

Original research

Chamaeamygdalus, a new genus segregated from *Amygdalus* sensu lato (*Prunus* sensu latissimo, Rosaceae), based on available morphological and phylogenetic evidence

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Abstract

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A rational generic concept in the group of *Prunus* sensu latissimo (Rosaceae) remains debatable, with two main approaches or traditions: one favouring a broad circumscription of *Prunus*, and another preferring its splitting into numerous segregate genera such as *Armeniaca*, *Cerasus*, *Emplectocladus*, *Laurocerasus*, *Maddenia*, *Padus*, *Persica*, *Prunus* s. str., *Pygeum*, etc. Members of these groups often hybridise with each other to form intermediates. This situation is parallel to the taxonomic options in another group of Rosaceae, the tribe Maleae, in which some authors recognise numerous genera (*Aria*, *Aronia*, *Chaenomeles*, *Cotoneaster*, *Cydonia*, *Eriobotrya*, *Malus*, *Photinia*, *Sorbus*, etc.). In contrast, others prefer a mega-genus *Pyrus* sensu latissimo. The genus *Amygdalus* (as well as other segregated genera mentioned above) is not recognised by many researchers and is considered a part of the genus *Prunus* s. l. However, species usually placed in *Amygdalus* are quite peculiar and habitually differ from other “prunoid” genera. The main feature distinguishing *Amygdalus* from closely related genera is the dry pericarp that opens when ripe. The group described as the section *Chamaeamygdalus* is the most isolated in *Amygdalus*. It includes low thornless shrubs with narrow leaves and small, densely tomentose-shaggy fruits. The shape of the calyx tube is a morphological feature that distinguishes the species of the section *Chamaeamygdalus* from the typical section of the genus. Phylogenetic analyses based on molecular data confirm the morphological differences between species of the section *Chamaeamygdalus*, which is the basis for assigning the generic rank to this group. The new genus *Chamaeamygdalus* is erected here, and three new species-rank nomenclatural combinations are validated for species of this genus.

Keywords: *Amygdalus*, *Chamaeamygdalus*, *Prunus*, molecular phylogeny, nomenclatural combinations, segregate genera.

INTRODUCTION

A rational generic concept for *Prunus* L. sensu lato (Rosaceae, Amygdaloideae, Amygdaleae) re-

mains controversial, with two main historically formed approaches or traditions: one favouring a wide circumscription of *Prunus* s. l., and another preferring its splitting into numerous segregate

genera such as *Amygdalus* L., *Armeniaca* Scop., *Cerasus* Mill., *Emplectocladus* Torr., *Laurocerasus* DuRoi, *Maddenia* Hook.f. & Thomson, *Padus* Mill., *Persica* Mill., *Prunus* s. str., *Pygeum* Gaertn. (Bortiri et al., 2001, 2006; Lee, Wen, 2001; Shaw, Small, 2004; Potter et al., 2007; Wen et al., 2008; Rahemi et al., 2012; Shi et al., 2013). Members of these groups often hybridise with each other to form intermediates. The “splitter’s” approach to genera in the group was dominant in East European botany in the 20th century (Komarov, 1941; Kostina, 1941; Kovalev, 1941; Linchevskiy & Fedorov, 1941; Pobjarkova, 1941; Kotov, 1954; Takhtajan, 1997; Buzunova, 2001), while the “lumper’s” approach, preferring *Prunus* sensu latissimo, was more common in West European and partly North American botany (Mason, 1913; Wight, 1915; Rydberg, 1918; Sterling, 1964; Webb, 1968; Robertson, 1974; Duncan & Duncan, 1988; Wilken, 1993; Kalkman, 2004; Shaw & Small, 2004). This situation is parallel to the taxonomic options in another group of Rosaceae, the tribe Maleae, in which many authors recognised numerous genera (*Pyrus* L. s. str., *Aria* Host, *Aronia* Medik., *Chaenomeles* Lindl., *Chamaemespilus* Medik., *Cotoneaster* Medik., *Cydonia* Mill., *Eriobotrya* Lindl., *Malus* Mill., *Photinia* Lindl., *Sorbus* L.). In contrast, others prefer a mega-genus *Pyrus* sensu latissimo (Christenhusz et al., 2018).

Recent molecular taxonomic results (Uematsu et al., 1991; Badenes & Parfitt, 1995; Bortiri et al., 2001; Potter et al., 2002, 2007; Wen et al., 2008; Shi et al., 2013) significantly clarified possible evolutionary relationships within the *Prunus* group and outlined several distinct clades, which, if a “splitter’s” approach is applied, may correspond to “narrow” traditionally recognised genera. However, in some cases, a re-circumscription of some genera is needed to match them with the newly outlined clades. In the present article, I, staying within the traditional approach of recognising several genera in the tribe *Amygdaleae* Juss., analyse available evidence of evolutionary lines within the group traditionally recognised as the genus *Amygdalus*.

The genus *Amygdalus* by many authors, both in the past (Koehne, 1893; Focke, 1894; Schneider, 1904, 1912) and in modern times (Mowrey & Werner, 1990; Zhang, 1992a, b; Kester & Gradziel, 1996;

Lersten & Horner, 2000; Lee & Wen, 2001; Shaw & Small, 2004; Bortiri et al., 2006), was not separated from *Prunus*, as well as other segregate genera, such as *Armeniaca*, *Cerasus*, *Emplectocladus*, *Laurocerasus*, *Maddenia*, *Padus*, *Persica*, *Prunus* sensu stricto and *Pygeum*, due to the presence of intermediate forms. Cross-pollination is characteristic of *Amygdalus* species and the whole group of the mentioned genera; they often hybridise, leading to the formation of morphologically transitional forms.

The main morphological feature that separates the traditionally circumscribed genus *Amygdalus* from closely related groups (often also recognised as genera, see above) is its dry pericarp that opens at maturity. However, this character is unreliable, as at least one species placed in the genus *Armeniaca*, *Armeniaca sibirica* (L.) Pers. (= *Prunus sibirica* L.) has a more or less dry pericarp, which sometimes opens when ripe. Thus, in many taxonomic schemes, *Amygdalus* (and the segregate genera mentioned above) is included in the broadly circumscribed genus *Prunus*. However, species placed in *Amygdalus* are morphologically quite peculiar and habitually different from most other species of “prunoid” genera. Recent estimates recognise in the genus *Amygdalus* from 26 species (Browicz & Zohari, 1996) to 40 or even more species (Linchevskiy & Fedorov, 1941; Vafadar et al., 2014) naturally occurring from the Mediterranean region to Central Asia, mainly in Algeria, the Balkan Peninsula, south-western Asia, the Caucasus, Iran, Afghanistan, Western Siberia (south), Central Asia, Mongolia, and mountains of Central China.

MATERIALS AND METHODS

Traditional methods of herbarium taxonomy were used in the work (De Vogel, 1987). Nomenclatural decisions are based on the current edition of the *International Code of Nomenclature for algae, fungi, and plants, Shenzhen Code* (Turland et al., 2018). The conclusions are also partly based on the analysis of the results of molecular phylogenetic studies as available in published sources, as well as the results of studying herbarium specimens at the National Herbarium of Ukraine (KW) and the memorial herbarium collection of W. Besser (KW-BESS).

RESULTS AND DISCUSSION

Taxonomic revisions of the genus *Amygdalus* and their analysis

The genus *Amygdalus* was first subdivided into two subgenera by Persoon (1806), who recognised *Amygdalus* subg. *Persica* (Mill.) Pers. (which includes the species of the traditionally circumscribed genus *Persica*) and the type subgenus, *Amygdalus* subg. *Euamygdalus* (which in that case, should be appropriately called *Amygdalus* subg. *Amygdalus* since it includes the genus type). Spach (1843), who has accepted the genus *Amygdalus* in a narrow sense (excluding *Persica*), distinguished within the genus two “series” (in fact, informal groups more or less corresponding to subgenera): *Amygdalus* “series” *Icosandrae* Spach (with four sections: sect. *Spartioides* Spach, sect. *Chamaeamygdalus* Spach, sect. *Leptopus* Spach, sect. *Euamygdalus* Spach), and “series” *Dodecandrae* Spach (with two sections: sect. *Lycioides* Spach and sect. *Scorpius* Spach). Linchevskiy (Linchevskiy & Fedorov, 1941) has added two more monotypic (monospecific) sections in *Amygdalus*, sect. *Amygdalopsis* (Carr.) Lincz. and sect. *Cerasioides* Lincz. Denisov (1988) and Browicz & Zohary (1996) somewhat modified the Spach system, subdividing the genus *Amygdalus* s. str. into two subgenera: subg. *Amygdalus* and subg. *Dodecandra* (Spach) Browicz. However, in the classification of Denisov, the type subgenus had four sections (sect. *Amygdalus*, sect. *Chamaeamygdalus*, sect. *Spartioides*, and sect. *Leptopus*). In comparison, in the system of Browicz & Zohary (1996), there are only three sections (sect. *Amygdalus*, sect. *Chamaeamygdalus*, sect. *Spartioides*). In all those systems, species of the genus *Persica* (in the strict sense) were excluded from the genus *Amygdalus*. Later, many other researchers adhered to this view of generic delimitation (Evreinov, 1952; Grasselly, 1976; Kester & Assay, 1975; Kester et al., 1991; Kester & Gradziel, 1996; and others).

Classifications in which the genus *Amygdalus* is not accepted as an independent genus but is treated as part of the subgenus *Amygdalus* of the genus *Prunus* (*Prunus* subg. *Amygdalus* (L.) Focke) are also mainly based on the Spach system. Thus, Grasselly (1976) has listed six sections of *Prunus* subg. *Amygdalus*: *Prunus* sect. *Euamygdalus* (Spach) Dippel, sect. *Spar-*

tioides (Spach) Schneider, sect. *Lycioides* (Spach) Schneider, sect. *Emplectocladus* (Torr.) Gray, sect. *Chamaeamygdalus* (Spach) Dippel, and sect. *Amygdalopsis* (Carr.) Bentham & Hooker), while Kester et al. (1991) have distinguished five sections: *Prunus* sect. *Euamygdalus*, sect. *Spartioides*, sect. *Lycioides*, sect. *Chamaeamygdalus*, and sect. *Leptopus* Spach. Recently, Gradziel & Martínez-Gómez (2013) have divided the subgenus *Amygdalus* of the genus *Prunus* into the “Almond group” with four sections (*Prunus* sect. *Euamygdalus*, sect. *Spartioides*, sect. *Lycioides*, sect. *Chamaeamygdalus*) and the “Peach group”.

The section *Chamaeamygdalus* includes low, thornless shrubs with relatively narrow leaves and small, tomentose fruits. The main morphological diagnostic character that distinguishes species of the section *Chamaeamygdalus* from the type section of the genus *Amygdalus* (if recognised) is the shape of the calyx tube: almost cylindrical, elongated at the base, reverse-conical or elongated in members of the *Chamaeamygdalus* group, while in species of the type section the calyx tube is cylindrical or bell-shaped. The sections also differ in their phenology: in the *Chamaeamygdalus* group, the leaves open simultaneously with the flowers, while in the type section, they emerge after the flowers. The genus *Emplectocladus* Torr. (*Prunus* sect. *Emplectocladus* (Torr.) A.Gray), including six species occurring in North America, has been accepted by some authors as a separate subgenus of the genus *Amygdalus*. This group seems to be morphologically close to the *Chamaeamygdalus* group. According to recent molecular data, the *Emplectocladus* group forms the earliest-diverging subclade of the *Amygdalus* clade (Lee & Wen, 2001; Wen et al., 2008; Shi et al., 2013; Chin et al., 2014; Li et al., 2021).

Other researchers have also paid attention to the morphological peculiarities of species of the section *Chamaeamygdalus*. For example, Focke (1894), who has treated the segregate genera mentioned above within the genus *Prunus*, has assigned almond species and related peach species to *Prunus* subg. *Amygdalus* (L.) Focke, and has placed the low-growing shrubby taxa in *Prunus* subg. *Chamaeamygdalus* (Spach) Focke. The subgenus rank for *Chamaeamygdalus* has also been accepted by Koehne (1893), who has distinguished it from the subgenus *Amygdalus* mainly by the shape of a calyx tube.

Modern molecular phylogenetic data confirm the morphological distinction and isolation of species of the *Chamaeamygdalus* group. According to the results of the analysis of DNA sequences carried out by Bortiri et al. (2002), *Prunus tenella* Batsch (= *Amygdalus nana* L.) has been revealed as a sister taxon to the clade formed by other species of the subgenus *Amygdalus* (containing *Amygdalus communis* L.; = *Prunus amygdalus* Batsch; = *Prunus dulcis* (Mill.) D.A. Webb, nom. illeg.), which indicates that the genus *Amygdalus*, if accepted in a traditional circumscription, is most probably paraphyletic or even polyphyletic. Similar results were also obtained by other researchers (Lee & Wen, 2001; Martinez-Gomez et al., 2003; Shaw & Small, 2004; Bortiri et al., 2006; Wen et al., 2008; Rahemi et al., 2012; Vafadar et al., 2014). As a result of these studies, it was established that *Prunus tenella* (= *Amygdalus nana* L.) and *Prunus petunnikovii* (Litv.) Rehder (≡ *Amygdalus petunnikovii* Litv.), which were usually placed in the section *Chamaeamygdalus*, do not belong to the same clade as other species of the genus (or clade) *Amygdalus* and its type, *Amygdalus communis* (*Prunus amygdalus*).

According to new studies based on results of the analysis of fruit morphology and DNA sequences, which have been carried out by Yazbek & Oh (2013), such species as *Prunus tenella*, *Prunus petunnikovii* (earlier placed in sect. *Chamaeamygdalus*), *Prunus triloba* Lindl., and *Prunus pedunculata* (Pall.) Maxim. (≡ *Amygdalus pedunculata* Pall.) (sect. *Leptopus*) form a sister clade to the rest of *Amygdalus* species and are excluded from the type subgenus. This is also confirmed by the data of Vafadar et al. (2014), who, based on the results of molecular studies (nrDNA ITS and cpDNA *trnS-trnG*), have excluded from the genus *Amygdalus* s. str. the following taxa: *Amygdalus mira* (Koehne) Ricker (≡ *Prunus mira* Koehne), *Amygdalus davidiana* (Carrière) de Vos ex L. Henry (≡ *Prunus davidiana* (Carrière) N.E.Br.; ≡ *Persica davidiana* Carrière), *Amygdalus triloba* (Lindl.) Ricker (≡ *Prunus triloba* Lindl.), and *Amygdalus nana* L. (= *Prunus tenella* Batsch), which emerged in several clades separate from the large clade containing other *Amygdalus* species.

Considering the morphological peculiarities and phylogenetic isolation of species of the section *Chamaeamygdalus*, which is also confirmed by recent

molecular phylogenetic data, I think it reasonable to elevate the section *Chamaeamygdalus* to the generic rank. Below is the nomenclature of the genus *Chamaeamygdalus*, its three species and their distribution.

***Chamaeamygdalus* (Spach) Fedoronchuk, comb. nov.**

Basionym: *Amygdalus* L. sect. *Chamaeamygdalus* Spach, Ann. Sc. Nat. ser. 2, 19: 110. 1843.

Typus: *Chamaeamygdalus nana* (L.) Fedoronchuk (≡ *Amygdalus nana* L.; = *Prunus tenella* Batsch).

1. *Chamaeamygdalus nana* (L.) Fedoronchuk, comb. nov.

Basionym: *Amygdalus nana* L., Sp. Pl.: 473. 1753.

≡ *Prunus nana* (L.) Stokes, Bot. Mat. Med. 3: 103, 1812, nom. illeg., non Du Roi, 1771.

= ?*Amygdalus campestris* Besser, Enum. Pl. Volhyn.: 46. 1822.

= *Amygdalus sweginzowii* (Koehne) Ricker, Proc. Biol. Soc. Washington, 30: 18. 1917.

= *Prunus sweginzowii* Koehne, Repert. Spec. Nov. Regni Veg. 8: 62. 1910.

= *Prunus tenella* Batsch, Beytr. Entw. Pragm. Gesch. Natur-Reiche, 1: 29. 1801.

Distribution: Central Europe (southern Germany), Balkan Peninsula, Eastern Europe (south), Caucasus, Western Asia (Anatolian Peninsula), Western Siberia (south), Central Asia. This species grows mainly in the zone of fescue-feathergrass and forb-meadow steppes, in depressions and slopes of ravines, in thickets, and sometimes on mountain slopes.

Note. The species was initially (before its valid publication in 1753) described by Linnaeus (1738) based on cultivated specimens grown in Clifford's Garden from seeds of unknown origin. Citing in the protologue the habitat of the species ("Habitat in Asia septentrionali?"), the author doubted whether it was possible to identify his species with the plant collected in Altai (the Bukhtarma River basin, the right tributary of the Irtysh River), illustrated in the book by J. Amman (1739). Most likely, the seeds of the (cultivated?) plants from which Linnaeus described the species were collected in the south of Europe [lectotype: Gerber, Herb. Linn. No. 639.6 (LINN), designated by Majorov & Sokoloff (Cafferty & Jarvis, 2002).

Occupying a large range, *Chamaeamygdalus nana* varies significantly in its morphological characteristics, as evidenced by the above synonymy (see also additional synonyms in POWO (2023)). Leaf sizes are especially variable. Plants from Southern Podolia, which differ from the typical ones in their high growth, broader leaves, shorter calyx tube, white petals and more than 1/3 of a bare column, were treated by Besser (1822) as *Amygdalus campestris* Besser. Preparing a treatment of the genus *Amygdalus* for the *Flora of Ukraine*, Kotov (1954), in a note under *Amygdalus nana*, has indicated that in the southern regions of Ukraine (the Dniester River basin, the south of Odesa and Kherson regions, near the Askania Nova Reserve), large specimens of plants with broad leaves often occur. However, Kotov (1954) has doubted to attribute them to *Amygdalus campestris* Besser, since the Besser (1822) has not indicated a specific place of growth, and herbarium specimens from Southern Podolia are absent in Besser's collection (KW-BESS), and Besser has identified his collections of plants from Podolia as *Amygdalus nana*. However, I (Fedoronchuk 2007) found out that Besser nevertheless clarified the place of growth of *Amygdalus campestris*, indicating: "A. campestem copiosum prope Iszkowce in distr. Cremenec. Vidit Hortul Wintzel", and in the collection of Besser (KW) in folder No. 232, I found two specimens from Podolia, which Kotov did not see, one of which I designated as the lectotype: "*Amygdalus campestris* Bess. Herb. W. Besser" (Fedoronchuk, 2007). In POWO (2023), the name "*Cerasus campestris* (Besser) Gueldenst. ex Ledeb." (Ledebour, 1843), pro syn.) is cited as a synonym for *Prunus tenella* Batsch. var. *campestris* (Besser) Rehder (1938). However, from Ledebour (1843), it is clear that (1) this name has not been validly published (mentioned only as a synonym) and, (2) it concerns an entirely different species, *Prunus fruticosa* Pall. (*Cerasus fruticosa* (Pall.) Borkh.). The name "*Amygdalus campestris* Besser" has been cited by Ledebour as a synonym of *A. nana* (Ledebour 1843).

2. *Chamaeamygdalus ledebouriana* (Schltdl.) Fedoronchuk, comb. nov.

Basionym: *Amygdalus ledebouriana* Schltdl., Abh. Naturf. Ges. Halle, 2: 21. 1854.

≡ *Prunus ledebouriana* (Schltdl.) Y.Y. Yao, Fl. Desert. Reipubl. Popul. Sin. 2: 161. 1987.

Distribution: Western Siberia (Altai), Central Asia (Tarbagatai). This species grows mainly in grassland habitats, on mountain steppe plateaus and slopes, in forb-meadow steppes at the foothills of mountain ridges, and along river valleys.

Note. The species has been described by Schlechtendahl (1854) based on plants grown from seeds sent to him by Bunge. According to the amended description (Linchevskiy & Fedorov, 1941), the species is very close to *Amygdalus nana*, differing from it mainly in having more vigorous growth, on the average larger leaves, slightly rougher stones with an oblique base. The species appears to be similar to *Amygdalus petunnikovii* Litv. in terms of stone shape (see below).

3. *Chamaeamygdalus georgica* (Desf.) Fedoronchuk, comb. nov.

Basionym: *Amygdalus georgica* Desf., Hist. Arbr. France, 2: 221. 1809.

Amygdalus nana L. var. *georgica* (Desf.) DC. ex Ser., in A.P. de Candolle, Prodr. 2: 530. 1825.

Prunus nana (L.) Stokes f. *georgica* (Desf.) Voss, in Vilm. Blumengärtn., ed. 3. 1: 232. 1894.

Prunus nana proles *georgica* (Desf.) Asch. & Graebn., in Syn. Mitteleur. Fl. 6(2): 141. 1906.

Prunus nana var. *georgica* (Desf.) C.K. Schneid., in Ill. Handb. Laubholz. 1: 599. 1906.

≡ *Prunus georgica* (Desf.) Eisenman, Phytotaxa, 222: 188. 2015.

Distribution: Caucasus (Transcaucasia). Grows on treeless mountain slopes.

Note: This species differs from typical *Chamaeamygdalus nana* in its somewhat higher growth, ciliated stipules and stones more pointed at the apex. Its type is a neotype represented by a cultivated garden specimen from the Desfontaines collection, collected by an unknown collector and deposited at the Webbia Herbarium in Florence: "*Amygdalus georgica* Desf. H[ort] Pari[s]. Herbarium Webbianum, ex Herb. Desfontaines", FI-W 055869 (Eisenman, 2015: 188).

Amygdalus petunnikovii Litv. (≡ *Prunus petunnikovii* (Litv.) Rehder), occurring in Central Asia (the Tian Shan: the Chirchik River basin, Kara-tau ridges, Talas Ala-tau, on gravelly mountain slopes

in the zone of arboreal and shrubby vegetation, at about 1400–1800 m above sea level) was sometimes placed in *Amygdalus* sect. *Chamaeamygdalus* and considered the most morphologically isolated species among other taxa related to *Amygdalus nana*. However, its proper phylogenetic placement remains problematic (Liu et al., 2013, Yazbek & Oh, 2013; Vafadar et al., 2014), and it is probably not directly related to *Chamaeamygdalus nana*. Because of that, I do not include this species in the newly re-circumscribed *Chamaeamygdalus*, pending further research.

CONCLUSIONS

The main character that separates the species placed in *Amygdalus* (in a traditional circumscription) from species of related genera is the dry mesocarp that opens (splits) when ripe. Species of the *Amygdalus* group are quite distinctive and habitually different from other “prunoid” genera. Also, the main morphological feature distinguishing the species earlier placed in the *Amygdalus* sect. *Chamaeamygdalus* from the typical section of the genus *Amygdalus* is the shape of the calyx tube (see above). These two groups (earlier mostly recognised as sections, see above) also differ in their phenology: in plants of the *Chamaeamygdalus* group, the leaves open simultaneously with the flowers, while in *Amygdalus* s. str. they open later than the flowers.

Morphological and phenological differences, also confirmed by molecular phylogenetics, give the reasons to consider the species formerly placed in the section *Chamaeamygdalus* as members of an independent genus. It should be noted that alternative views on generic circumscriptions in taxonomically complicated groups of *Rosaceae*, such as generic complexes of *Prunus* s. l. (Mason, 1913; Wight, 1915; Rydberg, 1918; Sterling, 1964; Webb, 1968; Robertson, 1974; Duncan & Duncan, 1988; Wilken, 1993; Kalkman, 2004; Shaw & Small, 2004), *Pyrus* L. s. l. (Christenhusz et al., 2018), or *Potentilla* L. s. l. (Mosyakin et al., 2020), have the right to exist, and thus, also my taxonomic and nomenclatural concept of *Amygdalus* and *Chamaeamygdalus* as genera distinct from each other and other segregate genera of the generic complex of *Prunus* sensu latissimo. The *Chamaeamygdalus* species are also distinguished

biogeographically, being widespread mainly at the northern border of the total range of taxa belonging to *Amygdalus* s. str., and are nearly restricted to the steppe region of Eurasia and the Caucasus.

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Author contribution. The author conducted all the research, analysed the data and wrote the text.

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