



Afrohybanthus (Violaceae), a new genus for a distinctive and widely distributed Old World hybanthoid lineage

BENJAMIN J. FLICKER¹ & HARVEY E. BALLARD, JR.^{1,2}

¹Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, USA

²Author for correspondence; email: ballardh@ohio.edu

Abstract

Recent traditional and molecular systematic studies of the violet family, Violaceae, have confirmed extensive polyphyly of the genus *Hybanthus* and substantial polyphyly in *Rinorea* as well. Phylogenetic analyses have proposed up to nine distinct hybanthoid clades. Broad studies of representative taxa within each clade have revealed coherent suites of macromorphological traits in foliage, flowers, fruits and seeds that easily discriminate the nine hybanthoid lineages from each other and from currently recognized genera in the family. Base chromosome numbers and biogeography also provide additional support for recognition of the hybanthoid clades as distinct segregate genera. Some hybanthoid clades have available older generic names, but one of the two Old World lineages, namely the *Hybanthus enneaspermus* group, is presently nameless. This clade, distinctive in its ellipsoid, pale yellow, often foveolate seeds, is the most diverse in the Paleotropics, with approximately 25 species distributed across Africa, Madagascar, southern Asia, northern Australia and the southwestern Pacific. The group is segregated here as *Afrohybanthus* gen. nov., with new combinations provided for existing names, all of which have thus far proven morphologically distinct and worthy of recognition at the rank of species. Imminent future studies will describe additional taxa in the new genus.

Key words: Generic circumscription, *Hybanthus*, Old World

Introduction

The Violaceae is a medium-sized family with 23 accepted genera and ca. 1,100 species of trees, shrubs, lianas, and herbs (Ballard, 2007; Ballard *et al.*, 2014; Paula-Souza & Ballard, 2014). The family consists primarily of woody genera of trees, shrubs and lianas in the New and Old World tropics—*Viola* being the only sizeable herbaceous temperate to montane genus. Genera possess great diversity in growth form, inflorescence architecture, floral morphology, and fruit type. The genus *Hybanthus* Jacq. is the third largest in the family with ca. 125 species (Ballard *et al.*, 2014), and is primarily native to the tropics and subtropics; only one species, *Hybanthus concolor* (T.F. Forst.) Spreng., is distributed in temperate eastern North America. Species in the genus range in habit from herbs or subshrubs to shrubs or (rarely) treelets, and have been traditionally characterized and distinguished from other Violaceae by their distinctly zygomorphic corolla with the bottom (anterior) petal noticeably or substantially longer than the lateral and upper ones, differently shaped and often strongly differentiated into an abruptly expanded blade and claw, and with a “saccate” base; usually free stamens, uncommonly with the filaments fused into a short ring, the bottom pair of stamens each bearing a gland; fruits a three-valved thin-walled capsule typical of most genera in the family; and globose to ellipsoidal unwinged seeds. Species inhabit a broad elevational range, from sea-level to 3000 m, and occupy various habitats from lowland rainforest, savanna and grassland, through temperate and cloud forests, to paramo, with the greatest diversity of species in forest openings, shrubland and grassland habitats in Latin America, Africa and Australia. Recent interest has spawned intensive investigations into a bioactive class of proteins, cyclic peptides, and comparative studies have shown the Violaceae to be particularly rich in these (Broussalis *et al.*, 2001; Ireland *et al.*, 2006). Studies of cyclic peptide diversity in species of Australian *Hybanthus* have revealed hundreds of forms and shown that peptide composition closely reflected apparent morphological relationships among taxa (Simonsen *et al.*, 2005).

Taxonomic history of Hybanthus

Nicolaus Jacquin first described *Hybanthus* in 1760 based on the type species *Hybanthus havanensis* Jacq. Several other genera were described as allies to *Hybanthus* by various authors over the next 160 years, including *Pombalia* Vand. (1771), *Solea* Spreng. (1800), *Ionidium* Vent. (1803), *Ionia* Pers. ex Steud. (1821), *Pigea* DC. (1824), *Ionia* Steud. (1840), *Vlamingia* De Vries (1845), *Acentra* Phil. (1870), *Cubelium* Raf. ex Britton & A.Br. (1897) and *Clelandia* J.M. Black (1932). Most of these names were based on various Neotropical hybanthoid taxa as type species. The exceptions are *Clelandia*, *Pigea* and *Vlamingia*, which have been erected for species of southern Australia, with *Pigea* the earliest available and validly published generic name, relating to taxa in the *Hybanthus caledonicus* group (Wahlert *et al.*, 2014). No generic names have ever been applied to Old World hybanthoid taxa outside of Australia, and particularly those of the *Hybanthus enneaspermus* group widespread through Africa and Madagascar, tropical Asia, and northern Australia.

During the last half-century there has been an increasing trend toward synonymy of segregate genera due to the lack of apparently consistent distinctions, favoring a broad concept of *Hybanthus*. Although Airy Shaw in 1966 recognized *Clelandia* as a distinct genus, and Hutchinson (1967) recognized *Cubelium*, all others have since followed Melchior (1925) in recognizing a single broadly defined genus, *Hybanthus*. This trend toward few, broadly delimited taxa at the generic level was also fostered extensively at the species level, especially in Africa and tropical Asia, resulting in comparatively few species (and in the case of *Hybanthus enneaspermus*, many infraspecific taxa; e.g., Grey-Wilson 1981). To date no comprehensive monograph has been published for the genus as presently circumscribed, although a few regional treatments have been completed. Bennett (1972) revised the Australian taxa of *Hybanthus* and described the section *Variabiles* for the southern Australian taxa based on differences in base chromosome number, calcium oxalate crystal shape and distribution, staminal gland morphology, and seed and embryo morphology. The remaining Australian taxa were left in sect. *Suffruticosi*.

Evidence from DNA, morphology, chromosome numbers and geography

Recent molecular phylogenetic results (Fig. 1) for the Violaceae have demonstrated that *Hybanthus* is polyphyletic, with species in nine morphologically and biogeographically distinct clades (Feng, 2005; Wahlert *et al.*, 2014). Results further show that the *Hybanthus enneaspermus* group to occupy a basal position in a broader clade with several other New World and Old World genera and hybanthoid groups, but well removed from the Old World *Hybanthus caledonicus* group and *Hybanthus sensu stricto*.

All hybanthoid clades can be easily distinguished by suites of morphological and anatomical characters including habit, degree of woodiness, branch and stipule morphology, inflorescence type, extent of zygomorphy (relative elongation of bottom petal to lateral and upper ones); basal expansion and differentiation of bottom petal; filament connation; staminal gland shape and position; seed number per valve and capsule, seed shape, size, color and surface sculpturing.

The overall phylogenetic distribution of inferred base chromosome numbers across the family also differentiates the *Hybanthus* clades into two assemblages, with basal genera possessing numbers based on $x = 6$ and derived ones (which form a monophyletic group including other genera) based on $x = 8$.

Geographic distributions of the nine clades are mostly non-overlapping, except for certain areas of Latin America. Seven clades are restricted to the New World, while two are confined to the Old World. The genus *Hybanthus* in the narrow sense is currently being re-circumscribed by the second author to represent a group of three Mesoamerican and Antillean species with woody shrub or treelet habit, long-pedunculate dichasial inflorescences, weakly zygomorphic corollas with a bottom petal greatly distended at base, filaments fully connate into a tube, a single lunate shield-like gland spanning the two bottom stamens, asymmetrical capsule with 1–2 seeds, and seeds large, subglobose, dark brown and minutely roughened.

The *Hybanthus enneaspermus* group represents one of two clades of *Hybanthus sensu lato* restricted to the Paleotropics, the other being the *Hybanthus caledonicus* group (Feng, 2005; Wahlert *et al.*, 2014). The *Hybanthus enneaspermus* group is phylogenetically distinct, and preliminary studies indicate that it possesses numerous macromorphological distinctions across foliage, flowers, capsules and seeds that set it apart from *Hybanthus sensu stricto* and all other hybanthoid groups revealed by recent phylogenetic investigations. Plants are typically herbs with some semi-woody subshrubs and shrubs. The clade is distributed broadly throughout most of the Old World Tropics, and has a center of taxonomic diversity in Tropical East Africa. Geographically, the clade overlaps only slightly with the *Hybanthus caledonicus* group in parts of central Australia. The objective of this study was to clarify the distinctions of the *Hybanthus enneaspermus* group from other hybanthoid groups, in particular *Hybanthus sensu stricto* and the *Hybanthus caledonicus* group, and to provide nomenclatural combinations for existing names under a new segregate genus.

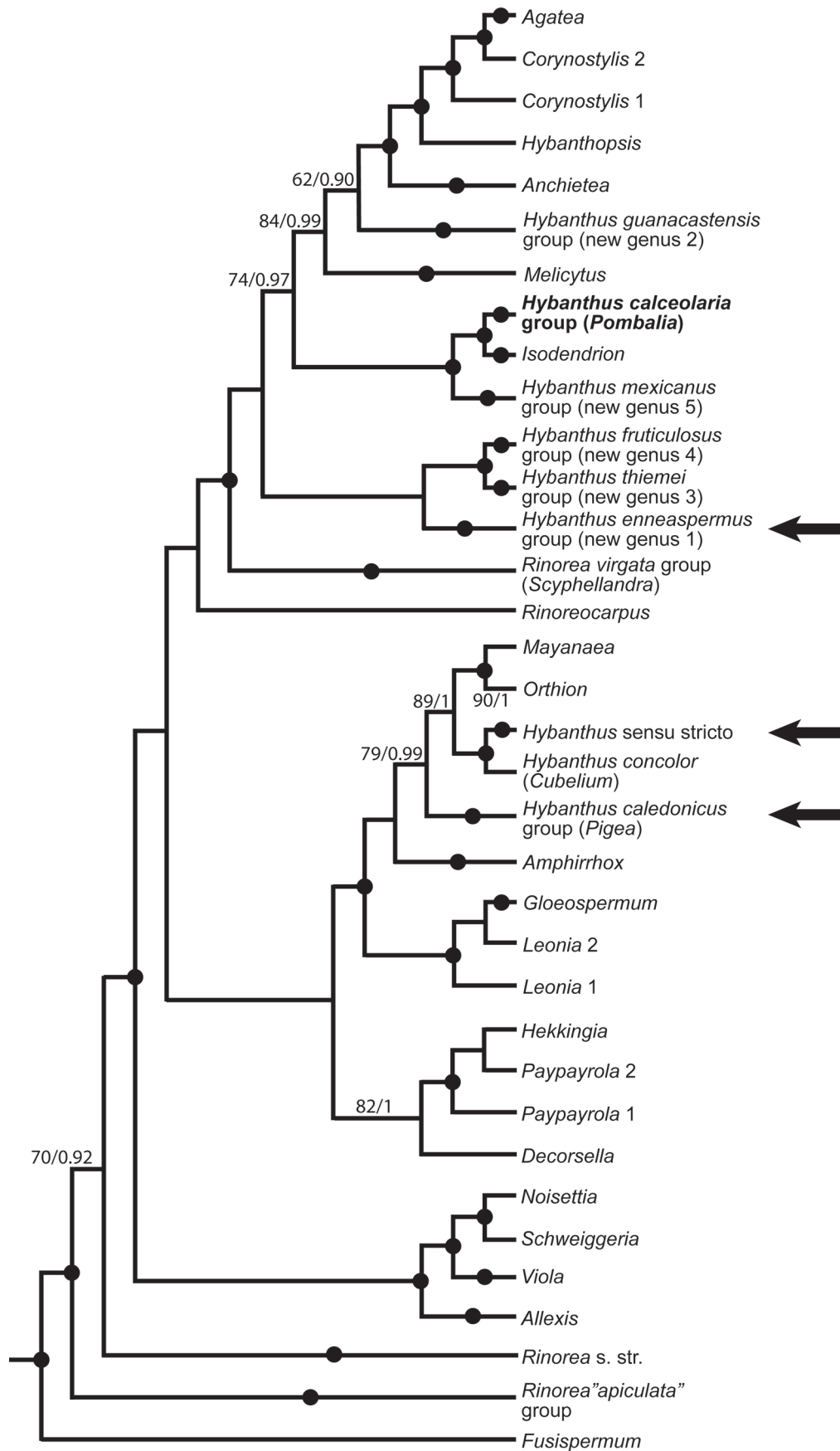


FIGURE 1. Chloroplast phylogeny of the Violaceae; arrows point to Old World groups and *Hybanthus* sensu stricto (redrawn from Wahlert *et al.*, 2014). Numbers above branches are maximum likelihood bootstrap/Bayesian posterior probabilities; solid circles indicate 100%/1.00 support for a branch.

Materials and methods

Morphology and distribution were determined from more than 900 herbarium specimens from A, B, BM, BR, BSM, C, CBG, CHAPA, DUKE, F, G, GH, HBG, IBUG, IEB, INB, K, L, LL, M, MEXU, MICH, MO, NY, P, POM, RSA, S, TEX, U, US, W, WAG, WIS, XAL and Z (herbarium acronyms follow Thiers 2014). Taxa in the three most relevant *Hybanthus* groups were compared in this study: *Hybanthus* sensu stricto, the *Hybanthus enneaspermus* group, and the *Hybanthus caledonicus* group. Flowers were dissected after briefly soaking in a weak soap water solution. Images of floral parts, capsules, seeds and other small structures were captured with an Olympus SZ61 dissecting microscope and an Olympus SC30 videocapture imaging system. Measurements of floral, capsule and seed traits were made using ImageJ software (Abromoff *et al.*, 2004).

Results

The *Hybanthus enneaspermus* group is immediately distinguishable morphologically from other hybanthoid groups by many characters. Characters particularly separating it from *Hybanthus* sensu stricto and the *Hybanthus caledonicus* group (Table 1) include differences in inflorescence type; degree of corolla zygomorphy; relative differentiation of the bottom petal; relative expansion or extension of the base of the bottom petal; extent of filament connation; number, shape and attachment of the staminal glands (Fig. 2, a–c); number of seeds per valve or capsule; and shape, color and surface ornamentation of the seed (Fig. 2, d–f).

TABLE 1. Overview of traits distinguishing *Afrohybanthus* from the type material of *Hybanthus sensu stricto* and the other Old World clade, the South Australian/ South Pacific *Hybanthus caledonicus* clade.

Group	Inflorescence Type	Base of bottom petal	Filament connation	Gland #	Seed surface	Seed color
Afrohybanthus	Solitary	Spurred	Short collar	2	Ribbed or foveolate (smooth)	Pale yellow
<i>Hybanthus</i> sensu stricto	Dichasium	Distended	Fully connate	1	Minutely roughened	Dark brown with pale markings
<i>Hybanthus caledonicus</i> group	Solitary (racemes, monochasium)	Spurred (saccate)	Short Collar	2	Pusticulate	Dark brown

TABLE 1. (Continued)

Group	Corolla zygomorphy (lateral: bottom petal)	Gland position on bottom stamen	Seeds per capsule	Distribution
Afrohybanthus	.38–.66	Medial to upper medial	(6) 9, 12, 15 (18)	Paleotropics
<i>Hybanthus</i> sensu stricto	.75–.89	Summit of filament tube	1–2	Antilles, Mesoamerica
<i>Hybanthus caledonicus</i> group	.30–.66	Basal	1–3 (6)	South Australia/ South Pacific

Chromosome numbers in the two Old World groups appear to parallel the two base numbers apparent in the family overall. Numbers appear to be based on $x = 8$ in the *H. enneaspermus* group (*Hybanthus aurantiacus* F. Muell. ex Benth., $n = 8$, Bennett, 1972; *H. enneaspermus* (L.) F. Muell., $n = 8$, Bennett, 1972, Peng and Chen, 1985; *H. enneaspermus*, $n = 16$, Mangenot and Mangenot, 1962, Sarkar *et al.*, 1980), as opposed to $x = 6$ for species of the *Hybanthus caledonicus* group in southern Australia and New Caledonia (see Bennett, 1972).

The numerous morphological distinctions of the *Hybanthus enneaspermus* group, its somewhat isolated cladistic position especially with regard to *Hybanthus* sensu stricto and the *Hybanthus caledonicus* group, its allopatric Old

World distribution, and different base chromosome number from the *Hybanthus caledonicus* group (and presumably *Hybanthus* sensu stricto), provide compelling evidence for recognition of the *Hybanthus enneaspermus* group as a separate genus. No available generic name exists that applies specifically to taxa in the group under scrutiny. Therefore, the *Hybanthus enneaspermus* group is described under a new name, *Afrohybanthus*.

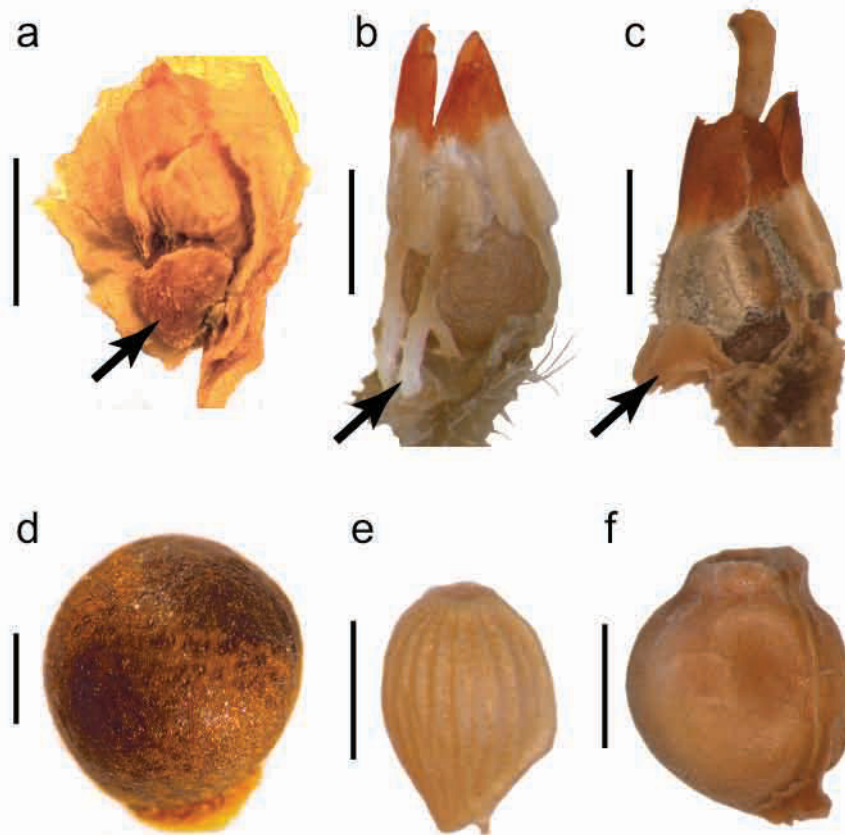


FIGURE 2. Staminal gland and seed morphologies of three different hybanthoid clades. a & d. *Hybanthus* sensu stricto (*H. havavensis*) (a. Contreras 8540 [MO], d. Lundell & Lundell 8540 [MO]). b & e. *Afrohybanthus* (*A. enneaspermus*) (b. Wood 2171 [K], e. Faden & Faden 74/1216 [K]). c & f. *Hybanthus caledonicus* group (*H. caledonicus*) (c. Melville & Coleman 4481 [K], f. Salasoo 4441 [K]). Arrows indicate the staminal glands, scale bars are all 1 mm.

Afrohybanthus Flicker gen. nov.

Diagnosis. The new genus is similar to southern Australian taxa in the Old World *Hybanthus caledonicus* group and many New World taxa, but divergent from *Hybanthus* sensu stricto in having solitary flowers, strongly zygomorphic corollas with a well differentiated bottom petal, filaments basally connate into a short “collar” with free portions to the filaments, two staminal glands, and 3–5 seeds per capsule valve. It shares with the *Hybanthus caledonicus* group a short but distinct spur at the base of the bottom petal, rather than a merely saccate or distended bottom petal characteristic of most New World taxa including *Hybanthus* sensu stricto. It is different from the *Hybanthus caledonicus* group in the elongate glands with medial or upper attachment on the filaments, and is unique in producing ellipsoid to narrowly ovoid, pale yellow or honey-colored seeds commonly with longitudinal ribs and/or foveolae in several to many lines.

Description. Herbs, subshrubs, occasionally shrubs 10 cm to 3 m. tall, stems glabrous to scarcely pubescent, occasionally densely pubescent. *Leaves* simple, alternate, occasionally fascicled, sessile to subsessile, linear to obovate, 0.5–8 cm long, 0.1–1.8 cm wide, base cuneate, lamina herbaceous to chartaceous, veins reticulate, margins entire to denticulate, occasionally with violoid gland on teeth and at apex, glabrous or pubescent, stipules persistent to deciduous, linear to lanceolate, apex acute, occasionally glandular tipped, 1.5–6 mm long, membranous to herbaceous, glabrous to sparsely

pubescent, ciliate along the margins. *Inflorescences* of axillary solitary flowers, peduncles 2–8 mm long, glabrous to pubescent, peduncle bracts subopposite, positioned in the apical half to third near articulation point, membranous, lanceolate, usually glandular tipped, glabrous to pubescent, up to 3 mm long, summit ending at articulation between peduncle and pedicel. *Flowers* borne on a pedicel (from articulation to base of flower) 5–30 mm long, glabrous to pubescent, 6–25 mm long, sepals 5, herbaceous, subequal, 2.5–4 mm long, pubescent along costa, occasionally ciliate along the entire margins, 3–7-nerved, upper 3 lanceolate, bottom 2 falcate-lanceolate, all with apex acute. Corolla strongly zygomorphic, petals white, yellow, pink or purple, herbaceous, glabrous, upper pair lance-ovate, 3–6 mm long, rarely exceeding the calyx, 3–5 nerved, lateral pair falcate, 4–7 mm long, slightly exceeding the calyx, 7–9-nerved, basal petal spurred, strongly clawed, with large blade exceeding the calyx, spatulate to orbicular, apex obtuse occasionally cuspidate or retuse, 8–20 mm long, 2–6 mm wide, often marked with a honey guide. Filaments 1.5–2.5 mm long, connate at base into a minute “collar” less than 1 mm long, free portion above filament tube about 1 mm long, the bottom pair of stamens each with a nectary gland attached medially or in the upper third of the free portion of the filament, glands petioled up to 1 mm long, occasionally sessile, glands usually with a tuft of hairs. Anthers 1.5–4 mm, glabrous, the bottom 2 occasionally with long hairs along the costa of the anther connective, dorsal connective scales short, ovate, glabrous, margin entire, apex rounded. Ovary globose, 1.1–2 mm long, 0.7–1.1 mm wide, glabrous, rarely densely short-pubescent. Style slightly exceeding the anthers, up to 4 mm long, thickened at the tip. *Fruit* a three-valved capsule, glabrous, rarely short-pubescent, straw-colored at maturity, occasionally pale green, 4–9 mm long. *Seeds* typically 9, 12 or 15 (3–5 per valve), rarely 6 or 18, pale yellow or honey-colored, typically ribbed and/or foveolate longitudinally in several to many lines, very rarely smooth, narrowly ovoid to ellipsoid, glabrous, 1.2–2.1 mm long, 0.6–1.8 mm wide. Chromosome numbers based on $x = 8$.

Type species: *Viola enneasperma* L.

Etymology:—The name is based on a combination of the regional center of taxonomic diversity for the *H. enneaspermus* group (Africa) and the broadly defined genus to which this and other hybanthoid lineages have previously been allied.

New Combinations

The following combinations are arranged alphabetically. New combinations are made at the species level. Herbarium investigations support recognition of most previously described taxa, and studies have confirmed that they diverge consistently in multiple features of habit, flowers, capsules and/or seeds. The substantial morphological differentiation, and also commonly non-overlapping geographic distributions and separate habitats, urges recognition of all taxa at the rank of species. In most cases of lectotypes designated in this manuscript, an image of the selected lectotype is presented as a figure.

Afrohybanthus aurantiacus (F. Muell. ex Benth.) Flicker, *comb. nov.* \equiv *Ionidium aurantiacum* F. Muell. ex Benth., *Fl. Austr.* 1: 102. 1863 \equiv *Hybanthus aurantiacus* (F. Muell. ex Benth.) F. Muell., *Pl. North West Austr.*: 5. 1881 \equiv *Hybanthus enneaspermus* var. *aurantiacus* (F. Muell. ex Benth.) F. Muell., *Pl. Indig. Shark Bay*: 6. 1883. Type:—NW Coast of Australia, *Byrnes s.n.* (lectotype K000327678!, designated here); Fig. 3.

Note: A lectotype was chosen from the two specimens cited by Bentham, who failed to designate a holotype.

Afrohybanthus buxifolius (Vent.) Flicker, *comb. nov.* \equiv *Ionidium buxifolium* Vent., *Jard. Malmaison*: sub pl. 27. 1803 \equiv *Viola buxifolia* (Vent.) Juss. ex Poir., *Encycl.* 8: 646. 1808 \equiv *Hybanthus buxifolius* (Vent.) Baill., *Bull., Soc. Linn.* 1: 584. 1886. Type:—Madagascar, *Commerson s.n.* (holotype P-JU!).

Afrohybanthus caffer (Sond.) Flicker, *comb. nov.* \equiv *Ionidium cafferum* Sond., *Linnaea* 23: 13. 1850 \equiv *Hybanthus caffer* (Sond.) Engl., *Bot. Jahrb.* 55: 400. 1919 \equiv *Hybanthus enneaspermus* (L.) F. Muell. var. *caffer* (Sond.) Robson, *Bol. Soc. Brot. Ser. 2A* 32: 169. 1958. Type:—Port Natal, South Africa, *Gueinzium 94* (holotype S!).



FIGURE 3. Lectotype designated here of *Ionidium aurantiacum* F. Muell. ex Benth.

Afrohybanthus danguyanus (H. Perrier) Flicker, *comb. nov.* \equiv *Hybanthus danguyanus* H. Perrier, *Memoires de l'Institut Scientifique de Madagascar, Serie B. Biologie Vegetale* 2: 312–313. 1949. Type:—Boina, Western Madagascar, middle basin upstream of Bemarivo, *Perrier 5070* (lectotype P030552!, designated here); Fig. 4.

Note: A lectotype was selected from the three specimens cited by Perrier, as none of them were explicitly identified by the author as the holotype.

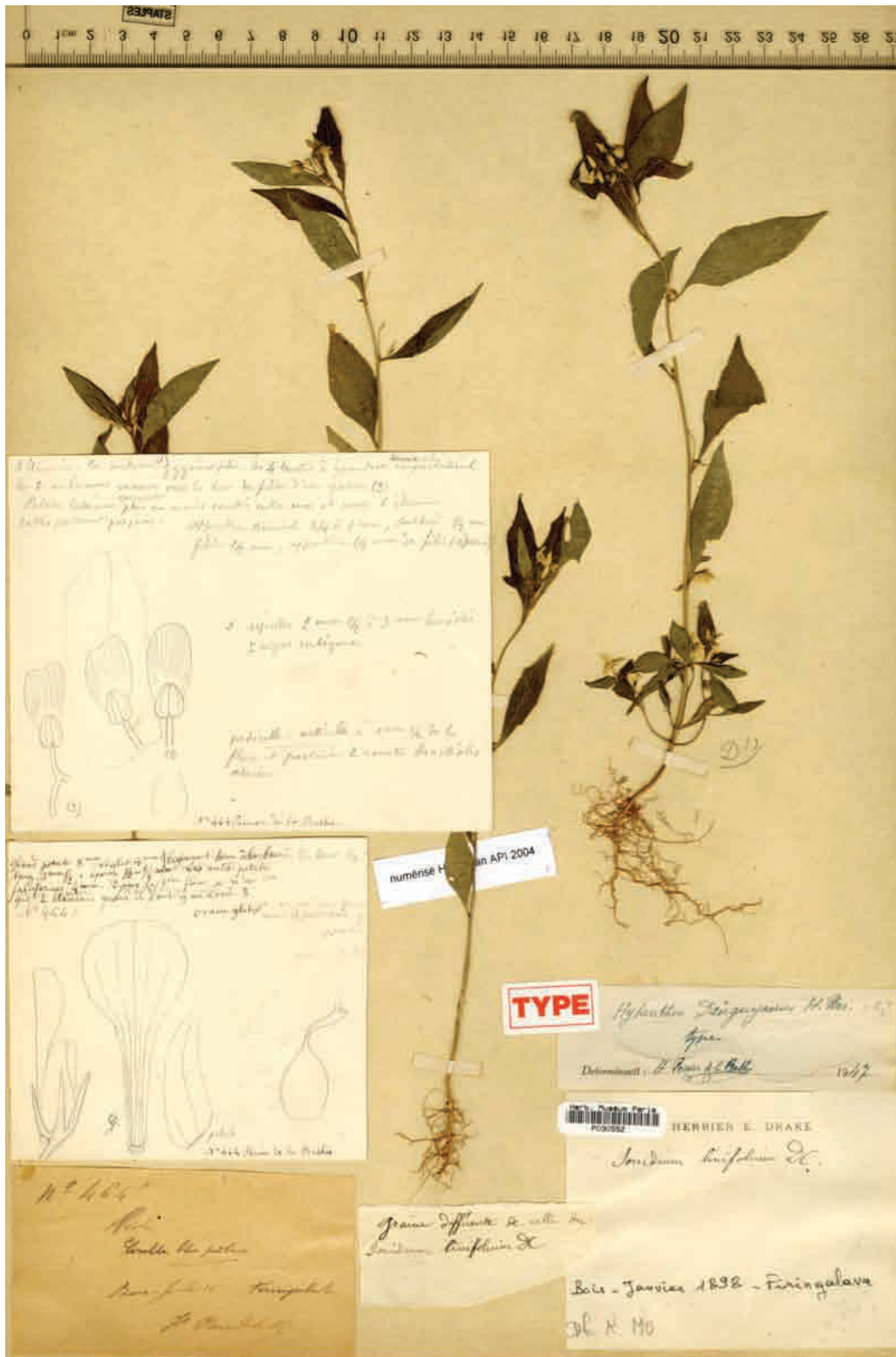


FIGURE 4. Lectotype designated here of *Hybanthus danguyanus* H. Perrier.

Afrohybanthus decaryanus (H. Perrier) Flicker, *comb. nov.* \equiv *Hybanthus decaryanus* H. Perrier, *Memoires de l'Institut Scientifique de Madagascar, Serie B, Biologie Vegetale* 2:312–313. 1949. Type:—Ikonka South of Ambovombe, Madagascar, *M. Decary* 9396 (holotype P!).

Afrohybanthus densifolius (Engl.) Flicker, *comb. nov.* \equiv *Hybanthus densifolius* Engl., *Bot. Jahrb.* 55: 398. 1919.
 Type:—Namibia, *Dinter 430* (lectotype P00631583!, designated here); Fig. 5.

Note: A lectotype was designated because the holotype at B was destroyed.



FIGURE 5. Lectotype designated here of *Hybanthus densifolius* Engl.

Afrohybanthus enneaspermus (L.) Flicker, *comb. nov.* \equiv *Viola enneasperma* L., *Sp. Pl.* 2: 937. 1753 \equiv *Ionidium enneaspermum* (L.) Vent., *Jard. Malmaison* 1 (5): sub. pl. 27. 1803 \equiv *Hybanthus enneaspermus* (L.) F.Muell., *Fragm. Phyt. Austr.* 10: 81. 1876.

Type:—Sri Lanka, *Hermann s.n.* in Vol. I, p. 19 of Hb. Hermann (lectotype BM!, designated by Grey-Wilson, 1986).

= *Viola suffruticosa* L., *Sp. Pl.* 2: 937. 1753 ≡ *Ionidium suffruticosum* (L.) Roem. & Schult., *Syst. Veg.* 5: 394. 1819 ≡ *Hybanthus suffruticosus* (L.) Baill., *Traite bot. med. Phan.* 2(3): 841. 1884. Type:—Sri Lanka, *Hermann s.n.* in Vol. I, p. 41 of Hb. Hermann (lectotype BM!, designated by Grey-Wilson, 1986).

= *Ionidium heterophyllum* Vent., *Jard. Malmaison* 1(5): sub pl. 27. 1803 ≡ *Hybanthus heterophyllus* (Vent.) Baill., *Traite bot. med. Phan.* 2(3): 841. 1884. Type:—China Herb., *d'Incarville 109* (holotype P-JU!).

= *Viola linifolia* Poir., *Encyc. Meth. Bot.* 8: 647. 1808 ≡ *Ionidium linifolium* (Poir) Roem. & Schultes, *Syst. Veg.* 5: 392. 1819 ≡ *Hybanthus linifolius* (Poir) Baill., *Bull. Mens. Soc. Linn. Paris* 1: 554. 1886. Type:—Madagascar, *Commerson s.n.* (holotype P-JU!).

= *Viola thesiifolia* Juss. ex Poir., *Encycl.* 8: 649. 1808. ≡ *Ionidium thesiifolium* (Juss. ex Poir.) Roem. & Schultes, *Syst. Veg.* 5: 398. 1819 ≡ *Hybanthus thesiifolius* (Juss. ex Poir.) Hutch. & Dalziel, *Fl. W. Trop. Afr.* 1: 97. 1927. Type:—Senegal, *Adanson IIIA* (holotype P-JU!).

= *Ionidium hexaspermum* Dalz., *Hooker's J. Bot. Kew Gard. Misc.* 4: 342. 1852. Type:—West India, near Belgaum, *Dalzell s.n.* (holotype K!).

= *Ionidium aethiopicum* Turcz., *Bull. Soc. Nat. Mosc.* 27(2): 339. 1854. Type:—Sudan, Mt. Arasch-Cool, *Kotschy 42* (holotype KW001000995, isotype K000231118!).

= *Ionidium hirtum* Klotsch, *Reise Mossamb. Bot.*: 148. 1861 ≡ *Ionidium enneaspermum* var. *hirtum* (Klotzsch) Oliv., *Fl. trop. Afr.* 1: 106. 1868 ≡ *Hybanthus hirtus* (Klotzsch) Engl., *Bot. Jahrb.* 55: 398. 1919. Type:—Kenya, Northern Frontier District, near Malka Korokoru in sandy steppe, *F. Thomas 88* (lectotype K!, designated here).

Note: A lectotype was designated because the holotype at B was destroyed.

= *Ionidium indicum* Capitaine *Bull. Soc. Bot. France* 57: 396. 1910.

= *Hybanthus enneaspermus* var. *diversifolius* Grey-Wilson, *Kew Bull.* 36: 106. 1981. Type: —Kenya, Arabuko, *R.M. Grahams 1983* (holotype K, seen as image!, isotype K000231110, seen as image!).

Afrohybanthus fasciculatus (Grey-Wilson) Flicker, *comb. nov.* ≡ *Hybanthus fasciculatus* Grey-Wilson, *Kew Bull.* 36 (1): 110. 1981. Type:—Meru National Park, Kenya, *P.H. Hamilton 163* (holotype K!).

Afrohybanthus latifolius (De Wild.) Flicker, *comb. nov.* ≡ *Ionidium enneaspermum* (L.) Vent. var. *latifolium* De Wild., *Pl. Thonn. Cong., ser. 2*: 238, fig. 17. 1911 ≡ *Hybanthus enneaspermus* (L.) F.Muell. var. *latifolius* (De Wild.) Engl., *Bot. Jahrb. Syst.* 55: 398. 1919 ≡ *Hybanthus latifolius* (De Wild.) A. Chev., *Fl. Afrique occ. Franc.* 1. 228. 1938. Type:—Ubangi, Democratic Republic of Congo, *Fr. Thonner 203* (holotype BR!).

Afrohybanthus nyassensis (Engl.) Flicker, *comb. nov.* ≡ *Ionidium nyassense* Engl., *Pflanzenw. Ost-Afr. C*: 277. 1895 ≡ *Hybanthus nyassensis* (Engl.) Engl., *Bot. Jahrb. Syst.* 55: 400. 1919 ≡ *Hybanthus enneaspermus* (L.) F.Muell. var. *nyassensis* N. Robson, *Bol. Soc. Brot. Ser. 2A* 32: 168. 1958. Type:—Shire Highlands, Blantyre, Malawi, *Last s.n.* (lectotype K!, designated by Grey-Wilson, 1986).

Note: This taxon has been raised to specific rank due to its combination of plentiful branching at the base, oblanceolate leaves, and bottom petal shape that is unique in the new genus.

Afrohybanthus pseudodanguyanus (Grey-Wilson) Flicker, *comb. nov.* ≡ *Hybanthus enneaspermus* (L.) F. Muell. var. *pseudodanguyanus* Grey-Wilson, *Kew Bull.* 39 (4): 771. 1984. Type:—Meru National Park, Kenya, *P.H. Hamilton 203* (holotype K!).

Note: This taxon has been raised to specific rank due to its combination of leaves with dentate margins; short, pubescent staminal glands; and seeds with lateral striations (foveolae longitudinally arranged in lines).

Afrohybanthus ramosissimus (Thwaites) Flicker, *comb. nov.* ≡ *Ionidium ramosissimum* Thwaites, *Enum. Pl. Zeyl.*: 21. 1864 ≡ *Hybanthus ramosissimus* (Thwaites) Melch. in Engl. & Prantl, *Nat. Pflanzenfam., ed. 2* 21: 360. 1925. Type:—Maharagama, Sri Lanka, *Thwaites 1084* (lectotype K000327681!, designated here, photo at US!); Fig. 6.

Note: Although a single collection was specified in the protologue, it is uncertain whether herbarium specimens at

K, PDA or both were used by Thwaites in describing the species (Stafleu & Cowan, 1986). Therefore, the K sheet is selected as the lectotype.



FIGURE 6. Lectotype designated here of *Ionidium ramosissimum* Thwaites.

Afrohybanthus serratus (Engl.) Flicker, *comb. nov.* \equiv *Hybanthus enneaspermus* (L.) F. Muell. var. *serratus* Engl., *Bot. Jahrb. Syst.* 55: 398. 1919. Type: South Africa *Schlechter* 4218 (lectotype K000231107!, designated here); Fig. 7.

Note: A lectotype was designated because the holotype at B was destroyed. This taxon has been raised to specific rank due to its serrate/dentate leaf margins and green capsules, the walls of which are thickened along the costa of each valve, appearing trilobate in cross section. This represents a unique combination of characters in the new genus.



FIGURE 7. Lectotype designated here of *Hybanthus enneaspermus* var. *serratus* Engl.

Afrohybanthus stellarioides (P.Forster) Flicker, *comb. nov.* \equiv *Hybanthus enneaspermus* var. *stellarioides* Domin, *Biblioth. Bot.* 89: 983. 1928 \equiv *Hybanthus enneaspermus* subsp. *stellarioides* (Domin) E. Bennett, *Nuytsia* 1: 229. 1972 \equiv *Hybanthus stellarioides* (Domin) P.Forster, *Muellaria* 8(1): 18. 1993. Type:—Cook District, Queensland, Australia. K. Domin 6794 (holotype PR, seen as image!).

Afrohybanthus travancoricus (Bedd.) Flicker, *comb. nov.* \equiv *Ionidium travancoricum* Bedd., *Icones Plantarum Indiae Orientalis* 1: 55. 1874. Type:—Sri Lanka, *Beddome* 320 (lectotype K000327683!, designated here); Fig. 8.

Note: Beddome used specimens and deposited types from BM, K and CAL (Stafleu & Cowan, 1976). Because the status of individual specimens is uncertain, a K sheet has been selected as the lectotype.



FIGURE 8. Lectotype designated here of *Ionidium travancoricum* Bedd.

Afrohybanthus tsavoensis (Grey-Wilson) Flicker, *comb. nov.* \equiv *Hybanthus enneaspermus* (L.) F. Muell. var. *tsavoensis* Grey-Wilson, *Kew Bull.* 36(1): 106. 1981. Type:—Tsavo Park, Kenya, *Greenway & Kanuri 12916* (holotype K!).

Note: This taxon has been raised to specific rank due to its distinctive dense woolly pubescence (unique in the new genus) as well as its floral size, basal petal shape, and corolla color that differentiate it from *A. enneaspermus*.

Afrohybanthus verbi-divini (Everaarts) Flicker, *comb. nov.* \equiv *Hybanthus enneaspermus* (L.) F.Muell. var. *verbi-divini* Everaarts, *Fl. Malesiana* 7: 831. 1971. Type:—Flores, Lower Sunda Islands, *Schmutz* 3135 (holotype L!).

Note: This taxon has been raised to specific rank due to its unique combination of large, dark red corollas, consistently larger height (up to 2 meters tall), and relatively large, smooth seeds atypical for the genus.

Uncertain taxa

All Engler names below were originally based on type material in Berlin, now destroyed. No duplicates have been located to serve as lectotypes, and no collections have been found that unambiguously match the protologues. Similarly, no type specimens have been verified for *Ionidium thymifolium*, and the protologue is vague; the taxonomic status of that name remains unclear. *Hybanthus enneaspermus* var. *pseudocaffer* retained here, as further studies are needed to determine whether it should be synonymized under *Hybanthus enneaspermus* or be recognized as distinct at some taxonomic rank.

Hybanthus fritzcheanus Engl., *Bot. Jahrb.* 55: 398. 1919.

Hybanthus hildebrandtii Engl., *Bot. Jahrb.* 55: 398. 1919.

Hybanthus hirtus (Klotzsch) Engl. var. *glabrescens* Engl., *Bot. Jahrb.* 55: 399. 1919.

Hybanthus hirtus (Klotzsch) Engl. var. *klotzschii* Engl., *Bot. Jahrb.* 55: 400. 1919.

Ionidium thymifolium Presl, *Bot. Bem.* 11. 1845.

Hybanthus enneaspermus var. *pseudocaffer* Grey-Wilson, *Kew Bull.* 36: 109. 1981. Type: —Tanganyika, Steinbruch forest area, *Faulkner* 2026 (holotype K000231111, image seen!).

Discussion

Distinctive androecial or seed traits alone are sufficient to confidently assign taxa to this or any other *Hybanthus* group; but the suite of distinctions in vegetative, floral and fruit structures cumulatively support recognition of this and other clades on par with other currently recognized genera of Violaceae. Fewer traits have been used to distinguish other long-recognized genera in the Violaceae, e.g., *Mayanaea* and *Orthion*, *Rinoreocarpus* and *Rinorea*, *Noisettia* and *Viola* (see Ballard *et al.*, 2014).

Nearly all hybanthoid taxa in Africa, southern Asia and northern Australia are here assigned to the new genus. However, *Hybanthus capensis* (Thunb.) Engl. from the Cape region of Africa possesses features of bottom petal spur, staminal glands and seeds that are diagnostic of the *Hybanthus caledonicus* group, and that species is tentatively excluded from *Afrohybanthus*. Future manuscripts will examine prospective new taxa under *Afrohybanthus*.

Acknowledgments

We thank the curators and collections managers at the herbaria mentioned in the Materials and Methods for access to specimens, and anonymous reviewers and editors for suggestions that improved the manuscript.

Literature Cited

- Airy-Shaw, H.K. (1966) *Revised 7th edition of J.C. Willis, A Dictionary of the Flowering Plants and Ferns*. Cambridge University Press, New York, New York, 1289 pp.
- Ballard, H.E. Jr. (2007) Violaceae. In: Heywood, V.H., Brummitt, R.K., Culham, A. & Seberg, O. (Eds.) *Flowering plant families of the world*. Royal Botanic Gardens, Kew, pp. 331–333.
- Ballard, H.E. Jr., Paula Souza, J. & Wahlert, G.A. (2014) Violaceae. In: Kubitzki, K. (Ed.) *The families and genera of vascular plants, Volume XI Flowering plants. Eudicots. Malpighiales*. Springer-Verlag, Berlin, pp. 303–322.
http://dx.doi.org/10.1007/978-3-642-39417-1_25

- Bennett, E.M. (1972) A Revision of the Australian species of *Hybanthus* Jacquin (Violaceae). *Nuytsia* 1: 218–241.
- Broussalis, A.M., Goransson, U., Coussio, J.D., Ferraro, G., Martino, P.V. & Claeson, P. (2001) First cyclotide from *Hybanthus* (Violaceae). *Phytochemistry* 58: 47–51.
[http://dx.doi.org/10.1016/S0031-9422\(01\)00173-X](http://dx.doi.org/10.1016/S0031-9422(01)00173-X)
- Feng, M. (2005) *Floral morphogenesis and molecular systematics of the family Violaceae*. Ph.D. dissertation. Ohio University, Athens, Ohio, 279 pp.
- Grey-Wilson, C. (1981) Notes on African Violaceae. *Kew Bulletin* 36: 103–126.
<http://dx.doi.org/10.2307/4119009>
- Grey-Wilson, C. (1986) Violaceae. In: Pothill, R.M. (Ed.) *Flora of Tropical East Africa*. A.A. Balkema, Rotterdam, pp. 27–37.
- Hutchinson, J. (1967) *The Genera of Flowering Plants*, vol. II. Clarendon Press, Oxford, England, 117 pp.
- Ireland, D.C., Colgrave, M.L., Nguyencong, P., Daly, N.L. & Craik, D.J. (2006) Discovery and characterization of a linear cyclotide from *Viola odorata*: implications for the processing of circular proteins. *Journal of Molecular Biology* 357: 1522–1535.
<http://dx.doi.org/10.1016/j.jmb.2006.01.051>
- Mangenot, S. & Mangenot, G. (1962) Enquete sur les nombres chromosomiques dans une collection d'especes tropicales. *Revue de Cytologie et de Biologie Vegetales, Paris* 25: 411–447.
<http://dx.doi.org/10.1080/00378941.1962.10838117>
- Melchior, H. (1925) Violaceae. In: Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien*, ed. 2, vol 21. W. Engelmann, Leipzig, pp. 329–377.
- Paula-Souza, J. & Ballard, H.E. Jr. (2014) Re-establishment of the name *Pombalia* and new combinations from the polyphyletic *Hybanthus* (Violaceae). *Phytotaxa* 183: 1–15.
<http://dx.doi.org/10.11646/phytotaxa.183.1.1>
- Paula-Souza, J. & Souza, V.C. (2003) A new species of *Hybanthus* (Violaceae) from north-eastern Brazil. *Botanical Journal of the Linnaean Society* 141: 503–506.
<http://dx.doi.org/10.1046/j.1095-8339.2003.00161.x>
- Peng, C.I. & Chen, Y.F. (1985) *Hybanthus* Jacq. (Violaceae), a new generic record for the flora of Taiwan. *Botanical Bulletin of Academia Sinica* 26: 213–220.
- Sarkar, A.K., Chakraverty, M., Das, S.K., Pal, C.R. & Hazara, D. (1980) *Hybanthus enneaspermus* (L.) F. Muell, in Chromosome number reports LXVII. *Taxon* 29: 358–360.
- Schulze, G.K. (1944) Morphologisch-systematische Studien über die Gattung *Hybanthus* mit besonderer Berücksichtigung der südamerikanischen Arten. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 67: 437–492.
- Seo, M.N., Sanso, A.M. & Xifreda, C.C. (2011) Foliar micromorphology in the classification of South American *Hybanthus* species (Violaceae). *Annales Botanici Fennici* 48: 247–255.
<http://dx.doi.org/10.5735/085.048.0305>
- Simonsen, S.M., Sando, L., Ireland, D.C., Colgrave, M.L., Bharathi, R., Goransson, U. & Craik, D.J. (2005) A continent of plant defense peptide diversity: cyclotides in Australian *Hybanthus* (Violaceae). *The Plant Cell* 17: 3176–3189.
<http://dx.doi.org/10.1105/tpc.105.034678>
- Stafleu, F.A. & Cowan, R.S. (1976) *Taxonomic literature: A selective guide to botanical publications and collections with dates, commentaries and types*, Volume I: A–G, ed. 2. Bohn, Scheltema & Holkema, Utrecht, 1136 pp.
- Stafleu, F.A. & Cowan, R.S. (1986) *Taxonomic literature: A selective guide to botanical publications and collections with dates, commentaries and types*, Volume VI: Sti-Vuy, ed. 2. Bohn, Scheltema & Holkema, Utrecht, 926 pp.
- Souza, J.P. (2002) *Levantamento das especies de Hybanthus Jacq. (Violaceae) do Brasil*. MS. Dissertation, Universidade de São Paulo, Brazil, 166 pp.
- Wahlert, G.A., Marcussen, T., de Paula-Souza, J., Feng, M. & Ballard, H.E. Jr. (2014) A phylogeny of the Violaceae (Malpighiales) inferred from plastid DNA sequences: Implications for generic diversity and intrafamilial taxonomy. *Systematic Botany* 39: 239–252.
<http://dx.doi.org/10.1600/036364414X678008>