

## **A synopsis of the Iberian clade of *Linaria* subsect. *Versicolores* (Antirrhineae, Plantaginaceae) based on integrative taxonomy**

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## Abstract

Integrative taxonomy, based on the combination of multiple lines of evidence, provides the foundations for a robust species delimitation. Here we provide a taxonomic synopsis of the Iberian clade of *Linaria* subsect. *Versicolores* based on recently published morphometric and phylogenomic data. This clade radiated in the Iberian Peninsula (western Mediterranean) during the Quaternary, and is being intensively studied from phylogenetic, evolutionary, biogeographic, ecological and developmental standpoints. Eight morphologically and genetically distinct species are recognized in the clade: *L. algarviana*, *L. becerrae*, *L. clementei*, *L. incarnata*, *L. onubensis*, *L. salzmännii*, *L. spartea* and *L. viscosa*. For each accepted species, the type material and notes on diagnostic characters, distribution, habitat and intraspecific variability are provided. Five names are typified (four neotypes and one lectotype are designated), and references to previous typifications are also presented. A distribution map and an identification key are presented. This synopsis will provide the basis for future research on speciation and evolution of the clade.

**Keywords:** Antirrhineae, integrative taxonomy, *Linaria*, nomenclature, radiation, typification

## Introduction

A robust species delimitation is critical for evolutionary studies focused on speciation patterns and processes (Wiens 2004) and can only be achieved through the combination of multiple lines of evidence (Dayrat 2005). Integrative taxonomy provides the theoretical and methodological framework for this endeavour, which typically involves the integration of statistically analysed morphological and genetic data, the latter preferably from multiple unlinked loci. These two data types can be complemented with ecological, biogeographical or physiological information, among others (Padial et al. 2010).

*Linaria* Mill. sect. *Versicolores* (Benth.) Wetst. (Antirrhineae, Plantaginaceae) is a clade of c. 30 species and subspecies of toadflax mainly distributed in the Mediterranean Region, with centres of diversity in north-western Africa and the Iberian Peninsula. It includes two sister clades: subsect. *Elegantes* (Viano) D.A.Sutton (two Iberian species) and subsect. *Versicolores* (c. 28 species and subspecies). The latter subsection is morphologically characterised by a bifid style with discrete stigmatic areas, and is in turn formed by two sister clades, one mainly North African (c. 20 species and subspecies, two of them distributed in both north-western Africa and the Iberian Peninsula) and the other Iberian. The Iberian clade of subsect. *Versicolores*, which is the focus of this study, is a monophyletic group of species (Figs. 1, 2) that are endemic or subendemic to the Iberian Peninsula, in the western Mediterranean (Fernández-Mazuecos et al. 2013a). This group diversified in the Quaternary, and has been intensively studied from phylogenetic, evolutionary, biogeographic and developmental standpoints (Fernández-Mazuecos and Vargas 2011; Fernández-Mazuecos et al. 2013a; Fernández-Mazuecos and Vargas 2015; Vigalondo et al. 2015; Cullen et al. 2018; Fernández-Mazuecos et al. 2018). The recent radiation of the clade and its considerable phenotypic variability (Fig. 1) make it an ideal study system to understand plant speciation and floral diversification. Remarkably, the group displays wide interspecific variation in the length of the nectar spur, a floral trait that is considered a key innovation promoting diversification in angiosperms (Hodges 1997; Fernández-Mazuecos and Glover 2017).

The species now included in the Iberian clade of *Linaria* subsect. *Versicolores* have undergone substantial taxonomic rearrangements in the last decades, as shown by three full taxonomic proposals (Viano 1978; Sutton 1988; Sáez 2009; see summary in Table 1), several partial treatments (Valdés 1987; Sáez and Sainz 2011; Vigalondo et al. 2015) and the description of a new species (Blanca et al. 2017). We have recently published detailed morphometric analyses and genome-wide phylogenetic results that support the recognition of eight species in the clade (Fig. 2; Fernández-Mazuecos et al. 2018). By integrating these data, and taking into account previous phylogenetic and taxonomic contributions, we are now in a position to make a well-grounded taxonomic proposal for the clade. Here we present a taxonomic and nomenclatural synopsis of the Iberian clade of *Linaria* subsect. *Versicolores*, including new typifications when necessary. This synopsis will provide the foundations for future research focused on speciation and evolution of this plant lineage.

## Materials and Methods

This taxonomic synopsis is mainly based on examination of 586 herbarium specimens and integration of previously published morphometric and phylogenetic results, the latter summarised in Fig. 2 (Fernández-Mazuecos et al. 2013a; Fernández-Mazuecos and Vargas 2015; Vigalondo et al. 2015; Fernández-Mazuecos et al. 2018). We examined specimens from the following herbaria: ABH, BC, BCN, BM, COI (incl. COI-WILLK), G (incl. G-DC and G-BOIS), HGI, HJBS, LINN, LISU, MA, MGC, MPU, P (incl. P-JUSS), SALA, SEV, UPS

(incl. UPS-THUNB) and VAL (acronyms according to Thiers 2018+). Plants from 21 localities in the Iberian Peninsula were collected by the authors.

Taxa are alphabetically arranged. Each entry includes the scientific name of the taxon, sometimes accompanied by synonyms requiring clarification (additional synonyms are provided by Sáez 2009), type locality, type material, reference to a detailed description, diagnosis, distribution range, habitat, additional observations and a list of specimens examined and included in the distribution map. Authors of cited taxa follow IPNI (2018). The type locality or stated provenance is the geographical entity cited in the protologue, an exact transcription of the relevant portions of the protologue with indication of the geographical location where the plant originates or was collected (in some cases coincident with the locality of the type specimen or the original materials' provenance). A transcription of the label and the herbarium acronym are shown when type specimens were studied. Bibliographic references to previous typifications are also included. Synonyms are indicated as “=” (heterotypic synonym or taxonomic synonym: a name based on a type different from that of another name referring to the same taxon) or “≡” (homotypic synonym or nomenclatural synonym: a name based on the same type as that of another name).

The diagnosis provided for each species summarises the main characters distinguishing it from other species of *Linaria* subsect. *Versicolores* in the Iberian Peninsula based on previously published descriptions and measurements (Sutton 1988; Sáez 2009; Fernández-Mazuecos et al. 2013a; Vigalondo et al. 2015; Blanca et al. 2017; Fernández-Mazuecos et al. 2018). Following Fernández-Mazuecos et al. (2013a), tube width is measured in ventral view at the flower opening level, while spur length is measured from the corolla–calyx insertion to the spur tip. Terminology for seed traits follows Sutton (1988).

For each accepted species we provide its geographical distribution (Fig. 3) based on studied specimens, including type specimens and the author's original material, and herbarium sheets preserved in the herbaria mentioned above (indicated with barcodes or herbarium numbers). Specimens of several species were also observed and collected in the wild, and additional occurrences were taken from the literature (Vigalondo et al. 2015; Blanca et al. 2017) and from online databases in specific cases: Flora-On ([www.flora-on.pt](http://www.flora-on.pt)) for *L. algarviana* and *L. incarnata* in Portugal; Biodiversity Data Bank of the Valencian Community ([bdb.cma.gva.es](http://bdb.cma.gva.es)) for *L. viscosa* in eastern Spain; online database of the P herbarium ([science.mnhn.fr/institution/mnhn/collection/p/item/search](http://science.mnhn.fr/institution/mnhn/collection/p/item/search)) and Inventaire National du Patrimoine Naturel ([inpn.mnhn.fr](http://inpn.mnhn.fr)) for *L. spartea* in France. Given the complex taxonomy of the study group, occurrences from online databases have to be treated with caution. Therefore, only carefully selected occurrences were included in the distribution map.

## Taxonomic Treatment

***Linaria algarviana*** Chav., Monogr. Antirrh.: 142. 1833. Ind. loc.: “Habitat in Algarviâ, prope Promontorium sacrum (Ant., Juss.; Isnard)... vid. sicc. in herb Isnardiano nunc Juss.”—LECTOTYPE (designated by Viano 1978: 54): P-JU [n.v.].

*Description:* Sáez (2009), Sutton (1988). For an image of the plant, see Fig. 1a.

*Diagnosis:* Annual; fertile stems decumbent to ascending. Inflorescence lax in flower and fruit, sparsely glandular-pubescent or rarely strongly pubescent. Pedicels not adnate to inflorescence axis. Calyx lobes 0.7–1.2 mm broad. Corolla violet-purple, the palate whitish with yellow spot and usually reticulated with violet; tube 4–6 mm broad; spur 8–15 mm. Capsule loculi equal. Seeds pyriform-triangular, transversely ridged or occasionally ruminant-alveolate.

*Habitats*: Open scrub and grassland, on quartzite soil; between 0 and 150 m a.s.l.

*Distribution area*: Endemic to southern Portugal (Algarve) (Fig. 3).

*Additional specimens examined*: See Online Resource 1a.

*Notes*: An endemic species from the Algarve, Viano (1978) suggests that specimens with strongly pubescent inflorescences may be hybrids with *L. incarnata*. However, no specimens clearly referable to *L. incarnata* have been found so far south (see below), making that hypothesis unlikely. Strong pubescence probably represents intraspecific variability not worthy of taxonomic recognition. *Linaria algarviana* is distinguished from *L. incarnata* by the decumbent to ascending stems and broad corolla tube (versus erect stems and narrow tube in *L. incarnata*).

***Linaria becerrae*** Blanca, Cueto & J.Fuentes, Phytotaxa 298: 262. 2017. Ind. loc.: SPAIN. Málaga: Ardales, El Chorro, near Iglesia Rupestre and Portezuelos, 450 m elevation.—HOLOTYPE: GDA 62532 [n.v.]; several paratypes are preserved at GDA, MA and MGC.

*Description*: Blanca et al. (2017), Sáez (2009, as *L. salzmannii*). For an image of the plant, see Fig. 1b.

*Diagnosis*: Annual; fertile stems ascending to erect. Inflorescence dense in flower, becoming lax in fruit, glandular-pubescent. Pedicels partially adnate to inflorescence axis. Calyx lobes 0.5–1.3 mm broad. Corolla deep violet-purple with yellow palate; tube 4–7 mm broad; spur 9–17 mm. Capsule loculi subequal. Seeds trigonous-reniform, transversely ridged.

*Habitats*: Grassland, scree and rocky places, on calcareous sandstones (calcarenites); between 200 and 550 m a.s.l.

*Distribution area*: Endemic to southern Spain (Málaga province) (Fig. 3).

*Additional specimens examined*: See Online Resource 1b.

*Notes*: A recently described narrow endemic from the province of Málaga (southern Spain), it is assumed that it was first collected by Salzman in the early 19<sup>th</sup> century (Blanca et al. 2017). Boissier (1841) assigned Salzman's materials to *L. salzmannii* var. *violacea* ("Varietas  $\alpha$  crescit in arenosis regionis montanae, in provinciâ Malacitanâ Salzman"). Although we have been unable to locate these specimens, the fact that no purple-flowered populations of *L. salzmannii* are currently known in Málaga province supports the assumption that Salzman's materials belonged to *L. becerrae*.

Prior to the description of *L. becerrae*, populations of this species were widely identified as *L. salzmannii* (or sometimes *L. viscosa* subsp. *salzmannii*) in the literature (Nyman 1878-1882; Viano 1978; Sutton 1988; Pérez Latorre et al. 2008; Sáez 2009; Fernández-Mazuecos and Vargas 2011; Fernández-Mazuecos et al. 2013a; Fernández-Mazuecos et al. 2013b; Fernández-Mazuecos and Vargas 2015; Vigalondo et al. 2015; Fernández-Mazuecos and Glover 2017). The morphological differences between these plants from Málaga province and the type specimens of *L. salzmannii* (from the province of Granada) led to the description of the former as a new species, *L. becerrae* (Blanca et al. 2017). Morphometry and phylogenomic analyses (Fig. 2) support the recognition of *L. becerrae* and *L. salzmannii* as independent species (Fernández-Mazuecos et al. 2018). *Linaria becerrae* resembles purple-flowered individuals of *L. salzmannii*, but it can be distinguished by the longer spur and deeper-coloured corollas, with hardly visible venation (Blanca et al. 2017).

*Linaria becerrae* is restricted to calcarenite substrates in the province of Málaga. The main populations are found in the surroundings of the village of El Chorro. A smaller population is found 17 km to the south, near the town of Pizarra.

*Linaria clementei* Haens., Ensayo Carratraca: 21. 1817. Ind. Loc.: “Habita en la falda de la sierra cerca de la Iglesia” [Carratraca, Málaga province].—NEOTYPE (**designated here**): [SPAIN, Málaga province], Carratraca et Junquera, G, barcode G00356847 [photo!] (Online Resource 2a; image also available at <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=252502&lang=en>).

– *Linaria clementei* Haens. ex Boiss., Elench. Pl. Nov.: 69. 1838, **nom. illeg.** (Art. 53.1 of the ICN)

*Description*: Sáez (2009), Sutton (1988). For an image of the plant, see Fig. 1c.

*Diagnosis*: Perennial; fertile stems erect. Inflorescence dense in flower and fruit, glandular-pubescent. Pedicels not adnate to inflorescence axis. Calyx lobes 0.7–1.5 mm broad. Corolla violet-purple with yellow palate; tube 4–7 mm broad; spur 2–5 mm. Capsule loculi more or less equal. Seeds trigonous-reniform, transversely ridged or ruminant-alveolate.

*Habitats*: Rocky places, open scrub and grassland, on calcareous and dolomitic substrates (marble); between 200 and 900 m a.s.l.

*Distribution area*: Endemic to southern Spain (Málaga province) (Fig. 3).

*Additional specimens examined*: See Online Resource 1c.

*Notes*: Several authors (Boissier 1838; Viano 1976: 143; 1978: 86; Sutton 1988: 444; Burdet et al. 1990: 613; Devesa and Viera 2001) have considered that this species was published by Boissier (1838) in his *Elenchus plantarum novarum*. However, it was validly described by Haenseler in 1817. Therefore, the name proposed by Boissier in 1838 is a homonym, and thus an illegitimate name according to Art. 53.1 of the ICN (see McNeill et al. 2012).

In the protologue, Haenseler (1817: 21) includes the name of this plant followed by a concise description: “*Foliis inferioribus subquaternis, superioribus semiteretibus, obtusis sparsis; corolla clausa, calcare brevi acuto recto, labio superior supra subvillosa*”. The geographical locality is also mentioned: “Habita en la falda de la sierra encima de la Iglesia” [“It inhabits the mountain slope above the church”] (Haenseler 1817: 19-20).

Plant specimens collected by Haenseler in Málaga are currently found in several herbaria. Pérez-Rubín (2012) mentions that some of Haenseler’s original specimens were in the Sociedad Malagueña de Ciencias (Málaga Society of Sciences), which at one point donated its entire collection to the Herbarium of the University of Granada (GDA). On the other hand, Barbey (1931) indicates that in 1931 John Briquet, curator of the herbarium of the city of Geneva, certified that Haenseler collected plants in Málaga, some of which were acquired by the De Candolle and Boissier herbaria at G (see also Pérez-Rubín 2012). Additionally, Pérez-Rubín (2012) indicates that, shortly before his death, Haenseler donated his herbarium (in poor condition) to Pablo Prolongo. According to Viano (1976: 143), the type of *L. clementei* from a Haenseler specimen is preserved at MA, and this material was acquired via the Prolongo herbarium. However, we have not found any of Haenseler’s specimens of *L. clementei* in the herbaria consulted (e.g. G, GDA, MA, MGC).

Prolongo certainly had in his possession part of the Haenseler herbarium, which was studied by Willkomm in 1845, but another part was lost (Willkomm 1845). Moreover, Haenseler and Prolongo had contact with Edmond Boissier (Boissier 1841; Burdet et al. 1990; González Bueno 2010). In the Boissier collection at G there are some herbarium sheets of this species (images available at [http://www.ville-ge.ch/musinfo/bd/cjb/chg/result.php?type\\_search=simple&lang=en&criteria=linaria+clementei&mode=tout](http://www.ville-ge.ch/musinfo/bd/cjb/chg/result.php?type_search=simple&lang=en&criteria=linaria+clementei&mode=tout)). Two of these, collected in 1837, correspond to the *Elenchus* exsiccata with

number 150, and the other three have no collection date. However, it is not possible to establish any link between this material and the author Haenseler.

All things considered, none of Haenseler's original material of *L. clementei* is extant, and therefore no material is available for lectotypification purposes. As a consequence, a neotype should be selected that matches Haenseler's description (Art. 9.7 of the ICN). We have chosen as the neotype a specimen preserved in the G herbarium (specifically in the Boissier collection) and collected in "Carratraca et Junquera", a geographical locality that agrees with that given in the protologue (Online Resource 2a). The specimen was studied by Boissier and matches the traditional concept and current use of the name *L. clementei* (e.g. Haenseler 1817; Boissier 1838; Sutton 1988; Sáez 2009).

*Linaria clementei* is an unmistakable species, given its short floral spur and perenniality. It is endemic to Málaga province, in southern Spain (Fig. 3). A herbarium specimen (MA 109504) was allegedly collected by E. Reverchon in Grazalema (Cádiz province), c. 40 km west of the currently known distribution. However, a labelling error (or a very broad interpretation of the locality) cannot be ruled out since there is no evidence of the presence of this species in Grazalema. Moreover, *L. clementei* was reported from Gibraltar (Willkomm 1893). This record is not supported by herbarium specimens and should be disregarded as being in all probability erroneous.

***Linaria incarnata*** (Vent.) Spreng., Syst. Veg. 2: 796. 1825.  $\equiv$  *Antirrhinum incarnatum* Vent. in Lam., Encycl. 4: 364. 1797. Ind. loc.: "Cette jolie plantes croît en Espagne, d'où elle fut rapportée par M. Antoine de Jussieu. (Ex adumbratione Aubriet & in herb. D. de Juss.)"—LECTOTYPE (designated by Lainz 1966: 66): P-JU [n.v.]; isoelectotype: G, barcode G00356844 [photo!] (image available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356844>).

*Description:* Vigalondo et al. (2015). For an image of the plant, see Fig. 1d.

*Diagnosis:* Annual; fertile stems erect. Inflorescence lax in flower and fruit, glandular-pubescent. Pedicels not adnate to inflorescence axis. Calyx lobes 0.3–1.3 mm broad. Corolla violet-purple, the palate whitish with yellow spot and usually reticulated with violet; tube 1–2 mm broad; spur 7–15 mm. Capsule loculi subequal. Seeds subtrigonus, ruminant-alveolate.

*Habitats:* Grassland and open scrub, usually on siliceous sandy soil; between 200 and 850 m a.s.l.

*Distribution area:* Endemic to western Iberian Peninsula (Portugal and Spain) (Fig. 3).

*Additional specimens examined:* See Online Resource 1d.

*Notes:* We follow the circumscription of *L. incarnata* proposed by Vigalondo et al. (2015), in which this taxon is considered distinct from the SW Iberian *L. onubensis* Pau and the NW African *L. mamorensis* Mazuecos, Vigalondo & L.Sáez, Bot. J. Linn. Soc. 177(3): 412 (2015). This treatment is supported by both morphometry and phylogenomic data (Fig. 2) that indicate that *L. incarnata*, *L. onubensis* and *L. mamorensis* are morphologically similar but independently evolved species (Vigalondo et al. 2015; Fernández-Mazuecos et al. 2018). The three species display similar narrow-tubed, purple-flowered corollas. *Linaria incarnata* can be distinguished from the other two by the densely glandular-pubescent inflorescences and subtrigonus seeds.

Reports of *L. incarnata* from northern Africa (Sutton 1988; Sáez 2009) are due to confusion with *L. mamorensis* (see Vigalondo et al. 2015). The presence of *L. incarnata* in the Algarve (southern Portugal) has been previously indicated (Vigalondo et al. 2015) based on specimens from the locality of Quarteira (MA 187813). After examining additional

material from the same area, we conclude that these specimens are referable to *L. algarviana*. *Linaria incarnata* seems to be absent from the Algarve (see also Clamote et al. 2017).

***Linaria onubensis*** Pau, Broteria, Ci. Nat. 2: 50. 1933. Ind. loc.: “Valverde (Huelva) (E. Gros)”.—LECTOTYPE (designated by Vigalondo et al. 2015: 412): MA, barcode MA 109497! (image available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.ma109497>); isoelectotypes: MA, barcodes MA 109496! and MA 109495! (images available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.ma109496> and <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.ma109495?loggedin=true>).

*Description:* Vigalondo et al. (2015). For an image of the plant, see Fig. 1e.

*Diagnosis:* Annual; fertile stems erect. Inflorescence lax in flower and fruit, glabrescent to sparsely glandular-pubescent. Pedicels not adnate to inflorescence axis. Calyx lobes 0.4–1 mm broad. Corolla violet-purple, the palate whitish with yellow spot and sometimes reticulated with violet; tube 1–3 mm broad; spur 5–10 mm. Capsule loculi subequal. Seeds reniform, transversely ridged.

*Habitats:* Grassland and open scrub, on sandy siliceous soil; between 3 and 280 m a.s.l.

*Distribution area:* Endemic to south-western Spain (Huelva Province) (Fig. 3).

*Additional specimens examined:* See Online Resource 1e.

*Notes:* *Linaria onubensis* was originally described by Pau (1933). Based on the original description, Sutton (1988) interpreted it as a likely synonym of *L. elegans* Cav. in subsect. *Elegantes*, while Valdés (1987) and later authors (Sáez 2009) considered it a synonym of *L. incarnata*. Morphometry and phylogenomic results (Fig. 2) confirm that *L. onubensis* is a distinct species in subsect. *Versicolores* endemic to SW Spain (Vigalondo et al. 2015; Fernández-Mazuecos et al. 2018). It can be distinguished from *L. incarnata* by its glabrescent or sparsely glandular-pubescent inflorescences and reniform seeds.

***Linaria salzmannii*** Boiss., Voy. Bot. Espagne 2: 456. 1841. [“salzmanni”] ≡ *Linaria viscosa* subsp. *salzmannii* (Boiss.) Nyman, Consp. Fl. Eur. 538. 1881. Ind. loc.: not expressly indicated. The protologue includes type localities for the two varieties of *L. salzmannii* circumscribed by Boissier (1841) (var. *violacea* and var. *flava*; see below).—LECTOTYPE (**designated here**): G, barcode G00356813 [photo!] (Online Resource 2b; images also available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356813>).

≡ *Linaria salzmannii* var. *violacea* Boiss., Voy. Bot. Espagne 2: 456. 1841. Ind. loc.: “Varietas α [violacea] crescit in arenosis regionis montanae, in provinciâ Malacitanâ Salzmann, in viâ à Granada ad pagum Guejar. Alt. circ. 3500”.—LECTOTYPE (designated by Burdet et al. 1990: 618; “le lectotype est le spécimen de gauche sur la feuille n° 2” [the lectotype is the left specimen on the sheet n. 2]): G, barcode G00356813 [photo!] (Online Resource 2b; image also available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356813>).

= *Linaria salzmannii* var. *flava* Boiss., Voy. Bot. Espagne 2: 456. 1841. Ind. loc.: “Varietas β [flava] in cultis regionis montanae superioris et alpinae, Sierra Nevada, en la Dehesa de San Gerónimo et in latere meridionali suprâ Trevezlez. Alt. 4000-7000”.—LECTOTYPE



(designated by Burdet et al. 1990: 618): G, barcode G00356800 [photo!] (image available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356800>).

= *Linaria spicata* Kunze, Flora 29(41): 645. 1846. ≡ *Linaria viscosa* subsp. *spicata* (Kunze) D.A. Sutton, Rev. Antirrhin.: 436. 1988. Ind. loc.: “Sierra Nevada, in latere australi ad rivulos regionis alpinae”.—NEOTYPE (**designated here**): [Spain, Granada] Sierra Nevada 6-7000', Aug 1844, *Willkomm*, BM, barcode BM001209124 [photo!] (Online Resource 2c; image also available at <http://data.nhm.ac.uk/object/ea611a3f-6b0e-4221-9d48-8e4cc41d610c>).

*Description*: Sáez (2009, as *L. viscosa* subsp. *spicata*), Sutton (1988, as *L. viscosa* subsp. *spicata*). For images of the plant, see Fig. 1f, g.

*Diagnosis*: Annual; fertile stems ascending to erect. Inflorescence dense in flower and fruit, glandular-pubescent. Pedicels frequently partially adnate to inflorescence axis. Calyx lobes 0.4–0.9 mm broad. Corolla deep yellow, sometimes light violet-purple with darker veins and yellow palate, rarely white with purple spur and yellow palate; tube 3–7 mm broad; spur 5–10 mm. Capsule loculi subequal. Seeds trigonous-reniform, transversely ridged or ruminant-alveolate.

*Habitats*: Grassland, scree and rocky places, on siliceous, calcareous or dolomitic substrate; between 600 and 2600 m a.s.l.

*Distribution area*: Endemic to south-eastern Spain (Fig. 3).

*Additional specimens examined*: See Online Resource 1f.

*Notes*: Burdet et al. (1990) designated the lectotypes of the names *L. salzmannii* var. *flava* and *L. salzmannii* var. *violacea*, but not the lectotype of the name *L. salzmannii* (Greuter, personal comm. *in litt.*). The lectotype of *L. salzmannii* designated in this work (with G00356813) is a specimen mounted on three herbarium sheets with several fragments and plants (sheet 1: five fragments, with an original label handwritten by Boissier “entre Grenade et Guejar”; sheet 2: two well developed and complete plants, with two original labels handwritten by Boissier “*Linaria fleurs roses / ds le sable ds collines / en montant / Guejar*” and “*Linaria Salzmannii! Boiss. / spartea v. violacea Salzm. / h. Boiss. / polygonifolia Chavan. / non Spreng.*”; sheet 3: two well developed and complete plants and an envelope with several fragments, and an original label handwritten by Boissier “*Lin. nova species / comparer avec le Spartea / infra Guejar.*”) According to Burdet et al. (1990), the lectotype of *L. salzmannii* var. *violacea* is the left specimen on sheet 2. However, all the material included within the sheet G00356813 belongs to a single collection made at the same time and belongs to the same taxon, so the specimen is composed of all plants and all fragments on the three sheets indicated at G with barcode G00356813, and all of them should have been therefore considered as the lectotype of *L. salzmannii* var. *violacea* (Greuter, personal comm. *in litt.*) because the Art. 9.14 of the ICN does not apply in this case. Nevertheless, the lectotype of *L. salzmannii* var. *violacea* designated by Burdet et al. (1990) (restricted only to the plant mounted on the left part of the sheet number 2) must be accepted. The other original material of *L. salzmannii* var. *violacea* cited by Boissier in the protologue and indicated by Burdet et al. (1990) as syntype is mounted on two sheets, with barcode G00356814 (image available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356814>). However, in both sheets the fragment on the right part of the sheet belongs to *L. verticillata* Boiss.

In addition to the lectotype of *Linaria salzmannii* var. *flava* designated by Burdet et al. (1990), there are two other specimens at G with original material cited by Boissier in the protologue, with barcodes G00356801 [photo!] and G00356799 [photo!], collected in Trévez and Sierra Nevada respectively. Both specimens are therefore syntypes (images available at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356801> and <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00356799>).

As type of *L. spicata*, Sutton (1988: 436) indicated: “Type: Spain: [Granada]; Sierra Nevada, ‘in latere australi ad rivulos regionis alpinae’, ix 1844 *Willkomm s. n.* Herb. Kunze (syn.? LZ†); Sierra Nevada, 6000-7000 ft, viii 1844 *Willkomm s. n.* (type collection? BM!)”. Indeed, the personal herbarium of Gustav Kunze was preserved at LZ, but was unfortunately destroyed (see Stafleu and Cowan 1979: 702). We have not found any of Kunze’s original material of *L. spicata* in any herbaria consulted (e.g. LZ, L, PH, UPS). In the Willkomm herbarium at COI there are two specimens of this plant, with barcodes COI00042770 and COICOI00042768

(<http://coicatalogue.uc.pt/?q=linaria+spicata&t=results&orderby=relevance&orderdirection=DESC&size=10>). However, neither of them is a duplicate of the specimens mentioned by Sutton (1988). In conclusion, no original material of *L. spicata* is extant, and therefore there is no material available for lectotypification. As a consequence, a neotype should be designated (Art. 9.7 of the *ICN*). As the neotype, we have chosen a specimen preserved in the BM herbarium, with barcode BM001209124, and collected in “Sierra Nevada” in August 1844 by Willkomm (Online Resource 2c). The geographical locality agrees with that given in the protologue, and the specimen (three well preserved and developed fragments) matches the traditional concept and current use of the name (e.g. Kunze 1846; Sutton 1988; Sáez 2009).

Boissier’s concept of *L. salzmännii* comprised plants now included in both *L. salzmännii* and *L. becerrae* (Boissier 1841). In fact, the name *L. salzmännii* has been widely assigned to the taxon currently known as *L. becerrae* in recent times (see Notes under *L. becerrae*). In turn, populations currently assigned to *L. salzmännii* were usually identified as *L. viscosa* subsp. *spicata* (Sáez 2009; Fernández-Mazuecos and Vargas 2011; Fernández-Mazuecos et al. 2013a; Fernández-Mazuecos and Vargas 2015; Vigalondo et al. 2015). After examining the lectotypes of *L. salzmännii* var. *violacea* and *L. salzmännii* var. *flava* (designated by Burdet et al. 1990) and plants recently collected at a location nearby the type locality of *L. salzmännii* var. *violacea* in Granada province (south-eastern Spain), Blanca et al. (2017) concluded that *L. salzmännii* and *L. viscosa* subsp. *spicata* are taxonomic synonyms. Morphometry and phylogenomic analyses (Fig. 2) support a species status for this taxon, as shown by a clear differentiation from both *L. viscosa* and *L. becerrae* (Fernández-Mazuecos et al. 2018). As a consequence, its correct name is *L. salzmännii* (see also Blanca et al. 2017). *Linaria salzmännii*, *L. viscosa* and *L. becerrae* are similar in displaying dense glandular-pubescent inflorescences and being annual. The shorter spur and smaller calyx lobes distinguish *L. salzmännii* from the other two, among other characters.

The corolla of *L. salzmännii* is yellow in most of the distribution range of the species (Fig. 1g). However, a few populations display individuals with violet-purple corollas with a yellow palate (Fig. 1f), or even white corollas with a purple spur and a yellow palate. Purple-flowered plants are currently found in at least two locations: Sierra de Huétor in Granada province (close to the type locality, now probably lost due to the construction of a reservoir; Blanca et al. 2017) and Sierra de Cazorla in Jaén province. The purple- and yellow-flowered morphs were originally detected by Boissier (1841), who described them as varieties (var. *violacea* and var. *flava* respectively). Morphometry and genome-wide molecular analyses (Fernández-Mazuecos et al. 2018) confirm that the two colour morphs are conspecific (see also Sáez 2009). Colour morphs do not form monophyletic entities within *L. salzmännii*, and they are sometimes mixed in populations (e.g. in Sierra de Cazorla). As a result, they are not worthy of recognition as infraspecific taxa.

***Linaria spartea*** (L.) Chaz., Suppl. Dict. Jard. 2: 38. 1790; ≡ *Antirrhinum sparteum* L., Sp. Pl.: 1197. 1753. Ind. loc.: “*Habitat in Hispania. Loefling*”.—NEOTYPE (**designated here**): Portugal: Alto Alentejo: Montemor-o-Novo, 38°38'22,7"N 8°13'45,1"W, 210 m, talud

arenoso junto a senda, 26/3/2009, M. Fernández-Mazuecos 18MF09, MA, barcode MA 911385! (Fig. 4); isoneotypes: MA, barcodes MA 911386!, MA 911387!, MA 911388!, MA 911389!

= *Linaria viscosa* var. *crassifolia* Cout., Fl. Portugal: 550. 1913, **syn. nov.** ≡ *Linaria viscosa* subsp. *crassifolia* (Cout.) D.A. Sutton, Rev. Antirrhin.: 436. 1988. Ind. loc.: “Prox. do Cabo da Roca”.—NEOTYPE (**designated here**): Portugal: Lisboa, in rupestribus graminosis l. Cabo da Roca, supra marem 50 m alt., 14 junii 1936, W. et M. Rothmaler, s.n., JE, barcodes JE00024668 [photo!] and JE00024669 [photo!] (Online Resource 2d).

*Description*: Sáez (2009), Sutton (1988). For images of the plant, see Fig. 1h, i.

*Diagnosis*: Annual; fertile stems usually erect, sometimes ascending. Inflorescence predominantly lax in flower and fruit, glabrous, sparsely glandular-pubescent or sometimes densely glandular-pubescent. Pedicels not adnate to inflorescence axis. Calyx lobes 0.5–1.5 mm broad. Corolla deep yellow; tube 3–8 mm broad; spur 5–15 mm. Capsule loculi subequal. Seeds trigonous-reniform, transversely ridged.

*Habitats*: Grassland, open scrub, embankments and scree, mainly on siliceous sandy soils (less frequently on calcareous substrate); between 0 and 1180 m a.s.l.

*Distribution area*: Iberian Peninsula (except most of the East) and south-western France (Fig. 3).

*Additional specimens examined*: See Online Resource 1g.

*Notes*: The currently accepted neotype of the name *Antirrhinum spartheum* L. (Viano 1978: 51) from a specimen cultivated in the *Hortus Upsaliensis*, Herb. Linn. No. 767.20 (LINN) (image available at <http://linnean-online.org/7077/>), does not correspond to what is generally understood as *L. sparthea*. Surprisingly, the specimen LINN 767.20 does not even belong to *Linaria* subsect. *Versicolores* as it does not exhibit a bifid stigma, but a capitate stigma (as can be easily seen in three flowers that have lost the corolla located at the bottom of the inflorescence; Fig. 5). This specimen probably corresponds to some species of *Linaria* sect. *Supinae*. No original material has been found in the herbarium collections consulted. The specimen Herb. Thunberg No. 14125 (UPS-THUNB): *Antirrhinum spartheum* “cult. in Horto Uppsaliensi. Thunberg” [handwriting of Thunberg] includes a perennial plant with capitate stigmas (Mats Hjertson, personal comm. 23 Aug 2016). According to Art. 9.19(b) of the *ICN*, the previous neotype published by Viano (1978) must be superseded. To rectify this situation, a suitable neotype for *A. spartheum* is designated in this paper. The neotype herein designated is a modern specimen collected in Portugal and preserved at MA (Fig. 4). It matches the traditional concept and current use of the name (e.g. Viano 1978; Sutton 1988; Sáez 2009). A specimen from the same collection was included in the phylogenomic analysis published by Fernández-Mazuecos et al. (2018).

*Linaria viscosa* var. *crassifolia* was described by Coutinho (1913) from plants collected in Cabo da Roca (western Portugal). Sutton (1988) raised this taxon to subspecific rank and considered it a local endemic from the area of Cabo da Roca, where it grows on coastal rocks. However, Sáez (2009) expressed doubts about its taxonomic value. Specimens collected in the *locus classicus* of *L. viscosa* var. *crassifolia* (Fig 1i) are morphologically and genetically indistinguishable from *L. sparthea* (Fernández-Mazuecos et al. 2018). Consequently, here we treat the name *L. viscosa* var. *crassifolia* as a synonym of *L. sparthea*.

Since we have been unable to trace any original material of *L. viscosa* var. *crassifolia* in any consulted herbaria (e.g. COI, LISI, LISU, , or LY; see <https://www.biodiversitylibrary.org/page/33120692#page/609/mode/1up>), and in order to fix the application of this name, we designate a neotype according to Art 9.7 of the *ICN*. The neotype designated is preserved at JE, and is mounted on two sheets clearly labelled as being

part of a single specimen (see Art. 8.3), with barcodes JE00024668 and JE00024669 (Online Resource 2d). This specimen is very complete and well preserved, was collected in the geographical locality cited in the protologue “Cabo da Roca” and was studied and identified in 1986 by Sutton as *L. viscosa* subsp. *crassifolia*, and also cited in his work (Sutton, 1988). The neotype matches the traditional concept and current use of the name *L. viscosa* var. *crassifolia* (e.g. Coutinho 1913; Sutton 1988; Sáez 2009).

Despite their overall morphological similarity, *L. spartea* and *L. viscosa* form distinct genetic clusters (see Fig. 2) (Fernández-Mazuecos et al. 2018). Morphologically, *L. spartea* is mainly distinguished by the predominance of lax inflorescences in populations, while dense inflorescences are predominant in *L. viscosa* (Fig. 1h, j). Plants morphologically similar to *L. spartea*, with lax inflorescences, co-occur with *L. viscosa* in SW Spain, but they seem to be genetically indistinguishable from *L. viscosa* (Fernández-Mazuecos et al. 2018). Similarly, certain individuals with dense inflorescences, sometimes identified as *L. viscosa*, occur in Portuguese populations belonging to the *L. spartea* genetic cluster. An example of this is the area of Cabo da Roca, where a high variability in inflorescence density is observed (see Online Resource 2d).

Some populations of *L. spartea* in eastern Spain (Alicante and Gerona provinces), disjunct from the main distribution range of the species (see Fig. 3), might be introduced, as suggested by their presence in highly anthropogenic habitats.

***Linaria viscosa*** (L.) Chaz., Suppl. Dict. Jard. 2: 39. 1790. ≡ *Antirrhinum viscosum* L., Cent. Pl. 2: 21. 1763. Ind. loc.: “*Habitat in Hispania*”.—LECTOTYPE (designated by Sutton in Jarvis 2007: 306): LINN 767.24 [photo!] (image available at <http://linnean-online.org/7081/>).

*Description*: Sáez (2009, as *L. viscosa* subsp. *viscosa*), Sutton (1988, as *L. viscosa* subsp. *viscosa*). For an image of the plant, see Fig. 1j.

*Diagnosis*: Annual; fertile stems usually erect, sometimes ascending. Inflorescence predominantly dense in flower and fruit, glandular-pubescent. Pedicels generally not adnate to inflorescence axis. Calyx lobes 0.9–1.8 mm broad. Corolla deep yellow; tube 3–8 mm broad; spur 7–15 mm. Capsule loculi subequal. Seeds trigonous-reniform, transversely ridged.

*Habitats*: Grassland, open scrub and embankments, mainly on siliceous sandy soils (rarely on calcareous substrate); between 0 and 800 m a.s.l.

*Additional specimens examined*: See Online Resource 1h.

*Distribution area*: Endemic to southern and eastern Iberian Peninsula (Fig. 3).

*Notes*: Despite their overall similarity, recent results support *L. viscosa* and *L. spartea* as morphologically and genetically distinct species, mainly distinguished by their dense and lax inflorescences respectively (Fig. 1h, j; Fig. 2) (Fernández-Mazuecos et al. 2018). *Linaria viscosa* seems to replace *L. spartea* in south-western Spain (Fig. 3). However, the exact limits of their distribution ranges in this region are yet to be determined, since Fernández-Mazuecos et al. (2018) detected some minor inconsistencies between morphology-based identifications and genetic clustering (see Notes under *L. spartea*). The presence of *L. viscosa* in Portugal is frequently indicated (Viano 1978; Sutton 1988; Sáez 2009), but most of the Portuguese specimens identified as *L. viscosa* that we have examined display somewhat lax inflorescences, and therefore have been assigned to *L. spartea*. Furthermore, two Portuguese specimens initially identified as *L. viscosa* were assigned to *L. spartea* based on phylogenomic data (Fernández-Mazuecos et al. 2018). Although *L. viscosa* may be present in southern Portugal, it is probably a rare species in this country (see also Pereira et al. 2017). Populations of *L. viscosa* just north of the Strait of Gibraltar (Cádiz province) require further examination to assess their potentially hybrid origin suggested by genetic data (Fernández-

Mazuecos and Vargas 2015; Fernández-Mazuecos et al. 2018) and some morphological traits (such as the presence of individuals with pedicels partially adnate to the inflorescence axis, a trait characteristic of *L. salzmännii* and *L. becerrae*). Some disjunct populations with dense inflorescences are found in eastern Spain (Barcelona, Gerona, Valencia and Alicante provinces; Fig. 3). The identity of a specimen from Valencia has been confirmed as *L. viscosa* based on phylogenomic data (Fernández-Mazuecos et al. 2018). The populations in Barcelona (Sáez et al. 2000) and Gerona are, in all probability, introduced. Reports from northern Africa are due to confusion with other species of the genus (Sáez 2009).

### **Identification key**

Species of *Linaria* subsect. *Versicolores* are distinguished from other species of *Linaria* by their distinctly bifid stigma (Sutton 1988). This identification key comprises the ten species of *Linaria* subsect. *Versicolores* present in the Iberian Peninsula, including the eight species of the Iberian clade revised in this paper (endemic or subendemic to the Iberian Peninsula) and two species of the North African clade distributed in both northern Africa and the Iberian Peninsula (*L. pedunculata* and *L. gharbensis*). The key is based on those previous published (Sutton 1988; Sáez and Bernal 2009; Vigalondo et al. 2015; Blanca et al. 2017), with some modifications.

- 1a. Smooth seeds ..... *L. pedunculata*
- 1b. Seeds with deep transverse crests ..... 2
- 2a. Perennial herb, with fertile stems erect; spur up to 5 mm ..... *L. clementei*
- 2b. Annual herb, with fertile stems decumbent, ascending or erect; spur more than 5 mm ..... 3
- 3a. Corolla violet, purple or pinkish, with a yellow spot on the palate ..... 4
- 3b. Corolla yellow or yellowish-white, sometimes with a violet spur ..... 8
- 4a. Pedicels ± adnate in his basal part to the inflorescence axis ..... 5
- 4b. Pedicels not adnate to the inflorescence axis ..... 6
- 5a. Corolla with clearly visible darker veins; spur 5–10 mm long, shorter than rest of corolla ..... *L. salzmännii*
- 5b. Corolla with hardly visible venation; spur 9–17 mm long, somewhat longer than rest of corolla ..... *L. becerrae*
- 6a. Fertile stems decumbent to ascending; corolla tube width more than 3 mm ..... *L. algarviana*
- 6b. Fertile stems erect; corolla tube width up to 3 mm ..... 7
- 7a. Inflorescence densely glandular-pubescent; seeds subtrigonus ..... *L. incarnata*
- 7b. Inflorescence glabrescent to sparsely glandular-pubescent; seeds reniform ..... *L. onubensis*
- 8a. Corolla yellowish-white with violet spur; upper locule of the capsule clearly more developed than the lower one ..... *L. gharbensis*
- 8b. Corolla deep yellow; upper locule of the capsule equally or slightly more developed than the lower one ..... 9
- 9a. Inflorescence predominantly lax, glabrous, sparsely glandular-pubescent or densely glandular-pubescent ..... *L. spartea*
- 9b. Inflorescence predominantly dense, corymbiform at anthesis, generally densely glandular-pubescent ..... 10
- 10a. Pedicels ± adnate in his basal part to the inflorescence axis; calyx lobes 0.4–0.9 mm wide ..... *L. salzmännii*
- 10b. Pedicels not adnate to the inflorescence axis; calyx lobes 0.9–1.8 mm wide ..... *L. viscosa*

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### Compliance with Ethical Standards

**Conflict of interest** The authors declare that they have no conflict of interest.

### Online Resources

**Online Resource 1** Additional specimens examined. **a** *L. algarviana*; **b** *L. becerrae*; **c** *L. clementei*; **d** *L. incarnata*; **e** *L. onubensis*; **f** *L. salzmännii*; **g** *L. sparteae*; **h** *L. viscosa*.

**Online Resource 2** Images of three neotypes and one lectotype designated in this study. **a** Neotype of *Linaria clementei* Haens. designated in this study (G, barcode G00356847). © Conservatoire et Jardin botaniques de la Ville de Genève. **b** Lectotype of *Linaria salzmännii* Boiss. designated in this study (G, barcode G00356813). © Conservatoire et Jardin botaniques de la Ville de Genève. **c** Neotype of *Linaria spicata* Kunze designated in this study (BM, barcode BM001209124). © The Trustees of the Natural History Museum, London. **d** Neotype of *Linaria viscosa* var. *crassifolia* Cout. designated in this study (JE, barcodes JE00024668 and JE00024669). © Herbarium Haussknecht, Institut für Spezielle Botanik, Friedrich-Schiller-Universität Jena.

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## Figure captions

**Fig. 1** Inflorescences of the eight species included in the Iberian clade of *Linaria* subsect. *Versicolores*: **a** *L. algarviana* (Portugal, Cabo de São Vicente); **b** *L. becerrae* (Spain, El Chorro); **c** *L. clementei* (Spain, Sierra Blanca); **d** *L. incarnata* (Spain, Sierra de la Peña de Francia); **e** *L. onubensis* (Spain, Valverde del Camino); **f** *L. salzmännii*, purple-flowered morph (Spain, Sierra de Huétor); **g** *L. salzmännii*, yellow-flowered morph (Spain, Sierra Nevada); **h** *L. sparteae* (Spain, Cabañeros); **i** *L. sparteae* (Portugal, Cabo da Roca); **j** *L. viscosa* (Spain, Doñana). Photographs a, d, h and j by José Quiles; b, c, f and g by Joaquín Ramírez; e by Pablo Vargas; and i by Llorenç Sáez

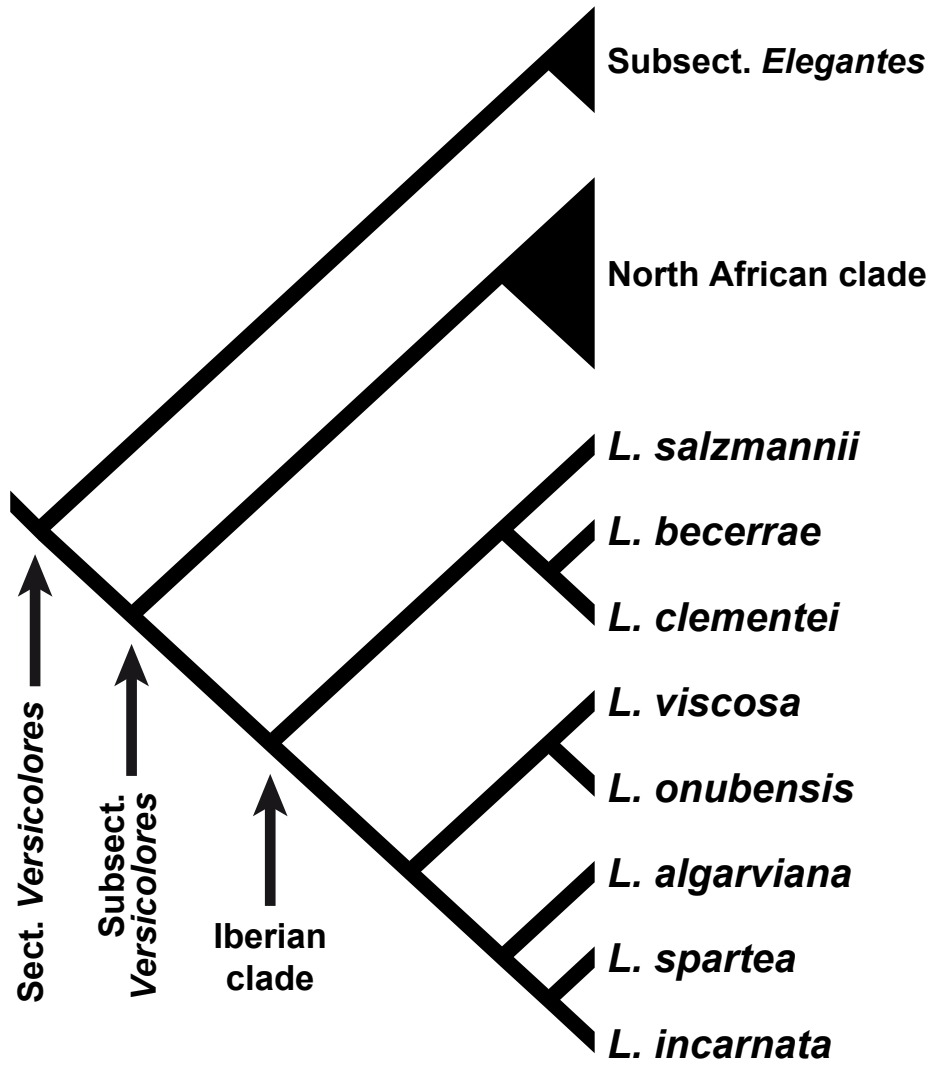
**Fig. 2** Phylogenetic hypothesis for the eight species of the Iberian clade of *Linaria* sect. *Versicolores* and closely related lineages based on genome-wide data (Fernández-Mazuecos et al. 2018)

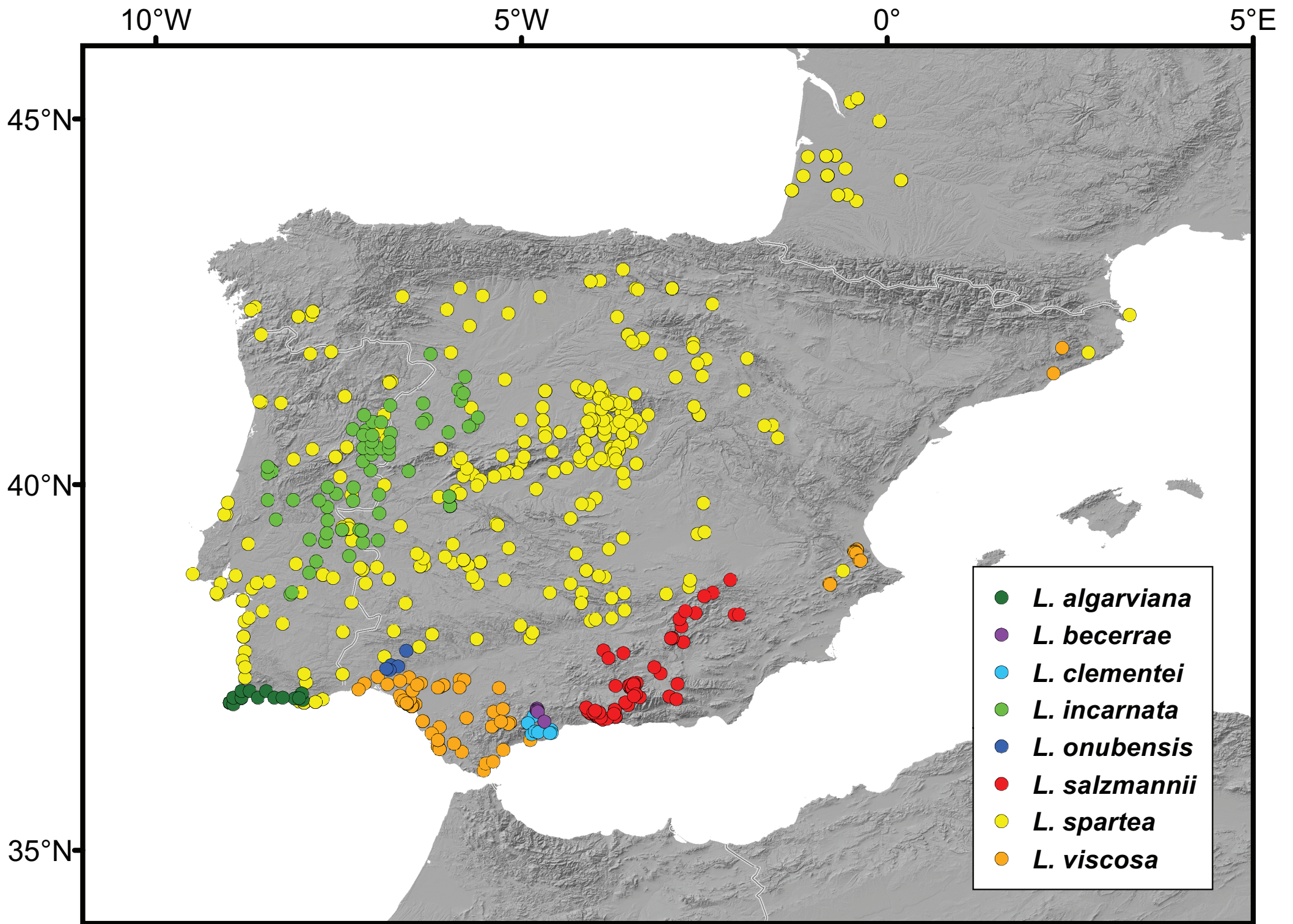
**Fig. 3** Distribution map of the eight species included in the Iberian clade of *Linaria* subsect. *Versicolores* (see Materials and methods for the origin of occurrence records)

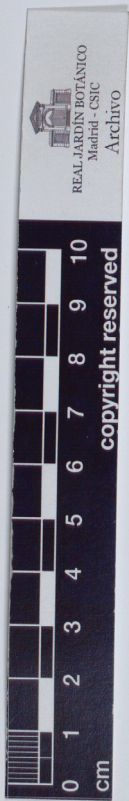
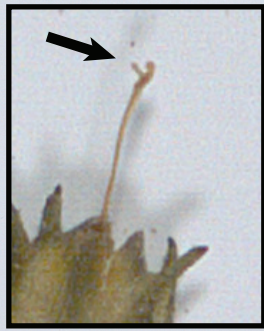
**Fig. 4** Neotype of *Linaria sparteae* (L.) Chaz. designated in this study (MA, barcode MA 911385). The inset shows the bifid stigma that is characteristic of *Linaria* subsect. *Versicolores* (cf. Fig. 5). Image provided by the MA herbarium (Real Jardín Botánico, RJB-CSIC, Madrid)

**Fig. 5** Stigmatic morphology of the specimen proposed by Viano (1978) as neotype of the name *Antirrhinum sparteum* L. (LINN 767.20). The capitate stigma shows that the specimen does not belong to *Linaria* subsect. *Versicolores*, where all species display a bifid stigma (cf. Fig. 4)









REAL JARDIN BOTANICO DE MADRID. HERBARIO MA  
*NEOTYPOS*

Revisado *Nario Fdez-Mazuecos* de 20.17

**Hortus Regius Matritensis (MA)**

**Scrophulariaceae**

*Linaria spartea* (L.) Chaz.

PORTUGAL: ALTO ALENTEJO: Montemor-o-Novo,  
38°38'22,7"N 8°13'45,1"W, 210 m, talud arenoso junto a senda,  
26-mar-2009, *M. Fernández-Mazuecos*, 18MF09.  
det. *M. Fernández-Mazuecos*

HERB. HORT. REG. MATRIT.  
911385  
MA



**Table 1.** Synoptic comparison of three major taxonomic treatments of taxa included in the Iberian clade of *Linaria* subsect. *Versicolores*.

<b>Viano (1978)</b>	<b>Sutton (1988), Sáez (2009)<sup>a</sup></b>	<b>This synopsis</b>
<i>L. algarviana</i>	<i>L. algarviana</i>	<i>L. algarviana</i>
<i>L. clementei</i>	<i>L. clementei</i>	<i>L. clementei</i>
<i>L. incarnata</i> p.p. <sup>b</sup>	<i>L. incarnata</i> p.p. <sup>b</sup>	<i>L. incarnata</i> <i>L. onubensis</i>
<i>L. viscosa</i> subsp. <i>salzmannii</i> <sup>c</sup>	<i>L. salzmannii</i> <sup>c</sup>	<i>L. becerrae</i>
	<i>L. viscosa</i> subsp. <i>viscosa</i>	<i>L. viscosa</i>
<i>L. viscosa</i> subsp. <i>viscosa</i>	<i>L. viscosa</i> subsp. <i>spicata</i>	<i>L. salzmannii</i>
	<i>L. viscosa</i> subsp. <i>crassifolia</i>	<i>L. spartea</i>
<i>L. spartea</i>	<i>L. spartea</i>	

<sup>a</sup>The only difference between these two treatments is that Sáez (2009) did not recognise *L. viscosa* subsp. *crassifolia* as distinct, pending further research.

<sup>b</sup>Viano (1978), Sutton (1988) and Sáez (2009) included North African populations (now *L. mamorensis*) in their concept of *L. incarnata*.

<sup>c</sup>Descriptions of *L. viscosa* subsp. *salzmannii* in Viano (1978) and of *L. salzmannii* in Sutton (1988) and Sáez (2009) are mostly based on plants now included in *L. becerrae*.