

RESEARCH ARTICLE

A new plant genus and species from south-eastern Spain: *Castrila latens* (Rubieae, Rubiaceae)

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Abstract A new genus and species, *Castrila latens*, native to the south-eastern Iberian Peninsula, is described here for the first time and compared with its closest relatives. The plant is characterized by being annual, glabrous, having reduplicate leaves in whorls of (5)6–7, inflorescences capitate and involucrate, corolla shortly hypocrateriform and white, with yellowish doliiform tube, stamens included, and ovary and mericarps densely papillose. An endemic plant, it grows on the calcareous mountains of the Sierra Seca, Sierra de Castril, and Sierra de la Cabrilla, between 1800 and 2100 m of elevation, in the Granada and Jaén provinces (eastern Andalusia, Spain). For this genus and species, a description, an illustration, a distribution map, the chromosome number, the assessment of the conservation status, an estimate of the breeding system, and the situation in the Rubieae phylogenetic tree are provided.

Keywords endemic plants; Iberian Peninsula; monospecific genus; paraphyly; phylogeny; taxonomy

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The tribe Rubieae Baill. (Rubiaceae) has a worldwide distribution with up to 1000 species in about 12 genera (Govaerts & al., 2021), which exhibit an enormous ecological diversity from tropical habitats, Mediterranean scrublands, and deciduous temperate forests to Arctic and alpine tundra. This is paralleled by considerable morphological diversity, with respect to life form, growth habit, leaves and stipules, inflorescences, flower and fruit morphology, and corresponding changes in pollination and dispersal ecology (Ehrendorfer & al., 2018).

Rubieae has been the subject of a number of molecular phylogenetic studies (e.g., Soza & Olmstead, 2010; Ehrendorfer & Barfuss, 2014; Ehrendorfer & al., 2018; Yang & al., 2018) that have helped researchers recognize the monophyly of the tribe, identify its main lineages, test hypotheses on the evolution of the morphological characters considered most relevant, and develop the possible biogeographical scenarios followed by its taxa. In general, the different studies are consistent in their results, although the identification of

the clades and subclades of Rubieae and the relationships between them have improved with the increased sampling of species and the number of molecular markers used. In addition, these studies have also shown the many problems of taxonomic and phylogenetic reconciliation still presented by some of its largest traditional genera, *Asperula* L. and *Galium* L., which are non-monophyletic.

According to Ehrendorfer & al. (2018), the tribe includes three major clades: the clade Kelloggiinae (one genus, *Kelloggia* Torr. ex Hook.f.); the clade Rubiinae (two genera, *Didymaea* Hook.f. and *Rubia* L.); and the most species-rich clade, Galiinae (the remaining nine genera included in this study). Within Galiinae, three clades were identified: *Asperula*, *Cymogalia*, and *Galium*. While the clade *Galium* contained exclusively species of *Galium*, the clade *Asperula* included members of *Galium* and the genera *Asperula*, *Callipeltis* Steven, *Crucianella* L., *Cruciata* Mill., *Mericarpea* Boiss., *Phuopsis* (Griseb.) Hook.f., *Sherardia* L., and *Valantia* L. *Asperula* was polyphyletic and most of the small genera were included in the different subclades formed by

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Galium and/or *Asperula* species. However, the small clades identified usually corresponded to recognized taxa (small genera or sections).

Yang & al. (2018), focusing on the clade Galiinae (referred to as *Galium* s.l.), with expanded sampling (especially of Chinese taxa) and using two nuclear and five plastid molecular markers, identified the three lineages cited by Ehrendorfer & al. (2018) but with a higher resolution within the clades *Asperula* and *Galium* (clade *Galium* s.str.). These authors treated the clade *Cymogalia* (most basally branching lineage with only one representative, *G. paradoxum* Maxim.) as a new genus, i.e., *Pseudogalium* L.E. Yang & al. The more thorough sampling and higher resolution achieved in that study suggested the non-monophyly of the sections described in *Galium* and provided phylogenetic placement of the monotypic genus *Micropophysa* Schrenk (not included in previous analyses).

Recently, Yang & al. (2022) carried out a biogeographical reconstruction of the tribe Rubieae based on a phylogeny including basically the same sequences as Yang & al. (2018), except that they expanded the sampling with some Australian and African species, as well as including other species of Rubiaceae as an outgroup to provide a family-level framework while considering *Didymaea* and *Rubia* as part of the ingroup. However, these authors did not consider *Kelloggia* to be part of the tribe Rubieae, but rather an outgroup. The authors distinguished five major clades: the clade *Didymaea* (with only *Didymaea*), the clade *Rubia* (only genus *Rubia*), the clade *Pseudogalium* (only genus *Pseudogalium*), the clade *Galium* (only species of the genus *Galium*), and the clade *Asperula* (the rest of the species of *Galium* and the remaining genera of the tribe).

The genera *Asperula* and *Galium* share similar morphological characters, being phylogenetically interdigitated and heterogenous (Chen & Ehrendorfer, 2011a,b), and therefore neither of the two genera is monophyletic (Natali & al., 1995; Ehrendorfer & al., 2005, 2018; Bremer, 2009; Soza & Olmstead, 2010; Ehrendorfer & Barfuss, 2014; Yang & al., 2018; Del Guacchio & Caputo, 2020). Because the current taxonomy of the tribe Rubieae does not reflect phylogenetic relationships, Ehrendorfer & Barfuss (2014) raised the need to accept paraphyletic taxa and discussed the pros and cons of taxonomic splitting versus lumping within the tribe. Ehrendorfer & al. (2018) advocated for moderate splitting, retaining the currently recognized small genera and adding new genera for the well-supported clades of *Galium* and *Asperula* (they predicted that in the future some 10 new genera could be segregated coinciding with recognized and molecularly supported sections). Indeed, this began to be a reality few years ago when Del Guacchio & Caputo (2020) raised three monophyletic sections of *Asperula* to generic rank to reconcile molecular results and morphological observations: *Cynanchica* P. Caputo & Del Guacchio, *Hexaphylla* (Klokov) P. Caputo & Del Guacchio, and *Thlipthisa* (Griseb.) P. Caputo & Del Guacchio.

In our fieldwork in eastern Andalusia (southern Spain), specifically around the Sierra Seca (municipality of Castril, northern Granada Province), we collected an undescribed

annual species of unknown identity, growing in therophytic grasslands on calcareous substrate. A preliminary identification, based on *Flora iberica* (Ortega-Olivencia & Devesa, 2007a,b), with reservations, led us to consider this plant as a species of the genus *Asperula*, i.e., *A. laevigata* L., whose closest areas lie in the north-eastern Iberian Peninsula and the Balearic Islands. However, the specimens did not resemble any species of *Galium* from the Iberian flora and only superficially resembled species of *Asperula* for having white hypocrateriform corollas, with the tube longer than the lobes, and with the ovary and fruit granulate. Moreover, *A. laevigata* is perennial, inhabits much lower elevations, and prefers non-calcareous substrates. In addition, a detailed comparison with *A. laevigata* revealed conspicuous morphological differences in both vegetative and floral features.

According to morphological characteristics, the two genera most closely related to the plant found in the Sierra Seca are *Asperula* and *Galium*. Both genera share many similar morphological characters, homoplasies and/or plesiomorphies, making it difficult to separate the two genera and, therefore, to assign many of the species to the correct genus, as reflected by the lack of agreement between traditional genus concepts and phylogenetic data (Natali & al., 1995; Ehrendorfer & al., 2005, 2018; Bremer, 2009; Soza & Olmstead, 2010; Chen & Ehrendorfer, 2011a,b; Ehrendorfer & Barfuss, 2014; Yang & al., 2018; Del Guacchio & Caputo, 2020). The two genera are conventionally distinguished by the presence of longer floral tubes in *Asperula* (note: several species of *Galium* have tubular-infundibuliform corollas, e.g., *G. boissierianum* (Steud.) Ehrend. & Krendl and *G. moralesianum* Ortega Oliv. & Devesa in *G. sect. Galium*), although in some species the tube is very short (e.g., corolla \pm rotate). Another distinguishing feature commonly used for differentiation is the frequent presence of bracteoles in *Asperula*. Although bracteoles are also found in many *Galium* species, they are only found on a few individual flowers and not in all the flowers of the same plant (e.g., *G. erythrorrhizon* Boiss. & Reut., *G. maritimum* L., *G. pulvinatum* Boiss., *G. talaveranum* Ortega Oliv. & Devesa, *G. tunetanum* Lam., etc.). In *Asperula*, the flowers are sessile or with pedicels shorter than the ovary, compared to *Galium*, in which the pedicels are often (but not always) longer than the ovary. Finally, in *Asperula*, the fruit, when hairy, does not have the hooked hairs that are common in *Galium*.

The genus *Asperula*, considered in a broad and traditional sense, includes mainly Eurasian species, reaching North Africa and extending into Australia and New Zealand, with the number of species varying according to the authors: 100–150 species (Ehrendorfer & al., 2005; Ortega-Olivencia & Devesa, 2007a); 192 species (Govaerts & al., 2021); or about 200 species (Pobedimova, 1978; Chen & Ehrendorfer, 2011a). The genus is represented by approximately 75 species and subspecies in the European flora (Ehrendorfer & Krendl, 1976), but only 10 species and subspecies are present in the Iberian Peninsula and Balearic Islands (Ortega-Olivencia & Devesa, 2007a).

The genus *Galium*, similarly considered in a broad sense, is by far the largest and most widespread genus within the tribe Rubieae, and includes more than 600 species (Chen & Ehrendorfer, 2011b; Yang & al., 2018) distributed worldwide, but with a strong representation in temperate regions. The genus is represented by 150 species and subspecies in the European flora (Ehrendorfer & al., 1976) and 60 species and subspecies in the Iberian Peninsula and Balearic Islands (Ortega-Olivencia & Devesa, 2007b; Blanca & al., 2021).

The plant, first collected in the Sierra Seca and Sierra de Castril (Granada Province) and then in the Sierra de la Cabrilla (Jaén Province), is characterized by being annual, glabrous, having reduplicate leaves in whorls of (5)6–7, inflorescences capitate and involucrate, corolla shortly hypocrateriform and white, with yellowish doliiform (barrel-shaped) tube, stamens included, and ovary and mericarps densely papillose. This combination of characters does not fit into either of the two genera mentioned above. Taking into account the great morphological differentiation as well as the reduced geographical distribution of this plant, and after reviewing the most major regional Floras from this area (e.g., Willkomm & Lange, 1865–1870; Willkomm, 1893; Tutin & al., 1976; Valdés & al., 1987; Devesa & al., 2007; Blanca & al., 2011; among others) as well as from other areas (e.g., Shishkin, 1958; Davis, 1982; Ehrendorfer & al., 2005; Fennane & al., 2014), we conclude that the Sierra Seca, Sierra de Castril and Sierra de la Cabrilla populations belong to a different taxon, which is described below as a new genus and species: *Castrila latens*. Its morphological characteristics, distribution and habitat are discussed, together with its breeding system, chromosome number, and its affinities in the Rubieae phylogenetic tree.

■ MATERIALS AND METHODS

Molecular analysis. — Samples of six individuals of *Castrila latens* were taken from two populations (Sierra de Castril and Sierra Seca, three individuals per population; see Appendix 1 for voucher accessions and geographic distribution of all specimens analysed). Total genomic DNA was extracted, using the CTAB method (Doyle & Doyle, 1987), from fresh leaves collected in the wild.

An initial analysis, to estimate the phylogenetic relationships of *Castrila latens* with the main clades within the tribe Rubieae, was implemented with the plastid sequences of the *atpB-rbcL* intergenic spacer (due to the higher availability of sequences in the nucleotide database), all taken from the GenBank database (accession numbers on the resulting tree; see Results section). Species of *Kelloggia* were used as outgroup on the basis of Ehrendorfer & al. (2018) and Yang & al. (2018). In total, the dataset contained 351 sequences. After establishing the relationship of *Castrila* with the clade *Galium* s.str., to avoid alignment ambiguities due to the large sequence divergences, we included species only from this clade in the rest of the analyses.

Plastid DNA for the intergenic spacers *rpl32-trnL* and *trnL-trnF*, and the *trnF* intron were amplified by polymerase chain reaction (PCR) in all six *Castrila latens* individuals. Taking into account the results of the initial analysis and those of Yang & al. (2018), these markers and *atpB-rbcL* were also amplified for three collections of three species representing clade II-E in Yang & al. (2018: fig. 1), and thus be able to have the whole set of markers combined in some of the species of this clade (*Galium cespitosum* Lam., *G. saxatile* L., *G. tenuissimum* M.Bieb.). *Callipeltis cucullaris* (L.) DC., *Pseudogalium paradoxum* (Maxim.) L.E. Yang & al., and *Sherardia arvensis* L. were selected as the outgroup for the phylogenetic analyses.

Accession numbers for the new sequences generated as part of this study are given in Appendix 1, while the accession numbers for the remainder are given on the phylogenetic trees.

PCR amplifications were conducted using primers Oligo 2 and Oligo 5 for *atpB-rbcL* (Manen & al., 1994), *rpl32-F* and *trnL(UAG)* for *rpl32-trnL* (Shaw & al., 2007), and primers C and F for the *trnL-trnF* region (Taberlet & al., 1991). PCR reactions were performed in 25 ml using the KAPA2G Robust HotStart ReadyMix PCR kit (Kapa Biosystems, Roche, Basel, Switzerland) and containing 12.5 ml of 5× KAPA2G Robust HotStart ReadyMix (1 U of KAPA2G Robust HotStart DNA Polymerase, 0.2 mM of each dNTP at 1×, 2 mM of MgCl₂ at 1×), 0.5 mM of each primer, and 50 ng of DNA. The amplification program consisted of an initial step of three minutes at 95°C followed by 30 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 30 s, plus a final extension step at 72°C for 5 min. Automated sequencing of the purified PCR products was performed by the sequencing service of Macrogen Spain (Madrid, Spain).

Nucleotide sequences were edited and aligned, using the Clustal algorithm, in the alignment editor BioEdit v.7.0.5.3 (Hall, 1999), and then adjusted by eye. The complete alignments are available as suppl. Appendices S1–S5.

Phylogenetic analyses were performed using Bayesian inference with MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003). Separate analyses were conducted on each plastid marker and on the combined plastid datasets in a single data matrix. When different accessions had the same sequence for a given species, only one was included. Ambiguous regions in the alignments were excluded from the analyses. Analyses were implemented using the best-fit nucleotide substitution model for each dataset (GTR + Γ). The model was selected using MrModeltest v.2.3 (Nylander, 2004) and the Akaike information criterion (Akaike, 1973). The analyses were based on two million generations with four simultaneous runs (16 Markov chain Monte Carlo chains) starting from random trees that were sampled every 100 generations. Tracer v.1.7 (Rambaut & al., 2018) was used to check the stationarity of the runs and the convergence between runs. The initial 25% of the trees were discarded as burn-in, and the remaining trees were used to build 50% majority-rule consensus trees.

Karyological analysis. — The chromosome number was counted at metaphase in root-tip meristems taken from

germinating seeds. Roots were pretreated with 8-hydroxyquinoline, fixed in ethyl alcohol–acetic acid (3:1), hydrolysed in 1 N HCl, stained in acetic orcein solution, and then flattened for light microscopy (Darlington & La Cour, 1969).

Morphology and conservation status. — Morphological observations and measurements of vegetative and reproductive parameters were undertaken on plant material kept at the herbaria GDA, HUAL, and UNEX, as provided in Appendix 1. For taxonomic identification and diagnostic characters, Spanish Floras and Floras from other territories, and specific scientific works (e.g., Shishkin, 1958; Ehrendorfer & al., 1976, 2005; Pobedimova, 1978; Ehrendorfer & Schönbeck-Temesy, 1980a,b, 1982a,b; Ortega-Olivencia & Devesa, 2004, 2007a,b, 2011; Chen & Ehrendorfer, 2011a,b; Ibn Tattou, 2014) were used. Additionally, other key features based on our field experience were included. The descriptive terminology follows Font Quer (2001) and Simpson (2020). To evaluate the conservation status of the new species we used the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee, 2024).

Breeding system. — The production of pollen grains and ovules was assessed in three populations and three flowers/population with the direct counting method. For each individual, we collected three floral buds near the anthesis, which were kept in 70% ethanol until laboratory examination. From each flower, we extirpated two anthers because the four anthers of the androecium were equal in size and shape. Each anther was split into its four pollen sacs and placed in a drop of lactophenol blue on a slide; they were squashed gently to spread the pollen. Grains were counted with the help of an eyepiece grid on a light microscope and a manual counter (López & al., 1999). Subsequently, we calculated the average number of pollen grains per anther and finally the total pollen grains per flower (multiplying by 4).

Pollen (P) and ovule (O) production per flower (only two ovules per ovary) were used to calculate the P/O ratio, and this ratio was used to classify the species according to the categories proposed by Cruden (1977). These categories are: cleistogamy (P/O = 4.7 ± 0.7), obligate autogamy (P/O = 27.7 ± 3.1), facultative autogamy (P/O = 168.5 ± 22.1), facultative xenogamy (P/O = 796.6 ± 87.7), and xenogamy (P/O = 5859.2 ± 936.5).

■ RESULTS

Phylogenetic analyses. — The six individuals of *Castrila latens* showed the same sequence for each molecular marker used, so only one representative of each of the two populations sampled was included in the analyses.

The initial phylogenetic analysis conducted with the *atpB-rbcL* sequences (351 sequences, 749 bp) positioned *Castrila latens* within the clade Galium, related to the taxa of *G. sect. Kolgyda* Dumort. s.l. (incl. sect. *Aspera* (Moench) Ledeb. according to Ehrendorfer & al., 2018), sect. *Microgalium* Griseb., and sect. *Leptogalium* Lange, with the

representative of *G. sect. Microgalium*, *G. tenuissimum* M.Bieb., being the most closely related (suppl. Fig. S1).

All analyses focusing on the clade Galium s.str. placed *Castrila* within a subclade together with species from the aforementioned sections, and *G. sect. Orientigalium* Ehrend. when the *trnL-trnF* region was considered. However, the relationship of *Castrila* to these species varied according to the marker used (suppl. Figs. S2–S4). Analysis of the *atpB-rbcL* region (140 sequences, 584 bp) resulted in the same relationship as the initial analysis, with *G. tenuissimum* being the sister taxon to *Castrila* (suppl. Fig. S2). With the *rpl32-trnL* spacer (69 sequences, 1029 bp), *Castrila* appeared as a basally branching lineage to the clade formed by species of *G. sect. Leptogalium*, while *G. tenuissimum* was related to *G. murale* (L.) All. (*G. sect. Kolgyda* s.l.) (suppl. Fig. S3). Finally, the *trnL-trnF* region (97 sequences, 1089 bp) offered the lowest resolution, with *Castrila* being part of a small, moderately supported group including *G. corsicum* Spreng., *G. pumilum* Murray, and *G. tenuissimum* (suppl. Fig. S4). In the combined analysis of the three plastidial markers (203 sequences, 2702 bp; Fig. 1, suppl. Fig. S5), the subclade of Galium s.str. in which *Castrila* is included exhibited very low resolution. *Castrila* was found to be part of a large polytomy, unrelated to any of the species included in the subclade (Fig. 1). In this subclade the relationships between the taxa of *G. sect. Kolgyda*, sect. *Leptogalium*, and sect. *Orientigalium* are poorly resolved, not being monophyletic and appearing scattered in the polytomy. *Galium tenuissimum* (*G. sect. Microgalium*) was part of this polytomy without being related to any of the species. The length of the *Castrila* branch is noteworthy, showing more sequence variation compared to the rest of the sampled taxa. A moderately well-supported group was formed by four annual species (*G. divaricatum* Lam., *G. murale*, *G. minutulum* Jord., *G. parisiense* L.) of *G. sect. Kolgyda* s.l. (sect. *Aspera* according to Ehrendorfer & al., 2018), but other species supposedly belonging to *G. sect. Aspera* remained either as part of the polytomy (*G. verticillatum* Danthoine ex Lam.) or as weakly related to species of *G. sect. Leptogalium* (*G. capitatum* Bory & Chaub.).

Morphology. — *Castrila* differs considerably in its morphological characters from all the above-mentioned sections (Table 1, suppl. Fig. S6), particularly in its smooth, glabrous and non-aculeolate stems, reduplicate leaves, capitate and involucrate inflorescence, shortly pedunculated and clustered cymes, shortly hypocrateriform corolla with doliiform tube, and included stamens (Figs. 2, 3). As shown in Table 1, with respect to the type of growth, the annual habit is shared only with the small *Galium* sect. *Microgalium* and sect. *Kolgyda* s.l. However, among other characters, in these two sections no capitate and involucrate inflorescences appear, and the corollas are cup-shaped or rotate, with the stamens exerted. On the other hand, the other two sections involved (*G. sect. Leptogalium* and sect. *Orientigalium*) host perennial species, with a great variety of types of inflorescences, their corollas vary from rotate, cup-shaped to infundibuliform, and the stamens are exerted.

Karyological analysis. — The chromosome number studied is $2n = 22$ (Fig. 3F), which is the most frequent in the tribe Rubieae (see Kiehn & Berger, 2023).

Breeding system. — In *Castrila latens* the total amount of pollen grains/flower varied within and between populations, with 1980–3060 in population 1, 2462–4404 in

population 2, and 2346–3386 in population 3. Consequently, the P/O ratio ranged between 990 and 1530, between 1231 and 2202, and between 1173 and 1693, respectively. At the species level, this ratio is 1396.67; therefore, according to Cruden (1977), these populations would present facultative xenogamy.

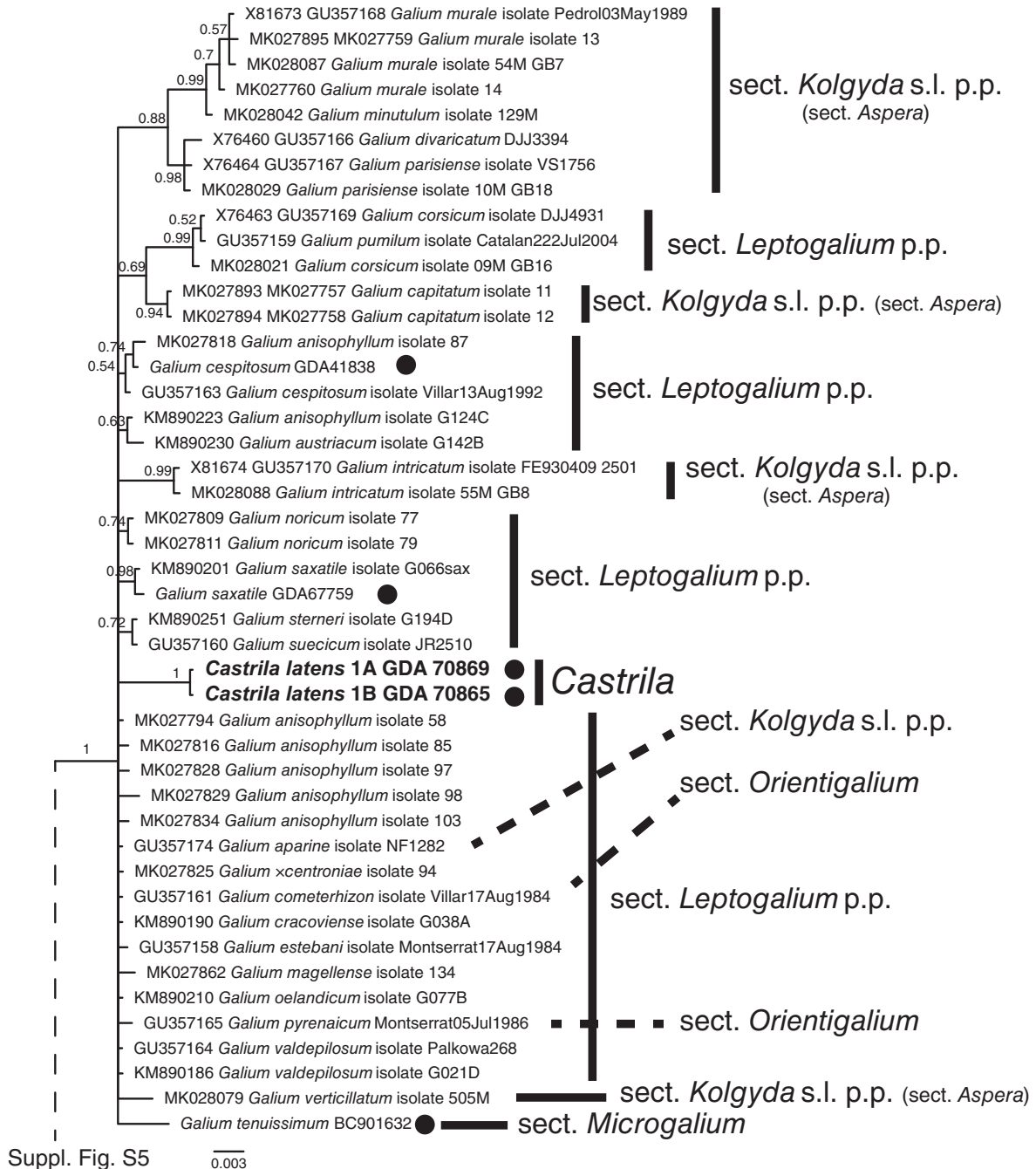


Fig. 1. Bayesian 50% majority-rule consensus tree inferred from the combined plastid data matrix of the clade *Galium* s.str. Only the group in which *Castrila* appears is shown; the rest of the tree can be seen in suppl. Fig. S5. Posterior probability values are shown above branches. The accession numbers (for the sequences taken from GenBank) are shown before each taxon name and collection/herbarium references (when available) are shown after each taxon name. Sequences generated in this study are marked with a dark circle (accession numbers in Appendix 1). Sectional classification and groupings are indicated on the right.

■ DISCUSSION

Knowledge about the diversity of our planet is increasing and new plant taxa are constantly being described, especially in areas less historically explored. Also, as a result of the phylogenetic research, some genera are newly created after nomenclatural combinations or changes to reduce the paraphyly of other old genera. However, it is more difficult to find

new genera from their discovery in the wild, especially in ostensibly well-sampled territories. The Iberian Peninsula is one of the two most species-rich areas of the Mediterranean Basin (Médail & Quézel, 1997), with almost a quarter of the area of the Mediterranean Basin biodiversity hotspot and nearly half of all European plants (Aedo & al., 2017; Buira & al., 2020). Within the Iberian Peninsula, the Baetic System, an area widely explored since ancient times, stands out for

Table 1. Main morphological characters of the genus *Castrila* and their comparison with those of the *Galium* sections located in the same clade.

Character	<i>G. sect. Microgalium</i>	<i>G. sect. Kolgyda</i> s.l.	<i>Castrila</i>	<i>G. sect. Leptogalium</i>	<i>G. sect. Orientalium</i>
Habit	Annual	Annual	Annual	Perennial	Perennial
Stems	4-angled, retrorsely aculeolate or retrorsely scabrid, rarely glabrescent to smooth	4-angled, retrorsely aculeolate, rarely smooth, glabrous or hairy	4-angled, smooth, glabrous	4-angled, hairy, smooth and glabrous or sometimes retrorsely aculeolate or papillose	4-angled, glabrous or hairy, never retrorsely aculeolate
Leaves (middle and upper)					
Arrangement	Whorls of (5)6–10	Whorls of (2)3–11	Whorls of (5)6–7	Whorls of 4–10(11)	Whorls of 4–8(9)
Shape	± flat, not or slightly revolute	± flat or sometimes revolute	Reduplicate	± flat or ± revolute, rarely recurved	± flat, rarely recurved or revolute
Inflorescence					
Shape	Lax, thyrsoid, ovoid to pyramidal, diffuse to intricate	Lax, pyramidal to oblong, (ob)ovoid or cylindrical	Capitate, involucrate	Eather lax, ovoid, oblong, pyramidal, corymbose or obovoid umbel	Ovoid to ± elongate, broadly pyramidal to very reduced corymbiform, subcapitate or subumbelate
Partial cymes	Few or moderately numerous flowers ± glomerate-capitate	Few-flowered or reduced to solitary, axillary flowers	Loose or clustered cymes	Corymbose, umbellate or reduced and few-flowered	Dense and few-flowered, subcapitate, dichasial, sometimes reduced to monochasial or solitary, axillary flowers
Calyx	Absent	Absent	Absent	Absent	Teeth usually absent, but sometimes persistent and enlarged in fruit
Corolla					
Shape	Cup-shaped or rotate	Usually rotate or cup-shaped	Shortly hypo-crateriform, with doliiform tube	Rotate	Infundibuliform, cup-shaped or rotate
Colour	Greenish-yellow, pale yellow, white or greenish-white	Reddish, pinkish, greenish, greenish-yellow, yellowish-red, yellowish-white, creamy, white, purplish or purplish-brown	White, with yellowish tube	Purple, pinkish, greenish, yellowish or white, sometimes pink tinted	White or pink, rarely yellowish, brownish, greenish or purple
Stamen attachment	Exserted	Exserted	Inserted	Exserted	Exserted
Mericaip surface	Smooth, glabrous, papillose, tuberculate, hairy, sometimes with hooked hairs	With patent hooked setae, uncinulate or ± hispid, papillose, microgranulate, mamilliferous or smooth	Densely and obtusely papillose	Acutely papillose or smooth, rarely hairy	Usually glabrous, smooth or finely granulate or papillose, more rarely with adpressed or spreading straight hairs

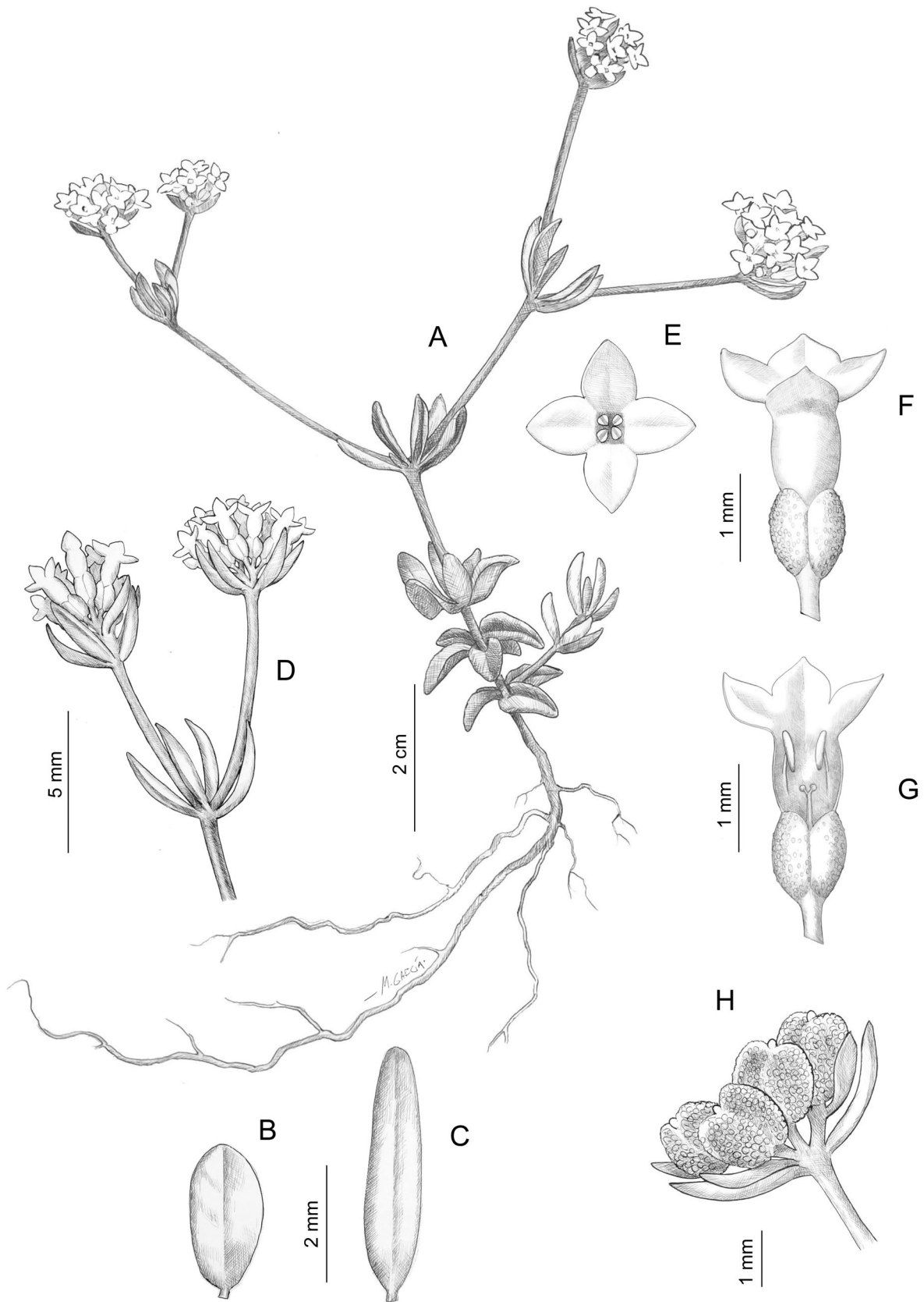


Fig. 2. *Castrila latens* (GDA 70863, holotype). **A**, General appearance; **B**, Basal leaf; **C**, Stem leaf; **D**, Inflorescence detail; **E**, Flower front view; **F**, Flower lateral view; **G**, Flower longitudinal section; **H**, Fruits. — Draw by Manuel García.

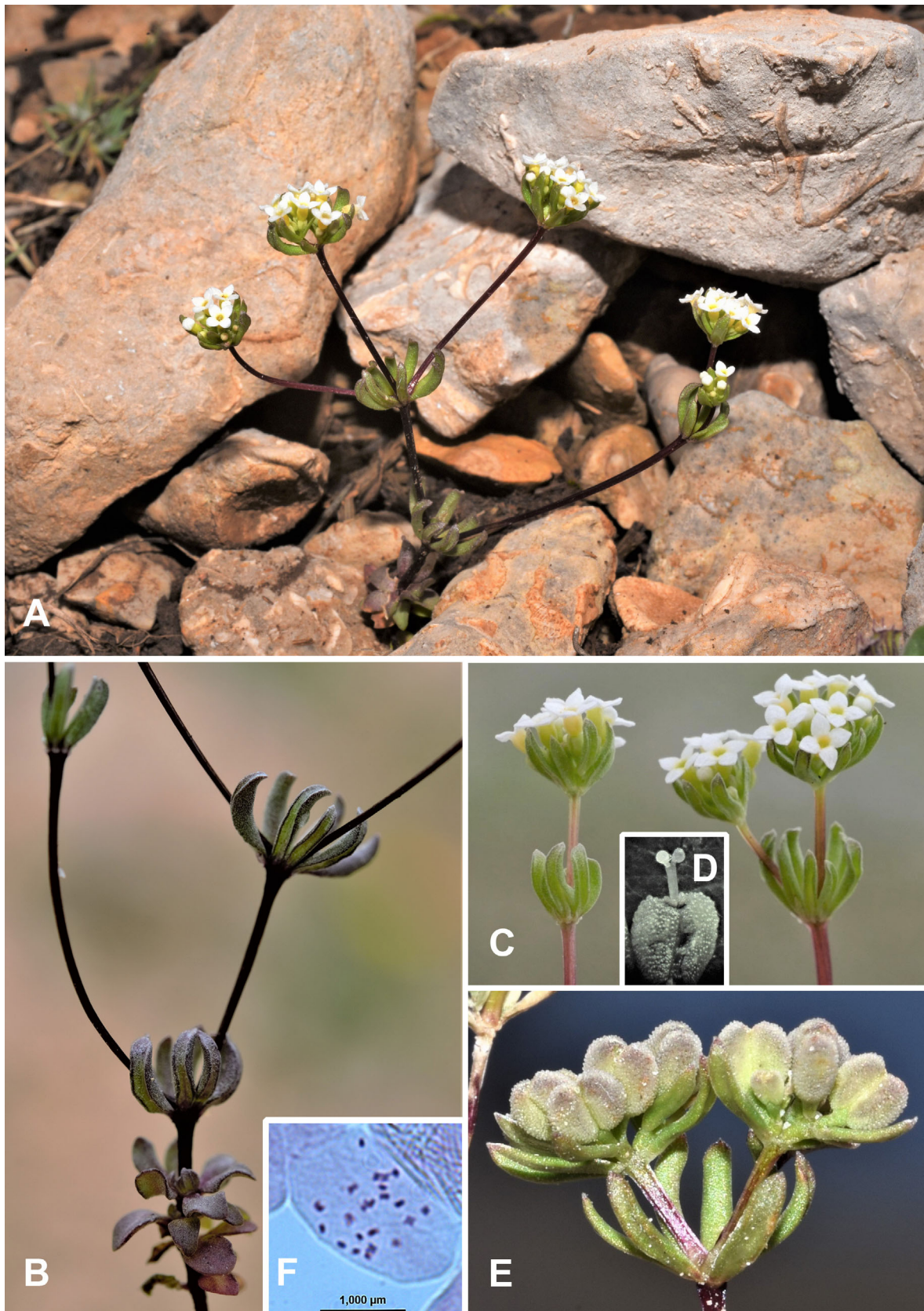


Fig. 3. *Castrila latens*. **A**, Habit; **B**, Leaves detail; **C**, Inflorescences detail; **D**, Ovary, style and stigmas; **E**, Fruits; **F**, Mitotic metaphase with $2n = 22$ chromosomes (Castril, Sierra Seca, GDA 70863). — Photos: A, D & E, Gabriel Blanca; B & C, Julián Fuentes; F, Víctor N. Suárez-Santiago.

having nearly 40% of all Iberian endemics (Buirea & al., 2017). How then did this new genus go unnoticed by botanists in this supposedly well-sampled territory? Probably, several factors interacted, such as: (1) the geographical isolation of the mountains which the plant inhabits (Sierra Seca, Sierra de Castril, Sierra de la Cabrilla), which are very difficult to access; (2) the predilection of botanists to visit and collect in other more emblematic mountains (e.g., Sierra Nevada, Sierra de Cazorla); (3) the small size of the flowers of the new species, which might have been easily confused, when viewed from above, with the tetrameric flowers of species from other families (e.g., Brassicaceae; the species in question blooms simultaneously with *Jonopsidium prolongoi* (Boiss.) Batt., appearing to be depauperate specimens). In just over six years, eastern Andalusia has given birth to two genera that do not come from nomenclatural combinations of pre-existing taxa, but from plant material not previously collected in nature: the genus *Gadoria* Güemes & Mota (Güemes & Mota, 2017) and the new one described here, *Castrila*.

Systematic relationships. — Our phylogenetic analysis places *Castrila* within the phylogenetic framework of Rubieae. The results clearly link *Castrila* to clade II sensu Yang & al. (2018) (clade III sensu Soza & Olmstead, 2010; clade VI sensu Ehrendorfer & Barfuss, 2014; clade Galium sensu Ehrendorfer & al., 2018; clade IV sensu Yang & al., 2022). To avoid confusion with the different denominations, we refer to it as clade Galium s.str. (as in Ehrendorfer & Barfuss, 2014; Yang & al., 2018). More specifically, *Castrila* is included in a group together with representatives of *Galium* sect. *Kolgyda* s.l., sect. *Leptogalium*, sect. *Microgalium*, and sect. *Orientigalium*. This group corresponds to the subclade B of Soza & Olmstead (2010), which included members of *G.* sect. *Kolgyda*, sect. *Leptogalium*, and sect. *Orientigalium*; with a subclade reported by Ehrendorfer & al. (2018: fig. 2; unnamed), formed by the annual species of *G.* sect. *Aspera* (this section is included in several Floras within the annual *G.* sect. *Kolgyda*; Ehrendorfer & al., 1976, 2005; Ehrendorfer & Schönbeck-Temesy, 1982a,b; Ortega-Olivencia & Devesa, 2007b), and several species of the perennial *G.* sect. *Leptogalium*; and with the subclade E in Yang & al. (2018), formed by species from the same aforementioned sections as well as the annual *G. tenuissimum*, which had not been sampled in previous studies.

According to the previous phylogenetic studies, the clade Galium s.str. is composed entirely of *Galium* species (*G.* sect. *Galium*, sect. *Hylaea* (Griseb.) Ehrend., sect. *Kolgyda* s.l., sect. *Leiogalium* (DC.) Ledeb., sect. *Leptogalium*, sect. *Microgalium*, sect. *Orientigalium*, and sect. *Trachygalium* K.Schum.), while the rest of the *Galium* species fall mainly into two subclades within the larger clade that includes *Asperula* species and the rest of the genera of the tribe (Soza & Olmstead, 2010; Ehrendorfer & Barfuss, 2014; Ehrendorfer & al., 2018; Yang & al., 2018). Members of the clade Galium s.str. are characterized by usually having one main vein, more than four leaf-like organs per whorl, pedunculated cymes, and rotate corollas (rarely funnel-shaped) (Ehrendorfer & Barfuss, 2014; Yang & al., 2018). Within the

clade Galium s.str. no other genus of Rubieae is described, but all small genera are included in the so-called clade *Asperula* by Ehrendorfer & al. (2018; clade III in Yang & al., 2018), making *Castrila* the first genus to split from this clade.

The relationship of *Castrila* to the species included in the subclade in which it occurs is not resolved, but it is part of a large polytomy together with species of non-monophyletic *Galium* sections. To classify a taxon with a rank higher than that of the taxa forming the group in which it is included can be controversial, as it renders the rest of the taxa paraphyletic and conflicts with the criterion of monophyly (Hörandl, 2006). However, it is known that many genera show a predominantly paraphyletic pattern (e.g., *Iberodes*, Otero & al., 2022). In fact, paraphyletic speciation has been indicated as common in groups showing recent local speciation (Rajakaruna, 2018; Otero & al., 2022). The recognition of small genera, several monotypic, with phylogenetic behaviour similar to *Castrila* is frequent in the tribe Rubieae (Soza & Olmstead, 2010; Ehrendorfer & Barfuss, 2014; Ehrendorfer & al., 2018; Yang & al., 2018; Del Guacchio & Caputo, 2020), and is justified on the basis of their monophyly and/or diagnosability due to their high morphological differentiation, despite being included in *Galium* or *Asperula* groups in the clade *Asperula* (Ehrendorfer & Barfuss, 2014; Ehrendorfer & al., 2018). Certainly, Ehrendorfer & Barfuss (2014) and Ehrendorfer & al. (2018), aligning with Hörandl (2006), Hörandl & Stuessy (2010), and numerous other researchers, acknowledged the numerous challenges in taxonomic and phylogenetic reconciliation within Rubieae. They endorsed the acceptance of paraphyletic taxa and advocated for a measured approach to splitting, supporting the retention of currently recognized small genera and the incorporation of new genera for well-supported clades of *Galium* and *Asperula*. According to its marked morphological differentiation, *Castrila* is easily diagnosable (see discussion on taxonomic characterization and genus key) and, in addition, differentiation of its sequences is highly pronounced with respect to the most closely related taxa, as shown by the great length of its branch.

Galium tenuissimum (*G.* sect. *Microgalium*) was the species most closely related to *Castrila* in the analyses made with each marker independently, appearing as a sister species to *Castrila* in the *atpB-rbcL* tree and forming part of the *Castrila* group together with *G. corsicum* and *G. pumilum* in the *trnL-trnF* tree. Yang & al. (2018) found *G. tenuissimum* as a sister group to a set of species of *G.* sect. *Leptogalium*; a relationship that is in line with the relationship suggested between the two sections by Ehrendorfer & Barfuss (2014), who proposed the perennial *G.* sect. *Leptogalium* as derived from the annual *G.* sect. *Microgalium* (embedded in many Floras within the *G.* sect. *Kolgyda*; e.g., Ehrendorfer & al., 1976, 2005; Ehrendorfer & Schönbeck-Temesy, 1982a,b). However, it should be noted that the relationship found by Yang & al. (2018) was based on only two plastid markers (*rpoB-trnC*, *trnC-psbM*), as the authors used only three plastid markers, out of the seven total, for *Leptogalium* species (the two mentioned and *trnL-trnF-ndhJ*; all obtained by Soza & Olmstead, 2010), and only

two matched the markers amplified in *G. tenuissimum* (the nuclear ribosomal markers ETS and ITS, and the plastid *rpoB-trnC*, *trnC-psbM*, *rps16* intron, and *atpB-rbcL*). Thus, the relationship between these two sections merits further investigation. Regarding *Castrila* and its relationship to *G. sect. Microgalium*, notable morphological differences and geographical separation suggest a lack of relationship (see below); however, our results with two of the three markers used indicate that *Castrila* should be considered in future studies attempting to decipher the relationships between *G. sect. Leptogalium* and *sect. Microgalium*.

Future analyses, incorporating phylogenomic approaches and/or utilising nuclear markers in conjunction with plastid markers, are likely to enhance our understanding of the evolutionary dynamics of the majority of species in the clade. This includes the identification of potential reticulation events that may explain morphological features observed in *Castrila*, some of which superficially resemble those in *Asperula*.

Taxonomic characterization. — The new genus *Castrila* can be distinguished morphologically from other genera of Rubiaceae, and more particularly from the genus *Galium*, by a combination of characters that includes its annual habit, non-aculeolate stems and leaves, reduplicate leaves, and type of corolla (Table 1, Figs. 2, 3). This latter character is one of the primary diagnostic characters of this new genus; observed from above, the corolla could give the impression of being rotate with patent lobes, but in lateral view it can be seen to have a doliiform tube larger than the lobes. We have found this type of corolla in no other species of *Galium*, and it may only superficially resemble the corolla of *Asperula fidanii* Eroğlu, recently described from south-eastern Anatolia (Turkey; Eroğlu, 2022). Therefore, the new genus appears to be molecularly embedded within sections of the genus *Galium*, but morphologically it shows more of an *Asperula* aspect.

Although the analysis of the *atpB-rbcL* region indicated that *Galium tenuissimum* (*G. sect. Microgalium*) is the sister taxon to *Castrila*, this species and *Castrila latens* are separated by a large geographical gap, since the distribution area of *G. tenuissimum* includes south-eastern Europe (Balkan Peninsula, Hungary), the Horn of Africa, and south-western and central Asia to north-western China (POWO, 2023). In addition, there are major morphological differences (see also Table 1 and suppl. Fig. S6), since *G. tenuissimum* has stems to 50(60) cm, intricate and divaricately branching from the base, and usually retrorsely aculeolate, leaves at middle stem region in whorls of (5)6–10, linear to oblanceolate, ± flat, not or slightly revolute, antrorsely aculeolate near margins and on veins abaxially, inflorescences broadly paniculate, very lax and loosely divaricate, pedicels capillate strongly elongating in fruit up to 20 mm and slightly reflexed, and corolla whitish, pale yellow, or greenish, rotate to slightly cup-shaped.

The species of *Galium* sect. *Kolgyda* s.l., which are also annual plants (see Table 1 and suppl. Fig. S6), are clearly separated by their flat or sometimes revolute leaves, lax inflorescences with few flowers or reduced to solitary, axillary, and usually rotate or cup-shaped corollas. Much more different

are the species of *G. sect. Leptogalium* and *sect. Orientigalium*, since they are perennial plants, with corollas infundibuliform, cup-shaped or rotate, among other characters (see Table 1 and suppl. Fig. S6).

To facilitate the identification of *Castrila*, a key is provided (see below) including the traditional sections of *Galium* and those of *Asperula*, recently dismembered, in the Mediterranean region.

Breeding system. — It is known that autogamous plants differ from other closely related xenogamous species mainly in the smaller size of the flower and its parts, as well as other characters such as the presence of funnelliform corollas cylindrical or closed, less contrasting floral colour patterns, reduced or absent nectaries, scentless flowers, no nectar guides, introrse anthers adjacent to stigma, fewer pollen grains, shorter pistil with style included, and stigma receptivity synchronous with anther dehiscence (Ornduff, 1969). Also, one of the principal adaptations of plant life in the Mediterranean region is an annual habit, and strongly associated with this habit is self-pollination (Zohary, 1997).

For several annual species with small and inconspicuous flower aggregates, selfing and autogamy have been documented in the family Rubiaceae, and more specifically in the genera *Galium* (e.g., *G. aparine* L., *G. setaceum* Lam., *G. spurium* L.), *Crucianella*, and *Cruciata* (Ehrendorfer, 1971; Chen & Ehrendorfer, 2011b). Given this background and the annual habit of the new species as well as the minute size of its flowers, we indirectly estimated its breeding-system data according to Cruden (1977). This author indicated that the P/O ratios are correlated with the breeding systems of plants, and consequently those with low P/O ratios would be considered autogamous.

Unexpectedly, the P/O results revealed that *Castrila latens* was facultatively xenogamous, indicating that it is regularly self-compatible and homogamous (Cruden, 1977). Given the characteristics of the flower and habit of the species, the expectation would have been to find a low P/O ratio (e.g., Cruden, 1977; Ortega-Olivencia & al., 1997; Amela García & al., 2014). In the flowers of this species, the globose stigmas either do not overlap with the anthers or they do so only in their lower third, so that a large number of pollen grains would fall by gravity onto the stigma or rub it directly, promoting self-pollination. However, the high pollen production per flower (1980–4404 grains) could be said to represent excessive energy expenditure to fertilize only two ovules/flower, so this high production could be interpreted as inviting pollen transfer between flowers or plants by small insects, which may mediate some outcrossing. In any case, caution must be exercised, as no pollinator observations or breeding experiments have been conducted in the field.

■ TAXONOMIC TREATMENT

Castrila Blanca, S.Ben-Menni, H.Blanca, Cueto, J.Fuentes, Ortega Oliv. & Suár.-Sant., **gen. nov.** — Type: *Castrila latens* Blanca & al.

Description. – Herbaceous annual, glabrous. Stems erect, simple or divaricate, delicate. Stem leaves in whorls of (5)6 or 7, sessile, uninervous, reduplicate. Inflorescences capitate, 1–3 on the top of the stems, involucrate, composed of shortly pedunculated and bracteolate cymes. Flowers hermaphrodite, tetramerous; calyx absent; corolla shortly hypocateriform, with tube doliiform, and lobes patent, triangular, obtuse, not apiculate, white. Stamens included, inserted near the base of the tube, with anthers linear, dorsifixed, yellow. Gynoecium with ovary papillose, topped in two globose stigmas. Mericarps ellipsoidal, densely papillose, blackish.

Castrila latens Blanca, S.Ben-Menni, H.Blanca, Cueto, J.Fuentes, Ortega Oliv. & Suár.-Sant., **sp. nov.** – Holotype: SPAIN. Granada Province: Castril, Sierra Seca, entre Morra de la Laguna y Cueva Tocino, pastizales terofíticos en sustrato calizo, 30SWG2799, 1980 m, 4 Jun 2020, *J. Fuentes s.n.* (GDA barcode GDA-Fanero 70863!).

The new species is illustrated in Figs. 2 and 3.

Description. – Annual plant, glabrous, non-aculeolate, with thin roots and without underground stolons. Stems 2.3–6 cm long, erect, 4-angled, smooth, brownish or reddish-purplish; nodes 5 or 6, lowest internodes 0.5–3.5 mm long, generally shorter than or subequal to the leaves. First leaves (cotyledons) 2, 2.3–3.8 × 0.8–1.8 mm, reflexed or patent, ovate or oblong, flat, pinnately veined, obtuse, emarginate, glabrous, brown or violaceous, shortly petiolate, with petioles 0.5–0.9 mm long. Basal leaves 2–4/node, similar or

unequal (sometimes two narrower in the same node), 1.3–3.4 × 0.8–1.9 mm, generally patent, ovate, obovate or suborbicular, flat, uninervous, obtuse, glabrous, brown or greenish-brown, cuneate and shortly petiolate, with petiole up to 0.9 mm long. Stem leaves (5)6 or 7/node, (1.9)3.3–6.4 × 0.4–1.1 mm, much shorter than the internode, erect-arched towards the internode, linear-oblongate, reduplicate, acute, sometimes mucronate, glabrous, green, sessile. Inflorescences capitate, 0.3–0.8 cm in diameter, involucrate, with (2)3–14 (17) flowers, composed of shortly pedunculated cymes (peduncles 1.5–3.8 mm long), loose or densely clustered. Involucral bracts leaf-like, (4)6 or 7/node, free, 2.4–4.8 × 0.4–0.9 mm, arched-introrse, linear or linear-oblongate, generally reduplicate or less frequently flat, uninervous, acute, sessile, glabrous; cyme bracts similar in size or larger than the flowers. Bracteoles scarce, 2–2.3(3.5) × 0.35–0.8 mm, free, sometimes surpassing the flowers, linear, oblong or oblongate, flat, acute, glabrous. Flowers tetramerous (rarely trimerous), pedicellate. Pedicels 0.3–1 mm long (up to 1.3 mm long at fruiting), smooth. Corolla 1.3–2.1 mm long, shortly hypocateriform; tube 0.6–1.1 × 0.5–0.6 mm, contracted at the base and under the lobes (doliiform), swollen, at first greenish and then yellowish; lobes 0.4–0.8 mm long, patent, triangular, welded at the base above the constriction of the tube, obtuse, not apiculate, glabrous, papillose on the adaxial face, white. Stamens included, with anthers 0.3–0.5 × 0.1 mm, linear, dorsifixed, yellow, and filiform filaments inserted ca. 0.3 mm above the base of the tube.

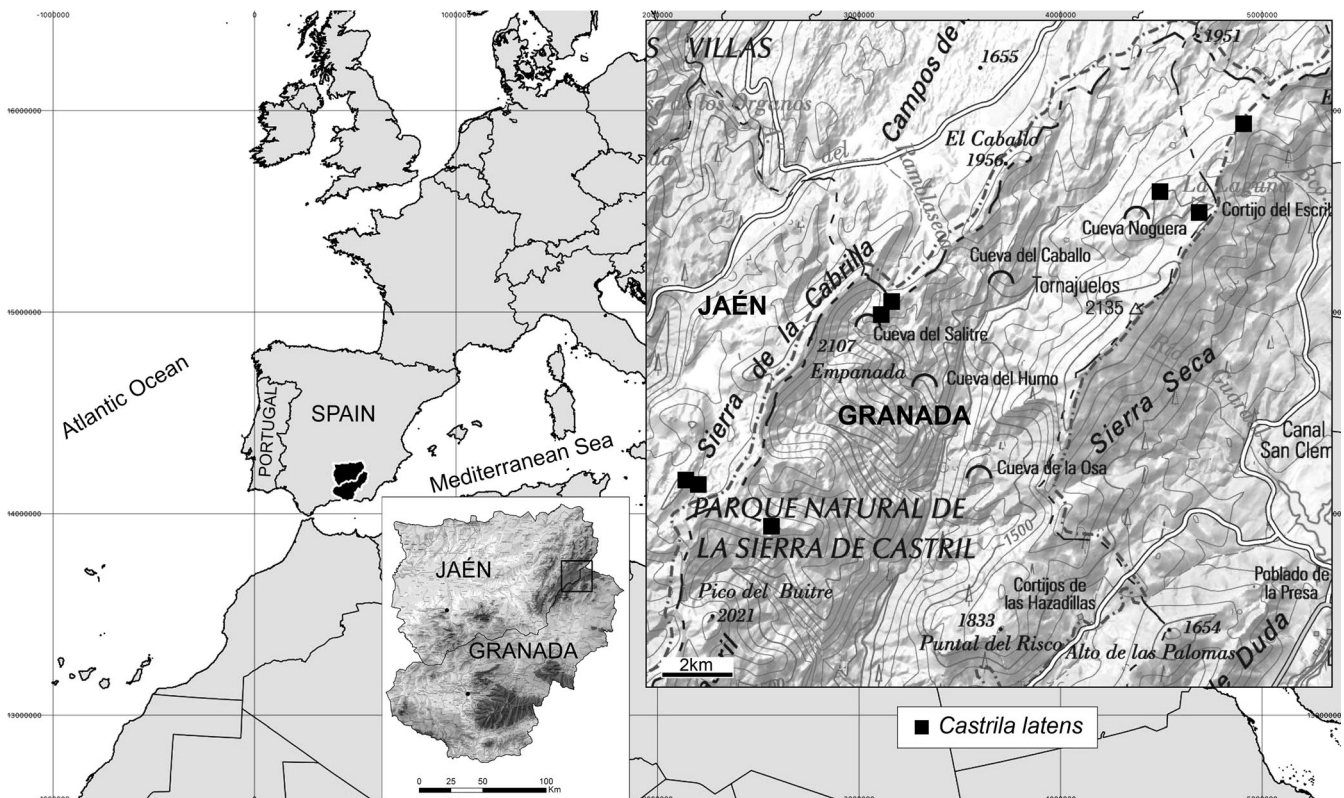


Fig. 4. Geographic distribution of *Castrila latens*.

Gynoecium with ovary 0.7–1.1 mm long in anthesis, papillose; style 0.1–0.4 mm long, topped in two globose stigmas. Mericarps 1.5–2.1 × 0.5–0.8 mm, ellipsoidal, papillose.

Etymology. – The genus name refers to the municipality of Castril (Granada Province, eastern Andalusia, south-eastern Spain) where the species was first found. The specific epithet “latens” comes from Latin, meaning “hiding” or “escaping notice”, because of the difficulty of detecting this plant in the field, mainly due to its small size, its mimicry with depauperate specimens of other tetramerous species and its brief flowering period.

Distribution and ecology. – *Castrila latens* should be considered an endemic species from the south-eastern Iberian Peninsula (Fig. 4), growing in ephemeral therophytic pastures of calcareous mountains, in the northern part of Granada Province (Sierra Seca, Sierra de Castril), and closely bordering areas in the province of Jaén (Sierra de la Cabrilla), both provinces of the Autonomous Community of Andalusia (Spain). Here it grows on poorly developed, stony soils between 1800–2100 m a.s.l., under an oromediterranean thermotype and a dry or sub-humid ombrotype (according to the terminology of Rivas-Martínez & al., 2017).

Phenology. – The flowering period spans mid-May to June, and fruiting time is in June to early July.

Additional specimens (paratypes). – See Appendix 1.

Conservation status. – The distribution area of *Castrila latens* is encompassed partially by the Sierra de Castril Natural Park (province of Granada), and the Sierra de Cazorla, Segura y las Villas Natural Park (province of Jaén), which were established in 1989 and 1986, respectively, so it has the protection that the Andalusian regional government established for natural parks. In addition, the Sierra Seca is included in a “Special Area of Conservation” (SAC) and therefore is part of a protected area of the Nature 2000 Network, preserved by European directive.

According to the IUCN categories and recommendations provided by the IUCN Standards and Petitions Committee (2024), we suggest labelling *Castrila latens* as Endangered (EN), according to the following criteria: B1ac(i,ii,iii) + 2ab (iii,iv)c(i,ii,iii). Further monitoring of the known populations is recommended for a more accurate evaluation of the conservation status of this newly described species. *Castrila latens* may require conservation measures and a management plan, and therefore it should be included in the Andalusian and Spanish Red Lists of vascular plants (i.e., Cabezudo & al., 2005 and Bañares & al., 2008, respectively).

Key to genera (*Asperula-Galium* complex including *Castrila*, *Cynanchica*, *Hexaphylla*, *Thliphthisa* and sections of *Galium*) in the Mediterranean Region

1. Annual plants2
1. Perennial plants, herbaceous or suffruticose4
2. Herbs with internodes retrorsely aculeolate or retrorsely scabridulous, at least at the base, if smooth then mericarps with hairs hooked, uncinulate or straight
 - *Galium* sect. *Kolgyda* s.l., sect. *Jubogalium* p.p. and sect. *Microgalium*

2. Herbs with internodes not retrorsely aculeolate; mericarps without hairs3
3. Involucral bracts ciliate-setose on the margins; corolla hypocrateriform, bright blue, bluish-violet or whitish; mericarps smooth, papillose or finely granulate; cauline leaves flat or ± revolute, non-reduplicate
 - *Asperula* s.str. (*A.* sect. *Asperula*)
3. Involucral bracts glabrous; corolla shortly hypocrateriform, white, with tube doliiform, at first greenish and then yellowish; mericarps papillose; cauline leaves reduplicate *Castrila*
4. Flowers 3-merous5
4. Flowers 4-merous6
5. Stems not retrorsely aculeolate; leaves 4–6(7) per whorl, ± 3-veined; mericarps granulate
 - *Asperula* sect. *Glabella* p.p.
5. Stems retrorsely aculeolate; leaves 4 per whorl, 1-veined; mericarps smooth *Galium* sect. *Aparinoides* p.p.
6. Leaves 4 per whorl, or opposite and sometimes with two vestigial minor stipules7
6. Leaves 4–10(12) per whorl9
7. Leaves 3-veined, sometimes inconspicuously, with swollen epidermal glands on the distal underside
 - *Galium* sect. *Platygalium*
7. Leaves 1–3-veined, without swollen epidermal glands on the distal underside8
8. Leaves 1- or 3-veined, generally reticulate, obtuse or with a very short cartilaginous point; flowers white or pale yellowish, sometimes tinged with pink or pale lilac to lilac-blue, smooth outside; ovary and fruit glabrous, smooth, papillose or granulate
 - *Asperula* sect. *Glabella* p.p.
8. Leaves 1-veined, with a hyaline apex or awn; flowers purplish, reddish, yellowish, pinkish, whitish or white pinkish, hairy, papillose or smooth outside; ovary and fruit papillose to tuberculate, rarely smooth or hairy
 - *Cynanchica*
9. Ovary and fruits with uncinulate hairs (0.5)0.6–1.3 mm; corolla infundibular or campanulate, whitish or greenish *Galium* sect. *Hylaea*
9. Ovary and fruits without uncinulate hairs, if with this type of hairs then up to 0.5 mm; corolla rotate, crateriform, infundibular, tubular-infundibuliform or subcampanulate, white, yellowish, pink, lilac, reddish, greenish or purple10
10. Partial inflorescences capituliform, globose or glomerular; corolla tubular-infundibuliform, infundibuliform or subcampanulate, never rotate; flowers sessile or subsessile11
10. Partial inflorescences not capitate, not globose, rarely glomerular; corolla mostly rotate, cup-shaped, crateriform to infundibular; flowers generally with pedicels, rarely sessile12
11. Leaves 6(7) per whorl; corolla purple, lilac to pink or white; mericarps glabrous, tuberculate or smooth, rarely hairy *Hexaphylla*

11. Leaves 6–10 per whorl; corolla yellowish or yellowish-brown; mericarps hirsute or pubescent, rarely glabrous.....*Galium* sect. *Galium* p.p.
12. Partial inflorescences with bracts and bracteoles; corolla cup-shaped to infundibuliform, purplish, reddish, brownish, greenish, or whitish, if rotate then bracts keeled and ciliate at margins or with leaves caducous; ovary and mericarps oblong, truncate at apex, glabrous and ± granulate, rarely hairy; leaves (4)6–8 per whorl*Thliphthisa*
12. Partial inflorescences with bracts, rarely with bracteoles and these not keeled or ciliated on the margins; corolla mostly rotate, less often ± crateriform, campanulate or infundibular, yellowish, greenish, reddish, purplish, pinkish or white; ovary and mericarps oblong, ovoid, subglobose or reniform, not truncate at apex, with surface smooth, granulate, rough, papillose, hispidulous or villous, sometimes somewhat fleshy, rarely with a commissural groove covered with yellowish glandular tissue; leaves 4–12 per whorl.....*Galium* sect. *Galium* p.p., sect. *Trachygaliu*m, sect. *Leiogaliu*m, sect. *Orientalgaliu*m, sect. *Leptogaliu*m and sect. *Jubogaliu*m p.p.

■ CONCLUSIONS

Tiny plants collected for the first time in nature during 2020–2022 in therophytic grasslands from mountainous areas of south-eastern Spain were deemed a species of the tribe Rubiaceae. Especially due to the type of corolla, the plants superficially resembled a species of *Asperula*. After taxonomic scrutiny, these plants were identified as a new species of that tribe, but they failed to fit into *Asperula* or its related genus *Galium*. The combination of morphological characters, the most important of which are the leaves reduplicate erect-arched, inflorescences capitate and involucrate, and corolla shortly hypocrateriform with tube doliiform, led to it being considered as a new genus, *Castrila*. Phylogenetic analyses, based on plastid markers, placed *Castrila* within the clade *Galium* s.str., in a subclade together with representatives of the annual *G.* sect. *Kolgyda* s.l., and species of *G.* sect. *Leptogaliu*m, sect. *Microgaliu*m, and sect. *Orientalgaliu*m. Future phylogenomic analyses are likely to unveil novel insights within that clade. The generic status of the new taxon might be reconsidered, despite the robust morphological distinctions observed in *Castrila* compared to the currently known species of the genera *Galium* and *Asperula*. Finally, the new taxon, confined to a few limestone montane zones of the Andalusian Baetic System, had remained unnoticed until now. The global conservation assessment conducted classifies the new species, *C. latens*, as Endangered (EN).

■ AUTHOR CONTRIBUTIONS

GB, MC, and JF found the plant and collected the samples. GB, MC, AOO and VNSS designed the study and undertook much of the

research, discussion, and analyses. HB and SBMS did the lab work. AOO prepared the genera key. GB, AOO and VNSS wrote the initial manuscript; all authors contributed to its completion.

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Appendix 1. Selected material studied: Voucher information, sequence accession numbers and populations studied to estimate breeding systems.

Taxon, country, political subdivision, locality, ecology, coordinates, altitude, date, collector (herbarium code and herbarium accession number or barcode), *atpB-rbcL*, *rpl32-trnL*, *trnL-trnF*, population for breeding system study.

Castrila latens* (paratypes)**, Spain, Granada, Castril, Sierra de Castril, entre Nava de los Troncos y Loma Alta, laderas calizas junto a dolinas, pastizales terofíticos en calizas, orientación norte y noroeste, 30SWG1692, 1950 m, 2 Jun 2022, *J. Fuentes & L. Gutiérrez s.n.* (GDA barcode GDA-Fanero 70864); Spain, Granada, Castril, Sierra Seca, entre Cerro La Laguna y Collado de los Tornajuelos, pastizales terofíticos de alta montaña, desarrollados en zonas de guijaral, sustrato calizo y calizo-dolomítico, 30SWG2798, 2000 m, 28 May 2021, *G. Blanca, J. Fuentes & A. Ortega s.n.* (GDA barcode GDA-Fanero 70865), PP297887, PP297892, PP297897 (UNEX No. 38089), population 2; Spain, Granada, Castril, Sierra Seca, Hoya de la Sabina, Parque Natural Sierra de Castril, pastizales terofíticos de alta montaña en orientación Norte, desarrollados en calizas, 30SWG2799, 1900 m, 23 May 2020, *J. Fuentes, J.M. Ortega & A. Delgado s.n.* (GDA barcode GDA-Fanero 70866); Spain, Granada, Castril, Sierra Seca, Parque Natural Sierra de Castril, Cueva del Tocino, pastizales terofíticos de alta montaña en orientación Noreste, desarrollados en sustratos calizos, 30SWG2799, 2000 m, 23 May 2020, *J. Fuentes, A. Delgado & J.M. Ortega s.n.* (GDA barcode GDA-Fanero 70867); Spain, Granada, Huéscar, carril entre Peña Vaquera y El Chaparral, litosuelos en zonas pedregosas, 1880 m, 21 Jun 2021, *G. Blanca, & M. Cueto s.n.* (HUAL barcodes HUAL 30043, HUAL 30044, HUAL 30045); Spain, Granada, Huéscar, Sierra Seca, entre Cruz de Marranero y El Chaparral, pastizales terofíticos de alta montaña en taludes y pedregales, sustrato calizo y calizo-dolomítico, 30SWH2800, 1880 m, 28 May 2021, *G. Blanca, J. Fuentes & A. Ortega s.n.* (GDA barcode GDA-Fanero 70868), (UNEX No. 38090), population 3; Spain, Granada, Sierra Seca, ca. Cueva Tocino, 1980 m, 28 May 2021, *G. Blanca, J. Fuentes & A. Ortega s.n.* (GDA barcode GDA-Fanero 70869), PP297888, PP297893, PP297898 (UNEX No. 38088), population 1. Spain, Jaén, Cazorla, Sierra de la Cabrilla, Nava de los Troncos, laderas de montaña en orientación noroeste, formando parte de pastizales terofíticos, 30SWG1692, 1960 m, 2 Jun 2022, *J. Fuentes & L. Gutiérrez s.n.* (GDA barcode GDA-Fanero 70870); Spain, Jaén, Sierra de la Cabrilla, en el límite provincial con Granada, entre Nava de los Troncos y Picón del Durillo, pastizales terofíticos sobre calizas, orientación noroeste, 30SWG1692, 1903 m, 2 Jun 2022, *J. Fuentes & L. Gutiérrez s.n.* (GDA barcode GDA-Fanero 70871). ***Galium cespitosum Lam., Spain, Huesca, Sallent de Gállego, ibones de Anayet, pastos malos y pedregosos silíceos, 30TYN0939, 2330 m, 20 Jul 1997, *I. Aizpuru s.n.* (GDA barcode GDA-Fanero 41838), PP297891, PP297896, PP297901. ***Galium saxatile*** L., Spain, La Coruña, Cedeira, parque eólico La Capelada, Sierra de La Capelada, prados sobre sustratos ultrabásicos, 497 m, 20 Jul 2017, *C. Quesada, M.T. Vizoso & P. Sánchez s.n.* (GDA barcode GDA-Fanero 67759), PP297889, PP297894, PP297899. ***Galium tenuissimum*** M.Bieb., Armenia, Vayoc Jor, Vajk Distr., ca. 2 km SE Vajk, gorge at road to Zaritap, shibliak communities, 39°40'N 45°31'E, 1330 m, *G. Fayvush & al. s.n.* (BC barcode BC 901632), PP297890, PP297895, PP297900.