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The rediscovery of *Nothoscordum modestum* (Amaryllidaceae) helps to understand the subordination of *Beauverdia* in *Nothoscordum*

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Abstract. The rediscovery of *Nothoscordum modestum* (Amaryllidaceae) helps to understand the subordination of *Beauverdia* in *Nothoscordum*
Nothoscordum modestum presents intermediate morphological characteristics between the genera *Nothoscordum* and *Beauverdia*. This species was known only by the type; however, new populations were found and during the analysis of specimens *in loco* it was evidenced that the taxon has flowers long pedicellate, morphological characteristic common in *Nothoscordum*; on the other hand, the scapes are curved at fruit maturity. The species is close related to *N. Marchesii*, *N. Ostenii*, *N. setaceum* and *N. vittatum*, and the main morphological differences between *N. modestum* and these species are commented. A list of species of *Nothoscordum* with one or two-flowered inflorescence is presented. As *Beauverdia* cannot be maintained as segregated from *Nothoscordum*, it is necessary to propose the new combination *Nothoscordum hirtellum* subsp. *glabratum*.
Key words: Allioideae, Grasslands, Leucocoryneae, Monanthoscordum, Pampa Biome, Uniflorum.

Resumo. A redescoberta de *Nothoscordum modestum* (Amaryllidaceae) ajuda a compreender a subordinação de *Beauverdia* em *Nothoscordum*
Nothoscordum modestum é uma espécie que apresenta características morfológicas intermediárias entre os gêneros *Nothoscordum* e *Beauverdia*. A referida espécie era conhecida apenas pelo tipo; no entanto, novas populações foram encontradas e durante a análise de espécimes *in loco* foi evidenciado que o táxon possui flores pediceladas, solitárias ou geminadas, características morfológicas comuns em *Nothoscordum*; por outro lado, o escapo curva-se na maturação do fruto. A espécie é próxima de *N. Marchesii, N. Osteni*, *N. setaceum* e *N. vittatum*, sendo comentada as principais diferenças morfológicas entre *N. modestum* e essas espécies. É apresentada lista de espécies de *Nothoscordum* que possuem flores solitárias ou geminadas. Como *Beauverdia* não pode ser sustentado como segregado de *Nothoscordum* é necessário propor a nova combinação *Nothoscordum hirtellum* subsp. *glabratum.*
Palavras chave: Allioideae, Bioma Pampa, Campos, Leucocoryneae, Monanthoscordum, Uniflorum.

The genus *Nothoscordum* Kunth (1843: 457) comprises between 20 or more than 80 species, with important center of diversity and endemism in Southern Brazil, Uruguay, Northeast Argentina and Paraguay. The species of *Nothoscordum* with solitary flowers present the most difficult taxonomy, and Beauverd (1908) included these taxa under the section *Uniflorum* Beauverd (1908: 1007). Later, Herter (1943, 1956) raised the new genus *Beauverdia* Herter (1943: 507) to place them. On the other hand, Guaglianone (1972) positioned the one-flowered species under *Ipheion* Rafinesque (1837: 2) sect. *Hirtellum* Guaglianone (1972: 178). Crosa (1975) re-established species with solitary flowers in *Nothoscordum* and Ravenna proposed the subgenus *Monanthoscordum* Ravenna (1978: 142) to accommodate them. For Crosa (2006) the subgenus *Monanthoscordum* and the section *Uniflorum* lack taxonomic value, since they are polyphyletic groups, but clearly separated from *Ipheion*.

On the other hand, Sassone et al. (2014) rehabilitated *Beauverdia* and including taxa previously recognized under *Ipheion* sect. *Hirtellum* and *Nothoscordum* subg. *Monanthoscordum*. Recently, Deble (2022) established *Nothoscordum Osteni* Beauverd (1908: 996) as segregated from *Beauveria hirtella* (Kunth 1843: 465) Herter (1931: 48) and

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indicated that *N. Ostenii* despite having solitary flowers, should be recognized as *Nothoscordum* because their flowers are supported by long pedicels and its scapes are not curved at fruit maturation. On the other hand, the separation of both genera becomes fragile and is only maintained by characteristics of scapes curvature at fruit maturation and often sessile or almost sessile flowers.

Taxonomic treatment

Identity and geographic distribution of Nothoscordum modestum

Nothoscordum modestum Ravenna (1991: 17) is known only from the type material, represented by exsiccate with several mounted specimens. Based on this material, it is possible to observe very peculiar characteristics, since the individuals have solitary or two-flowered inflorescence and flowers supported by long pedicels, morphological characteristics in agreement with those found in *Nothoscordum*, but the scapes apparently are curved at fruit maturity, as is found in the species of *Beauverdia*. With the discovery of new populations of *Nothoscordum modestum*, it was possible to prove that the scapes are curved at fruit maturity. As in the original description of *Nothoscordum modestum* there is no information about the curvature of the scapes at fruit maturity and about the morphology of the fruit, it is necessary to amend the original description and also add new information about this taxon.

Nothoscordum modestum Ravenna, Onira Botanical Leaflets 3 (6): 17. 1991. Typus: PARAGUAY. Without additional data, *P. Joergensen 4757* (holotype SI000433!). Figures 1 and 2.

Geophyte 1.5–5 cm high above the soil. Bulb 5–8 × 4–7 mm, ovoid, simple, with mild alliaceous smell when breaking; outer cataphylls dark-brown, the innermost whitish. Leaves at anthesis 1–6, spirally arranged; leaf sheaths 0.5–2 cm long, subterranean, straw-colored; leaf blades 8–60 × 0.6–2 mm, narrowly linear-filiform broadly elliptic in cross-section, 0.8–2 × 0.4–0.8 mm, grayish green or bluish green, ascendant-reflexes, glabrous, margin thickened and rigid due to the presence of fibrous vascular bundles. Scape solitary, inclined, 2.5–4 cm long, subcylindrical, grayish green or bluish green, become strongly curved at fruit maturity, glabrous. Bracts 2, ovate-elliptic, 6.5–9 × 2.5–3.5 mm, fused at base for 2–3 mm. Pedicels 11–25 mm long, reddish green or brownish green, glabrous. Inflorescence 1–2-flowered. Flowers 9–12 × 5.5–8mm, broadly campanulate, white, shiny. Tepals 6 (3 + 3), white become greenish white towards the base, shortly fused at base for ca. 0.5 mm, the outers ones, oblanceolate or elliptic, 6–7.5 × 2–2.4 mm, slight acute or obtuse at the apex, narrowed at the base; the inners ones elliptic, 5–7 × 1.8–2.3 mm; slight acute at the apex, narrowed at the base; tepal middle nerves purplish-brown, conspicuous, thicker towards the base. Staminal filaments 4.5–5.5 mm long, free at their bases, awl-shaped, translucent, whitish-cream; anthers 1–2 mm long, curved, pollen golden-yellow. Ovary obovate, 1.7–2.4 mm long; ovules 4–6 per locule; style greenish-white, 3–3.8 mm long, stigmatic portion capitate, greenish-yellow, shiny. Capsule nearly globose 2.5–4 × 2–4 mm. Seeds diminutive, brownish-black, ca. 0.8–1 mm, black, shiny, tetrahedrally angled.

Etymology— From the Latin *modestum* meaning "humble, modest", a reference to the weakly and delicate habit of the species.

Additional material examined— BRAZIL. Rio Grande do Sul: Dom Pedrito, estrada da Pedreira, 18 May 2021, *L.P. Deble et al. 18852* (PACA!).

Distribution, Habitat and Phenology — *Nothoscordum modestum* was described for Paraguay, but in the voucher and in the protologue the date of collection and habitat are not indicated. The two populations studied have a disjunct distribution in Paraguay and southern Rio Grande do Sul state, Brazil. However, the area of occurrence is possibly continuous in places with low drainage capacity and periodically flooded, associated with rocky outcrops, the preferred habitats of *N. modestum*. The few vouchers in herbaria probably is due to the small size of the specimens and the short time in which it emits leaves and flowers. Based on the populations analyzed *in loco*, this species is hidden most of the time, as the leaves only appear early May and the flowers bloom in mid-May. At the fruit maturation, the leaves are dry and the species is at rest from mid-June. *Nothoscordum modestum* is sympatric with several other species of *Nothoscordum*, among them *N. Gaudichaudianum, N. hirtellum, N. minarum, N. muscorum, N. Ostenii* and *N. vittatum*.

Discussion— *Nothoscordum modestum* differs from *N. Marchesii* by its scapes and leaves without alliaceous smell, by its shorter and ascendant-reflexes leaves, by its flowers white (vs. white-cream), borne in longer pedicels. From *Nothoscordum Ostenii* this species easily differs by its white flowers (vs. yellow) and by its scapes curved at fruit maturity (vs. non-curved). *Nothoscordum modestum* distinguishes from *N. setaceum* by its shorter leaves and flowers borne in longer pedicels and from *Nothoscordum vittatum* can be distinguished by its smaller habit, narrowly filiform leaves, scapes and pedicels glabrous and shorter tepals. From *N. Gaudichaudianum* it differs by its small size and few flowers per inflorescence (1–2 vs. 3–10).

Beauverdia under *Nothoscordum* again

Beauverdia was treated during a long time as subordinated in the genera *Nothoscordum* or *Ipheion* (see Guaglianone 1972, Crosa 1975). However, Sassone *et al.* (2014) rehabilitated the genus, posteriorly Sassone & Giussani (2018), in their reconstruction of phylogenetic history of the tribe Leucocoryneae in South America, based on inference of combined data using sequences of *ITS* region and two plastid genes: *matK* and *ndhF* demonstrated that *Beauverdia* and *Nothoscordum* forming a strongly supported clade. On the other hand, *Beauverdia* was treated as segregated from *Nothoscordum* in recent works (e.g. Deble 2021, Deble 2022). With the discovery of *Nothoscordum modestum* and also of some yet undescribed taxa that present intermediate characteristics between *Beauverdia* and *Nothoscordum* (Deble *et al.*, in preparation), it becomes impossible to separate both genera, both from a morphological and molecular point of view. Thus, the list of species of *Nothoscordum*, which has one or two flowers in the inflorescence and straight or curved scapes at fruit maturation, is updated below.

List of species of Nothoscordum with 1-2 flowered inflorescence

1. ***Nothoscordum dyalistemon*** (Guaglianone) Crosa, Darwiniana 19: 344. 1975. Bas.: *Ipheion dyalistemon* Guaglianone, Darwiniana 16: 800. 1971. ≡ *Beauverdia dyalistemon* (Guaglianone) Sassone & Guaglianone, Systematic Botany 39 (3): 774. 2014. Typus: ARGENTINA. Buenos Aires: Gonnet, ates de llegar a Cit Bell., camino Centenario, luego de un ponte calle Lacroce viniendo a La Plata a la izquierda …" 16 August 1967, *A.M. Ragonese & R. Guaglianone s.n.* (holotype SI000397! isotypes SI000398! K000524461 image seen!).

2. ***Nothoscordum Felipponei*** Beauverd, Bulletin de la Societé Botanique de Genèva 13: 7. 1921. ≡ *Brodiaea Felipponei* (Beauverd) Herter, Estudios Botánicos em la Región Uruguaya 4: 47. 1930. *Beauverdia Felipponei* (Beauverd) Herter, Boissiera 7: 510. 1943. ≡ *Ipheion Felipponei* (Beauverd) Traub, Plant Life (Stanford) 5: 50. 1949. ≡ *Tristagma Felipponei* (Beauverd) Traub, Plant Life (Stanford) 19: 61. 1963. Typus: URUGUAY. Montevideo: Cerro, "*in saxosis, perigonio flavo nitidis dorso atropurpureo-vittatis vel pictis; tepala basi connata, folia canaliculate dorso haud carinata*". Uruguay, Dep; Montevideo, Cerro *in saxosis*; leg Cornelius Osten" *C. Osten 3620* et Cuchilla de Pereira [Pereyra], Montevideo mense Junii 1920 (…), leg. Cl. Dr. F. Felippone cui hoc Nothoscordum insignum dicatum est (exsicc. No. 3493). Lectotypus (designated by Deble 2022: 5): URUGUAY. Montevideo: Cuchilla de Pereyra, June [August] 1920, *F. Felippone 3493* (G00098856! isolectotypes SI000426! MVM!).

3. ***Nothoscordum hirtellum***

3.1 ***Nothoscordum hirtellum*** (Kunth) Herter subsp. ***hirtellum***, Index Seminarum (Montevideo) 7: 12. 1926–27. Bas.: *Triteleia hirtella* Kunth. Enum. Pl. [Kunth] 4: 465.1843. ≡ *Milla hirtella* (Kunth) Baker, J. Linn. Soc., Bot.11: 385. 1871. ≡ *Brodiaea hirtella* (Kunth) Baker, Gard. Chron. ser 3, 20: 459. 1896. ≡ *Beauverdia hirtella* (Kunth) Herter, Boissiera 7:509.1943 ≡ *Ipheion hirtellum* (Kunth) Traub, Pl. Life (Stanford) 5: 50. 1949. ≡ *Tristagma hirtellum* (Kunth) Traub, Pl. Life (Stanford) 19: 61.1963. Typus: URUGUAY. Montevideo: without specific place [voyage M. Gaudichaud sur le Bonite], April 1836 [1841], *M. Gaudichaud* (holotype B 10 02477568 image seen! isotype P000852554 image seen! [p.p. left specimen]).

= *Triteleia Sellowiana* Kunth, Enum. Pl. [Kunth] 4: 4.66. 1843. ≡ *Milla sellowiana* (Kunth) Baker, J. Linn. Soc. Bot. 11: 383. 1871. ≡ *Brodiaea Sellowiana* (Kunth) Baker, Gard. Chron. ser. 3, 20: 459. 1896. ≡ *Beauverdia Sellowiana* (Kunth) Herter. Boissiera 7: 510. 1943. ≡ *Ipheion Sellowianum* (Kunth) Traub, Pl. Life (Stanford) 5: 50. 1949. ≡ *Tristagma Sellowianum* (Kunth) Traub, Pl. Life (Stanford) 19: 61. 1963.

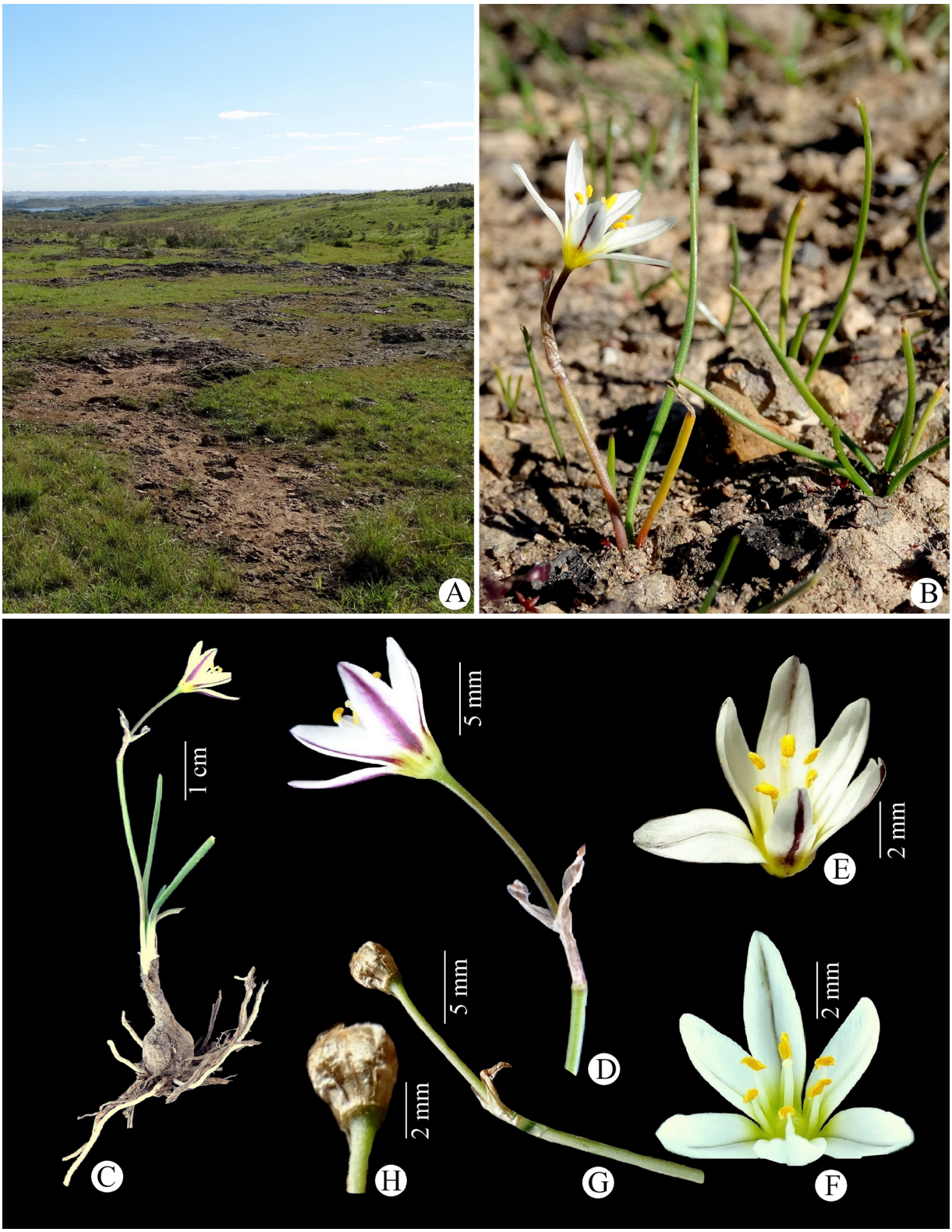

Figure 1. A. Habitat. B. Specimens in natural environments, in front, left in flowering, right and back in vegetative state. C. One entire specimen. D. Flower, lateral view, showing pedicels and bracts. E. Flower, lateral view. F. Flower, inclined view, showing stamens and pistil. G. Apex of the scape, showing the fruit. H. Fruit. All from *Deble & Moreira 18852*.

Typus: BRAZIL. Brasilia meridionalis [Rio Grande do Sul: ebenda von Alegrete über die Misiones dureh den nördlichen Teil des Staates nach Porto Alegre], May–November 1826, *F. Sellow 3664* (holotype B 10 0247567 image seen! isotypes: K000524640 image seen! K000524638 image seen!).

= *Nothoscordum canescens* Beauverd, Bulletín Herbier Boissier, ser. 2, 8: 998. 1909.—Typus: URUGUAY. Minas [Lavalleja]: "Depto. Minarum, in summo Monte Arequita, locis humidis, 18 Apr 1908 [August]" *C. Osten 5195* (holotype G00098878 image seen! isotype MVM 2899 [p.p.]!).

3.2. ***Nothoscordum hirtellum*** (Kunth) Herter subsp. ***glabratum*** (Deble) Deble, **comb. nova**. Bas. *Beauverdia hirtella* (Kunth) Herter subsp. *glabrata* Deble, Phytotaxa 527 (1): 22. 2021. Typus: BRAZIL. Rio Grande do Sul: Dom Pedrito, RS 630, "em afloramento rochoso à esquerda da estrada, após a ponte do rio Tacuarembó, na divisa com São Gabriel e Lavras do Sul", 18 May 2019, *L.P. Deble & B.P. Moreira 19451* (holotype PACA!).

3.3. ***Nothoscordum hirtellum*** (Kunth) Herter subsp. ***Lorentzii*** (Herter) Ravenna, Pl. Life (Stanford) 34: 144.1978. Bas.: *Beauverdia Lorentzii* Herter, Boissiera, 7: 509, Fig. 54. 1943. ≡ *Ipheion Lorentzii* (Herter) Traub, Plant Life (Stanford) 5: 50. 1949. ≡ *Tristagma Lorentzii* (Herter) Traub, Plant Life (Stanford) 19: 61. 1963. ≡ *Nothoscordum Lorentzii* (Herter) Ravenna, Plant Life (Stanford) 23: 50. 1967. ≡ *Nothoscordum Felipponei* Beauverd subsp. *Lorentzii* (Herter) Ravenna, Plant Life (Stanford) 25: 74–75, Fig. 21. 1969. ≡ *Beauverdia hirtella* (Kunth) Herter subsp. *Lorentzii* (Herter) Sassone & Guaglianone, Systematic Botany 39 (3): 773. 2014. Lectotypus (designated by Sassone et al. 2014: 773): ARGENTINA. Entre Ríos: Concepción del Uruguay, "en suelo arenoso al Norte del pueblo, flor anaranjado-amarilla", May 1877, *P.G. Lorentz 967* (BAF, not seen.).

4. ***Nothoscordum inundatum*** Ravenna, Onira Botanical Leaflets 7 (3): 7. 2002. Typus: ARGENTINA. Corrientes: Mburucuyá, Estancia Sta María, 8 May 1956, *T.M. Pedersen 3912* (holotype LP not seen, isotypes CTES0000187! C10005325!).

5. ***Nothoscordum Marchesii*** Crosa, Hickenia 3 (58): 254. 2005. Typus: URUGUAY. Rocha: Parque Nacional de San Miguel, "colecionado em el borde de afloramentos rochosos, entre el Fuerte San Miguel y el cerro Picudo" 6 June 2001, *O. Crosa s.*. (holotype MVFA 32139! isotype SI000430!).

6. ***Nothoscordum modestum*** Ravenna, Onira Botanical Leaflets 3 (6): 17. 1991. Typus: PARAGUAY. Without additional data, *P. Joergensen 4757* (holotype: SI000433!).

7. ***Nothoscordum Ostenii*** Beauverd, Bull. Herb. Boissier, ser. 2, 8: 996. 1909. Typus: URUGUAY. Paysandú: Los Molles, "Est Lawlor, Molles, in collibus lapidosis" 29 August 1898, *C. Osten 3611* (holotype G00191887! isotype SI000434!).

= *Nothoscordum luteominus* Ravenna, Onira Botanical Leaflets 8 (16): 63. 2003. Typus: ARGENTINA. Buenos Aires: Campana, 12 Oct 1953, *V.J. Mazzucconi 379* (BAB, not seen).

8. ***Nothoscordum setaceum*** (Baker) Ravenna, Plant Life (Stanford) 24: 68. 1968. Bas.: *Milla setacea* Baker, J. Linn. Soc., Bot. 11: 385. 1870. ≡ *Hookera setacea* (Baker) Kuntze, Revisio Generum Plantarum 2: 712. 1891. ≡ *Brodiaea setacea* (Baker) Baker Gard. Chron. ser. 3, 20: 459. 1896. ≡ *Ipheion setaceum* (Baker) Traub, Plant Life (Stanford) 9: 69. 1953. ≡ *Tristagma setaceum* (Baker) Traub, Plant Life (Stanford) 19: 61. 1963. Typus: ARGENTINA. Tucumán [probable southern Corrientes or Entre Ríos]: *G. Tweedie s.n.* (holotype K000524637 image seen!).

9. ***Nothoscordum subsessile*** Beauverd, Bulletín Herbier Boissier, ser. 2, 8: 997. 1909. ≡ *Beauverdia subsessilis* (Beauverd) Herter, Boissiera 7: 510. 1943.≡ *Ipheion subsessile* (Beauverd) Traub, Plant Life (Stanford) 5: 50. 1949. Typus: URUGUAY. Minas [Lavalleja]: "Depto. Minarum, in summo Monte Arequita, locis humidis, 18 Apr 1908 [August]" *C. Osten 5195b* (holotype G00191889 image seen! isotype MVM002899!).

= *Nothoscordum Izaguirreae* Crosa, Hickenia 3(61): 272. 2006. Typus: URUGUAY. Lavalleja: en pradera pastoreada, ubicada en la orilla del Río Santa Lucía, junto al puente del camino que pasa frente al cerro Arequita, 26 August 2001, *O. Crosa s.n.* (holotype MVFA 32803!)

10. ***Nothoscordum subtile*** Ravenna, Onira Botanical Leaflets 6 (4): 35. 2001. Typus: URUGUAY. Paysandú: Los Molles, "Culta in Santiago Chilae ex bulbis in glareosis humidis praedii Los Molles dicto, Paysandú Uruguariae collectis" October 1989, *P.F. Ravenna 3117* (holotype Herb. Rav., not seen).

11. *Nothoscordum vittatum* (Griseb.) Ravenna, Plant Life (Stanford) 24: 57.1968. Bas.: *Milla vittata* Griseb. Symb. ad. Fl. Argent. 318. 1879. ≡ *Brodiaea vittata* (Griseb.) Baker, Gard. Chon. ser 3. 20: 459. 1896. ≡ *Beauverdia vittata* (Griseb.) Herter, Boissiera 7: 511. 1943. ≡ *Ipheion vittatum* (Griseb.) Traub; Plant Life (Stanford) 5:50.1949. ≡ *Tristagma vittatum* (Griseb.) Traub, Plant Life (Stanford) 19: 61. 1963. Typus: ARGENTINA. Entre Ríos: Concepción del Uruguay, 1 May 1877, *P.G. Lorentz 968* (holotype GOET005392 image seen!).

= *Nothoscordum uniflorum* Baker, Bull. Misc. Inform. Kew 1898: 227. 1898. Typus: URUGUAY. Montevideo: "in Campos, near the city, Cantera 20" *C. Cantera s.n.* [ex herbarium José Arechavaleta y Balpardo 20] (holotype K000524634 image seen! isotype K000524635 image seen!).

= ? *Nothoscordum lloydiflorum* Beauverd, Bull. Herb. Boissier ser. 2, 8: 998. 1908. ≡ *Beauverdia lloydiflora* (Beauverd) Herter, Boissiera 7: 510. 1943. ≡ *Ipheion lloydiflorum* (Beauverd) Traub, Plant Life (Stanford) 5: 50.1949. ≡ *Tristagma lloydiflorum* (Beauverd) Traub, Plant Life (Stanford) 19: 61. 1963. Typus: URUGUAY. Canelones: Independencia "in campis, tepala alba, basi virescentia, extus medianus atroviolaceo, stigma flavum, antherae lutea", 3 May 1908, *C. Osten 5222* (holotype G00098836 image seen! isotypes SI000429!, MVM! US00091837 image seen!).

Declaration of competing of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to undermine the objectivity or integrity of the work reported in this paper.

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