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Identity and typification of *Linaria* ×*versicolor* (Antirrhineae, Plantaginaceae)

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Abstract. The identity of *Linaria* ×*versicolor* (Jacq.) Chaz. is discussed, supporting a hybrid origin in cultivation that involved species of the North African clade of *Linaria* subsect. *Versicolores* as parents. Due to the lack of original elements, a specimen from the SEV herbarium is designated as the neotype of the name. Ornamental plants usually known as "*Linaria maroccana* hort." correspond to this taxon, and not to *L. maroccana* Hook.f., one of the putative parents, native to the High Atlas (Morocco).
Keywords: *Linaria*, nomenclature, typification, hybrid, Jacquin.

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Introduction

Linaria Mill. sect. *Versicolores* (Benth.) Wettst. (Plantaginaceae) is a natural group comprising over 30 species and subspecies that occur mainly in northern Africa and southern Europe, with centres of diversity in northwestern Africa and the Iberian Peninsula (Sutton, 1988; Fernández-Mazuecos *et al.*, 2013a). Within this group, all but two species are included in *Linaria* subsect. *Versicolores*, which is also a natural group of species that are well differentiated morphologically from those of other *Linaria* lineages based on their distinctly divided style with discrete stigmatic areas (Sutton, 1988; Fernández-Mazuecos *et al.*, 2018a). Some species of this subsection, mainly *L. bipartita* (Vent.) Willd. and *L. maroccana* Hook.f., have been cultivated as ornamental plants (Chittenden, 1951). The members of this subsection are highly interfertile (Viano, 1978a), and the plants grown nowadays as "*L. maroccana* hort." (not *L. maroccana* Hook.f.) appear to be hybrids of different species within this subsection (Sutton, 1988; Sáez, 2024).

Nikolaus J.F. von Jacquin (1781: 336) described *Antirrhinum versicolor* Jacq. based on a plant cultivated in Schönbrunn's Imperial Garden (Vienna). In the protologue, Jacquin indicated that he received the seeds from the Botanic Garden of Paris, but no geographic origin was provided, and no herbarium specimen was specified. A year later, Jacquin (1782) published an illustration of *A. versicolor* (Plate 116). Chazelles de Prizy (1790: 38) transferred *A. versicolor* to the genus *Linaria*, as *L. versicolor* (Jacq.) Chaz. and noted its diverse flower colours. Ventenat (1797) reported a specimen of *A. versicolor* from André Thouin's herbarium, collected in Mont d'Or (nowadays Mont-Dore), in the south of France. Lamarck & Candolle (1805) cited *L. versicolor* as originating from the same area, as well as from the region of Narbonne, also in southern France. These references were accepted in subsequent publications (Willdenow, 1809; Aiton, 1812; Chavannes, 1833). However, Bentham (1846) mentioned *L. versicolor* as a taxon of hybrid origin raised in cultivation, and the species was eventually excluded from the Flora of France (Grenier & Godron, 1850).

Despite the epithet of *L. versicolor* suggesting that it should be the type species of *Linaria* sect. *Versicolores*, the name was largely ignored by subsequent authors, including the revision of the group by Viano (1978b). Sutton (1988), in the introductory section of his chapter on *Linaria* sect. *Versicolores*, discussed the identity of *L. versicolor* and confirmed that no native plants fitting the description provided by Jacquin (1781) occur in southern France. This author underlined the likely hybrid origin of this taxon (Sutton, 1988: 424–425),

most probably from parents originating in Morocco. In particular, he considered *L. gharbensis* Batt. & Pit. as one of the likely parents, along with other species such as *L. bipartita*, *L. maroccana*, or *L. incarnata* (Vent.) Spreng. (note that Moroccan populations included in *L. incarnata* by Sutton are now considered a separate species, *L. mamorensis* Mazuecos, Vigalondo & L. Sáez; see Vigalondo *et al.*, 2015). However, *L. versicolor* was not the subject of a complete taxonomic treatment in Sutton (1988).

The aim of this article is to clarify the identity of *L.* ×*versicolor* and propose a typification for the basionym, *A. versicolor*, which apparently has not yet been typified.

Materials and Methods

This study is based on an analysis of Jacquin's protologue (Jacquin, 1781) and illustration (Jacquin, 1782; Plate 116) of *Antirrhinum versicolor*, relevant literature, and specimens conserved in the following herbaria: B, BM, BR, CGE, G, G-BOIS, G-DC, H, JE, LAU, LINN, LIV, MPU, OXF, P, UPS, SEV and W (acronyms according to Thiers, 2024). The typification follows the International Code of Nomenclature for algae, fungi, and plants (Turland *et al.*, 2018).

Results and Discussion

The protologue of *Antirrhinum versicolor* provides a comprehensive description in Latin (Jacquin, 1781: 336). Based on this description and the illustration in Jacquin (1782; Plate 116), the following morphological details have been extracted. The distinctly divided style is characteristic of plants in the subsection *Versicolores*. Among putative parental species from northwestern Africa (Sutton, 1988), the relatively broad corolla tube resembles those of *L. gharbensis* and *L. maroccana* (versus the narrow tube of *L. bipartita* and *L. mamorensis*; see Fernández-Mazuecos *et al.*, 2013b). The shape and size of the calyx lobes are more similar to those of *L. maroccana*, but the yellow corolla with a purple spur, short fruiting pedicels, and leaf shape correspond to *L. gharbensis*. In contrast, the apparently equal or subequal capsule loculi represented are found in most other species of the section, including *L. bipartita* and *L. mamorensis* (Sutton, 1988; Vigalondo *et al.*, 2015).

The also northwestern African *L. bordiana* Santa & Simonneau subsp. *bordiana* displays a yellow corolla with a purple spur and equal or subequal capsule loculi. However, the shape and size of the calyx lobes do not correspond to those in Jacquin's protologue and plate. These morphological characteristics support a hybrid origin of *L. versicolor* in cultivation, possibly involving two or more species of the North African clade of subsection *Versicolores* (see Fernández-Mazuecos *et al.*, 2013b) as parents.

The protologue of *A. versicolor*, however, does not mention any potential type specimens (Jacquin, 1781), and it is known that Jacquin based some of his descriptions on living plants (Riedl-Dorn, 1988; Austin *et al.* 2014). As with other species described by Jacquin, this issue complicates its typification (D'Arcy, 1970). Based on Stafleu & Cowan (1979), the publication date of plate 116 of *A. versicolor* is 1782 (Jacquin, 1782). While valuable, this plate cannot be considered original material. To that end, it should have been available to the author prior to, or at the same time of, publication of the protologue according to Art. 9.4 of ICN (Turland *et al.*, 2018).

Jacquin's Herbarium at Vienna (W) holds specimens annotated by N.J.F. Jacquin or his son, J.F. Jacquin. Rechinger suggested (in D'Arcy, 1970: 555) that specimens labelled by J.F. Jacquin can be considered lectotypes when accompanied by the notes '*Hb. Jacqu. Hort. Bot. Vind.*' or '*Hort. Schönbr.*'. Only one specimen of *A. versicolor* with references to Jacquin is held at W: W0102197(!). However, it only contains the indication '*Hb. Jacq*.'.

Stafleu & Cowan (1979) list those herbaria where some of Jacquin's specimens can potentially be found. Inquiries for *A. versicolor* specimens were made to the following herbaria: B, BM, BR, CGE, H, JE, LINN, LIV, OXF, UPS, and W. No material attributed to N.J.F. Jacquin or J.F. Jacquin was identified. Additional material was requested and studied from G, G-BOIS, G-DC, LAU, MPU, P and SEV. A specimen with the indication of Mont d'Or and dated 1772 was located at MPU: MPU858479(!). This may be the specimen from A. Thouin's herbarium mentioned by Ventenat (1797). It displays intermediate characters between *L. maroccana* and *L. gharbensis*, which raises questions regarding its provenance, whether it was mistakenly labelled or the plants were cultivated or introduced to that region in France.

Since no original material was listed in the protologue, Plate 116 was published after the original description, the specimen W0102197 —according to D'Arcy (1970)— cannot be considered original material because it lacks the required indications, and we failed to locate any other potential original material, a neotype is here selected in accordance with Art. 9.11 and Art. 9.13 of the ICN (Turland *et al.*, 2018). The chosen neotype, housed at the Universidad de Sevilla (SEV 256697; Figure 1), is congruent with Jacquin's (1781) protologue of *A. versicolor* and with the current application of the name *Linaria versicolor*.

The specimen corresponds to an annual plant with erect fertile stems. The lower leaves are whorled in the sterile stems, the rest alternate, linear-lanceolate. Both the inflorescences and calyces are covered with glandular hairs, consistent with the original description. The oblong and subequal calyx lobes are also consistent with the original description. The original account does not differentiate between the lengths of fruit and flower peduncles, but the peduncles of the neotype align with the description when in flower. The corolla was described as pale yellow with a yellow palate and a violet spur. The shape and colour of the corollas in the neotype are congruent with the description, although the colour cannot be fully appreciated, and Verloove & Sánchez Gullón (2012), who reported this specimen, did not provide information on this character. While Jacquin (1781) did not mention the bifid styles, the seeds (originally described as small, rugose and black) of the neotype align with the original description, as they are wingless, blackish, and bearing transverse ridges that contribute to their rugose appearance. This neotype specimen was collected in an urban area of the southern

Figure 1. Neotype of *Antirrhinum versicolor* Jacq. designated in this study (SEV 256697). Image provided by the SEV herbarium (Universidad de Sevilla).

Iberian Peninsula (Matalascañas, Huelva, Spain) and reported as *L. maroccana* Hook.f. by Verloove & Sánchez Gullón (2012). These authors considered the plant adventitious and escaped from cultivation. In fact, its morphology matches that of ornamental plants known as "*L. maroccana* hort." rather than that of *L. maroccana* Hook.f., one of the putative parents, native to the High Atlas (Morocco). Genetic data for the same population, including internal transcribed spacer sequences (generated using the methods of Fernández-Mazuecos *et al.*, 2013a) and genotyping-by-sequencing data (generated using the methods of Fernández-Mazuecos *et al.*, 2018b), support a hybrid origin and close affinities with species of the North African clade of subsection *Versicolores* (which includes *L. bipartita*, *L. maroccana* Hook.f., *L. gharbensis* and *L. mamorensis*, among others; see Fernández-Mazuecos *et al.*, 2013b) (results not shown).

Linaria viscosa (L.) Chaz. was proposed by Viano (1978b) as the type species for *L.* sect. *Versicolores*. This proposal was subsequently adopted by Sutton (1988). We support maintaining *L. viscosa* as the type species for section *Versicolores*.

Taxonomic treatment

Linaria* ×*versicolor (Jacq.) Chaz., Suppl. Dict. Jard. 2: 38 (1790)
L. maroccana Hook.f. × *L.* spp. subsect. *Versicolores* (Benth.) Wettst.
Basionym:
Antirrhinum versicolor Jacq., Misc. Austr. Bot. 2: 336 (1781)
Type (neotype, designated here): SPAIN: Huelva: Matalascañas (UTM 29SQA1798), adventicio en aceras y arriates en jardines del casco urbano, 05.01.2008, *E. Sánchez Gullón s.n.* (SEV 256697!) (Figure 1).

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Authorship contribution

NR: conceptualization, data curation, investigation, methodology, resources, visualization, writing, original draft; MFM: conceptualization, methodology, resources, visualization, writing, review and editing; LS: conceptualization, methodology, resources, visualization, writing, review and editing.

Conflict of interest

None

References

Aiton, W.T. 1812. Hortus kewensis, or, A catalogue of the plants cultivated in the Royal Botanic Garden at Kew. Ed. 2. Vol. 4. Brown, London. doi: 10.5962/bhl.title.105339

Austin, D.F., Staples, G.W. & Bianchini, R. 2014. Typification of Ipomoea hederacea Jacq. (Convolvulaceae). Taxon 63(1): 167–171. doi: 10.12705/631.35

Bentham, G. 1846. Linaria. In: Candolle, A.P. de (Ed.) Prodromus systematis naturalis regni vegetabilis. Vol. 10. Pp. 266–288. V. Masson, Paris.

Chavannes, E. 1833. Monographie des Antirrhinées. Treuttel et Würtz, Paris. doi: 10.5962/bhl.title.59234

Chazelles de Prizy, L.M.D. 1790. Supplément au dictionnaire des jardiniers. Vol. 2. Claude Lamort, Metz.

Chittenden, F.J. (Ed.). 1951. Dictionary of Gardening. Vol. 3. Oxford Univ. Press, Oxford.

D'Arcy, W.G. 1970. Jacquin names, some notes on their typification. Taxon 19(4): 554–560. doi: 10.2307/1218948.

Fernández-Mazuecos, M., Blanco-Pastor, J.L. & Vargas, P. 2013a. A phylogeny of toadflaxes (Linaria Mill.) based on nuclear internal transcribed spacer sequences: systematic and evolutionary consequences. Int. J. Plant Sci. 174(2): 234–249. doi: 10.1086/668790

Fernández-Mazuecos, M., Blanco-Pastor, J.L., Gómez, J.M. & Vargas, P. 2013b. Corolla morphology influences diversification rates in bifid toadflaxes (Linaria sect. Versicolores). Ann. Bot. 112(9): 1705–1722. doi: 10.1093/aob/mct214

Fernández-Mazuecos, M., Ferrer-Gallego, P.P., Miguel, M., Glover, B.J. & Sáez, L. 2018a. A synopsis of the Iberian clade of Linaria subsect. Versicolores (Antirrhineae, Plantaginaceae) based on integrative taxonomy. Plant Syst. Evol. 304(7): 871–884. doi: 10.1007/s00606-018-1517-0

Fernández-Mazuecos, M., Mellers, G., Vigalondo, B., Sáez, L., Vargas, P. & Glover, B.J. 2018b. Resolving recent plant radiations: power and robustness of genotyping-by-sequencing. Syst. Biol. 67(2): 250–268. doi: 10.1093/sysbio/syx062

Grenier, J.C.M. & Godron, D.A. 1850. Flore de France ou description des plantes qui croissent naturellement en France et en Corse. Vol. 2. Sainte-Agathe Aîné, Besançon. doi: 10.5962/bhl.title.6635

Jacquin, N.J.F. von. 1781. Nicolai Josephi Jacquin Miscellanea austriaca ad botanicam, chemiam, et historiam naturalem spectantia, cum figuris partim coloratis. Vol. II. Ex Officina Krausiana, Vienna. doi: 10.5962/bhl.title.46949

Jacquin, N.J.F. von. 1782. Icones plantarum rariorum. Vol. 1. Antirrhinum versicolor. Plate 116. C.F. Wappler, Vienna; B. White et filium, London; S. et J. Luchtmans, Leiden; A. König, Strasbourg. doi: 10.5962/bhl.title.329

Lamarck, J.B. & Candolle, A.P. de. 1805. Flore Française, ou descriptions succinctes de toutes les plantes qui croissent naturellement en France. Ed. 3. Vol. 3. H. Agasse, Paris. doi: 10.5962/bhl.title.112968

Riedl-Dorn, C. 1988. Zum Problem der Lectotypifizierung nach lebenden Pflanzen beschriebenen Arten bei Nikolaus Joseph von Jacquin. Ann. Naturhist. Mus. Wien, B 90: 9–15.

Sáez, L. 2024. Linaria maroccana. In: Flora of North America Editorial Committee (Eds. 1993+). Flora of North America North of Mexico [Online]. Vol. 17. New York & Oxford. Available from: floranorthamerica.org/Linaria_maroccana [accessed 15 January 2024].

Stafleu, F.A. & Cowan, R.S. 1979. Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Vol. 2. H-Le. Bohn, Scheltema & Holkema, Utrecht. doi: 10.5962/bhl.title.48631

Sutton, D.A. 1988. A revision of the tribe Antirrhineae. British Museum (Natural History), Oxford Univ. Press, London, Oxford.

Thiers, B. 2024. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium, The New York Botanical Garden, New York. Available from: sweetgum.nybg.org/science/ih [accessed 25 January 2024].

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (Eds.). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Veg. 159. Koeltz Botanical Books, Glashütten. doi: 10.12705/Code.2018

Ventenat, E.P. 1797. Muflier. Antirrhinum. In: Lamarck, J.B. (Ed.). Encyclopédie méthodique. Botanique. Vol. 4. Pp. 347–366. Chez H. Agasse, Paris.

Verloove, F. & Sánchez Gullón, E. 2012. New records of interesting vascular plants (mainly xenophytes) in the Iberian Peninsula. II. Fl. Medit. 22: 5–24. doi: 10.7320/FlMedit22.005

Viano, J. 1978a. Croisements experimentaux interspecifiques au sein du genre Linaria. Caryologia 31: 383–425. doi: 10.1080/00087114.1978.10796761

Viano, J. 1978b. Les linaires à graines aptères du bassin méditerranéen occidental. 1. Linaria sect. Versicolores. Candollea 33: 33–88.

Vigalondo, B., Fernández-Mazuecos, M., Vargas, P. & Sáez, L. 2015. Unmasking cryptic species: morphometric and phylogenetic analyses of the Ibero-North African Linaria incarnata complex. Bot. *J*. Linn. *Soc*. 177(3): 395–417. doi: 10.1111/boj.12251

Willdenow, C.L. 1809. Enumeratio Plantarum Horti Regii Botanici Berolinensis: Continens descriptiones omnium vegetabilium in horto dicto cultorum. Taberna libraria Scholae Realis. Taberna libraria Scholae Realis, Berlin. doi: 10.5962/bhl.title.165500