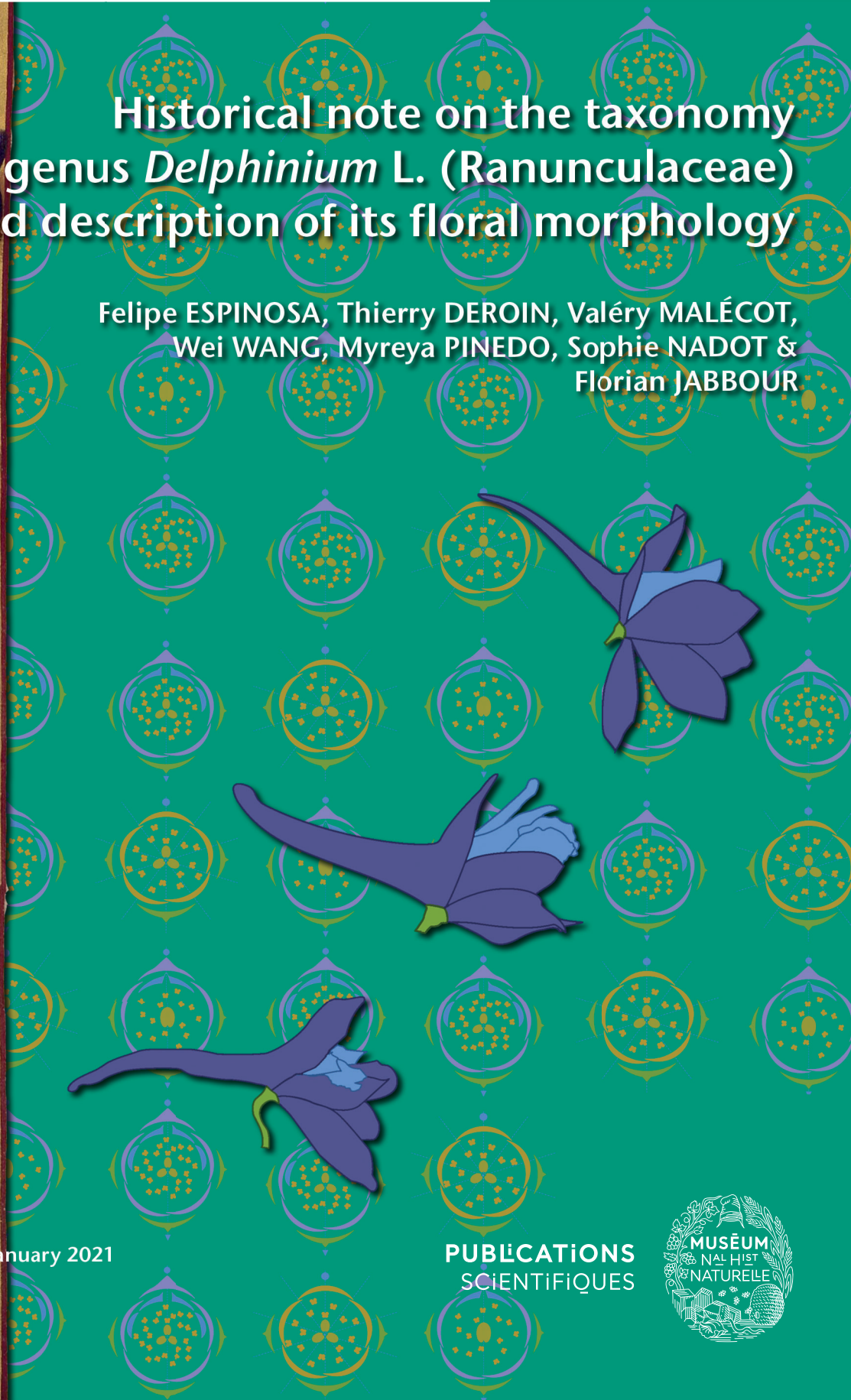




Historical note on the taxonomy of the genus *Delphinium* L. (Ranunculaceae) with an amended description of its floral morphology

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ABSTRACT

Since its first valid description by Linnaeus in 1753, the genus *Delphinium* L. has undergone numerous taxonomical changes that we synthesize here. The knowledge of the taxonomic history of the genus is essential to clarify its circumscription. For this purpose, we outline its pre-Linnean taxonomic history, from Dioscorides' translated works dating back to the 16th century to Tournefort's classification in 1694. Regarding its post-Linnean history, we discuss the three different lectotypifications proposed during in the 20th century. In addition, we amend the description of the typical flower of *Delphinium* by including the characteristics of the species *D. ecalcaratum* S.Y. Wang & K.F. Zhou and *D. turcicum* (H.Duman, Vural, Aytaç & Adigüzel) Espinosa with actinomorphic flowers.

RÉSUMÉ

Note historique sur la taxonomie du genre Delphinium L. (Ranunculaceae) et amendement de la description de la morphologie florale.

Depuis la première description valide du genre *Delphinium* L. en 1753 par Linné, celui-ci a subi de nombreuses modifications taxonomiques, dont la synthèse est proposée ici. Une connaissance de l'histoire taxonomique du genre est essentielle pour sa définition actuelle. Pour cela, d'une part, nous détaillons son histoire pré-linnéenne, depuis les traductions de Dioscoride datant du xvi^e siècle jusqu'à la classification de Tournefort en 1694. Nous présentons ensuite un historique de la taxonomie post-linnéenne du genre, en discutant les trois lectotypifications proposées au cours du xxe siècle. Nous exposons enfin sa taxonomie actuelle. D'autre part, nous amendons la description de sa fleur typique en y incluant les caractéristiques des espèces à fleurs actinomorphes *D. ecalcaratum* S.Y. Wang & K.F. Zhou et *D. turcicum* (H.Duman, Vural, Aytaç & Adigüzel) Espinosa.

INTRODUCTION

Dating back to the ancient Greeks, the term '*Delphinium*' was used in the first botanical treaties to refer to a Mediterranean group of plants. Today, this botanical name refers to a genus formed of approximately 350 species distributed in the Northern Hemisphere and tropical African mountains (Wang & Warnock 2001; Jabbour & Renner 2012a; Chartier *et al.* 2016). Over its long history, the genus has undergone numerous changes in its intrageneric composition and classification. These taxonomical reorganizations led to confusions in typification (Warnock 1993; Blanché *et al.* 1997). The knowledge of the taxonomical history of the genus is essential to clarify its circumscription and making a correct classification. In this context, the aim of this article is to outline the pre-Linnean taxonomic history of the genus *Delphinium*, to discuss the three different lectotypifications proposed during the 20th century and to amend the description of its typical flower.

PRE-LINNAEAN HISTORY OF THE GENUS *DELPHINIUM* L.

The first reference to the name '*Delphinium*' (in this article, pre-Linnean Latin botanical names are written between inverted commas) is found in the work of Dioscorides *De Materia Medica*, whom we became aware of thanks to anonymous Arab, Greek and Latin manuscripts from the 5th and the 6th centuries, and printed translations of the 16th century (Ruel 1527: 100; 1529: 180; Matthioli 1554: 367; 1565: 781; Laguna 1555: 318 ('*Delphinio*' in Spanish); Mathée 1559: 286). The name

is given to plants presenting long, thin and dissected leaves resembling dolphins (from the Greek δελφίνιον, [delphinion]). In these translations, confusion between the leaves and the floral parts is unlikely, because the vegetative and the reproductive parts of the plant are described separately. However (see below), a more recent translation compares the flower to a dolphin. Some works from the same century, very probably influenced by Dioscorides' translations, also include the name '*Delphinium*' (Dodoens 1554: 202; 1557: 123). A more detailed survey of the various Greek and Latin versions of Dioscorides' work may be necessary to trace a possible evolution in the name. Anyhow, Wellmann's edition (Wellmann 1906) provides the following text:

III.73.1 “δελφίνιον· οἱ δὲ διάχυτος, οἱ δὲ διάχυσις, οἱ δὲ παράλυσις, οἱ δὲ κάμματος, οἱ δὲ ὑάκινθος, οἱ δὲ ὑφαί-
 μον, οἱ δὲ ἄρας, οἱ δὲ δελφινιάς, οἱ δὲ Νήρειον, οἱ δὲ Νηρεί-
 α-διον, οἱ δὲ σώσανδρον, οἱ δὲ Κρόνιον, Ρωμαῖοι βουκίνους μίνον. κλώνας
 ἀνίησι δισπιθαμιαίους ἢ καὶ μείζονας ἀπὸ μιᾶς ῥίζης, περὶ οὓς
 φυλλάρια ἐπεσχισμένα, λεπτά, ἐπιμήκη, δελφινιοειδῆ, ὅθεν καὶ
 ὠνόμασται· ἄνθος δὲ ὅμοιον λευκοῖω, ἐμπόρφυρον, σπέρμα ἐν
 λοβοῖς κέγχρω ἐμφέρές.

2 τούτου τὸ σπέρμα βοηθεῖ ποθὲν σὺν οἴνῳ σκορπιοπλήκτοις
 ὥς οὐδὲν ἕτερον· φασι δὲ καὶ τοὺς σκορπίους παρατεθείσης
 τῆς πόας παραλύεσθαι ἀπράκτους τε καὶ ναρκῶδεις γίνεσθαι,
 ὑφαιρουμένης δὲ εἰς τὸ αὐτὸ καθεστάναι. φύεται ἐν τραχέσιν
 καὶ εὐήλοισ χωρίοις.

δελφίνιον ἕτερον· οἱ δὲ ὑάκινθον, Ρωμαῖοι βουκίνους· καὶ αὐτὸ
 ἐμφέρές τῷ πρὸ αὐτοῦ, τοῖς δὲ φύλλοις καὶ τοῖς κλωνίοις ἰσχνότερον
 πολλῶ, δύναμιν ἔχον καὶ αὐτὸ τὴν αὐτὴν τῷ προειρημένῳ, οὐχ
 οὕτως δὲ ἐνεργές.” (Wellmann 1906: 84).

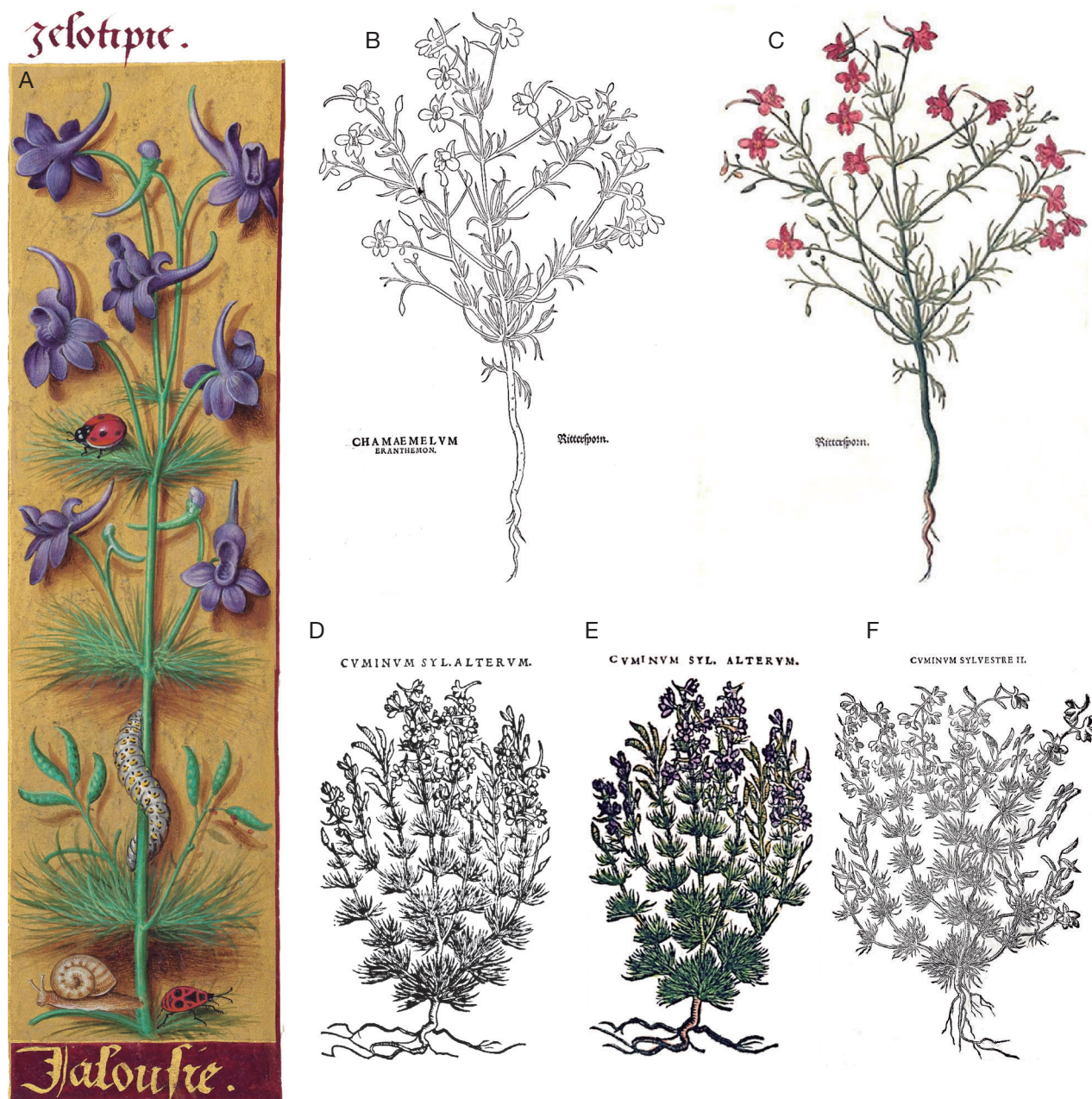


FIG. 1. — Illustrations showing specimen of *Consolida* (DC.) Gray with other names than '*Consolida*' or '*Delphinium*', reproduced from: **A**, Bourdichon (1505-1510: 35); **B**, Fuchs (1542: 27); **C**, Fuchs (1543: 15); **D**, Matthioli (1554: 357); **E**, Laguna (1555: 308); **F**, Matthioli (1565: 760). **A**, Plant called by the vernacular French name 'Jalousie'; **B**, Plant named by the erroneous name '*Chamaemelum eranthemon*' and **B**, **C**, by the vernacular German name 'Rittersporn' still in use; **D-F**, Plants are named by the erroneous name '*Cuminum syl. altervm*'.

Which translates as: "Delphinion [some call it Diachysis, other Diachytos, Paralysis, Kamaros, Hyakinthos, Delphinios, Nerion, Neriadion, Sosandron, Kronion, the Romans Bucinus minor] leaves are incised, tender, and elongated, and are borne on several stems arising from a single root. The purple flower looks like the flower of Matthiola and has a dolphin-like shape, whence the name. The seeds sit in capsules and are similar to millet seeds. Ingested with wine, they help against scorpion's sting like no other remedy. It is also said that the scorpions get paralyzed when getting close from the plant. It grows in harsh and sunny spots" (Wellmann 1906).

Interestingly, in the *Natural History* of Pliny the Elder, plants corresponding to '*Delphinium*' sensu Dioscorides appear under the name '*Hyacinthum*' (Gaius Plinius Secundus 1850: 537). There is no description of the plant, but the medicinal uses mentioned for '*Hyacinthum*' are the same as those described by Dioscorides for '*Delphinium*'. Additionally, some works dating back to the 16th century include illustrations showing specimen of *Consolida* (DC.) Gray, now included in *Delphinium* L. (Jabbour & Renner 2011a), associated with other names than '*Consolida*' or '*Delphinium*'. Some of these vernacular names are 'Jalousie', a French word used in olden days to refer to *Consolida* (DC.) Gray (Bourdichon 1505-1510: 35; Fig. 1A) or 'Rittersporn', a

German word still currently referring to *Delphinium* L. plants (Fuchs 1542: 27; 1543: 15, Fig. 1B, C). Other names, once used to refer to larkspurs, actually correspond to other genera showing vegetative characteristics similar to those of *Consolida*, such as thin and finely dissected leaves: '*Chamaemelum eranthemon*' (Fuchs 1542: 27, Fig. 1B), or in some translations of *De Materia Medica*, '*Cuminum syl. alternum*' (Matthioli 1554: 357; 1565: 760; Laguna 1555: 308; Fig. 1D-F). These names, corresponding to non-universal or artificial classifications, had been withdrawn in the last centuries.

In the first half of the 17th century, Bauhin proposed a group called '*Consolida regalis*' based on the name given by the 'ancient authors' (sic) (Bauhin 1623: 141). In this group, he included the '*Hyacinthum*' sensu Pliny the Elder and '*Delphinium*' sensu Dioscorides (Bauhin 1623: 141). Conversely, at the end of the same century, Tournefort (1694: 338) resurrected the name '*Delphinium*', considering '*Consolida regalis*' sensu Bauhin as synonym. Additionally, he suggested not to use Bauhin's '*Consolida regalis*' to avoid any confusion with the groups '*Consolida major*', '*media*' and '*minor*' (Tournefort 1694: 338). Tournefort explained that flower buds looked like the representations of dolphins made by painters (Tournefort 1694: 338). He described '*Delphinium*' flowers as having a pentamerous dorsally-spurred calyx and a capsule with three separate cavities (Tournefort 1694: 338). All these changes of name and circumscription of this group of plants in pre-Linnaean classifications already highlight the complexity of its morphology and the difficulty to disentangle its taxonomy.

A BRIEF MODERN TAXONOMIC HISTORY OF THE GENUS *DELPHINIUM* L. AND ITS INTRAGENERIC CLASSIFICATION

The first valid publication of the name *Delphinium* was made by Linnaeus (1753: 530). He placed the genus into the group called "*Polyandria trigynia*", which is characterized by an androecium with numerous stamens and a gynoeceum with three carpels, although this group also included species with a single carpel in *Delphinium*. Back then, the genus consisted of six species: *D. consolida* L., *D. ajacis* L., *D. peregrinum* L., *D. grandiflorum* L., *D. elatum* L., and *D. staphysagria* L.

In 1818, de Candolle (1818: 341) proposed an infrageneric classification of *Delphinium* L. where the genus was divided into four sections, one of which was called sect. *Consolida* DC., including *D. consolida* L. Three years later, Gray (1821: 711) raised sect. *Consolida* to generic status (*Consolida* (Brunfels) Gray) including *D. consolida* L. However, Spach (1839: 355) still adopted a broad *Delphinium* (L.) Spach that included *D. consolida* L. (Spach 1839: 355), but placed the species *D. aconitii* L. into another monospecific genus *Aconitella* Spach (1839:358).

Huth (1895) retained the name *Delphinium* L. for the genus and further split it into two subgenera: subg. *Consolida* (DC.) Gray and subg. *Eudelphinium* Huth. This classification was acknowledged by Dalla Torre & Harms (1901: 165).

Linnaeus did not assign any holotype for the genus *Delphinium*. This missing information led to major taxonomic controversy during the 20th century, urging the need for lectotypification.

THREE LECTOTYPIFICATIONS FOR A SINGLE GENUS NAME

Following the automatic typification of the American Code, Britton & Brown (1913: 84) proposed the first typification of *Delphinium* L., choosing the species listed first in the protologue: *D. consolida* L. (type: LINN 694.1 [http://linnean-online.org/6495/], Fig. 1A). However, in 1914, Nieuwland noted that *D. consolida* L., with a single carpel and a single petal (Fig. 2a1-a3), was standing apart from the rest of *Delphinium* L. He therefore decided to distribute the species among three different genera, namely *Delphinastrum* Spach, *Delphinium* L. and *Consolida* (DC.) Gray. He proposed a new lectotype for *Delphinium* L.: the type specimen of *D. peregrinum* L. (BM-000628786; Fig. 1B). This proposition was followed by Hitchcock & Green (1929). Pawłowski (1963; 1964) and Davis *et al.* (1965) also approved *Delphinium* L. and *Consolida* (DC.) Gray as distinct genera. In accordance with this classification, Munz (1967) also accepted the type of *D. peregrinum* L. (Fig. 2A) as type of *Delphinium* L.

The typification project of Linnean generic names favoured the selection of *D. peregrinum* L. as type species (Jarvis 1992) because, as Jarvis (1992) explained, the earlier adoption of a specimen of *D. consolida* L. (Fig. 2A) as type of the genus *Delphinium* L. may imply to make the combinations of all the species of *Consolida* (DC.) Gray using the name *Delphinium* L., and to find another generic name for the group *Delphinium* sensu stricto. He concluded that the lectotypification of *D. peregrinum* L. (Fig. 2B) was in agreement with the taxonomy of his time (Jarvis 1992). However, considering the genus *Consolida* (DC.) Gray, and anticipating the probable adoption of the sections *Delphinellum* and *Staphysagria* as new genera, Warnock (1993) decided to revise the typification of the genus and proposed as type of the genus name a specimen of *D. elatum* L. (S09-28218; Fig. 2C) providing, according to him, "the greatest nomenclature stability". However, this proposal was rejected during the nomenclature section held at the XV International Botanical Congress Tokyo (1993) (votes 4:8 [not recommended]) (Greuter *et al.* 1994; Brummitt 1995). Blanché *et al.* (1997) considered the second lectotypification (based on *D. peregrinum* L.) as the "traditional" typification.

Today, according to the Code and in agreement with Art. 10.5 (Turland *et al.* 2018), the valid lectotype of *Delphinium* L. is the specimen of *D. peregrinum* (Fig. 2B). In the Code, although Heath (1990) proposed the deletion of this example, the lectotypification of *Delphinium* L. using the specimen of *D. consolida* L. continues to be cited as a case of typification following the American code, later supplanted by a formal typification.

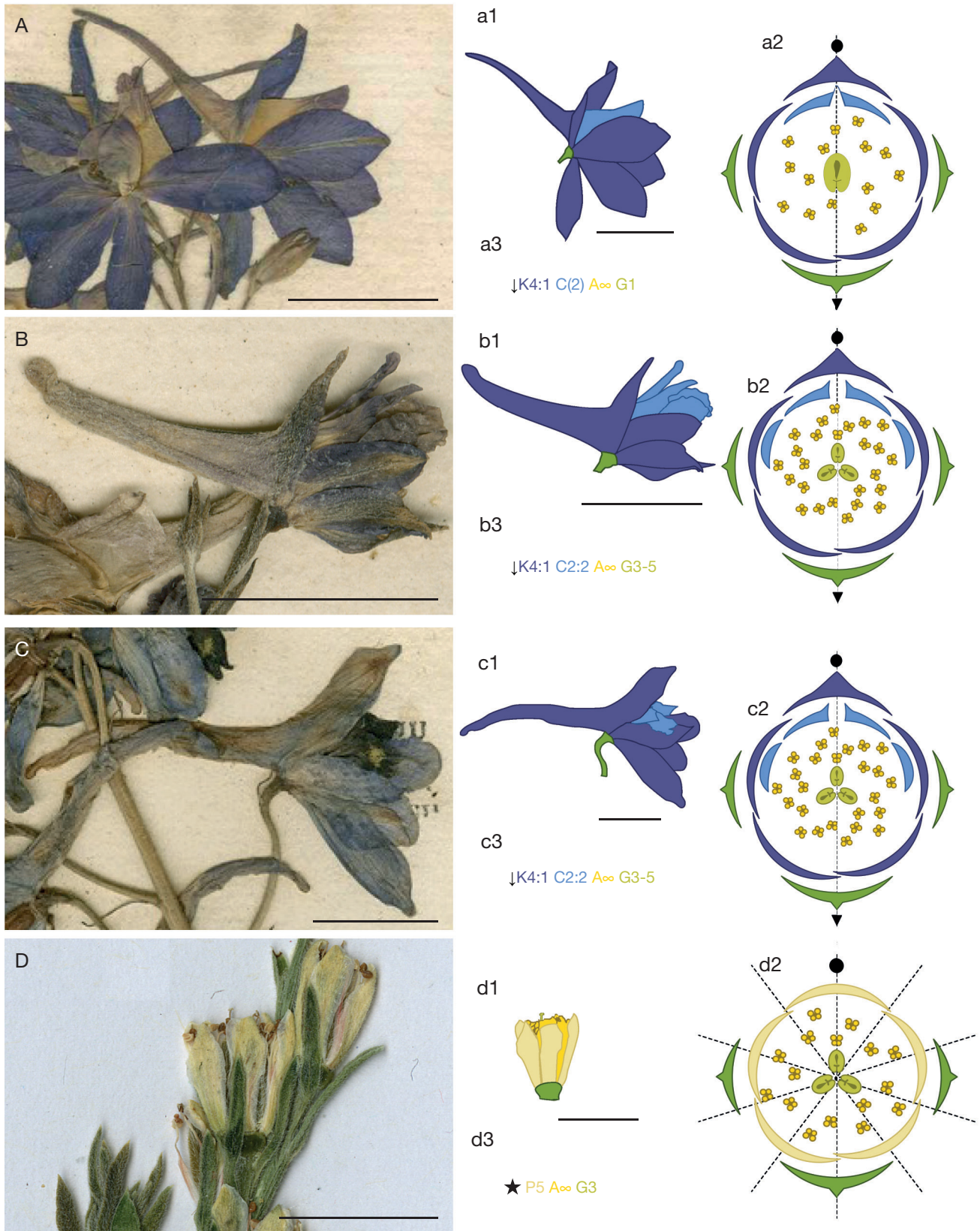


FIG. 2. — Photographs and drawings of flowers from herbarium specimens used for lectotypifying of the genus *Delphinium* L. or showing a peloric floral organization: **A, a1**, *Consolida regalis* Gray (LINN 694.1); **B, b1**, *Delphinium peregrinum* L. (BM-000628786); **C, c1**, *D. elatum* (S09-28218); **D, d1**, *D. turcicum* (H. Duman, Vural, Aytaç & Adigüzel) Espinosa (P04021863). Floral diagrams and formulae of: **a2, a3**, *Consolida regalis*; **b2, b3**, *D. peregrinum*; **c2, c3**, *D. elatum*; **d2, d3**, *D. turcicum*. **Dark green**, peduncle or receptacle, bract and bracteoles; **violet**, sepals; **blue**, petals; **yellow cream colour**, tepals; **yellow**, stamens; **light green**, carpels. Scale basr: 1 cm.

CURRENT TAXONOMY OF THE GENUS *DELPHINIUM* L.

To better understand the taxonomy of *Delphinium* L. and based on seed morphology, Malyutin (1987) divided the genus *Delphinium* L. into subg. *Staphisagria* (J. Hill) Peterm. and subg. *Delphinium*, and further divided the latter one in sect. *Anthriscifolium* Wang and sect. *Delphinium* (confirming Wang's (1979) classification for this subgenus). This classification was supported by a combination of morphological and cytological characters (Blanché 1990). Later, based on breeding systems, pollination ecology, cytology and isozyme variations, he proposed the division of the sect. *Delphinium* into four series *Cossoniana* C. Blanché, Molero & P. Simon, *Balansae* C. Blanché, Molero & P. Simon, *Macropetala* C. Blanché, Molero & P. Simon and *Halterata* B. Pawl. (Blanché *et al.* 1997). Integrating the results of molecular data, Jensen *et al.* (1995) placed *Delphinium* L. together with *Consolida* (DC.) Gray and *Aconitum* L. in the subtribe Delphiniinae Benth. (Delphinieae Warm., Ranunculoideae Hutch). Using 65 morphological characters combined with four plastid and nuclear DNA sequence data, Wang *et al.* (2009) placed the genera *Delphinium* L., *Consolida* (DC.) Gray and *Aconitum* L. within the tribe Delphinieae. Through a morphological analysis, Trifonova (1990) proposed to consider *Consolida* (DC.) Gray and *Aconitella* Spach as different genera based on morphological characters. However, this was challenged by Jabbour & Renner (2011a) who found that both genera were nested within *Delphinium* L. using molecular data and a large taxon sampling, leading them to proposed an extended genus *Delphinium* L. including both *Consolida* (DC.) Gray and *Aconitella* Spach. Based on the results of a molecular phylogenetic analysis, they decided to resurrect the genus *Staphisagria* J. Hill, including *D. staphisagria* L. (Jabbour & Renner 2011b). They recognized three genera in the tribe Delphinieae: *Delphinium* L., *Aconitum* L. and *Staphisagria* J. Hill. (Jabbour & Renner 2012a). The genus *Aconitum* L. was further split into *Aconitum* L. *sensu stricto* and the monotypic *Gymnaconitum* (Stapf.) Rapaics (Wang *et al.* 2013).

DESCRIPTION OF THE TYPICAL *DELPHINIUM* FLOWER

As seen in the above section, the genus *Delphinium sensu lato* (Jabbour & Renner 2011a) belongs to the tribe Delphinieae Warm. (Ranunculoideae Hutch, Ranunculaceae Juss.). This tribe is the only clade within the family Ranunculaceae with flowers that are bilaterally symmetrical.

Based on flowers of *D. peregrinum* L. (Fig. 2B-b3), *Delphinium* typical flowers are composed of four categories of organs: sepals and petals composing the perianth (the diversity of terms used in the bibliography of these organs is reviewed in Jabbour & Renner 2012b), and the two types of sexual organs, stamens and carpels (Blanché 1990; Fig. 2B-b3). From outside in, there are five free petaloid sepals quincuncially arranged: two ventral, two lateral and a spurred dorsal

one, four free petals located in the dorsal half of the flower: two dorsal organs forming nectariferous spurs inserted into the spur of the dorsal sepal and with an exserted limb, and two lateral organs with a wide limb and a narrow claw. The other petals (corresponding to four ventral primordia) stop developing shortly after organogenesis (Payer 1857; Jabbour & Renner 2012b). The stamens are arranged in eight spiral series, and the gynoecium is composed of 3(-5) free carpels (Pawłowski 1964) turning into follicles after fertilization. In *Delphinium*, bilateral symmetry is established through two phenomena: 1) the development of dorsal spurs; and 2) the arrested development of the ventral petals (Jabbour *et al.* 2009).

However, as mentioned earlier (see Current taxonomy of the genus), the genus *Delphinium* L. includes species with floral morphological particularities that should be included in the description of *Delphinium* L. flowers. These exceptions will be presented in detail in the next section.

AMENDING *DELPHINIUM* DESCRIPTION TO ACCOUNT FOR EXCEPTIONS IN FLORAL MORPHOLOGY

The inclusion of *Consolida* (DC.) Gray into *Delphinium* L. (Jabbour & Renner 2011a) implies an extension of the floral typical character states of the genus. The perianth of *Consolida* (DC.) Gray is bilaterally symmetrical and is composed of five petaloid sepals which arrangement and morphological characteristics are identical to those of *Delphinium* L. sepals. However, the inner perianth organs of *Consolida* (DC.) Gray consist of only two fused dorsal petals forming a single organ with a nectariferous spur inserted into the sepal spur (Fig. 2A-a3). The other petals (in this case six primordia) stop developing shortly after initiation (Jabbour & Renner 2012b). *Consolida* (DC.) Gray flowers are bisexual, with five spirals of stamens, three less than the typical *Delphinium* L. flowers and, a single carpel, as opposed to the three carpels of the *Delphinium* typical gynoecium (Pawłowski 1964). *Consolida* (DC.) Gray flowers exemplify a case of reduction in floral organ numbers (petals, stamens and carpels) compared to the typical *Delphinium* L. flowers (Fig. 2A-a3).

Recently, Vural *et al.* (2012) described a new genus named *Pseudodelphinium* H.Duman, Vural, Aytaç & Adigüzel, including the single species *Pseudodelphinium turcicum* H.Duman, Vural, Aytaç & Adigüzel. The description of this new species is based on a single population reported since 1997 in central Turkey. Plants of this species are herbaceous with radially symmetrical flowers presenting a perianth composed of five tepals (corresponding to petaloid sepals but considered as petals by the authors), numerous stamens, and three free carpels turning into follicles (Fig. 2D-d3). The authors noted its probable taxonomic affinity with the genus *Delphinium* L., but chose to establish a new genus based on the morphological particularities of the single population (no dorsal spurs, radial symmetry, perianth composed of a single type of organs) they decided to establish a new genus. Later, the genus was placed in *Delphinium* L. subg.



FIG. 3. — A, Flower drawing of *Chienia honanensis* W.T. Wang (modified from Wang [1964]); B, *Chienia honanensis* specimen [PE00026940] housed at PE herbarium (there are no scales on the original drawing and on the image of the original specimen); C, D, *D. grandiflorum* L. specimens [PE00477116 and PE00477117 respectively] housed at PE herbarium collected in the same province and the same year as the *Chienia honanensis* specimen and with which it matches morphologically speaking, excepted that PE00026940 specimen would show a teratological form of the floral structure.

Delphinium by Xiang *et al.* (2017) based on molecular data. Espinosa *et al.* (2017) found that in this species the perianth is exclusively composed of sepals, while petals seems to stop their development at a very early stage. By integrating lines of evidence from morphology, anatomy, palynology, and molecular phylogeny they further supported its inclusion in *Delphinium* L. and proposed the new combination *Delphinium turcicum* (H. Duman, Vural, Aytac & Adigüzel) Espinosa (Espinosa *et al.* 2017). Floral characteristics of this species are very similar to those of the Chinese species *D. ecalcaratum* S.Y. Wang & K.F. Zhou presenting spurless actinomorphic flowers with an uniseriate perianth. Flowers of this species include fewer stamens than *D. turcicum* (H. Duman, Vural, Aytac & Adigüzel) Espinosa (5 vs 15 respectively) but one additional carpel (Ding *et al.* 1981).

W. T. Wang (1964) published the new species *Chienia honanensis* W. T. Wang (Ranunculaceae), based on a single specimen bearing flowers with bilateral symmetry and a biseriate perianth. Calyx is composed by 5 free petaloid sepals quincuncially arranged and there are 5(-6) W2 organs, all in the dorsal half of the flower (Fig. 3A). The flowers present numerous stamens and the gynoecium is composed of three free carpels turning into follicles. Even if the author recognized the proximity of *C. honanensis* with the genus *Delphinium*, the higher number of petals (5-6 vs 4 in the typical *Delphinium* flower; Fig. 2b3, 3A) and the absence of dorsal spurs led him to propose the new genus *Chienia* W.T. Wang (Wang 1964). The species was later considered as based on a single teratological specimen of *Delphinium grandiflorum* L. by Warnock (1993). The vegetative parts of this specimen, conserved at PE (<http://www.cvh.ac.cn/cvh6/view/spms/info.php?id=cb003d8d>, Fig. 3B) match vegetatively with a specimen of *Delphinium grandiflorum* L. collected in the same province in the same year (<http://www.cvh.ac.cn/cvh6/view/spms/info.php?id=cef539df> and <http://www.cvh.ac.cn/cvh6/view/spms/info.php?id=cef53a7c>; Fig. 3B, C). Since the floral organization observed on the type material of the *Chienia honanensis* appears to be restricted to a single individual, and was apparently not transferred to progeny (no other collection exists, leading to the assumption that no permanent population ever occurred), we consider this as a non-heritable teratological variation, unable to be fixed in a population. Such teratological variation may occur in selected horticultural plants but it is not usual to include such variation in the description of the common morphology of a genus.

Thus, as far as floral morphology is concerned, and considering that the former genus *Consolida* (DC.) Gray is now included in *Delphinium* L., we state that the *Delphinium* flower is zygomorphic and characterized by a perianth consisting of five spirally-initiated sepals (the dorsal one being spurred) and four (two lateral, two dorsal spurred) or one (spurred) petals, all in the dorsal half of the flower. The spurred dorsal petals are nectariferous, and their spurs are nested within the spur of the dorsal sepal. The gynoecium consists of a single carpel, or 3(5) carpels. The description of

D. ecalcaratum (Ding *et al.* 1981) and the recent inclusion of *Delphinium turcicum* (Fig. 1D, d) into the genus *Delphinium* L. (Espinosa *et al.* 2017; Xiang *et al.* 2017) imply to amend the description of the genus, to indicate that there are exceptions to the typical floral morphology. The major diagnostic floral characters of *D. ecalcaratum* and *D. turcicum* are: 1) radial symmetry; 2) uniseriate perianth composed of tepals; and 3) the absence of spurs. More analyses relying on herbarium material and particularly living material are needed to better understand the origin of the morphological deviations. Regarding *Delphinium turcicum*, having access to seeds of this species would allow us to conduct a karyological analysis in order to identify possible recent hybridization events, and testing the stability of the phenotype on other substrates, as the only known population of this species grows in the basin of the hypersaline lake Tuz Gölü, known for high levels of plant endemism (Yaprak & Tug 2009; Vural *et al.* 2012; Espinosa *et al.* 2017; Xiang *et al.* 2017).

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REFERENCES

- BAUHIN G. 1623. — *Pinax Theatri Botanici*. Ludovici Regis, Basel, 522 p. <https://gallica.bnf.fr/ark:/12148/bpt6k97448m>
- BLANCHÉ C. 1990. — *Delphinium* L. subgen. *Delphinium*: origin and evolutionary trends. *Collectanea Botanica* 19: 75-95. <https://doi.org/10.3989/collectbot.1990.v19.118>
- BLANCHÉ C., MOLERO J., ROVIRA A. M., SIMON J. & BOSCH M. 1997. — *Delphinium* L. subgen. *Delphinium* in the Iberian peninsula and north Africa: a new taxonomic approach. *Lagascalia* 19: 59-82. <https://idus.us.es/handle/11441/62784>
- BOURDICHON J. 1505-1510. — *Horae ad usum Romanum*, dices *Grandes Heures d'Anne de Bretagne*. Jean Bourdichon, Tours, 238 p. <https://gallica.bnf.fr/ark:/12148/btv1b52500984v>
- BRITTON N. L. & BROWN A. 1913. — Ranunculaceae, in BRITTON N. L. & BROWN A. (eds), *An Illustrated Flora of the Northern United States, Canada and the British Possessions: from Newfoundland to the Parallel of the Southern Boundary of Virginia and from the Atlantic Ocean Westward to the 102nd Meridian*. Vol. 2. Scribner, New York: 84-126. <https://doi.org/10.5962/bhl.title.940>
- BRUMMITT R. K. 1995. — Report of the Committee for Spermatophyta: 43. *Taxon* 44: 607-612. <https://doi.org/10.2307/1223505>
- CANDOLLE A. P. DE 1818. — *Regni vegetabilis systema naturale*, Vol. 1. Treuttel et Würtz, Paris, 564 p. <https://doi.org/10.5962/bhl.title.59874>

- CHARTIER M., DRESSLER S., SCHÖNENBERGER J., ROJAS MORA A., SARTHOU C., WANG W. & JABBOUR F. 2016. — The evolution of afro-montane *Delphinium* (Ranunculaceae): morphospecies, phylogenetics and biogeography. *Taxon* 65: 1313-1327. <https://doi.org/10.12705/656.6>
- DALLA TORRE C. G. & HARMS H. 1901. — *Genera Siphonogamarum ad Systema Englerianum Conscripta*. Guilelmi Engelmann, Leipzig, 921 p. <https://doi.org/10.5962/bhl.title.26684>
- DAVIS P. H., CULLEN J. & COODE M. J. E. 1965. — Ranunculaceae in DAVIS P. H., CULLEN J. & COODE M. J. E. (eds), *Flora of Turkey and the East Aegean Islands*. Edinburgh University Press, Edinburgh: 95-203.
- DING B. Z., WANG S. Y. & GAO Z. Y. 1981. — *Delphinium* L., in DAVIS P. H., CULLEN J. & COODE M. J. E. (eds), *Flora henanensis*. Vol. 1. Henan People's Publishing House, Zhengzhou: 431-436.
- DODOENS R. 1554. — *Des Cruydeboeck*. Part 2. Netherlands, 346 p.
- DODOENS R. 1557. — *Histoire des plantes traduite par Charles de l'Écluse*. Imprimerie de Jean Loe, Anvers, 584 p.
- ESPINOSA F., DEROIN T., XIANG K.-L., WANG W., CASTRO M. P., BYNG J. W., AYTAÇ Z., NADOT S. & JABBOUR F. 2017. — The Turkish endemic *Pseudodelphinium turcicum* (Ranunculaceae): an unusual population of *Delphinium* with peloric flowers that has persisted in the wild for 20 years. *International Journal of Plant Sciences* 178: 546-555. <https://doi.org/10.1086/692764>
- FUCHS L. 1542. — *De Historia Stirpium Commentarii insignes*. Officina Isingriniana, Basel, 895 p. <https://gallica.bnf.fr/ark:/12148/bpt6k53240h>
- FUCHS L. 1543. — *New Kreüterbuch*. Officina Isingriniana, Basel, 892 p.
- GAIUS PLINUS SECUNDUS 1850. — *Histoire naturelle de Pline*. Dubochet J. J., Le Chevalier & Ciaie, Paris, 707 p.
- GRAY S. F. 1821. — *A Natural Arrangement of British Plants*. Vol. 2. Baldwin, Cradock & Joy, London, 757 p. <https://doi.org/10.5962/bhl.title.43804>
- GREUTER W., BARRIE F. R., BURDET H. M., CHALONER W. G., DEMOULIN V., HAWKSWORTH D. L., JØRGENSEN P. M., NICOLSON D. H., SILVA P. C. & TREHANE P. (eds) 1994. — *International Code of Botanical Nomenclature (Tokyo Code) Adopted by the Fifteenth International Botanical Congress, Yokohama, August-September 1993*. Koeltz Botanical Books, Königstein, 389 p.
- HEATH P. V. 1990. — Proposals to amend the Code. *Taxon* 39: 138-140. <https://doi.org/10.2307/1223211>
- HITCHCOCK A. S. & GREEN M. L. 1929. — Proposal by A. S. Hitchcock (Washington) and M. L. Green (Kew), in International Botanical Congress Cambridge (England), 1930, Nomenclature, Proposals by British Botanists. Wyman & Sons, London: 110-162. <https://bibdigital.rjb.csic.es/duel/1/13040>
- HUTH E. 1895. — Monographie der Gattung *Delphinium*. *Botanische Jahrbücher* 20: 322-499. <https://doi.org/10.5962/bhl.title.15558>
- JABBOUR F., RONSE DE CRAENE L. P., NADOT S. & DAMERVAL C. 2009. — Establishment of zygomorphy on an ontogenic spiral and evolution of perianth in the tribe Delphinieae (Ranunculaceae). *Annals of Botany* 104: 809-822. <https://doi.org/10.1093/aob/mcp162>
- JABBOUR F. & RENNER S. S. 2011a. — *Consolida* and *Aconitella* are an annual clade of *Delphinium* (Ranunculaceae) that diversified in the Mediterranean basin and the Irano-Turanian region. *Taxon* 60: 1029-1040. <https://doi.org/10.1002/tax.604007>
- JABBOUR F. & RENNER S. S. 2011b. — Resurrection of the genus *Staphisagria* J. Hill, sister to all the other Delphinieae (Ranunculaceae). *PhytoKeys* 7: 21-26. <https://doi.org/10.3897/phytokeys.7.2010>
- JABBOUR F. & RENNER S. S. 2012a. — A phylogeny of Delphinieae (Ranunculaceae) shows that *Aconitum* is nested within *Delphinium* and that Late Miocene transitions to long life cycles in the Himalayas and Southwest China coincide with bursts in diversification. *Molecular Phylogenetics and Evolution* 62: 928-942. <https://doi.org/10.1016/j.ympev.2011.12.005>
- JABBOUR F. & RENNER S. S. 2012b. — Spurs in a spur: perianth evolution in the Delphinieae (Ranunculaceae). *International Journal of Plant Sciences* 173: 1036-1054. <https://doi.org/10.1086/667613>
- JARVIS C. E. 1992. — Seventy-two proposals for the conservation of types of selected Linnaean generic names. *Taxon* 41: 552-583. <https://doi.org/10.2307/1222833>
- JENSEN U., HOOT S. B., JOHANSSON J. T. & KOSUGE K. 1995. — Systematics and phylogeny of the Ranunculaceae – a revised family concept on the basis of molecular data. *Plant Systematics and Evolution Supplement*: 273-280. https://doi.org/10.1007/978-3-7091-6612-3_27
- LAGUNA A. 1555. — *Pedacio Dioscorides Anazarbeo, Acerca de la Materia Medicinal y de los Venenos Mortíferos*. Juan Latio, Anvers, 616 p.
- LINNAEUS C. 1753. — *Species Plantarum*. T. 1. Laurentii Salvii, Stockholm, 560 p. <https://doi.org/10.5962/bhl.title.669>
- MALYUTIN N. I. 1987. — The system of genus *Delphinium* (Ranunculaceae) based on the morphological features of seeds. *Botanicheskii zhurnal* 72: 683-693.
- MATHÉE M. 1559. — *Les Six Livres de Pedacion Dioscoride d'Anazarbe de la Matière Médicinale, Translatez de Latin en François*. Thibault Payan, Lyon, 574 p. <https://gallica.bnf.fr/ark:/12148/bpt6k96067706>
- MATTHIOLI P. A. 1554. — *Commentarii, in Libros Sex pedacii Dioscoridis Anazarbei, De Medica Materia*. Vincentium Valgrisiurum, Venice, 707 p. <https://gallica.bnf.fr/ark:/12148/bpt6k58820r>
- MATTHIOLI P. A. 1565. — *Commentarii in Sex Libros Pedacii Dioscoridis Anazarbei De Medica Materia*. Officina Valgrisiurum, Venice, 1459 p. <https://doi.org/10.5962/bhl.title.61850>
- MUNZ P. A. 1967. — A Synopsis of African Species of *Delphinium* and *Consolida*. *Journal of the Arnold Arboretum* 48: 30-55.
- NIUWLAND J. A. 1914. — Critical Notes on New and Old Genera of Plants. I. *The American Midland Naturalist* 3 (7): 170-197. <https://doi.org/10.2307/2992842>
- PAWŁOWSKI B. 1963. — Disposition systematica specierum europaeorum generis *Delphinium* L. *Fragmenta Floristica et Geobotanica* 9 (4): 429-446.
- PAWŁOWSKI B. 1964. — *Delphinium*, in TUTIN T. G., HEYWOOD V. H., BURGESS N. A., VALENTINE D. H., WALTERS S. M., WEBB D. A. (eds), *Flora Europaea*. The University Press, Cambridge: 213-216.
- PAYER J. 1857. — *Traité d'organogénie comparée de la fleur*. Masson, Paris, 748 p. <https://doi.org/10.11588/diglit.9757>
- RUEL J. 1527. — *Pedacii Dioscoridis Anazarbei de medicinali materia libri quinq.* Joannem Antonium, Sabina, 212 p.
- RUEL J. 1529. — *P. Discoridiae Pharmacorum Simplicium, reique Medicae Libri VIII*. J. Schotrum, Strasbourg, 361 p. <https://gallica.bnf.fr/ark:/12148/bpt6k6156233r>
- SPACH É. 1839. — *Histoire naturelle des végétaux*. T. 7. Librairie Encyclopédique de Roret, Paris, 538 p. <https://doi.org/10.5962/bhl.title.44839>
- TOURNEFORT J. P. 1694. — *Éléments de botanique*. Imprimerie Royale, Paris, 561 p. <https://gallica.bnf.fr/ark:/12148/btv1b8454361d>
- TRIFONOVA V. I. 1990. — Comparative biomorphological study of the taxonomy and phylogeny of the genera *Consolida* (DC.) S.F. Gray and *Aconitella* Spach. *Collectanea Botanica (Barcelona)* 19: 97-110. <https://doi.org/10.3989/collectbot.1990.v19.119>
- TURLAND N. J., WIERSEMA J. H., BARRIE F. R., GREUTER W., HAWKSWORTH D. L., HERENDEN P. S., KNAPP S., KUSBER W.-H., LI D.-Z., MARHOLD K., MAY T. W., MCNEILL J., MONDO A. M., PRADO J., PRICE M. J. & SMITH G. F. (EDS) 2018. — *International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>
- VURAL M., DUMAN H., AYTAÇ Z., ADIGÜZEL N. 2012. — A new genus and three new species from Central Anatolia, Turkey. *Turkish Journal of Botany* 36: 427-433. Retrieved from <https://dergipark.org.tr/pub/tbtbotany/issue/11778/140841>

- WANG W. T. 1964. — Duo genera nova Ranunculacearum sinensium. *Acta Phytotaxonomica Sinica* 9: 103-107.
- WANG W. T. 1979. — *Delphinium*, in LIN L. (ed.), *Flora Reipublicae Popularis Sinicae*. Vol. 27. Science Press, Beijing: 326-462.
- WANG W., LIU Y., YU S. X., GAO T. G. & CHEN Z. D. 2013. — *Gymnaconitum*, a new genus of Ranunculaceae endemic to the Qinghai-Tibetan plateau. *Taxon* 62: 713-722. <https://doi.org/10.12705/624.10>
- WANG W., LU A. M., REN Y., ENDRESS M. E. & CHEN Z. D. 2009. — Phylogeny and classification of Ranunculales: evidence from four molecular loci and morphological data. *Perspectives in Plant Ecology, Evolution and Systematics* 11: 81-110. <https://doi.org/10.1016/j.ppees.2009.01.001>
- WANG W. T. & WARNOCK M. J. 2001. — *Delphinium*, in WU Z. Y. & RAVEN P. H. (eds), *Flora of China*. Vol. 6. Science Press/Missouri Botanical Garden, Beijing/St Louis: 223-237.
- WARNOCK M. J. 1993. — Proposal to conserve 2539 *Delphinium* L. (Ranunculaceae) with a conserved type author. *Taxon* 42: 453-456. <https://doi.org/10.2307/1223157>
- WELLMANN M. 1906. — *Pedanii Dioscuridis Anazarbei, De materia medica libri quinque*. Vol. 2. Weidmannos, Berlin, 339 p. <https://gallica.bnf.fr/ark:/12148/bpt6k6228793s>
- XIANG K.-L., AYTAÇ Z., LIU Y., ESPINOSA F., JABBOUR F., BYNG J. W., ZHANG C.-F., ERST A. S. & WANG W. 2017. — Recircumscription of *Delphinium* subg. *Delphinium* (Ranunculaceae) and implications for its biogeography. *Taxon* 66: 554-566. <https://doi.org/10.12705/663.3>
- YAPRAK A. E. & TUG G. N. 2009. — Halophytic endemics of Turkey, in IVANOVA D. (ed.), *Plant, Fungal and Habitat Diversity Investigation and Conservation*. Proceedings of IV BBC-Scientific Area B. Prof. Marin Drinov Academic Publishing House, Sophia: 234-238.

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