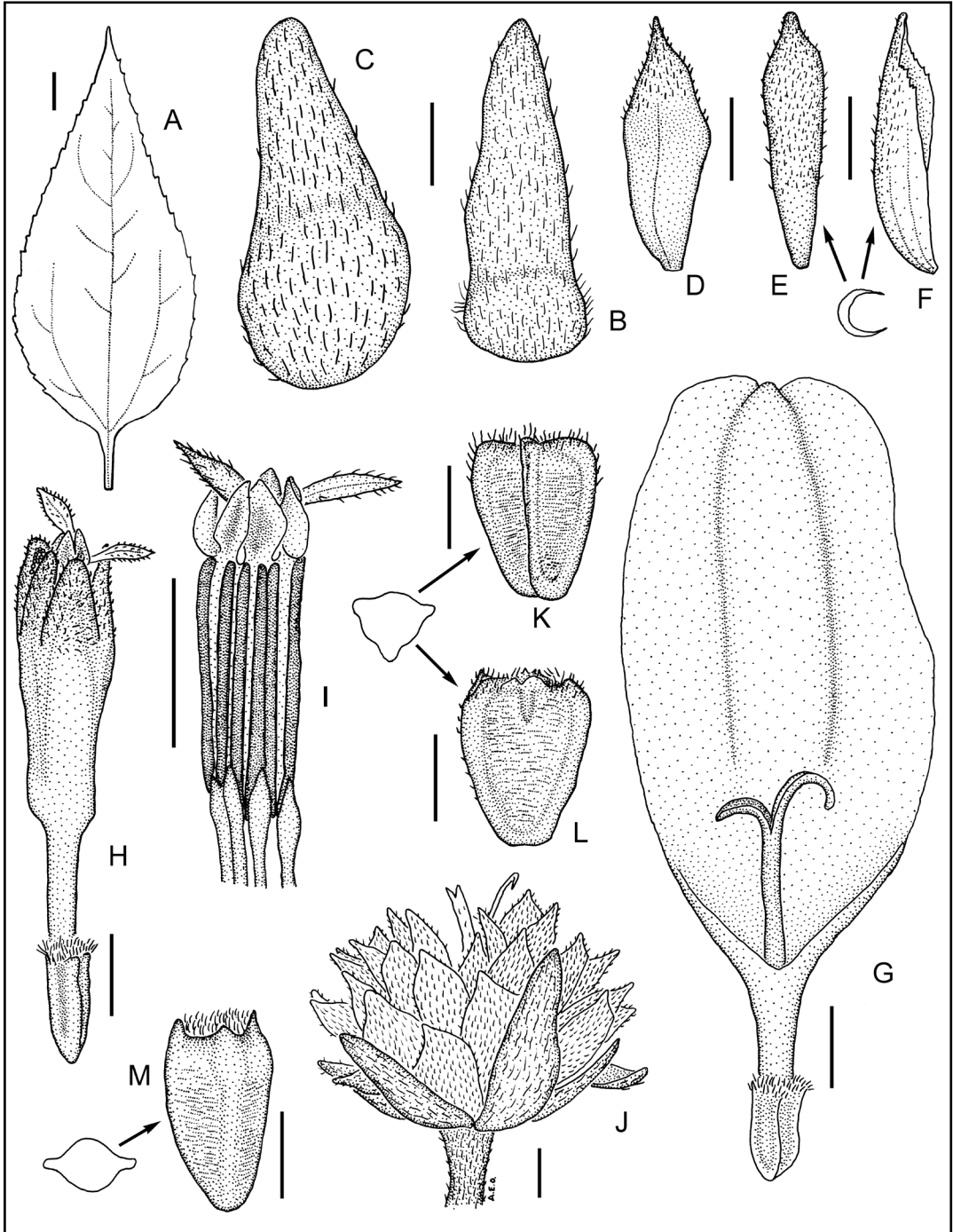


Figure 35. *Lipoblepharis floribunda*. A – leaf; B – outer involucral bract; C – median involucral bract; D – innermost involucral bract, transitional to paleae; E – palea, dorsal view; F – palea, lateral view; G – ray floret; H – disc floret; I – stamens and stigmas; J – fruiting capitulum; K, L – ray achenes, adaxial and abaxial views; M – disc achene. (All based on type specimen, *D. Mueller-Dombois* & *J. Wheatley* 88111107 (CANB)). Scale bars: A = 1 cm; B–M = 1 mm. Del. A.E. Orchard.

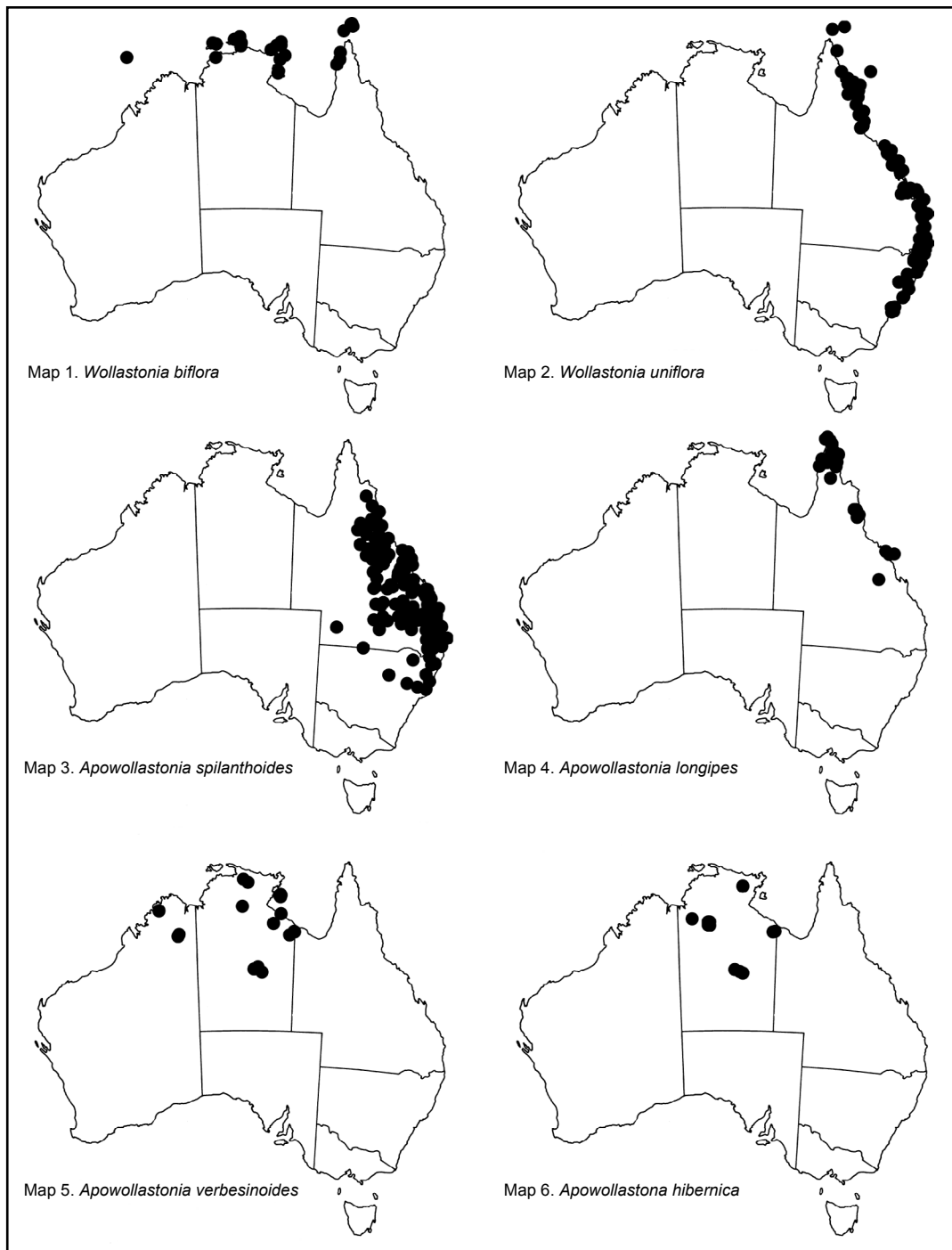


Figure 36. Map 1 – Australian distribution of *Wollastonia biflora* (var. *biflora*); map 2 – Australian distribution of *W. uniflora*; map 3 – distribution of *Apowollastonia spilanthoides*; map 4 – distribution of *A. longipes*; map 5 – distribution of *A. verbesinoides*; map 6 – distribution of *A. hibernica*.

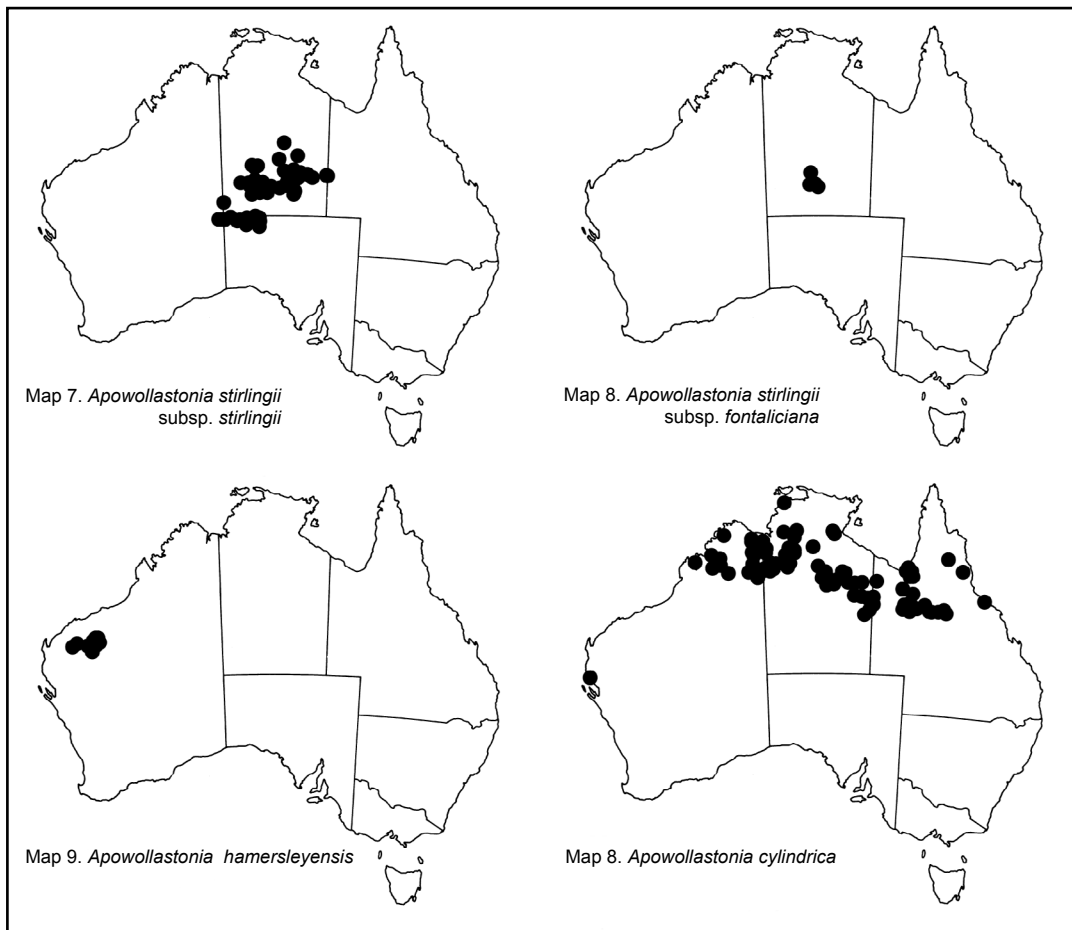


Figure 37. Map 7 – distribution of *Apowollastonia stirlingii* subsp. *stirlingii*; map 8 – distribution of *A. stirlingii* subsp. *fontaliciana*; map 9 – distribution of *A. hamersleyensis*; map 10 – distribution of *A. cylindrica*.

peduncles. The achenes are notable in apparently completely lacking awns, these being absent even in the young florets. The pappus consists of a few tiny, free scales amongst longer, dense, terminal hairs. Capitula contain about eight ray florets and 15 disc florets, all of which can develop into achenes, but do so irregularly.

5. *Lipoblepharis stenophylla* (Merr.) Orchard, *comb. nov.*

Wedelia stenophylla Merr., *Philipp. J. Sci.* 30: 429 (1926). *Type citation*: ‘Mindanao, Misamis Province, For. Bur. 29751 *Caster*, on the top of Angyar Ridge, altitude about 400 metres’ (*holo*: PNH, apparently destroyed; *iso*: UC 256909 photo!).

Perennial *herb* 1 m tall. *Leaves* grey-green, linear, 40–50(–70) mm long, 3–7 mm wide, shortly serrate (rarely almost entire), sparsely to moderately densely scabrous on margins and main veins. *Capitula* on peduncles 60–70(150) mm long; involucral bracts lanceolate, blunt, appressed-hairy abaxially. *Ray florets* with *corolla* lamina yellow, ovate, with sparse hairs abaxially. *Disc florets* with *corolla* yellow;

anther thecae black. *Paleae* light green, linear, acute, conduplicate, with a well-defined midrib and weak lateral striae, shortly appressed-scabrous distally. *Achenes* dull black, narrowly ovoid, c. 2 mm long, 1.5 mm wide, compressed, 2-angled, the angles produced as small vertical lobes apically, with short hairs apically, otherwise glabrous; *pappus* of 2 or 3 erect, persistent, antrorsely barbed awns 1–2 mm long. (Figures 33H–S)

Distribution and habitat. Found in the Philippines (Mindanao), Indonesia (Sulawesi [Celebes]), and Papua New Guinea, growing in secondary grassland with *Themeda triandra*, at altitudes of 600–1,370 m.

Phenology. Flowers October–November, fruits October–December.

Conservation status. Unknown. Collections widespread, sparse and variable. Possibly vulnerable, but poorly known.

Additional specimens. INDONESIA: Sangia-wita-Berg, Kabaena, 22 Oct. 1909, *J. Elbert* 3464 (CANB, G, K); Tangkeno, Rahadopi, Pula Kabaena, 3 July 1978, *E.A. Widjaja* 723 (K). PAPUAN NEW GUINEA: Kassam, 2 Nov. 1959, *L.J. Brass* 32354 (K); Kanojia, 7 Feb. 1935, *C.E. Carr* 11193 (BM); Baiune, 15 Dec. 1954, *E.E. Henty* NGF11640 (K).

Taxonomic notes. Plants from Papua New Guinea have ±entire leaves, while those of the Philippines and Sulawesi are usually shortly serrate (*Widjaja* 723 has entire leaves). Achene shape is very variable among the specimens cited here, and it is possible that more than one species is involved, but existing collections are too few and inadequate to resolve this. Some New Guinean specimens have broader leaves to 12 or 15 mm wide and achenes to 3 mm long and 1 mm wide (e.g. near Mount Hagen Stn, 15 Sep. 1956, *R.D. Hoogland* 6227 & *R. Pullen*, BM); bei Constantin Hafen, Mar. 1902, *R. Schlechter* 14252, BO). They approach *Apowollastonia major* in general appearance, but can be recognised by their weaker habit, smaller leaves, acute paleae, and achene shape.

11. *Lipochaeta* DC., *Prodr.* 5: 610 (1836).

Type: *L. lobata* (Gaud.) DC.

Microchaeta Nutt., *Trans. Amer. Philos. Soc.* (n.s.) 7: 450 (1841), *nom. illeg. superfl.*

Perennial *herbs*, erect, spreading, (0.2–)1–2 m tall, or prostrate and rooting at nodes (*L. succulenta*). *Leaves* opposite, simple, (linear-)lanceolate to ovate, deltate or spatulate, 6–12.5(–25) cm long, (1–)2–4(–12) cm wide, triplinerved, entire or deeply lobed, serrate, petiolate or sessile, both surfaces subglabrous or scabrous with glutinous dots. *Capitula* radiate, on short to medium peduncles, with 2 subequal series of bracts; *bracts* green (sometimes purple-tinged), stiffly herbaceous, sparsely hairy abaxially; inner bracts similar. *Ray florets* pistillate, fertile; *corollas* yellow. *Disc florets* bisexual; *corolla* yellow, 4-lobed; *anther thecae* black or brown. *Paleae* oblanceolate, conduplicate, stiff, coriaceous, subhyaline to opaque (often tinged purple), lacking an abaxial crest and apical lobes, with a midrib and numerous striae; margins entire; tip usually blunt and subhooded; abaxially and/or marginally shortly scabrous. *Achenes* dark brown to black, 1.5–3.0 mm long, slightly compressed, 3-angled (ray) or 4-angled (disc), sometimes shortly winged on angles, cylindrical to obcuneate, usually rugose at maturity, rounded or truncate apically, with minute hairs apically, lacking elaiosomes; *pappus* a ring of tiny scales, slightly fused basally, sometimes with 1–3 short awns.

A genus of six species and a number of infraspecific taxa, endemic to Hawai‘i. Distinguished from *Wollastonia* principally in having disc florets with 4-lobed corollas, a chromosome number of $n = 26$ (Rabakonandrianina 1980; Rabakonandrianina & Carr 1981), and both flavonols and flavones (5-lobed corollas, $n = 15$, flavonols only in *Wollastonia*). For keys, descriptions, illustrations and synonymies see Degener (1946–1962), Gardner (1979), Wagner *et al.* (1999), and Wagner and Robinson (2002).

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