

RESEARCH ARTICLE

A revised classification of Rubiaceae subfamily Rubioideae tribe Rubieae*

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Abstract In its current circumscription, Rubiaceae subfam. Rubioideae tribe Rubieae consists of 18 genera, i.e., *Asperula*, *Callipeltis*, *Castrila*, *Crucianella*, *Cruciata*, *Cynanchica*, *Didymaea*, *Galium*, *Hexaphylla*, *Kelloggia*, *Mericalpaea*, *Microphysa*, *Phuopsis*, *Pseudogalium*, *Rubia*, *Sherardia*, *Thliphthisa* and *Valantia*. It had long been recognized that the separation of *Asperula* with long corolla tubes from *Galium* with short corolla tubes is highly artificial, and indeed already the earliest molecular phylogenetic studies, confirmed by several studies since, could demonstrate the nonmonophyly of both *Asperula* and *Galium*. The combination of molecular phylogenetic studies based on several plastid DNA regions and partly also on nuclear ribosomal ITS and ETS, as well as sampling all genera of the tribe and all sections of *Asperula* and *Galium*, resulted in a widely resolved and well-supported phylogenetic tree. The morphological homogeneity and distinctness of most of the clades identified allow us to propose a robust reclassification of Rubieae in which only monophyletic groups are recognized. In addition to the genera listed above (except for *Castrila*, which is included in *Galium* s.str.), we here recognize *Cruciana* stat. nov. (for *Asperula* sect. *Cruciana*), *Hydrogalium* gen. nov. (for *Asperula* sect. *Dioicae*, A. sect. *Glabella* and *Galium* sect. *Aparinoides*), *Hamogalium* gen. nov. (for *Galium* sect. *Depauperata*), *Jubogalium* stat. nov. (for *Galium* sect. *Jubogalium*), *Altaiogalium* gen. nov. (for *Galium paniculatum*), and *Trichogalium* (for *Galium* sect. *Platygalium*) as additional segregate genera of *Asperula* and *Galium*. These 23 genera fall into three subtribes, i.e., Kelloggiinae (containing *Kelloggia*), Rubiinae (containing *Didymaea* and *Rubia*) and Galiinae subtr. nov. (containing the remaining genera). An unsampled lineage of Galiinae, sometimes recognized as *Leptunis*, which may have to be recognized at generic rank, is briefly discussed. Brief descriptions of all genera are provided and altogether 293 new combinations of species are made.

Keywords corolla tube length; Friedrich Ehrendorfer; homoplasy; monophyletic classification; paraphyly; polyphyly

■ INTRODUCTION

By containing approximately 14,000 species, Rubiaceae is the fourth-largest family of flowering plants (Razafimandimbison & Rydin, 2024a). In this largely tropical and subtropical family, tribe Rubieae is the only cosmopolitan lineage and the only lineage centred in temperate regions (Soza & Olmstead, 2010a and references therein). Following Bordbar & al. (2022) and Razafimandimbison & Rydin (2024a), Rubieae are part of the Spermacoceae alliance in subfam. Rubioideae, where they are sister to tribe Aitchisonieae, containing only one species (*Aitchisonia rosea* Hemsl. ex Aitch.) from south-central Iran to Pakistan. The distinction of Aitchisonieae from Rubieae has been discussed in detail by Bordbar & al. (2022). Whereas the circumscription of Rubieae is consolidated, a comprehensive generic classification based on phylogenetic principles is still lacking.

In the circumscription by Ehrendorfer & al. (2018), Rubiaceae-Rubieae consist of 13 genera, i.e., *Asperula* L., *Callipeltis* Steven, *Crucianella* L., *Cruciata* Mill., *Didymaea* Hook.f., *Galium* L., *Kelloggia* Torr. ex Benth. & Hook.f., *Mericalpaea* Boiss., *Microphysa* Schrenk, *Phuopsis* (Griseb.) Hook.f., *Rubia* L., *Sherardia* L., and *Valantia* L. It had long been recognized (Ehrendorfer, 1958) that the separation of *Asperula* with long corolla tubes from *Galium* with short corolla tubes, a separation which has been contentious for a long time, is highly artificial, and that accordingly the two genera may not be monophyletic. This could be confirmed by the first molecular phylogenetic studies of the tribe by Manen & al. (1994) and Natali & al. (1995), and all later molecular phylogenetic studies could demonstrate that subclades of *Asperula* and *Galium* are scattered across the phylogenetic tree of Rubieae (Soza & Olmstead, 2010a; Ehrendorfer & al., 2018; Yang & al., 2018, 2022).

*This paper is dedicated to the memory of Friedrich Ehrendorfer (26 July 1927–28 November 2023)

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If classification is to be phylogenetic, a claim made since Darwin (1859) according to Stuessy (2009), it needs to reflect phylogeny and recognize formally only those groups that are monophyletic (for opposing views on this, see Schmidt-Lebuhn, 2012 vs. Stuessy & Hörandl, 2014). On this background, Ehrendorfer & al. (2018) emphasized the need to account for phylogenetic relationships in the generic classification of Rubieae. No reclassification of the entire tribe was presented by Ehrendorfer & al. (2018), but Yang & al. (2018) raised *Galium* sect. *Cymogalium* Pobed. to generic rank as *Pseudogalium* L.E Yang & al., and Del Guacchio & Caputo (2020) introduced the genera *Cynanchica* P.Caputo & Del Guacchio, *Hexaphylla* (Klokov) P.Caputo & Del Guacchio and *Thliphthisa* (Griseb.) P.Caputo & Del Guacchio for *Asperula* sect. *Cynanchicae* DC. ex Boiss., sect. *Hexaphylla* Klokov and sect. *Thliphthisa* (Griseb.) Ehrend., respectively. Finally, the monospecific genus *Castrila* Blanca & al. has recently been described by Blanca & al. (2024). All the above genera were recognized as members of Rubieae by Razafimandimbison & Rydin (2024a,b) with the exception of *Cynanchica*. This likely is an accidental omission, as Razafimandimbison & Rydin (2024b) refer to Del Guacchio & Caputo (2020) without an indication of disagreement with their treatment. Consequently, Rubieae contains the genera *Asperula*, *Callipeltis*, *Castrila*, *Crucianella*, *Cruciata*, *Cynanchica*, *Didymaea*, *Galium*, *Hexaphylla*, *Kelloggia*, *Mericarpaea*, *Microphysa*, *Phuopsis*, *Pseudogalium*, *Rubia*, *Sherardia*, *Thliphthisa* and *Valantia*.

The studies by Soza & Olmstead (2010a), Ehrendorfer & al. (2018) and Yang & al. (2018) were jointly based on six plastid regions (*atpB-rbcL*, *rpl32-trnL* spacer, *rpoB-trnC*, *trnC-psbM*, *trnL-trnF-ndhJ*, *rps16*) as well as nuclear ribosomal ITS and ETS, and, jointly, all genera of the tribe and all sections of *Asperula* and *Galium* were sampled. The only exception to this is *Leptunis* Steven, a lineage of possibly one species only (Ehrendorfer & Barfuss, 2014; Ehrendorfer, 2017). This lineage will be briefly discussed below. Although the number of molecular markers used in the above studies is rather small, congruency in the recognition of major clades (although not necessarily their relationships to each other) among these studies, in combination with their morphological homogeneity and distinctness in most cases, leads us to conclude that the evidence available is strong enough to support a robust reclassification of Rubieae, as implied by Ehrendorfer & al. (2018) when indicating their preference for moderate splitting.

By proposing a new classification for Rubieae we intend to conclude and honour the life-long work of Friedrich Ehrendorfer (1927–2023) on *Galium* and its relatives.

■ MATERIALS AND METHODS

The new classification of Rubieae presented here is based mainly on the results of molecular phylogenetic studies by Soza & Olmstead (2010a), Ehrendorfer & al. (2018), and Yang & al. (2018); other phylogenetic evidence used is

referred to in the text. Of the core studies we rely on, Soza & Olmstead (2010a) and Ehrendorfer & al. (2018) used only plastid data, while the phylogenetic tree presented by Yang & al. (2018) is based on combined plastid and nuclear (ITS/ETS) sequences; ETS sequence data were also used by Soza & Olmstead (2010b), but in this study the focus was on New World *Galium* sect. *Platygalium* W.Koch with accordingly sparse sampling outside this group.

We acknowledge that relying mainly on plastid data may be prone to misrepresentation of phylogenetically coherent groups due to different placements of taxa in plastid versus nuclear based topologies. We are, however, confident in the phylogenetic delimitation of the groups recognized as genera by us for the following reasons: (i) taking evidence from nuclear data (Soza & Olmstead, 2010b; Yang & al., 2018), analysed either alone or in combination with plastid data, fully into account, the phylogenetic groups recognized as genera have been congruently inferred (or at least are not contradicted with high support by phylogenetic data) in all studies, notwithstanding that relationships among them may differ; (ii) although interspecific hybridization is deemed rather common in the entire tribe, although partly difficult to detect (Kästner & Ehrendorfer, 2016), well-documented cases of hybridization, partly confirmed by artificial crossings, are essentially restricted to *Galium* s.str. (Kästner & Ehrendorfer, 2016; Müller & al., 2021) and never involve species of lineages treated as different genera here; (iii) most clades treated as genera here are morphologically homogeneous and distinct.

The brief descriptions of the genera we will recognize below, including species number and geographical distribution, are mainly based on Ball (1976), Ehrendorfer & Krendl (1976a,b), Ehrendorfer & Puff (1976), Ehrendorfer & al. (2005), Chen & Ehrendorfer (2011), Kästner & Ehrendorfer (2016) and an unpublished manuscript by F. Ehrendorfer (Ehrendorfer, 2017); additional sources are cited in the text. In Rubieae, leaves mostly have one or three veins; leaf venation was only described when different. In general, flowers are arranged in more or less many-flowered and regular thyrses; inflorescences are only described when deviating from this pattern. In most genera calyx teeth are not recognizable and they were only described when being distinct. For description of the corolla tube as either short or long, the character traditionally used for the distinction of *Asperula* and *Galium*, we follow Ehrendorfer & al. (2018), who defined long corolla tubes as >1.5 mm and short corolla tubes as <1.5 mm. The two style branches normally are of equal length and were only described when not. Sex distribution was only described when flowers are not hermaphroditic.

Our classification also takes into account a scheme presented by F. Ehrendorfer at the XVIIIth International Botanical Congress at Melbourne (2011) (Fig. 1), which in slightly modified forms later was published by Ehrendorfer & Barfuss (2014) and Kästner & Ehrendorfer (2016). Both the Melbourne presentation and the unpublished manuscript (Ehrendorfer, 2017) were kindly made available to us by Dr. Luise Schratt-Ehrendorfer (Vienna, Austria).

■ RESULTS AND DISCUSSION

Figure 2 represents a simplification of the phylogenetic tree by Yang & al. (2018), modified by the addition of *Mericalpaea* and *Galium* sect. *Jubogalium* Ehrend. in the positions identified by Ehrendorfer & al. (2018). Support values (Bayesian posterior probabilities, maximum parsimony bootstrap values) were taken from Soza & Olmstead (2010a), Yang & al. (2018), and Ehrendorfer & al. (2018).

In principle, the phylogenetic tree seen in Fig. 2 would allow two major options for the classification of Rubieae. On the one hand, it would be possible to classify all lineages of Galiinae subtr. nov. (*Pseudogalium* through *Galium* s.str.; Fig. 2) as an enlarged genus *Galium* (or *Asperula* – both these names were introduced by Linnaeus, 1753, and to our knowledge it has not been settled which name to use in case of their synonymy). On the other hand, Galiinae can be split into several genera. In general, clade stability, clade diagnosability and the number of nomenclatural changes required are criteria commonly considered when discussing generic status of lineages (e.g., Funk, 1985; Entwistle & Weston, 2005; Humphreys & Linder, 2009; Vences & al., 2013). On this background, we decided to take the second approach, i.e., recognition of several segregates of *Asperula* and *Galium* as separate genera for mainly two reasons. First, treating

Galiinae as one large genus *Galium* (or *Asperula*) would abandon several long-established genera that are well characterized by apomorphic characters and are morphologically divergent. Second, the majority of lineages to be segregated from *Galium* and *Asperula* have clear apomorphies and accordingly can be easily diagnosed, as will be discussed in detail below. Considering that all major lineages of Rubieae have been sampled by Soza & Olmstead (2010a), Yang & al. (2018) and Ehrendorfer & al. (2018), and that the lineages we will treat at generic rank below have been congruently identified in these three studies (when included), we firmly believe that our classification will be stable, and that most of the genera recognized are easily diagnosable. The number of nomenclatural changes necessary in our approach is approximately the same as when incorporating all genera of Galiinae in *Galium* (or *Asperula*).

In the following, we will discuss and describe the lineages recognized by us on the basis of the phylogenetic tree shown in Fig. 2.

■ TAXONOMIC TREATMENT

ICN citations refer to the *Madrid Code* (Turland & al., 2025).

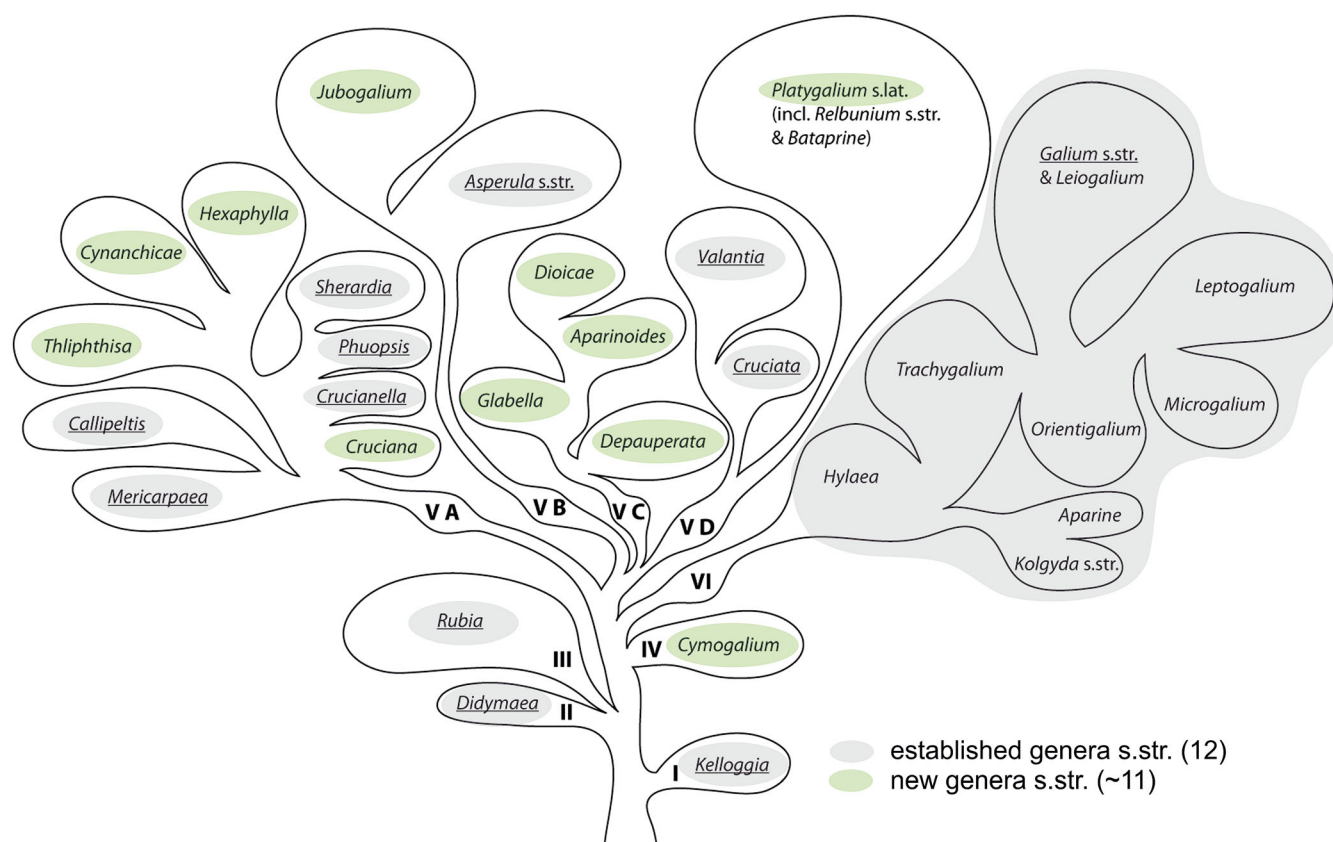


Fig. 1. Possible classification of tribe Rubieae using a narrow generic concept as presented by F. Ehrendorfer at the XVIIIth International Botanical Congress at Melbourne (2011). Roman numerals and letters at branches indicate major clades and subclades recognized by F. Ehrendorfer in his presentation.

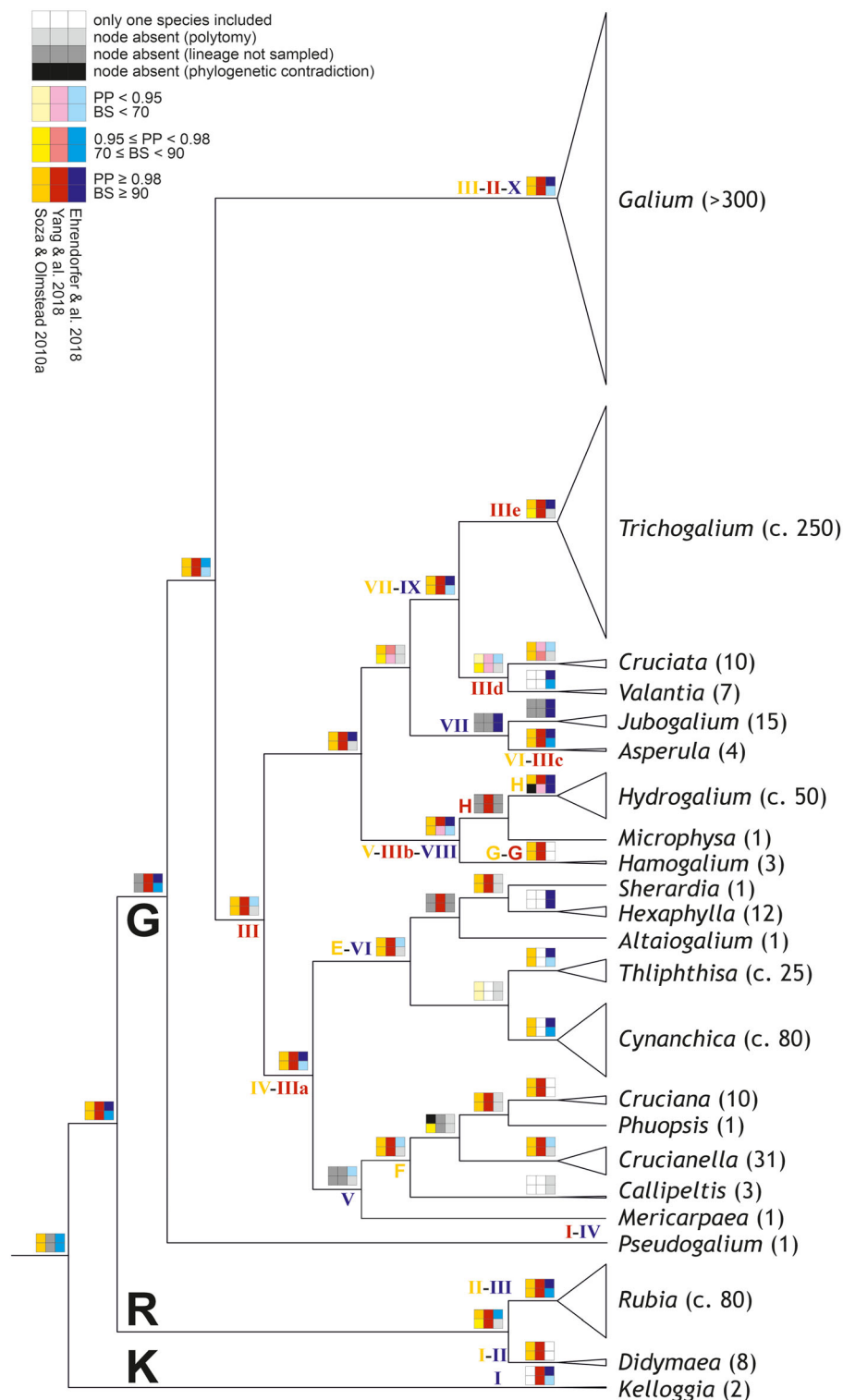


Fig. 2. Phylogenetic relationships among the genera of subtribe Rubieae recognized here as inferred by Yang & al. (2018; based on combined plastid and nuclear data, i.e. their fig. 1) modified by the addition of *Mericarphaea* and (*Galium* sect.) *Jubogalium* in the positions identified by Ehrendorfer & al. (2018). Subtribes are indicated at the base of the corresponding clades: G, Galiinae; K, Kelloggiiinae; R, Rubiinae. Height of triangles corresponds to species numbers which also are given after genus names. Colouration of grids at branches indicates level of support for each genus inferred by Soza & Olmstead (2010a; yellow), Yang & al. (2018; red) and Ehrendorfer & al. (2018; blue); grey indicates absence of support due to, e.g., lack of resolution in the source study or phylogenetic incongruency among source studies. Roman numerals or letters at branches indicate clade designations used by Soza & Olmstead (2010a; yellow), Yang & al. (2018; red) and Ehrendorfer & al. (2018; blue).

Rubiaceae Baill., Hist. Pl. 7: 365. 1880

With respect to the circumscription of Rubiaceae we follow Razafimandimbison & Rydin (2024a). Robbrecht & Manen (2006) considered Rubiaceae to additionally contain *Theligonum* (as subtribe Theligoninae), but in this broader circumscription Rubiaceae would be polyphyletic, hence *Theligonum* is treated as a separate tribe Theligoneae sister to Putorieae (Razafimandimbison & Rydin, 2024a). For the subtribal classification of Rubiaceae, we follow Ehrendorfer & al. (2018), who distinguished three major clades, i.e., Kelloggiinae, Rubiinae and Galiinae subtr. nov. (the latter two were merged into a single subtribe Rubiinae in the classification of Robbrecht & Manen, 2006). The name Galiinae was described but not published by Ehrendorfer (2017). Thus, Rubiaceae consists of three subtribes with altogether 23 genera. In order to account taxonomically for our changes in generic delimitation, altogether 293 new combinations were made.

Following Kästner & Ehrendorfer (2016), Rubiaceae (i.e., their Rubiaceae s.l.) contain herbaceous or woody perennials and annuals, have decussate leaves with very often leaf-like stipules, mostly hermaphroditic and homostylous flowers, a mostly rudimentary calyx without calyx teeth, valvate corolla lobes, 2-merous gynoecia with one anatropous and erect ovule per carpel, fleshy or dry fruits that mostly separate into two mericarps at maturity, and mostly polycarpate pollen grains. The tribe is of cosmopolitan distribution but clearly centred in temperate regions. Detailed information on the distribution of the genera is given below.

Key to the subtribes and genera of Rubiaceae

(for more detailed discussion of characters and generic delimitation see below)

1. Calyx with distinct teeth; interpetiolar stipules small, bi- to multifid; mericarps dry; perennial herbs from western North America or SW China... 1. *Kelloggia* (Kelloggiinae)
1. Calyx without distinct teeth, interpetiolar stipules not divided; if distinct teeth present (*Sherardia*), annual herbs from Eurasia; if stipules bifid (*Didymaea*), mericarps fleshy.....2
2. Mericarps fleshy; interpetiolar stipules either much smaller than leaves or leaf-like and leaves in whorls of 4–9; leaves not 3-veined, flowers hermaphrodite 3 (Rubiinae)
2. Mericarps dry; interpetiolar stipules never much smaller than leaves; if mericarps fleshy, leaves mostly 3-veined and in whorls of 4 (*Trichogalium*) or flowers unisexual and plants dioecious (*Hydrogalium* p.p.)4 (Galiinae)
3. Interpetiolar stipules small, entire or bifid; perennial procumbent or climbing herbs from Mexico to Panama 2. *Didymaea*
3. Interpetiolar stipules leaf-like, sometimes smaller; erect perennial herbaceous or woody plants from the Old World3. *Rubia*
4. Styles unequally long (Fig. 3A)5
4. Styles equally long6
5. Inflorescence spike-like..... 7. *Crucianella*

5. Inflorescence thyrsoid 9. *Cruciana*
6. Inflorescence capitate7
6. Inflorescence not capitate10
7. Bracts of capitate inflorescence basally fused 14. *Sherardia*
7. Bracts of capitate inflorescence free.....8
8. Outer surface of upper part of style strongly papillose, style greatly exerted8. *Phuopsis*
8. Outer surface of upper part of style not papillose, style not greatly exerted.9
9. Bracts of capitate inflorescence with stiff, long setae; mostly annual herbs..... 18. *Asperula*
9. Bracts of capitate inflorescence without stiff, long setae; perennial to basally woody herbs13. *Hexaphylla*
10. Flowers few or mostly solitary on long and distally recurved pedicels, fruits exposed (Fig. 3B)..... 15. *Hamogalium*
10. Flowers mostly many, pedicels not distally recurved; if recurved, fruits hidden11
11. Fruits enclosed by recurved, thickened and fused peduncles and pedicels, these spinulose-hispid above 20. *Valantia*
11. Fruits not enclosed by recurved, thickened and fused peduncles and pedicels.....12
12. Pedicels of flowers and fruits recurved, at least fruits mostly positioned below bracts 21. *Cruciata*
12. Pedicels of flowers and fruits not recurved13
13. Ovary not of separate mericarps but the 2 carpels united within $\pm$ inflated common pericarp 16. *Microphysa*
13. Ovary clearly of 2 mericarps14
14. Mericarps with 3 dorsal ridges with uncinat hairs..... 5. *Mericarpaea*
14. Mericarps not with 3 dorsal ridges.....15
15. Mericarps apically truncate11. *Thliphthisa*
15. Mericarps not apically truncate16
16. Furrow between mericarps of yellowish tissue different from mericarp surface (Fig. 3E)..... 19. *Jubogalium*
16. No distinct tissue present between mericarps.....17
17. Bracts of lateral fruits of a cyme enlarged, attached to fruits 6. *Callipeltis*
17. Bracts of lateral fruits of a cyme not enlarged18
18. Corolla tube long (>1.5 mm), leaves linear, 1-veined, in whorls of 4 or only 2 10. *Cynanchica*
18. Corolla tube short (<1.5 mm) or tube and lobes both ca. 1.5 mm; if tube longer than lobes leaves not linear and not 1-veined.....19
19. Corolla tube and lobes ca. 1.5 mm long..... 12. *Altaiogalium*
19. Corolla tube short (<1.5 mm), rarely long (in *Hydrogalium* p.p. and a few species of *Trichogalium* and *Galium*)20
20. Leaf venation pinnate 4. *Pseudogalium*
20. Leaf venation not pinnate21
21. Flowers unisexual (Fig. 3D), plants dioecious, from Australia, Tasmania or New Zealand 17. *Hydrogalium* p.p.

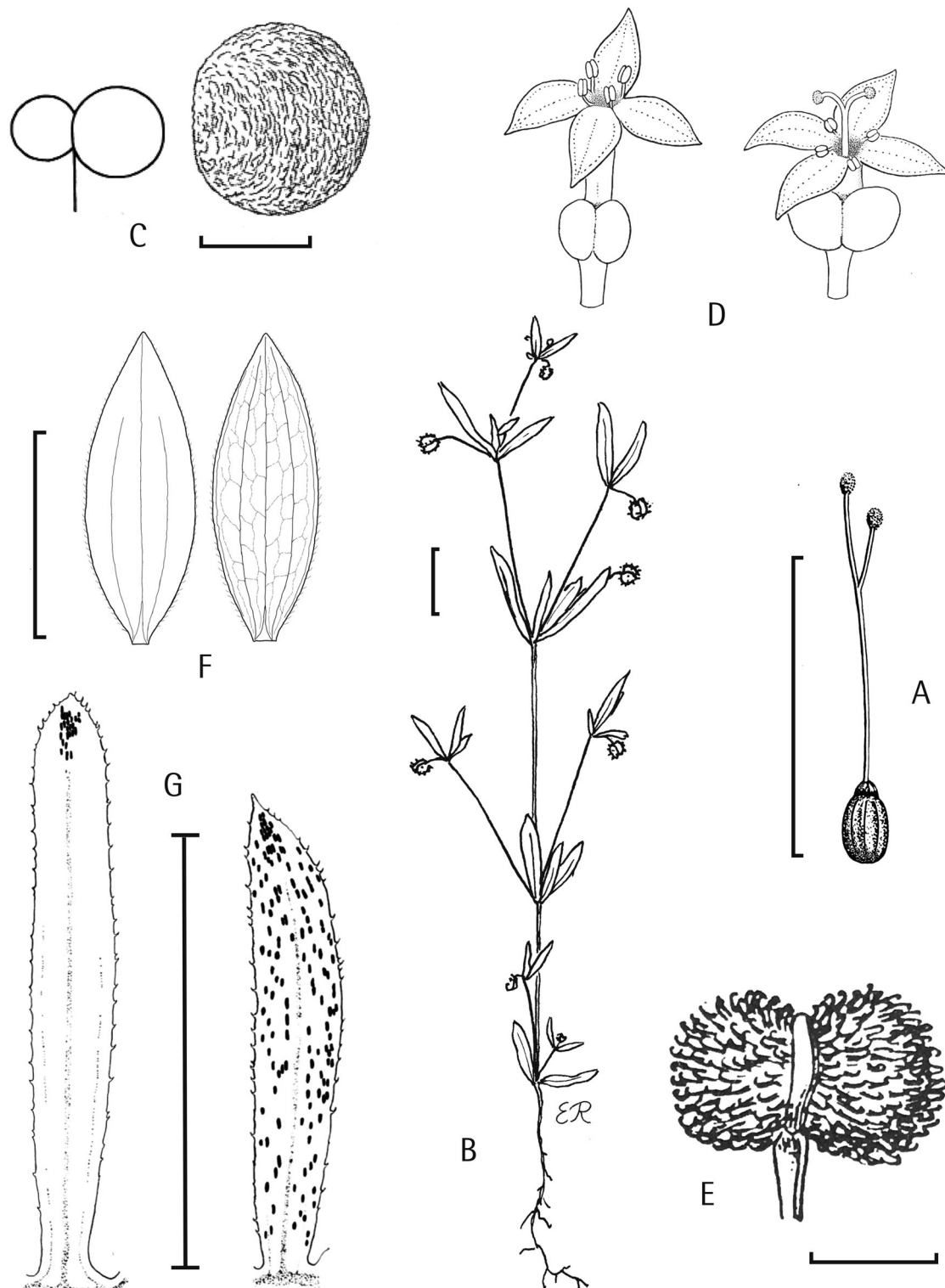


Fig. 3. **A**, *Cruciana glomerata*, ovary with styles of unequal length (modified from Nazimuddin & Qaiser, 1989); **B**, *Hamogalium bifolium* (from Baldwin & al., 2012; reprinted with permission from the Jepson Herbarium, UC Berkeley); **C**, *Hydrogalium elongatum*, globose mericarp (from Kästner & Ehrendorfer, 2016; reprinted with permission); **D**, *Hydrogalium*, male (left) and female (right) flower of former *Asperula* sect. *Dioicae*. Corolla 1.5–6 (male) and 0.8–3 mm (female) (from Thompson, 2009; reproduced with permission Royal Botanic Gardens Victoria); **E**, *Jubogalium setaceum*, furrow between mericarps without indumentum (from Fiori & Paoletti, 1933); **F**, *Trichogalium rubioides*, upper (left) and lower (right) surface of 3-veined leaves (from Kästner & Ehrendorfer, 2016; reprinted with permission); **G**, *Trichogalium johnstonii* (left) and *T. jepsonii* (right), cleared leaves showing glands (from Dempster & Stebbins, 1971; reprinted with permission). — Scale bars: A, B, F, G: 1 cm; C, E: 1 mm.

21. Flowers not unisexual; if unisexual, then plants not from Australia, Tasmania or New Zealand22
22. Leaf apex rounded, leaves in whorls of 4–8, mericarps (sub)globose (Fig. 3C)17. *Hydrogalium* p.p.
22. Leaf apex not rounded, mericarps mostly not (sub) globose23
23. Leaves in whorls of 4, often 3-veined (Fig. 3F), often with glands near apex on lower surface (Fig. 3G)..... 22. *Trichogalium*
23. Leaves in whorls of (4)5–10(12), mostly not 3-veined, without glands 23. *Galium*

Kelloggiinae Robbr. & Manen in Syst. Geogr. Pl. 76: 138. 2006 – Type: *Kelloggia* Torr. ex Benth. & Hook.f.

Kelloggiinae comprises only the genus *Kelloggia* (formerly classified as a member of Rubiaceae-Paederieae: Puff, 1982; Andersson & Rova, 1999) and was first described as a subtribe by Robbrecht & Manen (2006), who identified the position of *Kelloggia* as sister to all other Rubieae. The subtribe consists of perennial herbs with decussate leaves with two small interpetiolar stipules, flowers with distinct calyx teeth and long corolla tubes, tricolpate pollen grains (vs. polycolpate in all other Rubieae; possibly 5-colpate in *Didymaea*, see below) and mericarps with uncinat hairs (Ehrendorfer & al., 2018). Of these characters, the pollen grains are plesiomorphic within Rubieae (Ehrendorfer & al., 2018). *Kelloggia* also lacks a 50 bp deletion in the *atpB-rbcL* region of the plastid genome that is found in the remainder of Rubieae (Manen & Natali, 1996; Nie & al., 2005).

1. *Kelloggia*

Kelloggia is a well-supported monophyletic genus (Nie & al., 2005; Ehrendorfer & al., 2018; Yang & al., 2018), recognizable by the combination of small interpetiolar stipules that are bi- to multifid, the presence of distinct calyx teeth and 3-colpate pollen grains.

Kelloggia Torr. ex Hook.f. in Bentham & Hooker, Gen. Pl. 2(1): 137. 1873 – Type: *Kelloggia galioides* Torr.

Diagnosis. – Plants perennial, herbaceous. **Leaves 2, with 2 small bi- to multifid stipules.** Flowers 4- or 5-merous, **calyx with distinct teeth**, corolla funnel-shaped, tube long. **Pollen 3-colpate.** Mericarps 2, narrowly ovoid, dry, with uncinat trichomes, separating or tardily separating.

Number of species and geographical distribution. – *Kelloggia* contains two perennial herbaceous species distributed in western North America and in SW China, respectively (Nie & al., 2005).

Rubiinae Robbr. & Manen in Syst. Geogr. Pl. 76: 138. 2006, **emend.** Kadereit & Schneew. – Type: *Rubia* L.

The narrow concept of Rubiinae adopted here, including only *Didymaea* and *Rubia*, follows Ehrendorfer & al. (2018). In contrast, Robbrecht & Manen (2006), who introduced the name at subtribal rank, applied a broader concept by including all genera with leaf-like stipules and polycolpate

pollen grains. This corresponds to Rubieae s.str. of Käßner & Ehrendorfer (2016), thus also including Galiinae (see below). Rubiinae, as circumscribed here, consists of herbaceous or woody perennials with either small and sometimes bifid or leaf-like stipules, 4- or 5-merous flowers without calyx teeth and mostly short corolla tubes, polycolpate pollen grains and mostly fleshy fruits that lack hooked hairs (Ehrendorfer & al., 2018). Fleshy fruits can also be found in some lineages of Galiinae (see below).

2. *Didymaea*

Didymaea (two species sampled) is a well-supported monophyletic genus (Soza & Olmstead, 2010a; Yang & al., 2018). Like *Kelloggia*, *Didymaea* has small interpetiolar stipules that can be entire or bifid, but in contrast to *Kelloggia* it has fleshy fruits. Fleshy fruits can also be found in *Rubia* as well as some members of Galiinae (some species of *Trichogalium* and *Hydrogalium* gen. nov.; see below). From the former, *Didymaea* can be distinguished by its tetramerous (vs. mostly pentamerous) flowers and its distribution in the New World (vs. Old World), and from the latter by its stipules: these are small in *Didymaea* but leaf-like in *Trichogalium* and *Hydrogalium*. Bremekamp (1966) reported that the seeds of *Didymaea* do not adhere to the pericarp, which may be a synapomorphy of the genus. For *D. mexicana*, Halbritter (2016) reported 5-colpate pollen grains. If such pollen grains would be found in all other species, this would be another synapomorphy of the genus.

Didymaea Hook.f. in Bentham & Hooker, Gen. Pl. 2(1): 150. 1873 ≡ *Balfourina* Kuntze, Revis. Gen. Pl. 2: 954. 1891, nom. superfl. – Type: *Didymaea mexicana* Hook.f.

Diagnosis. – Plants perennial, herbaceous, procumbent or climbing. **Leaves 2, venation palmate or sometimes pinnate, stipules 2, small, entire to bifid, never leaf-like.** Corolla 4-merous, campanulate to rotate, tube short. **Mericarps 2, ovoid, fleshy, glabrous** (rarely with uncinat trichomes).

Number of species and geographical distribution. – Eight species from central Mexico to Panama (Pacheco-Trejo & al., 2009).

Nomenclatural note. – Kuntze (1891) introduced the name *Balfourina* as a replacement for *Didymaea* because he considered the name *Didymaea* too similar to *Didymium* Schrad., a genus of Myxomycetes.

3. *Rubia*

Rubia is a well-supported monophyletic genus (Soza & Olmstead, 2010a: 6 spp. sampled; Yang & al., 2016: 27 spp. sampled; Ehrendorfer & al., 2018: 8 spp. sampled; Yang & al., 2018: 7 spp. sampled). Like *Didymaea*, *Rubia* has fleshy fruits, but the flowers are predominantly pentamerous. Tetramerous species of *Rubia* can be distinguished from *Didymaea* by their geographical distribution as *Rubia* is distributed only in the Old World. There, its distribution does not overlap with the distribution ranges of those species with fleshy fruits of *Hydrogalium* (Australia).

Rubia L., Sp. Pl.: 109. 1753 – Type: *Rubia tinctorum* L.

Diagnosis. – Plants perennial, herbaceous to woody. Leaves in whorls of 4–9, venation pinnate, palmate or reduced, stipules leaf-like, sometimes smaller. **Corolla (4) 5-merous**, funnel-shaped to mostly rotate, tube short. **Mericarps 2, ovoid, fleshy, glabrous.**

Number of species and geographical distribution. – About 80 species from tropical and temperate Asia to Japan and Indonesia, through the Himalaya to SW Asia, E to S Africa, through the Mediterranean to western Europe, Macaronesia and the Azores (Ball, 1976; Puff, 1986; Chen & Ehrendorfer, 2011; Yang & al., 2016).

Galiinae Ehrend. ex Kadereit & Schneew., **subtr. nov.** – Type: *Galium* L.

Galiinae as a formal name at subtribal rank was introduced by F. Ehrendorfer (Ehrendorfer, 2017), but the name has not yet been validly published. Ehrendorfer & al. (2018) had referred to the “Galiinae Clade”. Galiinae includes mostly herbaceous perennials and annuals with stipules that are mostly leaf-like (although smaller in some groups; see below), with predominantly tetramerous flowers with short or long corolla tubes, and with most commonly dry fruits.

Nomenclatural note. – The authorship of Galiinae was given as “Galiinae K. Schum. in H.G.A. Engler & K.A.E. Prantl, Nat. Pflanzenfam. IV, 4: 16. Dec 1891 (Galieae). Validated by a diagnosis in German. – T: *Galium* L.” by Reveal (2012). As Schumann (1891) in his account of Rubiaceae used the name Galieae and clearly and consistently referred to this taxon (and other taxa with the same ending) as a tribe (Tribus), and also divided other tribes of Rubiaceae (Cinchoneae and Gardenieae) into subtribes, we can see no reason to question that the name Galieae as used by Schumann was meant for a taxon at tribal rank. Accordingly, the name Galiinae has not yet been validly published.

4. *Pseudogalium*

Pseudogalium, a lineage clearly unrelated to any other lineage of *Galium* (Jeong & al., 2016; Ehrendorfer & al., 2018; Yang & al., 2018), was erected as a genus for *Galium* sect. *Cymogalium* by Yang & al. (2018). Although the leaves of *Pseudogalium paradoxum* (Maxim.) L.E. Yang & al., the only species of the genus, were described as having one median and two lateral veins by Schönbeck-Temesy & Ehrendorfer (1989), they clearly are pinnately veined as described and illustrated by Chen & Ehrendorfer (2011: fig. 82/2) and Yang & al. (2018: fig. 3B). Pinnately veined leaves can also be found in *Rubia* (Yang & al., 2016) and *Didymaea* (Pacheco-Trejo & al., 2009), but *Pseudogalium* has dry mericarps with uncinat hairs instead of fleshy fruits. Also, the two stipules of *Pseudogalium*, although leaf-like, are distinctly smaller than the leaves.

Pseudogalium L.E. Yang, Z.L. Nie & H. Sun in Molec. Phylog. Evol. 126: 231. 2018 – Type: *Pseudogalium paradoxum* (Maxim.) L.E. Yang, Z.L. Nie & H. Sun = *Galium paradoxum* Maxim.

Diagnosis. – Plants perennial, herbaceous. **Leaves 2, venation pinnate, stipules leaf-like, smaller than leaf blades.** Corolla 4-merous, rotate, tube short. Mericarps 2, ovoid, dry, with uncinat trichomes.

Number of species and geographical distribution. – One species (*Pseudogalium paradoxum*) with three subspecies (Yang & al., 2018) widespread in Bhutan, China, India, Japan, Korea, Nepal and Russia (Chen & Ehrendorfer, 2011).

5. *Mericarpacea*

As *Mericarpacea* was sampled only by Ehrendorfer & al. (2018), its relationships are based on plastid data only. *Mericarpacea* is part of a large clade containing *Callipeltis*, *Crucianella*, *Phuopsis*, *Cruciana* stat. nov., *Cynanchica*, *Thliphthisa*, *Altaigalium* gen. nov., *Hexaphylla* and *Sherardia*, but its exact relationships within this clade are uncertain due to insufficient support values. It is, however, morphologically clearly distinct from all these genera. Although sharing its peculiar inflorescence morphology with *Callipeltis*, the molecular data of Ehrendorfer & al. (2018) do not suggest a close relationship between the two genera. *Mericarpacea* is best characterized by its mericarps with three dorsal and longitudinal crests loosely covered by broadly based uncinat hairs (Ehrendorfer & al., 2005; for illustration see Schumann, 1891: fig. 47H). The cymes appear to be extra-axillary, i.e., cymes are positioned opposite to leaves (Eig, 1927; Ehrendorfer & al., 2005). Following Ehrendorfer & al. (2005), this seemingly extra-axillary position of cymes is the result of unusual inflorescence branching. Specifically, the main axis of the stem ends in a ± reflexed cyme; usually one lateral branch continues to grow monopodially, overtopping and seemingly continuing the main axis; this lateral branch ends in a reflexed cyme that is overtopped by the next lateral branch. This pattern continues several times and causes the (morphologically) terminal inflorescences to be displaced laterally and thus to appear extra-axillary.

Mericarpacea Boiss., Diagn. Pl. Orient., ser. 1, 3: 51. 1843 – Type: *Mericarpacea ciliata* Boiss.

Diagnosis. – Plants annual. Leaves in whorls of 4(5), stipules leaf-like. **Apical cymes seemingly extra-axillary.** Corolla 4-merous, rotate, tube short. **Mericarps 2, ovoid, dry, with three dorsal ridges with uncinat trichomes.**

Number of species and geographical distribution. – One species, *Mericarpacea ciliata*, in the E Mediterranean area, Syria, Palestine, Jordan and Iraq.

6. *Callipeltis*

Despite the unique morphology of *Callipeltis*, molecular phylogenetic support for its monophyly is still lacking. The genus was sampled with only one species by Soza & Olmstead (2010a) and by Yang & al. (2018) and it was inferred as unresolved by Ehrendorfer & al. (2018), who sampled two species (three when *Callipeltis aperta* Boiss. & Buhse is accepted as separate species). In *Callipeltis*, the lateral flowers of 3-flowered cymes are subtended by bracts that become

enlarged and ± membranous (for illustration see Stopp, 1971: fig. 8a). They remain attached to the fruits (and in some species envelope the fruits) and serve their dispersal by wind (for detailed description of dispersal see Eig, 1927, and Stopp, 1971). Like *Mericalpaea*, *Callipeltis* has been described as having extra-axillary cymes (Eig, 1927; Ehrendorfer & al., 2005). In the fruits, often only one mericarp develops to maturity.

Callipeltis Steven in Observ. Pl. Ross 2: 6. 1828 ≡ *Cucullaria* Kuntze, Revis. Gen. Pl. 1: 279. 1891, nom. superfl. – Type: *Callipeltis cucullaris* (L.) DC. ≡ *Valantia cucullaris* L.

= *Warburgina* Eig in Bull. Agric. Exp. Sta. Zionist Organ. Inst. 1927: 6, 33. 1927 – Type: *Warburgina factorovskiyi* Eig.

Diagnosis. – Plants annual. Leaves in whorls of 4(–6), stipules leaf-like. **Apical cymes seemingly extra-axillary.** Corolla 4(3)-merous, funnel-shaped to rotate, tube short. Mericarps 1 or 2, ovoid, dry, **bracts of lateral fruits enlarged, membranous, attached to fruits.**

Number of species and geographical distribution. – Three species in the Mediterranean area and in SW Asia (Ehrendorfer & al., 2005).

Nomenclatural notes. – Kuntze (1891) explicitly cited *Callipeltis* Steven as a synonym of his *Cucullaria*, rendering his name a nomen superfluum.

Eig (1927) described *Warburgina* for an annual species newly described by him, *W. factorovskiyi* Eig. Differing from other *Callipeltis* species by having two fertile mericarps and narrow greenish bracts, the species later has been transferred by Ehrendorfer (1964) to *Callipeltis* as *C. factorovskiyi* (Eig) Ehrend. Although no molecular data are available, morphological evidence does not support separation of *Warburgina* from *Callipeltis*.

7. *Crucianella*

Crucianella is a well-supported monophyletic genus (Soza & Olmstead, 2010a: 4 spp. sampled; Yang & al., 2018: 5 spp. sampled). Like *Cruciana* (see below), *Crucianella* has long corolla tubes and styles of unequal length. However, *Crucianella* is well characterized by its spike-like inflorescences where mostly one or more rarely two flowers with two bracteoles each are found in the axils of often overlapping bracts arranged in two to four rows (for illustration see Kästner & Ehrendorfer, 2016: fig. 22d,f).

Crucianella L., Sp. Pl.: 109. 1753 ≡ *Rubeola* Tourn. ex Adans., Fam. Pl. 2: 144. 1763, nom. superfl., nom. illeg., non Mill. 1754 – Type (designated by Hitchcock in Sprague, Nom. Prop. Brit. Bot.: 124. 1929): *Crucianella latifolia* L. ≡ *Rubeola* Mill., Gard. Dict. Abr., ed. 4.: [s.p.]. 1754, nom. superfl. – **Type (designated here):** *Crucianella latifolia* L.

Diagnosis. – Plants perennial, herbaceous to woody, or annual. Leaves in whorls of 4–10, stipules leaf-like.

Inflorescence spike-like. Corolla 4–5-merous, funnel-shaped, tube long, **styles unequally long.** Mericarps 2, narrowly ovoid, dry, glabrous.

Number of species and geographical distribution. – About 31 species in the Mediterranean area and in SW Asia (Kästner & Ehrendorfer, 2016).

Nomenclatural note. – The nine species listed under *Rubeola* by Miller (1754) were not listed with binomials and belong to different genera as understood today. In order to place *Rubeola* Mill. in synonymy, we here choose *Crucianella latifolia* as type based on the following consideration. The first species listed by Miller is “*Rubeola latiori folio*” of Tournefort (1700: 130). Although not including the lectotype of the Linnean name *Crucianella latifolia*, both Tournefort and Linnaeus (1753) list Bauhin’s “*Rubia latifolia spicata*” (Bauhin, 1623: 334) as synonym of their names, implying that Tournefort’s (and thus Miller’s) species indeed is the same as Linnaeus’s species. Adanson (1763) also used Tournefort’s genus name, but Adanson’s name is illegitimate on account of both being a younger homonym (of Miller’s name) and of being a nomen superfluum (*Crucianella* L. is explicitly cited as synonym). *Rubeola* Mill. and *Rubeola* Tournf. ex Adans. are now isonyms by typification.

8. *Phuopsis*

Phuopsis has capitate inflorescences surrounded by leaf-like bracts. Most importantly, its pentamerous flowers with a long corolla tube show secondary pollen presentation, where pollen is deposited on the coarsely papillate outer surface of the upper part of the style, which after deposition of the pollen grains becomes strongly exserted (Yeo, 1993; Erbar & Leins, 1995; Puff & al., 1996; for illustration, see Schumann, 1891: fig. 47E; Erbar & Leins, 1995: figs. 25–29).

Phuopsis (Griseb.) Hook.f. in Bentham & Hooker, Gen. Pl. 2: 151. 1873 ≡ *Nemostylis* Steven in Bull. Soc. Imp. Naturalistes Moscou 29(II): 361. 1856, non Herb. 1840 – Type: *Phuopsis stylosa* (Trin.) Hook.f. ≡ *Crucianella stylosa* Trin.

– “*Laxmannia* S.G.Gmel. ex Trin.” in Mém. Acad. Imp. Sci. St. Pétersbourg Hist. Acad. 6: 492. 1818, not validly published.

Diagnosis. – Plants perennial, herbaceous. Leaves in whorls of (6)–8–10, stipules leaf-like. **Inflorescence capitate with leaf-like bracts, bracts free.** Corolla 5-merous, salver-shaped, tube long. Flowers with secondary pollen presentation, **pollen deposited on coarsely papillate outer surface of upper part of style, style strongly exserted afterwards.** Mericarps 2, ovoid, dry, glabrous.

Number of species and geographical distribution. – One species, *Phuopsis stylosa* (Trin.) Hook.f., in SW Asia (Azerbaijan, NW Iran; Chen & Ehrendorfer, 2011).

Nomenclatural notes. – *Nemostylis* Steven appears to be an older name for *Phuopsis*. Steven’s name may be considered a younger homonym of “*Nemostylis* Herb.” (in Bot. Mag. 66: sub t. 3779. 1840). When using the name *Nemostylis*, Herbert,

on page 2 of the text accompanying plate 3779, explicitly refers to Nuttall (“closely allied to *Nemostylis* of Nuttall, Flora of Arkansas [Territory], in Amer. Phil. Trans. [= Trans. Amer. Phil. Soc.], read 1834, p. 157”, followed by a copy of the verbal diagnosis of Nuttall). Although Nuttall (correct date of publication: 1837: 157) gave the genus as *Nemastylis*, it is clear from the context that Herbert did not intend to erect a new genus but simply referred to Nuttall’s taxon, albeit using a misspelled name (*Nemo-* instead of *Nema-*). In consequence, there is no name “*Nemostylis* Herb.” and *Nemostylis* Steven does not constitute a younger homonym. For the sake of nomenclatural stability, and because the name *Nemostylis*, to our knowledge, has never been used, we will propose conservation of *Phuopsis* over *Nemostylis* and continue to use the name *Phuopsis* in this paper.

Trinius (1818) listed *Phuopsis stylosa* explicitly as *Crucianella stylosa* and simply mentioned that Gmelin called this species differently (p. 492: “plantam elegantissimam a Gmelino *Laxmannia fasciculata* dictam”). Hence, Trinius did not validate Gmelin’s name (Art. 36.1).

9. *Cruciana*

We here erect the genus *Cruciana* for *Asperula* sect. *Cruciana*. While Ehrendorfer & al. (2018) sampled only one species of this section, which was positioned in a polytomy with *Phuopsis*, *Crucianella* and *Callipeltis*, the three species sampled by Soza & Olmstead (2010a) and the two species sampled by Yang & al. (2018) fell into a fully supported clade. As a long-tubed lineage, thus traditionally placed in *Asperula*, *Cruciana* can be distinguished from other such lineages primarily by its styles, which are unequal in length (Fig. 3A) (Ehrendorfer & al., 2005), but also by its mostly pentamerous flowers. Unequal styles can also be found in *Crucianella*, but *Cruciana* has thyrsoid instead of spicate inflorescences as found in *Crucianella*.

Cruciana (Griseb.) Kadereit & Schneew., stat. nov. ≡ *Asperula* sect. *Cruciana* Griseb., Spic. Fl. Rumel. 2: 166. 1846 – Type: *Cruciana glomerata* (M.Bieb.) Kadereit & Schneew. ≡ *Crucianella glomerata* M.Bieb.

Diagnosis. – Plants perennial, herbaceous to woody. Leaves in whorls of 4–12(16), stipules leaf-like. **Corolla 5 (4)-merous**, salver-shaped, funnel-shaped or bowl-shaped, tube long, **styles unequally long**. Mericarps 2, ellipsoid, dry, glabrous or pilose.

About 10 species from SW to central Asia (Kästner & Ehrendorfer, 2016). For species combinations, see Appendix 1.

10. *Cynanchica*

Based on *Asperula* sect. *Cynanchicae*, *Cynanchica* is well supported molecularly (Soza & Olmstead, 2010a; Ehrendorfer & al., 2018; only one species included by Yang & al., 2018) and has been described only recently (Del Guacchio & Caputo, 2020). It is, however, difficult to identify easily observable characters differentiating *Cynanchica* from other

members of former *Asperula*. Although characterized by whorls of four mostly linear leaves with only one vein, with often only two leaves per node through the absence of stipules in the upper part of the axis, 4-whorled taxa can commonly be found elsewhere in Rubieae. The flowers in *Cynanchica* often are sessile or have an only very short pedicel. Following Kästner & Ehrendorfer (2016), *Cynanchica* has a chromosome base number of $x = 10$, which otherwise, considering *Asperula* s.str. and segregates of *Asperula*, can only be found in *Cruciana*, which has styles of unequal length. Although chromosome base number clearly is an inconvenient character for delimitation of a genus, nonrecognition of this clade at generic rank is no feasible solution in view of its relationships (Fig. 2).

Cynanchica P.Caputo & Del Guacchio in Pl. Biosyst. 154: 769. 2020 – Type: *Cynanchica pyrenaica* P.Caputo & Del Guacchio ≡ *Asperula cynanchica* L.

Diagnosis. – Plants perennial, herbaceous to woody. Leaves in whorls of 4, sometimes reduced to 2, stipules leaf-like when present. Corolla 4-merous, salver- to funnel-shaped, tube long. Mericarps 2, obovoid, dry, glabrous or sparsely hairy.

Number of species and geographical distribution. – About 80 species mostly in SE Europe and Anatolia with some species reaching central and western Europe and NW Africa in the west and Syria, Iraq and Lebanon and the Caucasus area in the east (Kästner & Ehrendorfer, 2016). Del Guacchio & Caputo (2020) published combinations for 83 species.

Nomenclatural note. – For discussion of type, see Del Guacchio & Caputo (2020). These authors described *Cynanchica* as a new genus although referring to *Asperula* sect. *Cynanchicae* (DC.) Boiss.

11. *Thlipthisa*

Based on *Asperula* sect. *Thlipthisa*, a clade well supported molecularly (Soza & Olmstead, 2010a; Ehrendorfer & al., 2018; only one species included by Yang & al., 2018), *Thlipthisa* has been erected only recently (Del Guacchio & Caputo, 2020). *Thlipthisa* can be diagnosed by its mericarps, which are apically distinctly truncate (Ehrendorfer & al., 2005; Kästner & Ehrendorfer, 2016; for illustration see Schönbeck-Temesy & Ehrendorfer, 1985: figs. 4b, 8b).

Thlipthisa (Griseb.) P.Caputo & Del Guacchio in Pl. Biosyst. 154: 776. 2020 ≡ *Galium* sect. *Thlipthisa* Griseb., Spic. Fl. Rumel. 2: 161. 1846 – Type: *Thlipthisa rupestris* P.Caputo & Del Guacchio ≡ *Galium rupestre* Vis.

Diagnosis. – Plants perennial, herbaceous to basally woody. Leaves in whorls of (4)–6–9(–11), stipules leaf-like. Corolla 4-merous, funnel-shaped to subrotate, tube short or long. **Mericarps 2, dry, glabrous or rarely sparsely hairy, apically truncate.**

Number of species and geographical distribution. – About 25 species mostly from the eastern Mediterranean area (Kästner & Ehrendorfer, 2016). Del Guacchio & Caputo (2020) published combinations for 22 names.

12. *Altaigalium*

Galium paniculatum (Bunge) Pobed., sampled only by Yang & al. (2018, 2022), was identified as strongly supported sister to *Hexaphylla* and *Sherardia* in the phylogenetic tree based on combined nuclear and plastid data by Yang & al. (2018). In the absence of species of these two genera in the nuclear-based phylogenetic tree of Yang & al. (2018) it was sister to *Cynanchica* in that tree. Most importantly, it seems well-established that the species is not closely related to any other lineage of *Galium* s.l. The species originally had been described as *Asperula paniculata* based on its campanulate to funnellform corolla, but was included in *Galium* by Pobedimova (1971), a transfer supported by Kästner & Ehrendorfer (2016). Its assessment as a species of either *Asperula* or *Galium* might have resulted from the length of its corolla tube (half as long as flower, ca. 1.5 mm; for illustration see Pobedimova, 1958a: plate XIV, fig. 1), which is just on the border of the categories long (>1.5 mm) and short (<1.5 mm) used by Ehrendorfer & al. (2018). Although characterized as “problematic” (Ehrendorfer, 2017) or “relatively isolated” (Chen & Ehrendorfer, 2011), its position within *Galium* s.str. has not been questioned. Therefore, the same characters allowing it to be readily differentiated from closely related genera (several lineages formerly placed in *Asperula* and *Sherardia*) render it difficult to be distinguished from the phylogenetically more distant *Galium* s.str. Finally, distinction from those sections of *Galium* s.str. with partly glabrous mericarps and partly long corolla tubes (*G.* sect. *Trachygalium* K.Schum. and sect. *Galium*) is difficult. Following Kästner & Ehrendorfer (2016), 4-leaved whorls as found in the lower part of the yearly shoots of *G. paniculatum* cannot be found in *G.* sect. *Galium* and are rare in *G.* sect. *Trachygalium* (but note that the first whorls on the first shoot formed after germination always consist of four elements only; Kästner & Ehrendorfer, 2016). Its position as sister to *Hexaphylla* and *Sherardia* fits in terms of leaf number, which is four in the lower and never more than six in the upper part of the stem (Pobedimova, 1958a). From these two genera it differs by its inflorescence which is not capitate.

In summary, of all genera recognized by us, distinction of *Galium paniculatum* is most difficult but possible by a combination of its morphology and its geographical distribution (Altai to middle Yenisei and Dzungarian Alatau in Xinjiang; Chen & Ehrendorfer, 2011).

Altaigalium Kadereit & Schneew., **gen. nov.** – Type: *Altaigalium paniculatum* (Bunge) Kadereit & Schneew. ≡ *Asperula paniculata* Bunge.

Diagnosis. – Plants perennial, herbaceous. Leaves in whorls of 4–6, stipules leaf-like. Corolla 4-merous, campanulate to funnel-shaped, tube ca. 1.5 mm, as long as lobes. Mericarps 2, ellipsoid, dry, glabrous.

Number of species and geographical distribution. – One species, *Altaigalium paniculatum* comb. nov., from Altai to middle Yenisei and Dzungarian Alatau in Xinjiang (Chen & Ehrendorfer, 2011). For combination of this one species, see Appendix 1.

Etymology. – The name of this new genus refers to the distribution of its sole species in the Altai.

13. *Hexaphylla*

Based on *Asperula* sect. *Hexaphylla*, a clade well supported molecularly (Ehrendorfer & al., 2018; only one species included by Soza & Olmstead, 2010a, and by Yang & al., 2018), *Hexaphylla* has been erected only recently (Del Guacchio & Caputo, 2020). *Hexaphylla*, with 1-veined leaves in whorls of 6, is characterized by its partial inflorescences that are subcapitate and subtended by bracts. Capitate inflorescences can also be found in *Phuopsis* (see above), *Sherardia* (see below) and *Asperula* s.str. (see below). Of these, as discussed above, *Phuopsis* has pentamerous flowers and shows secondary pollen presentation, and *Sherardia* has distinct calyx teeth (see below) and the bracts of its capitate inflorescences are basally fused. In *Asperula* s.str., which except for *A. taurina* L. contains only annuals, the bracts of the subcapitate inflorescences are stiffly long-ciliate.

Hexaphylla (Klokov) P.Caputo & Del Guacchio in Pl. Biosyst. 154: 778. 2020 ≡ *Asperula* sect. *Hexaphylla* Klokov, Fl. RSS Ucr. 10: 458. 1961 – Type: *Hexaphylla allionii* P.Caputo & Del Guacchio ≡ *Asperula hexaphylla* All.

Diagnosis. – Plants perennial, herbaceous to basally woody. Leaves in whorls of 6(7), stipules leaf-like. **Partial inflorescences capitate, bracts free, without long, stiff ciliae.** Corolla 4-merous, salver- to funnel-shaped, tube long. Mericarps 2, ovoid, dry, glabrous or hairy.

Number of species and geographical distribution. – Twelve species, mostly in the Mediterranean area (Ehrendorfer & Krendl, 1976a; Kästner & Ehrendorfer, 2016). Del Guacchio & Caputo (2020) published one new name and combinations for 12 names.

Nomenclatural note. – For discussion of the type, see Del Guacchio & Caputo (2020).

14. *Sherardia*

The annual *Sherardia* is easily recognizable by its calyx with distinct teeth and its capitate inflorescence with basally fused bracts.

Sherardia L., Sp. Pl.: 102. 1753 ≡ *Rubeola* Hill, Brit. Herb.: 396. 1756, nom. superfl., nom. illeg., non Mill. 1754 ≡ *Dillenia* Heist. ex Fabr., Enum., ed. 2: 57. 1763, nom. superfl. ≡ *Hexodontocarpus* Dulac, Fl. Hautes-Pyrénées: 467. 1867, nom. superfl. – Type: *Sherardia arvensis* L.

Diagnosis. – Plants annual. Leaves in whorls of 4–6, stipules leaf-like. **Partial inflorescences capitate, bracts basally fused. Calyx with distinct teeth,** corolla 4-merous, salver-shaped, tube long. Mericarps 2, obconical, dry, scabrid.

Number of species and geographical distribution. – One species, *Sherardia arvensis*, native to the E Mediterranean area and SW Asia (Kästner & Ehrendorfer, 2016).

Nomenclatural notes. – *Rubeola* Hill not only is a younger homonym of *Rubeola* Mill. (see above), but also a nomen superfluum, as Hill (1756) explicitly used *Rubeola* instead of the valid Linnean name *Sherardia* (p. 396: “He [Linnaeus] takes away the received name *rubeola* [sic!], and calls the genus *sherardia* [sic!]”).

The name *Dillenia* Heist. ex Fabr. is a younger homonym of *Dillenia* L. (Sp. Pl.: 535. 1753) and, at the same time, a nomen superfluum, as Fabricius (1763) explicitly gives Linnaeus’s *Sherardia arvensis* (using the Linnean nomen specificum legitimum, though) as synonym.

Dulac (1867) explicitly listed *Sherardia* as a synonym of his genus, rendering his name a nomen superfluum.

15. *Hamogalium*

We here erect the genus *Hamogalium* for *Galium* sect. *Depauperata* Pobed. as emended by Ehrendorfer & al. (2005), a lineage supported as monophyletic in Soza & Olmstead (2010a) and Yang & al. (2018). The genus consists of annuals where the two interpetiolar stipules are leaf-like but smaller than the leaves. Pedicels are long and distally recurved, flowers mostly are solitary, and the mericarps have uncinat hairs (Fig. 3B).

Hamogalium Kadereit & Schneew., **gen. nov.** – Type: *Hamogalium songaricum* (Schrenk ex Fisch. & C.A.Mey.) Kadereit & Schneew. ≡ *Galium songaricum* Schrenk ex Fisch. & C.A.Mey.

Diagnosis. – Plants annual. **Leaves 2, stipules leaf-like, smaller than leaf blades. Flowers few or mostly solitary on long and distally recurved pedicels.** Corolla 3(4)-merous, rotate, tube short. Mericarps 2, reniform, dry, with uncinat trichomes.

Number of species and geographical distribution. – Probably not more than three species (Ehrendorfer & al., 2005) from SW Asia to W China and in western North America (one species: *Hamogalium bifolium* (S.Watson) Kadereit & Schneew.). For species combinations, see Appendix 1.

Etymology. – The name of this new genus refers to the distally recurved pedicels (hamosus: hooked).

16. *Microphysa*

Although *Microphysa*, based on *Asperula elongata*, was accepted by Chen & Ehrendorfer (2011), these authors argued that it better should be included in *Galium* sect. *Platygalium* (now *Trichogalium* (DC.) Fourr.: see below). However, considering its well-supported phylogenetic position (both in the combined and nuclear phylogenetic trees) distant from *G. sect. Platygalium* in Yang & al. (2018; the species was neither sampled by Soza & Olmstead, 2010a, nor by Ehrendorfer & al., 2018), *Microphysa* should be continued to be accepted as a separate genus as done by Yang & al. (2018). The genus is well-characterized by its fruit where the two parts of the inferior ovary do not develop into separate mericarps, each with its own pericarp, but remain united within a ± inflated

leathery and common pericarp (for illustration, see Pobedimova, 1958c: plate XXI, fig. 4). Following Chen & Ehrendorfer (2011), such fruits also occur in the *G. boreale* L.-*G. rubioides* L. group of *Trichogalium*. However, *Microphysa* has, in contrast to these species of *Galium*, long corolla tubes.

Microphysa Schrenk in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Petersbourg 2: 115. 1844 – Type: *Microphysa elongata* (Schrenk ex Fisch. & C.A.Mey.) Pobed. ≡ *Asperula elongata* Schrenk ex Fisch. & C.A.Mey.

Diagnosis. – Plants perennial, herbaceous. Leaves in whorls of 4, stipules leaf-like. Corolla 4-merous, funnel-shaped, tube long. **Ovary not of separate mericarps but the 2 carpels united within a ± inflated leathery and common pericarp.**

Number of species and geographical distribution. – One species, *Microphysa elongata* (Schrenk) Pobed., in NW China, Kazakhstan, Uzbekistan and Kyrgyzstan (Chen & Ehrendorfer, 2011).

17. *Hydrogalium*

The three groups included in this new genus (the name chosen by us had been suggested by Fischer, 2015 based on the habitat preference of *Galium* sect. *Aparinoides* (Jord.) Gren.) are *Asperula* sect. *Glabella* Griseb., *A. sect. Dioicae* Airy Shaw & Turrill and *G. sect. Aparinoides*. Ehrendorfer & al. (2018) identified a fully supported clade in which *A. sect. Glabella* (4 of ca. 12 species sampled) is paraphyletic in relation to a polytomy of *G. sect. Aparinoides* (5 of ca. 17 species sampled) plus *A. sect. Dioicae* (2 of ca. 21 species sampled). Soza & Olmstead (2010a), who did not sample *A. sect. Dioicae*, identified a fully supported clade in which two lineages of *A. sect. Glabella* form a trichotomy with *G. sect. Aparinoides*. Yang & al. (2018), who also did not sample *A. sect. Dioicae*, found a fully supported clade containing *A. sect. Glabella* again paraphyletic in relation to *G. sect. Aparinoides*. Yang & al. (2022), who sampled two species of *A. sect. Dioicae*, found them to be sister to each other and to be nested in *G. sect. Aparinoides*. No species of *A. sect. Glabella* was sampled in the nuclear-based tree of Yang & al. (2018). A close relationship between *A. sect. Glabella* and *G. sect. Aparinoides* had already been found by Manen & al. (1994) and Natali & al. (1995, 1996). Although it seems possible that additional sampling may warrant further splitting, in light of current phylogenetic data we consider combining *A. sect. Glabella*, *A. sect. Dioicae* and *G. sect. Aparinoides* in a single genus the most prudent option. Combination of these three groups in one genus creates a lineage that cannot be identified by a single character. Morphological similarities between *A. sect. Glabella* and *G. sect. Aparinoides* had already been noted by Manen & al. (1994) and Natali & al. (1995, 1996) and include mostly obtuse leaves in whorls of four to eight, 4- to 3-merous flowers and (sub)globose mericarps. However, mericarp shape in *A. sect. Glabella* can be both subglobose (Ehrendorfer & al., 2005)

and ovoid (Kästner & Ehrendorfer, 2016); additionally, subglobose mericarps can also be found in *Asperula*, some species of *Trichogalium* and in *G.* sect. *Hylaea* (Griseb.) Ehrend., and ovoid mericarps can also be found in *Galium* s.str.

Of the three groups included in *Hydrogalium*, *Galium* sect. *Aparinoides* is best characterized by its chromosome base number of $x = 12$, a number not found in any other lineage of *Galium* s.l. or Rubieae (Kästner & Ehrendorfer, 2016). As pointed out before (Manen & al., 1994; Natali & al., 1995, 1996), *G.* sect. *Aparinoides* and *Asperula* sect. *Glabella* share morphological characters. Inclusion of *A.* sect. *Dioicae* in this clade, as far as we can see, is not supported by any morphological character. *Asperula* sect. *Dioicae*, with two leaves and two smaller stipules or whorls of four to eight equal elements, was described by Shaw & Turrill (1928). Following Thompson (2009), this perennial herbaceous group is characterized, apart from its dioecy (Fig. 3D), by fleshy mericarps that do not separate at maturity. Interestingly, 8 of the 21 species are distinctly associated with wet habitats, providing a tentative link to *G.* sect. *Aparinoides*. However, the chromosome number of $2n = 88$ reported for *A. perpusilla* Hook.f. (de Lange & al., 2004) does not fit the typical chromosome number of $x = 12$ of *G.* sect. *Aparinoides* but represents the plesiomorphic base number $x = 11$ also found in *A.* sect. *Glabella*.

Hydrogalium Kadereit & Schneew., **gen. nov.** – Type: *Hydrogalium palustre* (L.) Kadereit & Schneew. $\equiv$ *Galium palustre* L.

– “*Chrozorrhiza* Ehrh.”, Beitr. Naturk. 4: 147. 1789, not validly published (ICN App.).

Diagnosis. – Plants perennial, herbaceous. Leaves **obtuse** or not (*Asperula* sect. *Dioicae*), mostly in whorls of 4–8, sometimes 2 leaves and 2 smaller stipules (*A.* sect. *Dioicae*). Corolla 4–3-merous, funnel-shaped (*A.* sect. *Glabella* and sect. *Dioicae*) or shortly campanulate to cup-shaped (*Galium* sect. *Aparinoides*) tube short, long or about as long as lobes, flowers hermaphroditic **or unisexual and then plants dioecious** (*A.* sect. *Dioicae*). Mericarps 2, broadly ellipsoid (*A.* sect. *Dioicae*) **to (sub)globose**, dry or somewhat fleshy (*A.* sect. *Dioicae*), glabrous, smooth to granulate, separating **or not separating** (*A.* sect. *Dioicae*) at maturity.

Number of species and geographical distribution. – About 17 species of more or less cosmopolitan distribution and from mostly mesic habitats in former *Galium* sect. *Aparinoides* (Kästner & Ehrendorfer, 2016; Puff, 1975: 20 spp.); about 12 species in SW Asia and the Mediterranean area in former *Asperula* sect. *Glabella* (Kästner & Ehrendorfer, 2016); 21 species in SE Australia and Tasmania (Thompson, 2009), one species in New Zealand (*A. perpusilla*; listed as *G. perpusillum* in the Flora of New Zealand: <https://www.nzflora.info/factsheet/Taxon/Galium-perpusillum.html>) in former *A.* sect. *Dioicae*. For species combinations, see Appendix 1.

Etymology. – The name of this new genus, first suggested by Fischer (2015), refers to the often mesic habitat of

members of former *Galium* sect. *Aparinoides* and former *Asperula* sect. *Dioicae*.

Nomenclatural note. – “*Chrozorrhiza* Ehrh.” is a name not validly published, as Ehrhart’s (1789) *Index phytophylacii Ehrhartiani* is suppressed (ICN App. 1).

18. *Asperula*

Asperula is a well-supported monophyletic genus (Soza & Olmstead, 2010a; Ehrendorfer & al., 2018: PP only; Yang & al., 2018). In contrast to *Hexaphylla* discussed above, the bracts surrounding the capitate partial inflorescences of *Asperula* s.str. are stiffly long-ciliate (for illustration see Kästner & Ehrendorfer, 2016: fig. 41). Although *Asperula* s.str. had been described as annual by Ehrendorfer & Krendl (1976a) and Ehrendorfer & al. (2005), inclusion of *A. taurina* in this lineage (Soza & Olmstead, 2010a; Kästner & Ehrendorfer, 2016; Ehrendorfer & al., 2018; Yang & al., 2018) makes this character nondiagnostic. All species of *Asperula* are diploid (Kästner & Ehrendorfer, 2016).

***Asperula* L., Sp. Pl.: 103. 1753, nom. cons.** – Type: *Asperula arvensis* L.

= *Blepharostemma* Fourr. in Ann. Soc. Linn. Lyon, n.s., 16: 398. 1868 – Type: *Blepharostemma taurina* (L.) Fourr. $\equiv$ *Asperula taurina* L.

Plants mostly annual, one species (*Asperula taurina*) perennial. Leaves in whorls of 4–8, stipules leaf-like. **Partial inflorescences capitate, bracts free, stiffly long-ciliate.** Corolla 4-merous, tubular to funnel-shaped, tube long. Mericarps 2, subglobose, dry, mostly glabrous.

Number of species and geographical distribution. – Four species in the Mediterranean area, S central Europe and SW Asia (Kästner & Ehrendorfer, 2016).

Nomenclatural note. – Fourreau (1868) did not provide a diagnosis, but refers to Lange (in Willkomm & Lange, 1868) in a short, yet unambiguous, way: “Lange, loc. cit. ex parte. (in sect.).”; “loc. cit.” refers to Lange’s *Prodromus florae Hispanicae*, given (as “Prodr. fl. hisp.”) at the genus preceding *Blepharostemma*. *Asperula* sect. *Blepharostemma* Lange (Prodr. Fl. Hispan. 2: 300. 1868) is a nomen superfluum as it contains the type of the genus *Asperula* (i.e., *A. arvensis*). When erecting the genus *Blepharostemma*, Fourreau (1868) excluded the type of Lange’s eponymic section (*A. arvensis*, kept by Fourreau in the genus *Asperula*) and thus created a new name; therefore, the correct citation is *Blepharostemma* Fourr. (instead of *Blepharostemma* (Lange) Fourr.). The type of *Blepharostemma* Fourr. is *Asperula taurina* L. Although it would be justifiable phylogenetically to separate *Blepharostemma* from *Asperula* (*A. taurina* was consistently inferred as sister to a clade comprising the other species of *Asperula* s.str.: Soza & Olmstead, 2010a; Ehrendorfer & al., 2018; Yang & al., 2018), *Asperula* as circumscribed here is well diagnosable morphologically and we consider further splitting, essentially based on life-form only (perennial versus annual), not necessary; hence, Fourreau’s name is a younger synonym of *Asperula*.

19. *Jubogalium*

We here erect the genus *Jubogalium* for *Galium* sect. *Jubogalium* originally described by Ehrendorfer (1958). *Jubogalium*, sampled only by Ehrendorfer & al. (2018), is a well-supported monophyletic genus. *Jubogalium* is easily recognizable by a furrow between the two mericarps that is occupied by yellowish tissue and that has been suspected to function as nectary tissue (Fig. 3E) (Ehrendorfer, 1958; Ehrendorfer & Krendl, 1976b; Ehrendorfer & al., 2005). When hairs are found on the mericarps, these do not cover this furrow. In addition to this character, upper inflorescence branches and pedicels often are almost capillary. In some species stipules are absent, in others the two stipules are smaller than the leaves, and in yet others they are leaf-like and whorls can consist of 4–10 elements.

Jubogalium (Ehrend.) Kadereit & Schneew., **stat. nov.** ≡ *Galium* sect. *Jubogalium* Ehrend., Oesterr. Bot. Z. 105: 212. 1958 – Type: *Jubogalium graecum* (L.) Kadereit & Schneew. ≡ *Galium graecum* L.

Diagnosis. – Plants perennial, herbaceous, or annual. Leaves 2 without stipules, 2 and 2 smaller leaf-like stipules, or leaves in whorls of 4–10, stipules leaf-like. Corolla 4-merous, rotate to funnel-shaped, tube short. Mericarps 2, ovoid, dry, glabrous or only dorsally pilose, **furrow between mericarps of yellowish (possibly secretory) tissue.**

Number of species and geographical distribution. – Fifteen species mainly in the E Mediterranean area and in SW Asia (Ehrendorfer, 1958; Ehrendorfer & Schönbeck-Temesy, 1982b; Ehrendorfer & al., 2005). For species combinations, see Appendix 1.

Etymology. – The name of this genus refers to the indumentum of the mericarps, which does not cover the furrow between the mericarps but is limited to their dorsal and lateral sides (juba: mane).

20. *Valantia*

Valantia is a well-supported monophyletic genus (Ehrendorfer & al., 2018, 5 spp. sampled).

In *Valantia*, the fruits are enclosed by the recurved, thickened and fused peduncles and pedicels that are spinulose-hispid above (Ehrendorfer & al., 2005; for illustration, see Stopp, 1971: fig. 5a,e).

Valantia L., Sp. Pl.: 1051. 1753 – Type: *Valantia muralis* L. = *Meionandra* Gauba in Oesterr. Bot. Z. 86: 62. 1937 – Type: *Meionandra columella* (Ehrenb. ex Boiss.) Gauba. – “*Vaillantia* Hoffm.”, Deutschl. Fl. 4: 274. 1804, not validly published.

Diagnosis. – Plants annual, one species perennial (*Valantia aprica* (Sm.) Tausch). Leaves in whorls of 4, stipules leaf-like. Corolla 4- (central flower) or 3-merous (lateral flowers), rotate or cup-shaped, tube short. Mericarps 2, reniform, dry, glabrous. **Fruits enclosed by recurved, thickened and fused peduncles and pedicels that are spinulose-hispid above.**

Number of species and geographical distribution. – One perennial (*Valantia aprica*) and six annual species of essentially circum-Mediterranean distribution (Kästner & Ehrendorfer, 2016).

Nomenclatural notes. – Hoffmann (1804) spelled the name as *Vaillantia*, corresponding to the spelling of the name of the commemorated person (Vaillant), but Linnaeus deliberately used the latinized form (*Valantia*). Hoffmann's correction, therefore, is not permissible (see Ex. 33 in Art. 60.10). Gauba (1937) described *Meionandra* based on *Meionandra columella* (Ehrenb. ex Boiss.) Gauba. This species is accepted as *Valantia columella* (Ehrenb. ex Boiss.) Bald., and there is no morphological evidence (Aiello & al., 1981; molecular data are still lacking) to separate *Meionandra* from *Valantia*.

21. *Cruciata*

Despite its unique morphology, support of *Cruciata* as a monophyletic group is strong only in Soza & Olmstead (2010a, four spp. sampled) and Soza & Olmstead (2010b, five spp. sampled), but not in Ehrendorfer & al. (2018, five spp. sampled) and Yang & al. (2018, five spp. sampled). In the nuclear-based tree by Yang & al. (2018), *Cruciata* is polyphyletic and nested within *Trichogalium*, a topology not supported by the nuclear data (ETS only) of Soza & Olmstead (2010b), where *Cruciata* is a well-supported monophyletic group in an unresolved position relative to *Trichogalium*. *Cruciata* can easily be recognized by its inflorescence and infructescence where the pedicels of flowers and especially of fruits are recurved and are, therefore, often positioned below the recurved bracts (for illustration see Stopp, 1971: fig. 3). In the few-flowered cymes, the central flower is hermaphroditic whereas the lateral flowers often are male.

Cruciata Mill., Gard. Dict. Abr., ed. 4. 1754 – Type: *Cruciata laevipes* Opiz

Diagnosis. – Plants perennial or annual. Leaves in whorls of 4, stipules leaf-like. **Pedicels of flowers and fruits recurved and, especially the fruits, often positioned below recurved bracts.** Corolla 4-merous, cup-shaped, tube short. **Central flower (of cyme) hermaphroditic, lateral flowers male or sterile.** Mericarps 2, ovoid to reniform, dry, glabrous or hairy.

Number of species and geographical distribution. – About 10 species centred in SW Asia, some species more widespread from the Mediterranean area and central Europe to central Asia (Kästner & Ehrendorfer, 2016).

22. *Trichogalium*

We here resurrect the genus *Trichogalium* for *Galium* sect. *Platygalium* s.l. *Trichogalium* is a mostly well supported monophyletic genus (Soza & Olmstead, 2010a,b; Ehrendorfer & al., 2018; Yang & al., 2018). However, in nuclear-based trees, *Trichogalium* is either unresolved (Soza & Olmstead, 2010b) or paraphyletic in relation to a polyphyletic *Cruciata* (Yang & al., 2018). Although this genus cannot easily be distinguished from *Galium* s.str., all its species have leaves in

whorls of four (a rather rare condition in *Galium* s.str.), and leaves often, but by no means always, have three veins (Fig. 3F). Also, many species have secretory glands on the lower surface of the leaves, often concentrated near the leaf apex (Fig. 3G). While Dempster (1978) stated that “for some obscure reason, this feature is rarely found except in species with 4 leaves to a node”, implying that it may be limited to *Trichogalium*, such glands are not always present. Whereas in the *Flora Iranica* area such glands are always present in the five species of *Trichogalium* present (Ehrendorfer & al., 2005), for the *Flora Europaea* area they have been described for four of nine species (Nicholas, 1929; Ehrendorfer & Krendl, 1976b), and in *Flora of China* (Chen & Ehrendorfer, 2011) 8 of 25 species considered to fall into *G.* sect. *Platygalium* were described as having glands. For Australia, Thompson (2009) described 15 of 17 native *Galium* species to have glands, and presence and absence of glands clearly is variable in the Americas (Dempster & Ehrendorfer, 1965; Dempster & Stebbins, 1971; Dempster, 1978, 1980, 1981, 1982, 1990). Interestingly, Nicholas (1929) also described *Cruciata* as having glands. *Trichogalium* includes *G.* sect. *Lophogalium* K.Schum., “*Baccogalium*”, which was never formally described as a section of *Galium* (Soza & Olmstead, 2010b) as well as the genera *Bataprine* Nieuwl. and *Relbunium* (Endl.) Hook.f. (Soza & Olmstead, 2010b). The genus contains species that have either hermaphroditic flowers or unisexual flowers, and plants can then be polygamous or dioecious; mericarps can be dry and glabrous, can have straight or uncinat hairs, or often can be fleshy. The evolution of these latter characters in (mostly) New World taxa of *Trichogalium* has been analysed by Soza & Olmstead (2010b).

***Trichogalium* (DC.) Fourr. in Ann. Soc. Linn. Lyon, n.s., 16: 396. 1868 ≡ *Galium* [unranked] *Trichogalia* DC., Prodr. 4: 599. 1830 – Type (designated here): *Trichogalium rotundifolium* (L.) Fourr. ≡ *Galium rotundifolium* L.**

= *Relbunium* (Endl.) Hook.f. in Bentham & Hooker, Gen. Pl. 2: 149. 1873 ≡ *Galium* sect. *Relbunium* Endl., Gen. Pl.: 523. 1839 – Type: *Relbunium hypocarpium* subsp. *nitidum* (Kunth) Ehrend.

= *Bataprine* Nieuwl. in Amer. Midl. Naturalist 1: 264. 1910 – Type: *Bataprine hispidula* (Michx.) Nieuwl.

Diagnosis. – Plants perennial, herbaceous or basally woody. **Leaves in whorls of 4, mostly (1–)3-veined**, stipules leaf-like, sometimes smaller, **often with glands mostly near apex on lower surface**. Corolla 4-merous, mostly rotate, tube short, rarely long. Flowers hermaphroditic or unisexual, plants polygamous or dioecious. Mericarps 2, reniform to subglobose, dry or fleshy, glabrous or with straight or uncinat hairs.

Number of species and geographical distribution. – According to Ehrendorfer (2017) about 80 spp. in Eurasia, 21 spp. in Australia and New Zealand, and 150 (>200 in Kästner & Ehrendorfer, 2016) in the Americas. Considering the number of names we identified for our combinations (see Appendix 1) using the literature given there, the numbers given by Ehrendorfer (2017) and Kästner & Ehrendorfer (2016) may be overestimates.

Nomenclatural notes. – Fourreau (1868) does not provide a diagnosis, but refers to, though in a rather minimalistic manner (“*D. C. in sect.*”; usually a slightly more elaborate form, “*D. C. Prodr. (in sect.)*”, is used by him), to the diagnosis provided by Candolle in his *Prodromus* for *Galium* “§ 3. *Trichogalia*” (Candolle, 1830: 599).

The typification of *Trichogalium* with *T. rotundifolium* by Kästner & Ehrendorfer (2016) is not valid because these authors failed to include a typification statement such as “designated here” (ICN Art. 7.11).

Species of both *Bataprine* and *Relbunium* have been shown to be nested in *Trichogalium* (Soza & Olmstead, 2010b) and, thus, are younger synonyms of *Trichogalium*.

23. *Galium* s.str.

Galium s.str. is a well-supported monophyletic genus (Soza & Olmstead, 2010a; Ehrendorfer & al., 2018; Yang & al., 2018). With the exception of *G. paniculatum*, all lineages segregated above from *Galium*, i.e., *Pseudogalium* (*G.* sect. *Cymogalium*: pinnately veined leaves), *Jubogalium* (*G.* sect. *Jubogalium*: furrow between mericarps), *Hydrogalium* p.p. (*G.* sect. *Aparinoides*: (sub)globose mericarps), *Hamogalium* (*G.* sect. *Depauperata*: stipule and pedicel structure) and *Trichogalium* (*G.* sect. *Platygalium*: see preceding paragraph) can more or less easily be distinguished from *Galium* s.str. by their unique apomorphies. This leaves *Galium* s.str. to contain *G.* sect. *Aparine* DC., sect. *Aspera* (Moench) Ledeb., sect. *Galium*, sect. *Hylaea*, sect. *Kolgyda* Dumort., sect. *Leiogalium* Ledeb. (included in sect. *Galium* by Kästner & Ehrendorfer, 2016 and found to be closely related to that section by Ehrendorfer & al., 2018 and Yang & al., 2018), sect. *Leptogalium* Lange, sect. *Orientogalium* Ehrend. and sect. *Trachygaleum*. *Galium* sect. *Microgalium* Griseb., recognized by Yang & al. (2018), was included in *G.* sect. *Aspera* by Kästner & Ehrendorfer (2016), but found to be sister to *G.* sect. *Leptogalium* by Yang & al. (2018). Of the listed recognized sections only *G.* sect. *Orientogalium* had not been sampled by Ehrendorfer & al. (2018). However, this section was sampled both by Soza & Olmstead (2010a) and Yang & al. (2018) and fell into *Galium* s.str. where it grouped within *G.* sect. *Leptogalium*. *Castrila*, a monospecific genus recently erected by Blanca & al. (2024), and accepted as part of Rubieae by Razafimandimbison & Rydin (2024b), clearly is part of *Galium* s.str. in an unresolved position.

In agreement with their position in one clade, close morphological links among all those sections of *Galium* s.str. listed above had been pointed out by Kästner & Ehrendorfer (2016), and several sections were found to be nonmonophyletic (Soza & Olmstead, 2010a; Jeong & al., 2016; Ehrendorfer & al., 2018; Yang & al., 2018).

***Galium* L., Sp. Pl.: 105. 1753 – Type: *Galium verum* L.**

= *Asterophyllum* K.F.Schimp. & Spenn. in Spenner, Fl. Friburg. 3: 1077. 1829, nom. superfl. – **Type (designated here): *Galium verum* L.**

- = *Aparine* Tourn. ex Guett. in Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris, 4to) 1750: 189. 1754 – **Type (designated here):** *Galium aparine* L.
- = *Aspera* Moench, Meth.: 641. 1794 ≡ *Aparinanthus* Fourr. in Ann. Soc. Linn. Lyon, n.s., 16: 397. 1868, nom. superfl. – **Type (designated here):** *Sherardia muralis* L.
- = *Aparinella* Fourr. in Ann. Soc. Linn. Lyon, n.s., 16: 397. 1868 – **Type (designated here):** *Galium parisiense* L.
- = *Castrila* Blanca, S.Ben-Menni, H.Blanca, Cueto, J.Fuentes, Ortega Oliv. & Suár.-Sant. in Taxon 73: 1010. 2024 – Type: *Castrila latens* Blanca, S.Ben-Menni, H.Blanca, Cueto, J.Fuentes, Ortega Oliv. & Suár.-Sant.
- = *Chlorostemma* Fourr. in Ann. Soc. Linn. Lyon, n.s., 16: 398. 1868 – Type: *Chlorostemma odoratum* (L.) Fourr. ≡ *Asperula odorata* L.
- “*Eyselia* Neck.”, Elem. Bot. 1: 199. 1790, not validly published (ICN App. 1).
- “*Gallion* Pohl”, Tent. Fl. Bohem. 1: 126. 1809.
- “*Galiopsis* Fourr.” in Ann. Soc. Linn. Lyon, n.s., 16: 398. 1868, nom. nud.
- “*Galion* St.-Lag.” in Ann. Soc. Bot. Lyon 7: 113. 1880, orthographical variant.

Diagnosis. – Plants perennial, herbaceous to basally woody. Leaves in whorls of (4)5–10(12), stipules leaf-like. Corolla 4-merous, mostly rotate, more rarely funnel- or cup-shaped, tube short; sometimes central flower (of cyme) hermaphroditic, lateral flowers male. Mericarps 2, ovoid, ob-ovoid, ellipsoid, reniform or rarely subglobose, dry, glabrous or hairy or with uncinat trichomes.

Number of species and geographical distribution. – *Galium* s.str. contains >300 spp. (Kästner & Ehrendorfer, 2016) distributed largely in Eurasia, reaching North America with *G.* sect. *Hylaea* and sect. *Trachygalium* and Africa with *G.* sect. *Galium* and sect. *Trachygalium*.

Nomenclatural notes. – Schimper & Spenner in Spenner (1829) merged the genera *Galium*, *Asperula*, *Sherardia* and *Valantia* in a single genus and gave it the new name *Asterophyllum*. This is, however, a nomen superfluum, as one of the available equally eligible Linnaean names should have been chosen. We here select *Galium verum* L. (explicitly listed by Schimper & Spenner in Spenner, 1829, as *Asterophyllum Galium*) as type of *Asterophyllum* in order to place *Asterophyllum* in the synonymy of *Galium*.

Miller (1754) used the spelling of pre-Linnaean authors: *Gallium* Mill. (Gard. Dict. Abr., ed. 4.: [s.p.]. 1754). As Miller gave Ladies-bedstraw as the English name of his *Gallium*, and this name today is used for *Galium verum*, it seems justified to assume that Miller’s *Gallium* has the same type as Linnaeus’s *Galium*. Also, of the four species listed by Miller (1754), two clearly belong to *Galium* s.str. (*G. rubrum* L., *G. saxatile* L.), and his *Gallium luteum* most likely refers to *G. verum* because Linnaeus (1753) listed *Gallium luteum* as the name used by Bauhin (1623) for this species. Hence, Miller’s name is best considered an orthographic variant.

Tournefort (1700) distinguished *Aparine* with rough or hairy leaves from *Gallium* (sic) without such leaf

indumentum. Guettard (1754), when discussing the two groups, modified this by emphasizing that in *Aparine* the fruits have hooked hairs or warts, which are lacking in *Galium*. Guettard used these characters to justify keeping the two genera separate, while dismissing the diagnostic characters originally used by Tournefort. As Guettard (1754) clearly referred to Tournefort’s *Institutiones rei herbariae* (Guettard, 1754: 190: “mais de treize qui le sont dans les Instituts, il n’y a que celui de Narbonne, & celui des Pyrénées qui ressemble à de la mousse, que je n’aie pas vûs”), where Latin diagnoses for both genera are provided, Tournefort’s name *Aparine* is validated by Guettard. As type for *Aparine* we choose *Galium aparine* L., which corresponds to *Aparine vulgaris*, as this species has hooked hairs on its fruits, leaves and stems, thus perfectly fitting the diagnostic characters emphasized by Tournefort and Guettard. As *G. aparine* is clearly nested within *Galium* s.str., *Aparine* is a synonym. The same name *Aparine* was also published by Hill (1756) in his *British herbal: Aparine* Hill (Brit. Herb.: 398. 1756). Although there is no direct reference to Tournefort, Hill bemoaned that Linnaeus, in his *Species plantarum* (Linnaeus, 1753), does not separate *Aparine* from *Galium* as done in his *Genera plantarum* (Linnaeus, 1737). As in Linnaeus (1737) there is a clear reference to Tournefort’s genus *Aparine*, the type for Hill’s name has to be the same as the one for Guettard’s name, rendering Hill’s *Aparine* an isonym (Art. 6.3 Note 2).

Moench (1794) introduced the name *Aspera* for what is now known as *Galium murale* (L.) All. (the name of Moench, *A. nutans*, is a nomen superfluum as it does not use the oldest available species epitheton), a species that clearly falls into *Galium* s.str.

Fourreau (1868) does not provide a diagnosis for his genus *Aparinanthus*, but refers to Lange (in Willkomm & Lange, 1868: 309), specifically to *Galium* sect. *Pseudovallantia* Lange, in his usual minimalistic way: “*Pseudo-Vallantia* Lange loc. cit. (in sect.)”. As *Aparinanthus* includes the type of *Aspera* Moench (as *A. muralis* (L.) Fourr.) and as there is no evidence that the second species included within the genus, *A. verticillatus* (Danthoine ex Lam.) Fourr., would be the type of the genus (no indication of type is given by Fourreau), we consider *Aparinanthus* Fourr. a nomen superfluum with respect to the name *Aspera* Moench. Taxonomically, both species are clearly nested within *Galium* s.str.

Fourreau (1868) did not provide a diagnosis for his genus *Aparinella*, but refers to Lange (in Willkomm & Lange, 1868: 322), specifically to *Galium* sect. *Pseudoparine* Lange: “*Pseudoparine* Lange Prodr. fl. hisp. (in sect.)”. According to Lange (in Willkomm & Lange, 1868), this group contains annual species with terminal inflorescences. Of the species listed by Fourreau (1868), *G. setaceum* Lam. (Encycl. 2: 584. 1788), belongs to what we here call *Jubogalium*, whereas all other species belong to *Galium* s.str. As Fourreau did not indicate any type for his genus, we here typify *Aparinella* with *G. parisiense* L., the species most widespread in the study area of Fourreau (1868: 397, “assez commun”). This typification places *Aparinella* Fourr. as a

synonym of *Galium* str. and makes impossible the resurrection of the name *Aparinella* for what we prefer to call *Jubogalium*.

Chlorostemma (Lange) Fourr. can be readily traced to *Asperula* sect. *Chlorostemma* Lange via a short reference (Fourreau, 1868: 398): “*Lange Prodr. fl. hisp. (in sect.)*”. This genus only contains a single species, *C. odoratum* (L.) Fourr. (corresponding to *Galium odoratum* (L.) Scop.), which clearly falls into *Galium* s.str.; hence, Fourreau’s name is a synonym.

“*Eyselia* Neck.” is a name not validly published, as all editions of Necker’s *Elementa botanica* are suppressed (ICN App. 1).

“*Gallion* Pohl” is a linguistically motivated modification of the original spelling. In a footnote, Pohl (1810: 137) stated: “Die unbeständige Schreibart der Botaniker verleitete mich, diese Pflanzengattung nach der griechischen Ursprache zu benennen. [...] Ich erlaubte mir daher nicht nur diese Benennung mit zwey l zu schreiben, sondern behielt auch noch die griechische Endung ov bey “(The variable spelling used by botanists prompted me to name this plant genus using ancient Greek. [...] I took the liberty not only to spell the name with two l, but also to keep the Greek ending ov”). Such modifications of names are not permitted (Art. 60.1).

“*Galiopsis* Fourr.” was published without any description or reference to a diagnosis elsewhere and, therefore, is a nomen nudum. Even if validly published, “*Galiopsis* Fourr.” would fall into the synonymy of *Galium* s.str. as “*Galiopsis*” contains only a single species corresponding to *Galium glaucum* L. Strangely enough, also the homonymic “*Galiopsis* St.-Lag.” (in Ann. Soc. Bot. Lyon 7: 79. 1880) is a nomen nudum. Saint-Lager’s name simply appears to be a misspelling of *Galeopsis* L., as the name is given in a list of genera of Lamiaceae on p. 24 and in a list including several generic names ending with *-is* on p. 79.

As for the name of Pohl (1810), “*Galion* St.-Lag.” is a linguistically motivated but nomenclaturally not permitted modification of the original spelling. Saint-Lager (1880: 118) wrote: “Afin de donner des exemples des diverses modifications proposées, nous avons restitué aux noms de genre d’origine grecque la désinence qui leur appartient” (Translating to: “In order to give examples of the various proposed modifications, we have restored the proper ending of the genus names of Greek origin”).

There exists one unsampled lineage that possibly deserves recognition at genus rank. This is the genus *Leptunis* Steven, containing, as far as known, only one species, *L. trichodes* (J.Gay ex DC.) Schischk., based on *Asperula trichodes* J.Gay ex DC. *Leptunis* is an annual with filiform leaves which is characterized particularly by its fruits, in which the obovoid mericarps are very strongly incurved at their apical ends (for illustration see Pobedimova, 1958d: plate XV, fig. 4). Whereas generic rank for *Leptunis* was accepted by Pobedimova (1958d) and Chen & Ehrendorfer (2011), Ehrendorfer & al. (2005) did not accept generic rank. They argued that *Asperula seticornis* Boiss., a species from Iran, has fruits intermediate between *Leptunis* and *Asperula* in the traditional

broad sense (where mericarps are more or less ellipsoid and straight), and concluded that *L. trichodes* (as *Asperula trichodes*) and *A. seticornis* should be placed in *A.* sect. *Trichodes* Boiss.

The phylogenetic position of this lineage remains unclear. Whereas Ehrendorfer & Barfuss (2014) suggested a close relationship of *Leptunis* to a clade comprising our genera 5 to 14 (*Mericarpha* to *Sherardia*), Ehrendorfer (2017) suggested a close relationship to the clade comprising our genera 5 to 9 (*Mericarpha* to *Cruciana*; i.e., clade V of Ehrendorfer & al., 2018).

In the absence of any molecular evidence, we tentatively maintain this genus in its original circumscription (i.e., with one species), acknowledging that circumscription and/or distinctness at the generic level may be subject to future change.

Genus incertum: *Leptunis*

Leptunis Steven in Bull. Soc. Imp. Naturalistes Moscou 29(2): 366. 1856 – Type: *Asperula trichodes* J.Gay ex DC., Prodr. 4: 582. 1830.

Diagnosis. – Plants annual. Leaves in whorls of 10–16, **filiform to subulate**. Corolla 4-merous, funnel-shaped, tube long. Mericarps 2, obovate, dry, **strongly incurved at apical end** when mature, sparsely appressed puberulent.

Number of species and geographical distribution. – One species from SW to central Asia and China (Chen & Ehrendorfer, 2011).

AUTHOR CONTRIBUTIONS

JWK initiated and JWK and GMS conducted this study and wrote and revised this paper.

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Appendix 1.

In this Appendix we provide the combinations necessary as a result of our reclassification of Rubiaceae-Rubieae. Species belonging to those lineages newly treated or resurrected at generic rank by us were identified in the literature, which is given after each genus name. Discrepancies between numbers of species given in the generic accounts and number of combinations made can be explained either by the fact that we missed species belonging in the respective genera or that species numbers indicated in the literature cited are estimates only.

Cruciana (Griseb.) Kadereit & Schneew.

(Pobedimova, 1958a; Ehrendorfer & Schönbeck-Temesy, 1982a; Ehrendorfer & al., 2005; Öztürk, 2013)

Cruciana anatolica (M.Öztürk) Kadereit & Schneew., **comb. nov.** = *Asperula anatolica* M.Öztürk in Turk. J. Bot. 37(1): 47. 2012

Cruciana asterocephala (Bornm.) Kadereit & Schneew., **comb. nov.** = *Asperula asterocephala* Bornm. in Bull. Herb. Boissier 7: 116. 1899

Cruciana comosa (Schönb.-Tem.) Kadereit & Schneew., **comb. nov.** = *Asperula comosa* Schönb.-Tem. in Pl. Syst. Evol. 127: 301. 1977

Cruciana glomerata (M.Bieb.) Kadereit & Schneew., **comb. nov.** = *Crucianella glomerata* M.Bieb., Fl. Taur.-Caucas. 1: 107. 1808

Cruciana kotschyana (Boiss. & Hohen.) Kadereit & Schneew., **comb. nov.** = *Crucianella kotschyana* Boiss. & Hohen. in Boissier, Diagn. Pl. Orient., ser. 1, 3: 28. 1843

Cruciana laxiflora (Boiss.) Kadereit & Schneew., **comb. nov.** = *Asperula laxiflora* Boiss., Fl. Orient. 3: 37. 1875

Cruciana molluginoides (M.Bieb.) Kadereit & Schneew., **comb. nov.** = *Crucianella molluginoides* M.Bieb., Fl. Taur.-Caucas. 1: 106. 1808

Cruciana prostrata (Adams) Kadereit & Schneew., **comb. nov.** = *Crucianella prostrata* Adams in Weber & Mohr, Beitr. Naturk. 1: 46. 1805

Cruciana szovitsii (Ehrend. & Schönb.-Tem.) Kadereit & Schneew., **comb. nov.** = *Asperula szovitsii* Ehrend. & Schönb.-Tem. in Rechinger, Fl. Iranica 176: 112. 2005

Altaiogalum Kadereit & Schneew.

Altaiogalum paniculatum (Bunge) Kadereit & Schneew., **comb. nov.** = *Asperula paniculata* Bunge in Ledebour, Fl. Altaic. 1: 140. 1829

Hamogalum Kadereit & Schneew.

(Ehrendorfer & al., 2005)

Hamogalum bifolium (S.Watson) Kadereit & Schneew., **comb. nov.** = *Galium bifolium* S.Watson, Botany (Fortieth Parallel): 134. 1871

Hamogalum exile (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Galium exile* Hook.f., Fl. Brit. India 3: 207. 1881

Hamogalum songaricum (Schrenk ex Fisch. & C.A.Mey.) Kadereit & Schneew., **comb. nov.** = *Galium songaricum* Schrenk ex Fisch. & C.A.Mey., Enum. Pl. Nov. 1: 57. 1841

Hydrogalium Kadereit & Schneew.

Species formerly classified in *Asperula* sect. *Dioicae*

(Thompson, 2009)

Hydrogalium acuminatum (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Asperula acuminata* I.Thomps. in Muellera 27: 63. 2009

Hydrogalium ambly (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula ambleia* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 99. 1928

Hydrogalium asthenes (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula asthenes* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 99. 1928

Hydrogalium charophyton (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula charophyton* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 101. 1928

Hydrogalium confertum (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula conferta* Hook.f. in London J. Bot. 6: 464 bis. 1847

Hydrogalium cunninghamii (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula cunninghamii* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 97. 1928

Hydrogalium euryphyllum (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula euryphylla* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 100. 1928

Hydrogalium geminifolium (F.Muell.) Kadereit & Schneew., **comb. nov.** = *Asperula geminifolia* F.Muell., Fragm. 5: 147. 1866

Hydrogalium gemellum (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula gemella* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928(3): 102. 1928

Hydrogalium gunnii (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula gunnii* Hook.f. in London J. Bot. 6: 464 bis. 1847

Hydrogalium hoskingii (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Asperula hoskingii* I.Thomps. in Muellera 27: 54. 2009

Hydrogalium minimum (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula minima* Hook.f. in London J. Bot. 6: 464 bis. 1847

Hydrogalium oblanceolatum (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Asperula oblanceolata* I.Thomps. in Muellera 27: 68. 2009

Hydrogalium perpusillum (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula perpusilla* Hook.f., Fl. Nov.-Zel. 1: 114. 1853

Hydrogalium polymerum (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Asperula polymera* I.Thomps. in Muellera 27: 61. 2009

Hydrogalium pusillum (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula pusilla* Hook.f. in London J. Bot. 6: 463 bis. 1847

Hydrogalium scoparium (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula scoparia* Hook.f. in London J. Bot. 6: 463 bis. 1847

Hydrogalium subsimplex (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Asperula subsimplex* Hook.f. in London J. Bot. 6: 463 bis. 1847

Hydrogalium subulifolium (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula subulifolia* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 98. 1928

Hydrogalium syrticola (Miq.) Kadereit & Schneew., **comb. nov.** = *Rubia syrticola* Miq. in Ned. Kruidk. Arch. 4: 111. 1856.

Hydrogalium tetraphyllum (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula euryphylla* var. *tetraphylla* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 100. 1928 = *Asperula tetraphylla* (Airy Shaw & Turrill) I.Thomps. in Muellera 27: 64. 2009

Hydrogalium wimmeranum (Airy Shaw & Turrill) Kadereit & Schneew., **comb. nov.** = *Asperula wimmerana* Airy Shaw & Turrill in Bull. Misc. Inform. Kew 1928: 94. 1928.

Species formerly classified in *Asperula* sect. *Glabella*

(Pobedimova, 1958a; Ehrendorfer & Krendl, 1976a; Ehrendorfer & Schönbeck-Temesy, 1982a; Ehrendorfer & al., 2005; Kästner & Ehrendorfer, 2016)

Hydrogalium bargyli (Gomb.) Kadereit & Schneew., **comb. nov.** = *Asperula bargyli* Gomb. in Bull. Soc. Bot. France 105: 255. 1958

Hydrogalium cymulosum (Post) Kadereit & Schneew., **comb. nov.** = *Galium cymulosum* Post in J. Linn. Soc., Bot. 24: 432. 1888

Hydrogalium gracile (C.A.Mey.) Kadereit & Schneew., **comb. nov.** = *Asperula gracilis* C.A.Mey., Verz. Pfl. Casp. Meer.: 154. 1831

Appendix 1. Continued.

Hydrogalium involucreatum (Wahlenb.) Kadereit & Schneew., **comb. nov.** = *Asperula involucreata* Wahlenb. in J. Berggr., Resor. Eur. Österl. 2, Bih.: 21. 1826
Hydrogalium laevigatum (L.) Kadereit & Schneew., **comb. nov.** = *Asperula laevigata* L., Mant. Pl.: 28. 1767
Hydrogalium libanoticum (Boiss.) Kadereit & Schneew., **comb. nov.** = *Asperula libanotica* Boiss., Diagn. Pl. Orient., ser. 1, 10: 59. 1849
Hydrogalium maximoviczii (Kom.) Kadereit & Schneew., **comb. nov.** = *Asperula maximoviczii* Kom. in Trudy Glavn. Bot. Sada 39: 109. 1923
Hydrogalium platygaleum (Maxim.) Kadereit & Schneew., **comb. nov.** = *Asperula platygaleum* Maxim. in Bull. Acad. Imp. Sci. Saint-Petersbourg, sér. 3, 19: 284. 1874

Hydrogalium suave (Fisch., C.A.Mey. & Avé-Lall.) Kadereit & Schneew., **comb. nov.** = *Asperula suavis* Fisch., C.A.Mey. & Avé-Lall., Index Seminum (Petropolitanus) 9: 62. 1843

Hydrogalium shikokianum (Nakai) Kadereit & Schneew., **comb. nov.** = *Galium shikokianum* Nakai in Bot. Mag. (Tokyo) 23: 103. 1909
= *Asperula trifida* Makino in Bot. Mag. (Tokyo) 17: 72. 1903

Note: As the epithet *trifidum* is already used in the combination for *Galium trifidum* L., we chose *Hydrogalium shikokianum* as a new name for the combination concerning *Asperula trifida* Makino (in Bot. Mag. (Tokyo) 17: 72. 1903) using the oldest synonym of *Asperula trifida*.

Hydrogalium tinctorium (L.) Kadereit & Schneew., **comb. nov.** = *Asperula tinctoria* L., Sp. Pl.: 104. 1753

Hydrogalium xylorrhizum (Náb.) Kadereit & Schneew., **comb. nov.** = *Asperula xylorrhiza* Nábělek in Spisy Přír. Fak. Masarykovy Univ. 35: 133. 1923

Species formerly classified in *Galium* sect. *Aparinoides*

(Puff, 1974, 1975, 1979; Ehrendorfer & Puff, 1976; Ehrendorfer & Schönbeck-Temesy, 1982b; Ehrendorfer & al., 2005; Chen & Ehrendorfer, 2011; Kästner & Ehrendorfer, 2016)

Hydrogalium antarcticum (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Galium antarcticum* Hook.f., Fl. Antarct. 2: 303 bis. 1846

Hydrogalium brevipes (Fernald & Wiegand) Kadereit & Schneew., **comb. nov.** = *Galium brevipes* Fernald & Wiegand in Rhodora 12: 78. 1910

Hydrogalium chonoense (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Galium chonoense* Hook.f., Fl. Antarct. 2: 303 bis. 1846

Hydrogalium claytonii (Michx.) Kadereit & Schneew., **comb. nov.** = *Galium claytonii* Michx., Fl. Bor.-Amer. 1: 78. 1803

= *Galium tinctorium* L. Sp. Pl.: 106. 1753

Note: As the epithet *tinctorium* is already used in the combination for *Asperula tinctoria* L., we chose *Hydrogalium claytonii* as a new name for the combination concerning *Galium tinctorium* L. (Sp. Pl.: 106. 1753) using the oldest synonym of *Galium tinctorium*.

Hydrogalium constrictum (Chaub.) Kadereit & Schneew., **comb. nov.** = *Galium constrictum* Chaub. in Saint-Amans, Fl. Agen.: 66. 1821

Hydrogalium debile (Desv.) Kadereit & Schneew., **comb. nov.** = *Galium debile* Desv., Observ. Pl. Angers: 134. 1818

Hydrogalium elongatum (C.Presl) Kadereit & Schneew., **comb. nov.** = *Galium elongatum* C.Presl, Delic. Prag.: 119. 1822

Hydrogalium innocuum (Miq.) Kadereit & Schneew., **comb. nov.** = *Galium innocuum* Miq., Fl. Ned. Ind., Eerste Bijv. 2: 341. 1861

Hydrogalium karakulense (Pobed.) Kadereit & Schneew., **comb. nov.** = *Galium karakulense* Pobed. in Komarov, Fl. URSS 23: 712. 1958

Hydrogalium labradoricum (Wiegand) Kadereit & Schneew., **comb. nov.** = *Galium tinctorium* L. var. *labradoricum* Wiegand in Bull. Torrey Bot. Club 24: 398. 1897 = *Galium labradoricum* (Wiegand) Wiegand in Rhodora 6: 21. 1904

Hydrogalium obtusum (Bigelow) Kadereit & Schneew., **comb. nov.** = *Galium obtusum* Bigelow, Fl. Boston., ed. 2: 55. 1824

Hydrogalium palustre (L.) Kadereit & Schneew., **comb. nov.** = *Galium palustre* L., Sp. Pl.: 105. 1753

Hydrogalium scioanum (Chiov.) Kadereit & Schneew., **comb. nov.** = *Galium scioanum* Chiov. in Ann. Bot. (Rome) 9: 322. 1911

Hydrogalium stenophyllum (Baker) Kadereit & Schneew., **comb. nov.** = *Galium stenophyllum* Baker in Bull. Misc. Inform. Kew 1895(99): 69. 1895.

Hydrogalium tanganyikense (Ehrend. & Verdc.) Kadereit & Schneew., **comb. nov.** = *Galium tanganyikense* Ehrend. & Verdc. in Kew Bull. 28(3): 488. 1974

Hydrogalium trianae (Wernham) Kadereit & Schneew., **comb. nov.** = *Galium trianae* Wernham in J. Bot. 50: 244. 1912

Hydrogalium trifidum (L.) Kadereit & Schneew., **comb. nov.** = *Galium trifidum* L., Sp. Pl.: 105. 1753

Jubogalium (Ehrend.) Kadereit & Schneew.

(Ehrendorfer, 1958; Ehrendorfer & Schönbeck-Temesy, 1982b)

Jubogalium canum (Req. ex DC.) Kadereit & Schneew., **comb. nov.** = *Galium canum* Req. ex DC., Prodr. 4: 602. 1830

Jubogalium cappadocicum (Boiss.) Kadereit & Schneew., **comb. nov.** = *Galium cappadocicum* Boiss., Diagn. Pl. Orient., ser. 1, 3: 43. 1843

Jubogalium cassium (Boiss.) Kadereit & Schneew., **comb. nov.** = *Galium cassium* Boiss., Diagn. Pl. Orient., ser. 1, 10: 68. 1849

Jubogalium dumosum (Boiss.) Kadereit & Schneew., **comb. nov.** = *Galium dumosum* Boiss., Diagn. Pl. Orient., ser. 1, 3: 44. 1843

Jubogalium exstipulatum (P.H. Davis) Kadereit & Schneew., **comb. nov.** = *Galium exstipulatum* P.H. Davis in Kew Bull. 4: 102. 1949

Jubogalium graecum (L.) Kadereit & Schneew., **comb. nov.** = *Galium graecum* L., Mant. Pl.: 38. 1767

Jubogalium jemense (Kotschy) Kadereit & Schneew., **comb. nov.** = *Galium jemense* Kotschy in Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Cl., Abt. 1, 52: 257. 1866

Jubogalium jungermannioides (Boiss.) Kadereit & Schneew., **comb. nov.** = *Galium jungermannioides* Boiss., Diagn. Pl. Orient., ser. 1, 3: 43. 1843

Jubogalium kahelianum (Deflers) Kadereit & Schneew., **comb. nov.** = *Galium kahelianum* Deflers, Voyage Yemen: 145. 1889

Jubogalium pamphylicum (Boiss. & Heldr.) Kadereit & Schneew., **comb. nov.** = *Galium pamphylicum* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 10: 69. 1849

Jubogalium parvulum (Hub.-Mor. ex Ehrend. & Schönb.-Tem.) Kadereit & Schneew., **comb. nov.** = *Galium parvulum* Hub.-Mor. ex Ehrend. & Schönb.-Tem. in Notes Roy. Bot. Gard. Edinburgh 37: 257. 1979

Jubogalium petrae (Oliv. ex Hart) Kadereit & Schneew., **comb. nov.** = *Galium petrae* Oliv. ex Hart in Trans. Roy. Irish Acad. 28: 433. 1885

Jubogalium polatiense (H.Duman & E.Doğan) Kadereit & Schneew., **comb. nov.** = *Galium polatiense* H.Duman & E.Doğan in Nordic J. Bot. 2025(8)-e04747: 2. 2025.

Jubogalium setaceum (Lam.) Kadereit & Schneew., **comb. nov.** = *Galium setaceum* Lam., Encycl. 2: 584. 1788

Jubogalium sinaicum (Delile ex Decne.) Kadereit & Schneew., **comb. nov.** = *Asperula sinaica* Delile ex Decne. in Ann. Sci. Nat., Bot., sér. 2, 2: 268. 1834

Jubogalium thiebautii (Ehrend.) Kadereit & Schneew., **comb. nov.** = *Galium thiebautii* Ehrend. in Ark. Bot., n.s., 5: 421. 1960

Trichogalium (DC.) Fourr.

(Ehrendorfer, 1955, 1956; Pobedimova, 1958b; Dempster, 1959, 1978, 1980, 1981, 1982, 1990; Dempster & Ehrendorfer, 1965; Dempster & Stebbins, 1971; Ehrendorfer & Krendl, 1976b; Porto & al., 1977; Puff, 1978; Ehrendorfer & Schönbeck-Temesy, 1982b; Lee, 1985; Yamazaki, 1993; Ehrendorfer & al., 2005; Thompson, 2009; Soza & Olmstead, 2010a,b; Chen & Ehrendorfer, 2011; Breitwieser & al., 2023; Natural Resources Conservation Service, 2025)

Trichogalium albescens (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Galium albescens* Hook.f. in London J. Bot. 6: 462 bis. 1847

Trichogalium ambiguum (W.Wight) Kadereit & Schneew., **comb. nov.** = *Galium ambiguum* W.Wight in Zoë 5: 55. 1900

Appendix 1. Continued.

- Trichogalium amblyophyllum* (Schrenk ex Fisch. & C.A.Mey.) Kadereit & Schneew., **comb. nov.** = *Galium amblyophyllum* Schrenk ex Fisch. & C.A.Mey., Enum. Pl. Nov. 1: 56. 1841
- Trichogalium amurense* (Pobed.) Kadereit & Schneew., **comb. nov.** = *Galium amurense* Pobed. in Komarov, Fl. URSS 23: 716. 1958
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- Trichogalium articulatum* (Lam.) Kadereit & Schneew., **comb. nov.** = *Galium articulatum* Lam., Encycl. 1: 260. 1792
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- Trichogalium aschenbornii* (S.Schauer) Kadereit & Schneew., **comb. nov.** = *Galium aschenbornii* S.Schauer in Linnaea 20: 701. 1847
- Trichogalium atherodes* (Spreng.) Kadereit & Schneew., **comb. nov.** = *Galium atherodes* Spreng., Syst. Veg. 4(2): 39. 1827
- Trichogalium australe* (DC.) Kadereit & Schneew., **comb. nov.** = *Galium australe* DC., Prodr. 4: 608. 1830
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- Trichogalium cotinoides* (Cham. & Schltdl.) Kadereit & Schneew., **comb. nov.** = *Galium cotinoides* Cham. & Schltdl. in Linnaea 3: 227. 1828
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- Trichogalium desereticum* (Dempster & Ehrend.) Kadereit & Schneew., **comb. nov.** = *Galium desereticum* Dempster & Ehrend. in Brittonia 17: 314. 1965
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- Trichogalium ericoides* (Lam.) Kadereit & Schneew., **comb. nov.** = *Galium ericoides* Lam., Encycl. 2: 583. 1786
- Trichogalium eriocarpum* (Bartl. ex DC.) Kadereit & Schneew., **comb. nov.** = *Galium eriocarpum* Bartl. ex DC., Prodr. 4: 600. 1830
- Trichogalium espiniacicum* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium espiniacicum* Dempster in Allertonia 5: 299. 1990
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- Trichogalium fuegianum* (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Galium fuegianum* Hook.f., Fl. Antarct. 2: 302. 1846
- Trichogalium fuscum* (M.Martens & Galeotti) Kadereit & Schneew., **comb. nov.** = *Galium fuscum* M.Martens & Galeotti in Bull. Acad. Roy. Sci. Bruxelles 11(1): 126. 1844
- Trichogalium galapagoense* (Wiggins) Kadereit & Schneew., **comb. nov.** = *Galium galapagoense* Wiggins in Madroño 20: 250. 1970
- Trichogalium gaudichaudii* (DC.) Kadereit & Schneew., **comb. nov.** = *Galium gaudichaudii* DC., Prodr. 4: 607. 1830
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- Trichogalium glaberrimum* (Hemsl.) Kadereit & Schneew., **comb. nov.** = *Galium glaberrimum* Hemsl., Diagn. Pl. Nov. Mexic. 3: 53. 1878
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- Trichogalium guadalupense* (Spreng.) Kadereit & Schneew., **comb. nov.** = *Rubia guadalupensis* Spreng., Syst. Veg. 1: 397. 1824
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- Trichogalium hatschbachii* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium hatschbachii* Dempster in Allertonia 5: 303. 1990
- Trichogalium hilendiae* (Dempster & Ehrend.) Kadereit & Schneew., **comb. nov.** = *Galium hilendiae* Dempster & Ehrend. in Brittonia 17: 310. 1965
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- Trichogalium hirtiflorum* (Req. ex DC.) Kadereit & Schneew., **comb. nov.** = *Galium hirtiflorum* Req. ex DC., Prodr. 4: 600. 1830
- Trichogalium hirtum* (Lam.) Kadereit & Schneew., **comb. nov.** = *Galium hirtum* Lam., Encycl. 2: 583. 1786
- Trichogalium hispidulum* (Michx.) Kadereit & Schneew., **comb. nov.** = *Galium hispidulum* Michx., Fl. Bor.-Amer. 1: 79. 1803
- Trichogalium huancavelicum* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium huancavelicum* Dempster in Allertonia 2: 400. 1981
- Trichogalium humile* (Cham. & Schltdl.) Kadereit & Schneew., **comb. nov.** = *Galium humile* Cham. & Schltdl. in Linnaea 3: 226. 1828
- Trichogalium humilioides* (M.L.Porto & Ehrend.) Kadereit & Schneew., **comb. nov.** = *Relbunium humilioides* M.L.Porto & Ehrend. in Pl. Syst. Evol. 128: 179. 1977
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- Trichogalium iltisii* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium iltisii* Dempster in Univ. Calif. Publ. Bot. 73: 8. 1978
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- Trichogalium indecorum* (Cham. & Schltdl.) Kadereit & Schneew., **comb. nov.** = *Rubia indecora* Cham. & Schltdl. in Linnaea 3: 229. 1828
- Trichogalium jepsonii* (Hilend & J.T.Howell) Kadereit & Schneew., **comb. nov.** = *Galium jepsonii* Hilend & J.T.Howell in Leaf. W. Bot. 1: 135. 1934
- Trichogalium johnstonii* (Dempster & Stebbins) Kadereit & Schneew., **comb. nov.** = *Galium johnstonii* Dempster & Stebbins in Madroño 21: 84. 1971
- Trichogalium juniperinum* (Standl.) Kadereit & Schneew., **comb. nov.** = *Galium juniperinum* Standl. in Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 114. 1940
- Trichogalium kamtschaticum* (Steller ex Schult. & Schult.f.) Kadereit & Schneew., **comb. nov.** = *Galium kamtschaticum* Steller ex Schult. & Schult.f., Mant. 3: 186. 1827
- Trichogalium killipii* (Dempster & Ehrend.) Kadereit & Schneew., **comb. nov.** = *Galium killipii* Dempster & Ehrend. in Allertonia 2: 262. 1980
- Trichogalium kinuta* (Nakai & H.Hara) Kadereit & Schneew., **comb. nov.** = *Galium kinuta* Nakai & H.Hara in J. Jap. Bot. 9: 518. 1933
- Trichogalium kunmingense* (Ehrend.) Kadereit & Schneew., **comb. nov.** = *Galium kunmingense* Ehrend. in Novon 20: 270. 2010
- Trichogalium lacrimiforme* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium lacrimiforme* Dempster in Madroño 23: 110. 1975
- Trichogalium lanceolatum* (Torr. & A.Gray) Kadereit & Schneew., **comb. nov.** = *Galium circaezans* Michx. var. *lanceolatum* Torr., Cat. Pl. New York: 23. 1819 = *Galium lanceolatum* (Torr.) Torr., Fl. N. Middle United States: 168. 1824
- Trichogalium latifolium* (Michx.) Kadereit & Schneew., **comb. nov.** = *Galium latifolium* Michx., Fl. Bor.-Amer. 1: 79. 1803
- Trichogalium latoramosum* (Clos) Kadereit & Schneew., **comb. nov.** = *Galium latoramosum* Clos in Gay, Fl. Chil. 3: 187. 1848
- Trichogalium leiocarpum* (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Galium leiocarpum* I.Thomps. in Muelleria 27: 79. 2009
- Trichogalium leptogonium* (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Galium leptogonium* I.Thomps. in Muelleria 27: 84. 2009
- Trichogalium leptum* (Phil.) Kadereit & Schneew., **comb. nov.** = *Galium leptum* Phil. in Anales Univ. Chile 85: 734. 1894
- Trichogalium lilloi* (Hicken) Kadereit & Schneew., **comb. nov.** = *Galium lilloi* Hicken in Darwiniana 1: 140. 1924
- Trichogalium linearifolium* (Turcz.) Kadereit & Schneew., **comb. nov.** = *Galium linearifolium* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 7: 152. 1837
- Trichogalium liratum* (N.A.Wakef.) Kadereit & Schneew., **comb. nov.** = *Galium liratum* N.A.Wakef. in Vict. Naturalist 72: 70. 1955
- Trichogalium longipedunculatum* (Mariath & Ehrend.) Kadereit & Schneew., **comb. nov.** = *Relbunium longipedunculatum* Mariath & Ehrend. in Pl. Syst. Evol. 128: 184. 1977
- Trichogalium magellanicum* (Hook.f.) Kadereit & Schneew., **comb. nov.** = *Galium magellanicum* Hook.f., Fl. Antarct. 2: 302 bis. 1846
- Trichogalium magnifolium* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium matthewsii* A.Gray var. *magnifolium* Dempster in Brittonia 10: 189. 1958 = *Galium magnifolium* (Dempster) Dempster in Brittonia 11: 111. 1959
- Trichogalium mandonii* (Britton) Kadereit & Schneew., **comb. nov.** = *Galium mandonii* Britton in Bull. Torrey Bot. Club 18: 263. 1891
- Trichogalium martirensense* (Dempster & Stebbins) Kadereit & Schneew., **comb. nov.** = *Galium martirensense* Dempster & Stebbins in Madroño 18: 110. 1965
- Trichogalium masafueranum* (Skotts.) Kadereit & Schneew., **comb. nov.** = *Galium masafueranum* Skotts., Phanerogams Juan Fernandez Isl. [extr. Nat. Hist. Juan Fernandez 2]: 174. 1921
- Trichogalium matthewsii* (A.Gray) Kadereit & Schneew., **comb. nov.** = *Galium matthewsii* A.Gray in Proc. Amer. Acad. Arts 19: 80. 1883
- Trichogalium mazocarpum* (Greenm.) Kadereit & Schneew., **comb. nov.** = *Relbunium mazocarpum* Greenm. in Proc. Amer. Acad. Arts 41: 250. 1905
- Trichogalium mechudoense* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium mechudoense* Dempster in Univ. Calif. Publ. Bot. 73: 15. 1978
- Trichogalium megapotamicum* (Spreng.) Kadereit & Schneew., **comb. nov.** = *Galium megapotamicum* Spreng., Syst. Veg. 4(2): 39. 1827
- Trichogalium microlobum* (I.Thomps.) Kadereit & Schneew., **comb. nov.** = *Galium microlobum* I.Thomps. in Muelleria 27: 100. 2009
- Trichogalium microphyllum* (A.Gray) Kadereit & Schneew., **comb. nov.** = *Galium microphyllum* A.Gray in Smithsonian Contr. Knowl. 3(5): 80. 1852
- Trichogalium migrans* (Ehrend. & McGill.) Kadereit & Schneew., **comb. nov.** = *Galium migrans* Ehrend. & McGill. in Telopea 2: 362. 1983
- Trichogalium miguelense* (Greene) Kadereit & Schneew., **comb. nov.** = *Galium miguelense* Greene in Pittonia 1: 34. 1887

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- Trichogalium moranii* (Dempster) Kadereit & Schneew., **comb. nov.** = *Galium moranii* Dempster in Brittonia 22: 190. 1970
- Trichogalium morii* (Hayata) Kadereit & Schneew., **comb. nov.** = *Galium morii* Hayata, Icon. Pl. Formos. 7: 32. 1918
- Trichogalium muelleri* (K.Schum.) Kadereit & Schneew., **comb. nov.** = *Relbunium muelleri* K.Schum. in Martius, Fl. Bras. 6(6): 406. 1889
- Trichogalium multiflorum* (Kellogg) Kadereit & Schneew., **comb. nov.** = *Galium multiflorum* Kellogg in Proc. Calif. Acad. Sci. 2: 97. 1861
- Trichogalium munzii* (Hilend & J.T.Howell) Kadereit & Schneew., **comb. nov.** = *Galium munzii* Hilend & J.T.Howell in Leaflet. W. Bot. 1: 135. 1934
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Appendix 1. Continued.

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