New combinations in the tribe Urgineae (Asparagaceae subfam. Scilloideae) with comments on contrasting taxonomic treatments

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Abstract

As part of a taxonomic revision of tribe Urgineae, and informed by morphological and phylogenetic evidence obtained in the last decade, we present 17 new combinations in Austronea, Indurgia, Schizobasis, Tenicroa, Thuranthos, Urgineopsis, and Vera-duthiea. These are for taxa recently described in Drimia sensu latissimo or otherwise named during the past century. We include type information for all considered taxa and designate lectotypes for Drimia pauciflora, Urginea salmona and U. sebirii. We discuss recent analytic and synthetic approaches to taxonomic arrangements for the Urgineae and reinforce the support of an analytic treatment that recognises several genera characterised by distinct syndromes of morphological, biogeographical, and molecular evidence.

Keywords: Austronea, Hyacinthaceae, Indurgia, nomenclature, Schizobasis, taxonomy, Tenicroa, Thuranthos, typification, Urgineoideae, Urgineopsis, Vera-duthiea

Introduction

Asparagaceae subfamily Scilloideae tribe Urgineae (Chase et al. 2009, APG 2016) includes ca. 200 bulbous plants occurring in Africa, Europe, and southwestern Asia, which show spurred bracts, at least in the basal portion of the inflorescence, and capsules dehiscing completely to the base of valves. Alternatively, Urgineae is treated as Hyacinthaceae subfam. Urgineoideae sensu (APG 2003), a treatment favoured by our research group. Generic circumscriptions within Urgineoideae have been especially controversial in recent decades. Pfosser & Speta (1999, 2001, 2004) presented the first extensive analytic phylogenetic work in Urgineoideae informed by ca. 120 samples of ca. 40 taxa and a single plastid region (trnL-F). Based on morphological, phylogenetic and biogeographic evidence, several new genera were established by Speta (1998a, b, 2001), who accepted 19 urgineoid genera, excluding Igidia Speta (1998b: 70), currently classified within Ornithogaloideae (Wetschnig et al. 2007).

The synthetic approach to the taxonomy of the Urgineoideae began with a phylogenetic work by Manning et al. (2004), based on two plastidial regions (trnL-F and rbcL) and limited sampling (21 samples representing 13 genera). These authors do not seem to have considered morphological and biogeographic evidence presented by Pfosser & Speta (1999, 2001, 2004), but focused rather on molecular findings. Of the 19 urgineoid genera recognised by Speta (1998a, 2001), only 13 were included in the analysis of Manning et al. (2004). Some 15 years later, the relevant sequence data are yet to be deposited in GenBank, which has prevented other research groups from confirming even
these preliminary findings, on which basis radical nomenclatural proposals were nonetheless made by Manning et al. (2004). Their phylogenetic tree revealed *Bowiea* Harvey ex Hooker (1867: t. 5619) as diverging earlier than other Urgineoideae, with both clades strongly supported. The core samples in the non-*Bowiea* clade covered 12 genera: *Boosia* Speta (2001: 168), *Charybdis* Speta (1998b: 58), *Drimia* Jacq. ex Willdenow (1799: 165), *Fusifilum* Rafinesque (1837: 27), *Litanthus* Harvey (1844: 314), *Rhadamantus* Salisbury (1866: 37), *Rhadamanthopsis* Obermeyer (1980a: 137) Speta (1998b: 74), *Schizobasis* Baker (1873a: 105), *Sekanama* Speta (2001: 168), *Teniroca* Rafinesque (1837: 52), *Thuranthos* Wright (1916: 233), and *Urginavia* Speta (1998b: 86). These authors argued the seeming paraphyly or polyphyly of some of these genera to promote an extremely broad *Drimia* concept. In doing so, they placed all the aforementioned genera in synonymy, resulting in extraordinarily wide variability in floral and vegetative morphology in *Drimia sensu latissimo*. Manning et al. (2004) motivated in support of their broad *Drimia* concept that: “*Teniroca* Raf. is paraphyletic unless *T. nana* Snijman is segregated as a monotypic genus, and the recently revived segregate *Fusifilum* Raf. (which includes several of the southern African species previously placed in *Urginea*), is polyphyletic”. Subsequently, Pinter et al. (2013) have presented clear morphological evidence to support the acceptance of *T. nana* Snijman (1985: 284) as the monotypic genus *Mucinaea* Pinter et al. (2013: 296). Morphological differences distinguishing *Mucinaea* from *Teniroca* include anther dehiscence by short apical slits resembling pores, the purplish-pink tepals bearing a double-eyed green marking at their base and a unique bulb structure, among other characters (Pinter et al. 2013). Whereas the species labeled as *Fusifilum* in the tree of Manning et al. (2004) resolve in three different and distant clades, it is disconcerting that of the four samples treated under *Fusifilum* by these authors, i.e. *F. calcarata*, *F. marginata*, *F. physodes* and *F. dregei*, two are without formal combination in this genus, viz. *F. calcarata* and *F. marginata*, and that only *F. physodes* (Jacquin 1795: tab. 418) Raf. ex Speta (1998b: 69) is included in the revision of *Fusifilum* by Müller-Doblies et al. (2001). Manning et al. (2004) record that these “terminal taxa [were] labelled according to the generic concepts of Speta (1998a, 2001)”. We argue that the correct genus adscription of these species would, in fact, dissolve the polyphyly of *Fusifilum* and support an analytic rather than a synthetic treatment in the subfamily, since “*F. dregei*” is a species in *Urgineopsis* Compton (1930: 107) (as accepted in this work), “*F. marginata*” belongs to *Austronea* (Martínez-Azorín et al. 2018a: 105), a genus sister to *Fusifilum* (see Martínez-Azorín et al. 2018a) and “*F. calcarata*” is related to *Boosia*.

Pfosser et al. (2012) published further phylogenetic findings that strengthen the case for an analytic approach in the Urgineoideae, as there are well-supported clades that correspond to previously described genera, fitting clear syndromes of morphological characters and biogeographic patterns, although some genera require a new circumscription to include some taxa previously described in other genera.

Manning & Goldblatt (2018) recently published a revision of *Drimia sensu latissimo* in southern Africa, where they persist in proposing a synthetic approach, with only two genera accepted for the whole Urgineoideae: *Bowiea*, monotypic in their sense, and *Drimia* with 70 species, eight of which are new. In this concept, *Drimia* is extremely broad morphologically, as it is the result of synonymising several traditionally accepted genera such as *Litanthus*, *Rhadamantus*, *Rhodododon* Baker (1880: 280), *Schizobasis*, *Teniroca*, *Thuranthos*, and *Urginea* Steinheil (1834: 321), as well as others recognised by Speta (1998b, 2001), Martínez-Azorín et al. (2013, 2017, 2018a, b), Pinter et al. (2013) and Crouch et al. (2018), all of which are characterised by distinct syndromes of morphological characters. Manning & Goldblatt (2018) opted for a counter-intuitive concept of *Drimia*, particularly difficult to understand based on its morphological variability, especially in relation to flower morphology. This is evident in their morphological characterization of the genus (Manning & Goldblatt 2018: 10), which contains multiple exceptions or opposites in the characterization of vegetative and most notably of reproductive organs (e.g., flowers diurnal or nocturnal, nodding to suberect; tepals free or fused in a long tube, erect to strongly reflexed; filaments free or fused in a long tube, spreading or connivent to the ovary, anthers free or connate; and seeds from flattened with loose testa and very light to subglobose, heavy and with tightly attached testa). This approach led inevitably to the recognition of 19 sections in *Drimia*, most of which correspond to previously described genera, in an attempt to navigate relationships within an overly-broad genus concept. While Manning & Goldblatt (2018) accept 70 species of *Drimia* s.l. for southern Africa and ca. 110 species classified into two genera globally, our studies suggest that this group includes at least 200 species arranged in ca. 30 genera. Manning & Goldblatt (2018) state that “a synthetic approach to the circumscription of *Drimia* is a far less radical departure from the traditional generic concepts in the subfamily than is the alternative multi-genus option”. We do not agree with this assertion, given our global perspective on Urgineoideae, including both the Eurasian and southern African centres of diversity. The merging of *Thuranthos*, *Litanthus*, *Rhodododon*, *Rhadamantus*, *Sagittanthera* Mart.-Azorin, M.B.Crespo, A.P.Dold & Van Jaarsv. in Martínez-Azorín et al. (2013: 46), *Aulostiemon* Martínez-Azorin et al. (2017: 288), *Drimia* s.str., and *Urginea* s.str. (all characterised by distinct flower morphologies) into one single genus, renders a gross underestimation of the evolutionary significance represented by the striking differences in floral
morphology. If this synthetic approach is accepted, a consistent solution should logically also apply to the sister group Hyacinthoideae, including many taxa of horticultural importance: genera such as Massonia Houttuyn (1780: 424), Lachenalia J.Jacq. ex Murray (1784: 314), Spetaea Wetschnig & Pfosser (2003: 87), Eucomis L’Hérit (1789: 11), Ledebouria Roth (1821: 194), Schizocarpus Van de Merwe (1943: 904), and Merwilla Speta (1998b: 107), among others, should similarly be merged into a broadly-conceived genus as well. Similarly, in the phylogeny of petaloid monocots, the clades sister to Asparagaceae would require revisiting, and genera within Liliaceae, Amaryllidaceae and Iridaceae should arguably be lumped, as they would not show a sufficient level of floral divergence to represent separate genera.

Based on our morphological and taxonomic studies on Urgineoideae performed during the last decade, and following an analytic taxonomic treatment of genera that fit clear syndromes of morphological characters, we provide 17 new combinations in Austronea, Indurgia, Schizobasis, Tenicroa, Thuranthos, Urgineopsis, and Vera-duthiea for those species newly described by Manning & Goldblatt (2018) under Drimia, and new combinations for other taxa named during the past century. These taxa are moved to genera that are traditionally accepted and morphologically well-defined; accompanying notes and new information are based on field and herbarium work. Additionally, phylogenetic analyses, based on more than 250 samples of all published genera in Urgineoideae from the global distribution range, each including trnL-F, matK, and ycf plastid nucleotide sequences as well as a selection on nuclear (Agrl) regions (see Fig. 3 in Martínez-Azorín et al. 2018b), also support the multigeneric treatment proposed here.

New combinations

Combination in Austronea

As recently reported by Martínez-Azorín et al. (2018a), the capitate to subcorymbose inflorescences of some Urgineoideae commonly nod at early development stages, one of the key characters of Austronea. Additional features of this genus include: reddish to yellowish-green tepals, rarely white, which are usually connate at the base to form a distinct cup and patent free lobes; filaments linear to lanceolate, smooth or rarely papillate below; ovary green to yellow-orange; and seeds commonly trigonous in outline, tetrahedrally folded and narrowly winged along the angles. This genus concept is supported by our phylogenetic studies (Fig. 3 in Martínez-Azorín et al. 2018b), with the genus forming a strongly supported clade sister to Fusifilum. The latter genus differs from Austronea by an inflorescence that is erect during all developmental stages; stellate flowers with free white tepals; filaments fusiform and widened in the middle, distinctly papillate on the lower portion; ovary white or tinged with violet or purple; and seeds commonly elliptical in outline, flat and widely winged on the margins.

Austronea represents a distinct group also recognised by Manning & Goldblatt (2018) as D. sect. Capitatae Manning & Goldblatt (2018: 76). Only Drimia virens Schlechter (1897: 433) J.C.Manning & Goldblatt in Goldblatt & Manning (2000: 712) was not included in this group by Manning & Goldblatt (2018), since they placed it in D. sect. Physodia Manning & Goldblatt (2018: 92) (= Fusifilum). Manning & Goldblatt (2007, 2018) considered Drimia virens as conspecific with D. minor (Duthie 1928: 11) Jessop (1977: 306). However, the latter is a true member of Fusifilum as presented in the revision of this genus by Müller-Doblies et al. (2001), and shown in the line drawing and original description of flower morphology of this species (Duthie 1928) (see also Martínez-Azorín et al. 2018a).

On the contrary, Urginea virens Schlechter (1897: 433) should be assigned to Austronea based on flower and seed morphology (Martínez-Azorín et al. 2018a), in agreement with the discussion by Müller-Doblies et al. (2001) of the status of Fusifilum minus (Duthie 1928: 11) Speta (1998b: 69). They argued that both Urginea pygmaea Duthie (1928: 10) and U. minor Duthie (1928: 11) are good “Urginea” (Austronea sensu Martínez-Azorín et al. 2018a) species, and should not be included in Fusifilum.

The newly described Drimia ciliolata J.C.Manning & J.M.J.Deacon in Manning & Goldblatt (2018: 89) belongs to Austronea based on the single hysteranthous, ciliate leaf; the inflorescence corymbose-capitate, nodding in bud; the pale-brown flowers with tepals fused at the base to form a cup; filaments glabrous; and the yellow-green ovary. Accordingly, here we present the necessary combination:

Combination in *Indurgia*

*Indurgia* Speta (2001: 169) includes species of Urgineoideae from India and neighbouring countries, related to *I. indica* (Roxburgh 1832: 147) Speta (2001: 170). Our phylogenetic findings (Fig. 3 in Martínez-Azorín et al. 2018b) show that all studied samples of Urgineoideae from that region form a well-supported clade which we accept as *Indurgia*. Moreover, samples from Africa usually identified as “*Drimia indica*” belong instead to *Vera-duthiea* Speta (2016: 154) or *Zingela* Crouch et al. (2018: 36), as shown by Crouch et al. (2018) and by Martínez-Azorín et al. (2018c). Therefore, we here combine *Urginea raogibikei* Hemadri (2006a: 386) in *Indurgia*, a species described from the Nellore district in India and fitting the morphology of that genus.


Combination in *Schizobasis*

*Schizobasis* is a distinct genus easily characterised by the branched, wiry inflorescence, widely recognised by researchers on Urgineoideae (including Jessop 1977), since its description by Baker (1873). However, Manning et al. (2004) and Manning & Goldblatt (2018) synonymised this genus to *Drimia*, despite accepting *Bowieuia*, with its similarly branched inflorescence. Their recognition of *Bowieuia* was mostly based on its phylogenetic position, diverging early from other clades in the subfamily. Our studies confirm the generic status of *Schizobasis*, supported by morphological, phylogenetic and biogeographic data, and we accordingly provide the necessary combination for a recently described species from the southern Richtersveld.


Combinations in *Tenicroa*

*Tenicroa* is a distinct genus characterised by leaves surrounded with membranous sheathing cataphylls with dark, raised, transversal ridges; stellate flowers with subpatent, free tepals and a narrow, longitudinal dark band on the abaxial side; stamens spreading, somewhat curved, with subbasifixed anthers, and ovary ovate-oblong, with elongate, deflexed and curved style, and papillose stigma. Based on these synapomorphies, most researchers in Urgineoideae agreed on the circumscription of *Tenicroa* deflexed and curved style, and papillose stigma. Based on these synapomorphies, most researchers in Urgineoideae agree on the circumscription of *Tenicroa* (J.C.Manning & Goldblatt) Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig comb. nov. = *Drimia decipiens* Manning & Goldblatt (2018: 109) and *D. juncifolia* J.C.Manning & J.M.J.Deacon in Manning & Goldblatt (2018: 107), including the two new species *D. decipiens* Manning & Goldblatt (2018: 109) and *D. juncifolia* J.C.Manning & J.M.J.Deacon in Manning & Goldblatt (2018: 107), basionym. Type:—SOUTH AFRICA: Western Cape, Wuppertal (3219): Swartruggens, near turnoff to Kagga Kamma at summit of Skitterykloof, (–DC), 27 November 2017, J. Manning 3637 (holotype, NBG).


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Combination in *Thuranthos*

Manning & Goldblatt (2018) included *Drimia pauciflora* Baker (1892: 6) as an uncertain species, because they were not able to find a type specimen for this taxon, but commented that the description suggests its inclusion in *Thuranthos*, and that in the case that *D. pauciflora* is a synonym of *Thuranthos basuticum*, the former would be the priority name. The type collection of *D. pauciflora* (Ecklon & Zeyher Asphod. 102) is kept at B (B100167472!) and available online at http://herbarium.bgbm.org/object/B100167472. We confirm that *Drimia pauciflora* represents the same species currently known as *Thuranthos basuticum* and therefore we propose a new combination in *Thuranthos*.


**Combinations in Urgineopsis**

The genus *Urgineopsis* was described for a single species “differing from *Urginea* in the gamophyllous perigone, from *Drinia* in the erect perigone segments and non-connivent stamens, and from *Rhodanthis* in the erect flowers lacking connivent stamens” (Compton 1930). These differences are still valid when *Drinia* and *Urginea* are considered in a narrow sense. Whereas Speta (1998a, b, 2001) accepted *Urgineopsis* based on morphological and phylogenetic data, Manning & Goldblatt (2018) proposed to place it in synonymy together with *Geschollia* Speta (2001: 169) under *Drinia* sect. *Ledebouriopsis* (Baker 1873b: 284) Manning & Goldblatt (2018: 24). They established this section to accommodate 11 species despite their different flower, fruit and seed morphologies. Our fieldwork combining morphological and corological studies supports the acceptance of *Urgineopsis* and *Geschollia* as distinct genera, in agreement with our phylogenetic results (Fig. 3 in Martinez-Azorin et al. 2018b).

During a field trip to Namibia in August 2016, an undescribed species of *Urgineopsis* was encountered in the Luderitz Peninsula (M. Martinez-Azorin et al. MMA1659, ABH74040!). It shows a single, leathery, terete leaf, tepals fused for ca. 3 – 4 mm to form a cup; spreading tepal tips, stamen filaments arising at the mouth of the perigone tube and slightly incurved, and with a distinctly puberulous perigone tube within. The study of herbarium collections at NBG revealed that it is conspecific with a plant collected and subsequently illustrated in 1977 by M. Bayer (Bayer 1013 (perhaps holotype, BOL; isotypes, NBG!, K!)). From south of Alexander Bay (Northern Cape, South Africa). Bayer identified it as *Urginea* sp. nov. This species has been recently described by Manning & Goldblatt (2018) as *Drinia barbata* J.C.Manning & J.M.J.Deacon in Manning & Goldblatt (2018: 47). Below we provide the necessary combination of the latter taxon into *Urgineopsis*. The population of *U. barbata* from Luderitz represents the first record of this genus for Namibia.

In establishing *Urgineopsis*, Compton accepted only one species, *Urgineopsis saltleri* Compton (1930: 107), a small taxon restricted to the mountains of the Cape Peninsula. Speta (1998a, b, 2001) later also recognised it as monotypic. Our studies evidence the existence of 5 additional taxa, originally described in *Urginea*, but which fit the flower, fruit and seed morphology profile of *Urgineopsis*. We here provide the necessary combinations in this genus. Notably, further studies are needed to resolve the taxonomy of this group, the taxa of which presently exhibit large morphological variability, including within populations.

**Urgineopsis arenosa** (Adamson) Mart.-Azorin, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = *Urginea arenosa* Adamson (1942: 239), basionym. Type:—SOUTH AFRICA: Western Cape, Simonstown (3418): ‘Cape Peninsula, Red Hill’, (–AB), *Salter 8321* (holotype, BOL!; isotypes, NBG!, K!).

**Urgineopsis barbata** (J.C.Manning & J.M.J.Deacon) Mart.-Azorin, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = *Drinia barbata* J.C.Manning & J.M.J.Deacon in Manning & Goldblatt (2018: 47), basionym. Type:—SOUTH AFRICA: Northern Cape, Oranjemund (2816): Boegoeberg, S of Alexander Bay, (–DA), only materials in flower ex hort. on 1 February 1980, *M. Bayer 1013* (NBG121176!), from south of Alexander Bay (Northern Cape, South Africa). Bayer identified it as *Urginea* sp. nov. This species has been recently described by Manning & Goldblatt (2018) as *Drinia barbata* J.C.Manning & J.M.J.Deacon in Manning & Goldblatt (2018: 47). Below we provide the necessary combination of the latter taxon into *Urgineopsis*. The population of *U. barbata* from Luderitz represents the first record of this genus for Namibia.

**Urgineopsis dregei** (Baker) Mart.-Azorin, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = *Urginea dregei* Baker (1897: 467), basionym. Type:—SOUTH AFRICA: Western Cape, Worcester (3319): ‘Worcester Div., Dutoitskloof’, (–CC), 1840, *Drège 1501* (lectotype designated by Manning & Goldblatt (2018), K!; isolecotype, S [only the four fruiting specimens]).


**Urgineopsis gracilis** (A.V.Duthie) Mart.-Azorin, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = *Urginea gracilis* Duthie (1928: 12), basionym. Type:—SOUTH AFRICA: Western Cape, Cape Town (3318): ‘Stellenbosch flats, in low-lying, clayey area’, (–DD), March 1925, *A. Duthie 1446a* (holotype, NBG!; isotype, BOL!).

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Urgineopsis pedunculata (Adamson) Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = Urginea pedunculata Adamson (1944: 134), basionym. Type:—SOUTH AFRICA: Western Cape, Simonstown (3418): ‘Cape Peninsula, Kalk Bay Mountains’, (–AB), M. R. Levyns sub Adamson 3483 (holotype, BOL!).

**Combinations in Vera-duthiea**

Based on morphology, biogeography and phylogenetic data, Martinez-Azorin *et al.* (2018c) showed that *Vera-duthiea* is a distinct African genus, recently identified from southern Africa following the description of *V. zebrina* Martinez-Azorín *et al.* (2018c: 285). Manning & Goldblatt (2018) described *Drimia vespertina* Manning & Goldblatt (2018: 65) for plants occurring in Kaokoland in northwestern Namibia, but which match *Vera-duthiea* in morphology. We accordingly provide below the necessary new combination.

*Urginea amboensis* Baker (1903: 665) and *Albuca reflexa* K.Krause & Dinter in Krause (1914: 445) were also described from northern Namibia and are similar to *V. vespertina*, but type material and the protologues of these taxa are insufficient to allow a credible taxonomic assessment. Further studies are required in the field and in herbaria to elucidate the relationships among these taxa.

Manning & Goldblatt (2009, 2018) accepted *Drimia indica* (Roxburgh 1832: 147) Jessop (1977: 272) as occurring in southern Africa and included *U. zambesiaca* Baker (1873b: 223), *U. amboensis* and *Albuca reflexa* as synonyms. Our phylogenetic studies (Fig. 3 in Martinez-Azorín *et al.* 2018b) reveal that samples from southwestern Asia belong to *Indurgia* Speta (2001: 169) and those superficially similar plants from Africa, to which the name *D. indica* has been misapplied, are included for the most part in *Vera-duthiea*. Moreover, the concept of *Drimia indica* by Manning & Goldblatt (2018) is overly broad as it also includes the collections Pooley 661 (NU!) and Moll 4309 (PRE!) from northeastern KwaZulu-Natal, South Africa. These collections represent two different genera: the former corresponds to *Zingela pooleyorum* Crouch *et al.* (2018: 36) while the latter is known as *Vera-duthiea zebrina* (Martínez-Azorín *et al.* 2018c: 285). Both taxa are quite distinct morphologically and ecologically as well as from the molecular-phylogenetic point of view (M. Martínez-Azorín and collaborators, in preparation). Crouch *et al.* (2018) discussed the history of their treatment in herbaria and literature.

Here we transfer to *Vera-duthiea* five species described from west-central Africa and southern Africa and which fit the morphology and biogeography of this genus, to facilitate future taxonomic work.


*Vera-duthiea salmonea* (Berhaut) Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = *Urginea salmonea* Berhaut (1967: 428), basionym. Type **(lectotype, designated here)**—SENEGAL: Mbao, 15 June 1954, Berhaut 1682 (P00349754!; isolectotype, P00349756!; syntypes: P00349752!, P00349753!, P00349755!).

Although Berhaut (1967) indicated the existence of the type collection *U. salmonea* at P under the number 1682, which would represent the holotype, two sheets belonging to *Berhaut 1682* currently exist at P with different P barcode numbers, and therefore we select here a lectotype.

*Vera-duthiea sebirii* (Berhaut) Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig **comb. nov.** = *Urginea sebirii* Berhaut (1954: 7), basionym. Type **(lectotype, perhaps holotype, designated here)**—SENEGAL: in “savane boisée” Ngasobil, June-July 1951, Berhaut 461 (P00349746!).

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