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The genus *Amygdalus* L. (*Rosaceae*): Species relationships, distribution and evolution under domestication

Kazimriez Browicz[1] & Daniel Zohary[2]
[1]*Institute of Dendrology, Polish Academy of Sciences, PL 62-035 Kórnik near Poznań, Poland;* [2]*Department of Evolution, Systematics and Ecology, The Hebrew University, Jerusalem 91904, Israel*

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Summary

The paper reviews the taxonomic relationships, morphological distinction, geographical distribution and ecological specificities of the twenty six species recognized (by us) in *Amygdalus* L. It also surveys the intra-genetic structure in this genus stressing the fact that they fall into five groups of closely related vicarious species: (i) *Communis* group (9 species), (ii) *Orientalis* group (6 species), (iii) Sect. *Chamaeamygdalus* (4 species), (iv) Sect. *Spartioides* (2 species), and (v) Subgenus *Dodecandara* (5 species). Within each group, species are separated from one another geographically (in few cases by altitude). The only major exception to such allopatric distribution is found in *A. communis* L., and this is interpreted as an outcome of domestication. Interspecific sterility barriers are absent, or only weakly developed in *Amygdalus*, and numerous inter-specific hybrids (particularly between the crop and various wild almond species) have been detected. Therefore most (may be all) wild almond species constitute the primary gene-pool of the cultivated nut crop.

The combined botanical and archaeological evidene points to the Levant countries as the place where the almond was taken into cultivation. Wild forms of *A. communis* are very likely native only to this area. Also the earliest archaeological signs of almond domestication come from this area.

Introduction

In the last thirty years the genus *Amygdalus* L. was subject to intensive investigation by several botanists who studied the flora and vegetation of southwest Asia and middle Asia. The scope of this effort becomes apparent when one examines the publications by Pachomova (1961), Zaprjagaeva (1964) and Browicz & Zielińkski (1984, 1990); or when one leafs through the treatments of *Amygdalus* in the various Floras covering these regions and published since 1960. A list of publications dealing with taxonomy and distribution of the almonds has been compiled (Browicz, 1989).

Progress was also made in almond genetics. Breeders experimented with interspecific hybridization in *Amygdalus* and crossed the cultivated almond with numerous wild species (Kester & Asay, 1975; Grasselly & Crossa-Raynaud, 1980; Denisov, 1988; Kester et al., 1991). The results obtained provided insight into the genetic affinities among *Amygdalus* species and the reproductive isolation barriers operating in this genus.

All in all, *Amygdalus* L. is already a relatively well studied genus. Yet no modern monographic treatment is available for the almonds, and the existing monograph by E. Spach (1843) is more than 150 years old. Also the information concerning the various species is splintered in numerous (frequently hard to obtain) reports, and fragmented country-wise. The aim of the present paper is to bring together this documentation and to sketch the evolutionary divergence in *Amygdalus*. We survey the species, their taxonomic relationships, ecological specificities and genetic affinities, and we map their geographic distribution. The paper also examines the effects of domestication in

Table 1. Species in *Amygdalus* L. and their taxonomic grouping

I. Subgenus *Amygdalus*

(i) Section *Amygdalus* [Syn.: Sect. *Euamygdalus* Spach]

(a) *Communis* species group:

1. *A. communis* L. [including *A. korshinskyi* (Hand.-Mazz.)Bornm.]
2. *A. trichamygdalus* (Hand.-Mazz.) Woronow
3. *A. fenzliana* (Fritsch) Lipsky
4. *A. webbii* Spach
5. *A. haussknechtii* (C. Schneider) Bornm.
6. *A. browiczii* Freitag [including *A. zabilica* Seraf.]
7. *A. kuramica* Korsh.
8. *A. bucharica* Korsh.
9. *A. tangutica* (Batalin) Korsh. [including *A. dehiscens* Koehne]

(b) *Orientalis* species group:

10. *A. orientalis* Duhamel
11. *A. graecae* Lindley
12. *A. elaeagnifolia* Spach [including *A. leiocarpa* Boiss.]
13. *A. kotschyi* Boiss. & Hohen.
14. *A. carduchorum* Bornm.
15. *A. mongolica* Maxim

(ii) Section *Chamaeamygdalus* Spach

16. *A. nana* L.
17. *A. georgica* Desf.
18. *A. ledebouriana* Schlecht.
19. *A. petunnikovii* Litv.

(iii) Section *Spartioides* Spach

20. *A. arabica* Olivier [including *A. agrestis* Boiss.]
21. *A. scoparia* Spach

II. Subgenus *Dodecandra* (Spach) Browicz [Syn.: Sect. *Lycioides* Spach]

22. *A. lycioides* Spach [including *A. horrida* Spach]
23. *A. spinosissima* Bunge [including *A. turcomanica* Lincz.]
24. *A. eburnea* Spach
25. *A. brahuica* Boiss. [including *A. afghana* Pachom.]
26. *A. erioclada* Bornm.

Amygdalus and defines the wild genetic resources of the cultivated almond.

Infrageneric structure of *Amygdalus*

The genus *Amygdalus* L. (many botanists follow Rehder, 1940 and regard it only as a subgenus within *Prunus* L.) contains some 26 well defined species (Table 1), as well as a long list of additional binomials. The latter comprise some twenty botanical names given to spontaneous interspecific hybrids (Table 2), and several problematic taxa, the description of which is based only on a solitary collection, or on very fragmentary material (for enumeration see Browicz, 1989).

Almonds are deciduous shrubs and small trees adapted to arid or semi-arid environments. They flower before the appearance of the leaves and bear fruits in which the pericarp ("hull") dries out at maturity, splits at the ventral suture and separates from the hard endocarp ("shell"). This is a principal diagnostic trait that distinguishes *Amygdalus* from *Prunus* in which the fleshy pericarp of the ripe fruit remains attached to the stone. Almonds are mostly allogamous; and almost

Table 2. Spontaneous interspecific hybrids in *Amygdalus* L.

Hybrid's name	Parents involved	Locality	Fertility	References
(i) Hybrids between wild species				
A. × *pabotii* Browicz	*A. carduchorum* & *A. haussknechtii*	W. Iran	fruiting	Browicz (1984)
A. × *aitchisonii* Korsh.	*A. kuramica* & subgenus *Dodecandra*	Pakistan	fruiting	Korshinskij (1904)
A. × *andarobii* Seraf.	*A. kuramica* & *A. spinosissima* subsp. *spinosissima*	Afghanistan	fruiting	Serafimov (1971)
A. × *insuenta* Seraf.	*A. zabulica* & *A. erioclada*	Afghanistan	not "	Serafimov (1977)
A. × *saviczii* Pachom.	*A. bucharica* & *A. spinnsissima* subsp. *spinosissima*	Uzbekistan	fruiting	Pachomova (1954)
A. × *podperae* (Náb.) Woronow	*A. elaeagnifolia* & *A. eburnéa*	S. Iran	?	Nábělek (1923)
A. × *Kamiaranensis* Khatamsaz	*A. scoparia* & *A. haussknechtii*	W. Iran	fruiting	Khatamsaz (1988)
A. × *yasujensis* Khatamsaz	*A. scoparia* & *A. elaeagnifolia*	S.W. Iran	not "	Khatamsaz (1988)
A. × *keredjensis* Browicz	*A. scoparia* & *A. lycioides*	N. Iran	not "	Browicz (1969)
A. × *iranshahrii* Khatamsaz	*A. scoparia* & *A. eburnea*	S.W. Iran	fruiting	Khatamsaz (1988)
A. × *mozaffarianii* Khatamsaz	*A. scoparia* & *A. brahuica*	S.E. Iran	fruiting	Khatamsaz (1988)
(ii) Hybrids between cultivated almond and wild species				
—	*A. communis* & *A. fenzliana*	Armeniya	fruiting	Denisov et al. (1973)
—	*A. communis* & *A. webbii*	Crete	fruiting	Browicz field observations
A. × *uzbekistanica* Sabirov	*A. communis* & *A. bucharica*	Uzbekistan, Tadzhikistan	fruiting	Sabirov (1959)
A. × *rhodia* Browicz	*A. communis* & *A. graeca*	Rodhos	fruiting	Browicz (1985)
A. × *balansae* Boiss.	*A. communis* & *A. orientalis*	Anatolia	fruiting	Boissier (1859)
A. × *sefinensis* Bornm.	*A. communis* & *A. kotschyi*	N. Iraq	not "	Bornmüller (1938)
A. × *kalmykovii* O. Lincz.	*A. communis* & *A. spinosissima* subsp. *spinosissima*	S. Kazakhstan	fruiting	Linczevskij (1951)
A. × *vavilovii* Popov	*A. communis* & *A. spinosissima* subsp. *turcomanica*	S. Turkmeniya	fruiting	Popov (1929)

all wild species (as well as most cultivars) tested were found to be self-incompatible. Chromosome counts are available from some 10 wild species, and from cultivated *A. communis* (Kester & Asay, 1975; Grasselly, 1977). All were found to be diploid, with $2n = 16$ chromosomes.

Amygdalus L. is a distinct Irano-Turanian genus (Browicz, 1989). Most of its species are distributed over southwest Asia. A few species extend the natural distribution range of the genus to southeast Europe, to the central Mediterranean basin, and to south Mongolia and west China (Map 1). The species placed in *Amygdalus* L. fall into the following two subgenera and four sections (see also Table 1):

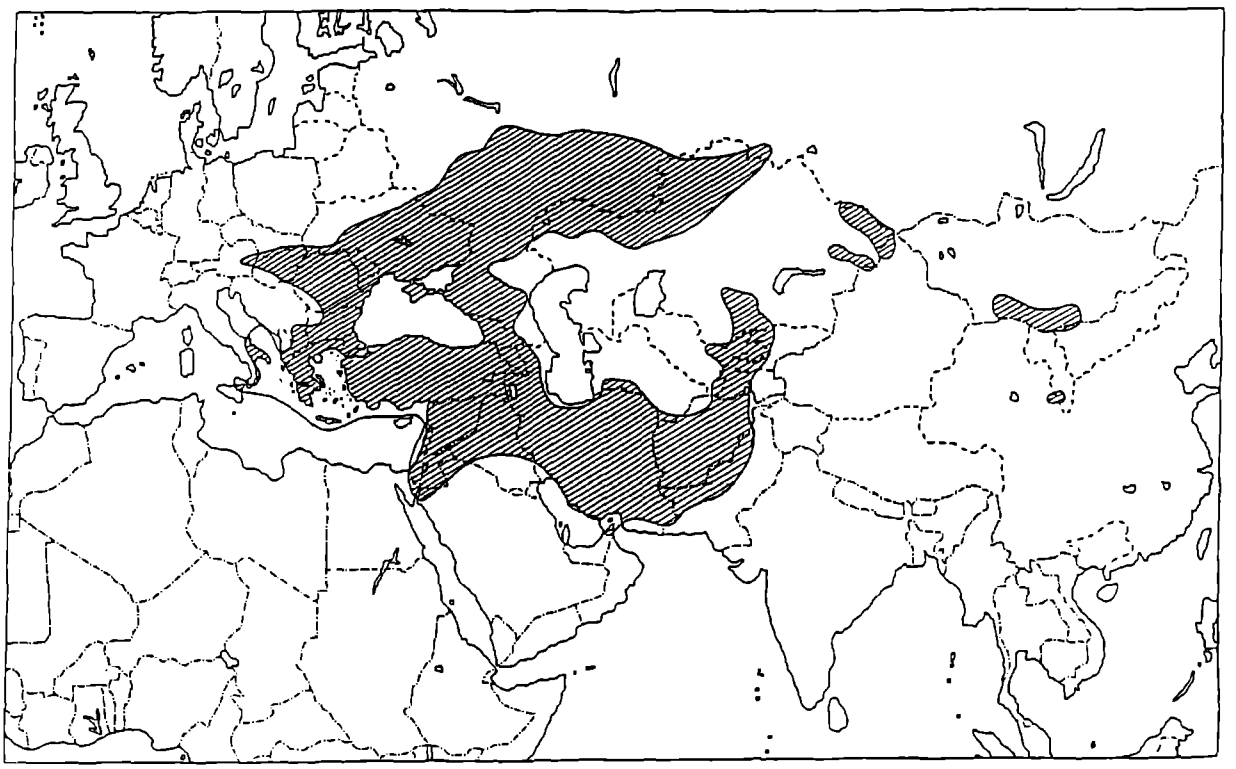
I. Subgenus Amygdalus *[Syn.: Ser.* Icosandrae *Spach, Ann. Sci. Nat. (Paris) ser. 2, 19: 107 (1843).]*

This is the larger and the more diversified subgenus, and it is further subdivided into 3 sections. All are characterized by broad short-tubed flowers, containing numerous (20–30) stamens (Figs. 1–3).

(i) Section Amygdalus *[Syn.: Sect.* Euamygdalus *Spach, Ann. Sci. Nat. (Paris) ser. 2, 19: 114 (1843).]*

Unarmed or somewhat spinescent shrubs or trees with twigs containing numerous brachyblasts bearing relatively large leaves (Fig. 1). This is the largest and the most widely distributed section in the genus *Amygdalus*. It contains two species clusters:

(a) *Communis* group: Relatively large and mostly non-spiny almonds morphologically resembling *A. commu-*



Map 1. Distribution area of the genus *Amygdalus* L., excluding cultivation.

nis. When not stunted they tend to develop into small or medium sized trees. This group contain both the cultivars and the wild forms of *A. communis* (=*Prunus amygdalus*), and 8 additional wild species (Table 1).
(b) *Orientalis* group: Smaller and more subspinescent almonds. Even when not coppiced they attain only bushy proportions or an "almost" tree size. This group contains 5–6 species (Table 1). All resemble *A. orientalis*.

(ii) Section Chamaeamygdalus *Spach. Ann. Sci. Nat. (Paris) ser. 2, 19: 100 (1843).*
Low, suckering, spineless bushes with narrow leaves and small, consipicuously woolly fruits (Fig. 2). A small section comprising 4 closely related species (Table 1), occupying the northern segment of the distributional range of the genus.

(iii) Section Spartioides *Spach, Ann. Sci. Nat. (Paris) ser. 2, 19: 107 (1843)*
Spineless, broom-like bushes or small trees, with long green twigs devoid of brachyblasts, which shed their leaves at the beginning of the dry season (Fig. 3). This is the smallest section in *Amygdalus* L., comprising 2 species.

II. Subgenus Dodecandra *(Spach) Browicz, in Rechinger Fl. Iran. 66: 166 (1969). [Syn.: Ser. Dodecandrae Spach, Ann. Sci. Nat. (Paris) ser. 2, 19: 120 (1843); Sect.* Lycioides *Spach, Ann. Sci. Nat. (Paris) ser. 2, 19: 120 (1843).]*

This is a smaller and much more uniform subgenus. Its members are characterized by rather small, narrow-cylindrical flowers which are more or less inflated at their base (Fig. 4). The flowers bear relatively few (up to 17) stamens. This subgenus contains 5–6 closely related and morphologically similar species (Table 1) distributed over the deserts and semi-deserts of Middle Asia, Afghanistan, Iran, and east Turkey. All are dense, very spiny bushes (rarely small trees) with rather small, narrow leaves and relatively small fruits. Some species are armed with compound spines (Fig. 4).

Speciation patterns in the genus *Amygdalus* L. are distinctly allopatric. The genus contains 5 natural groups, each representing a cluster of taxonomical-

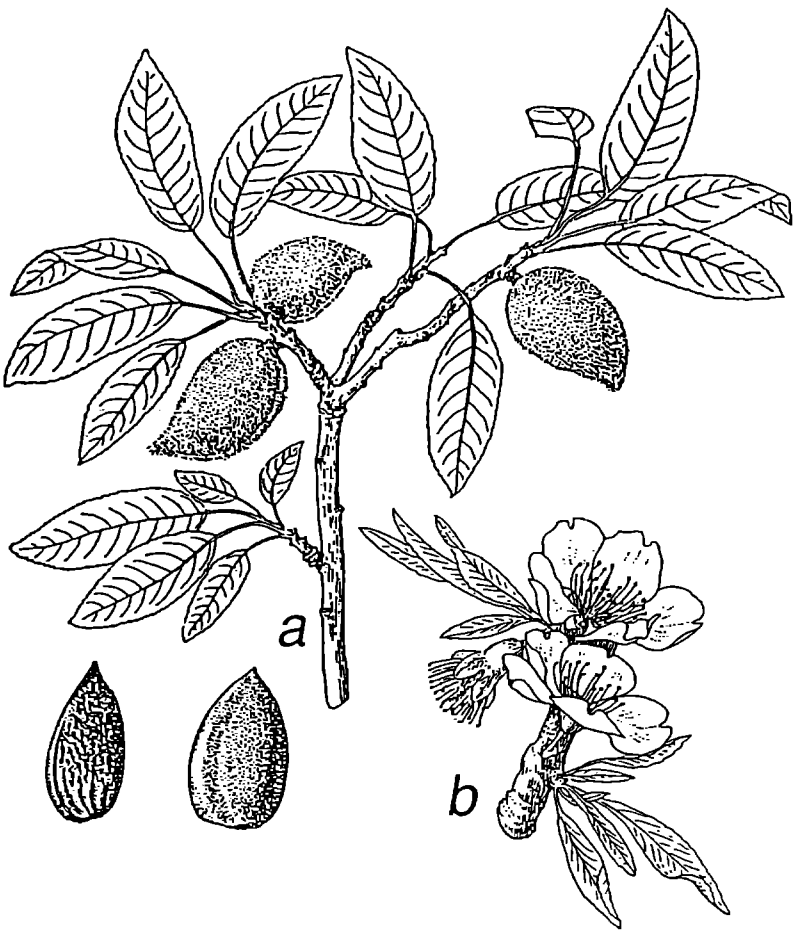


Fig. 1. Characteristic morphological features of members of Sect. *Amygdalus* as seen in: (a) *A. bucharica* (after Zapryagaeva, 1964) and (b) *A. communis* (after M. Zohary, 1972). ×0.7.

ly closely related, largely vicarious species ("semispecies" sensu Grant 1981, p. 71). Within each such natural group, member species seem to be fully (or almost fully) interfertile — but they occupy separate geographic territories. Thus, each of the 9 wild members in the *Communis* group (Table 1) has a distinct (and sometimes very restricted) area of distribution (Maps 2, 3). Similar allopatric distribution characterizes the *Orientalis* group of Sect. *Amygdalus* (Map 4), the species grouped in Sect. *Chamaeamygdalus* (Map 5), in Sect. *Spartioides* (Map 6), and in Subgenus *Dodecandra* (Map 7). In some cases the geographic isolation is replaced by altitude separation. *A. communis* seems to be the only marked exception to this rule. Domestication of this fruit tree and the subsequent spread of almond cultivation brought it in contact with several of its formerly well separated vicarious relative.

Species and their characterization

Twenty six species are recognized by us in *Amygdalus* (Table 1). The available taxonomic and ecological information on these species can be summarized as follows:

I. Subgenus Amygdalus
(i) Section Amygdalus *[syn: Sect.* Euamygdalus *Spach]*
(a) Communis *species group*

1. *Amygdalus communis* L., Sp. Pl. 473 (1753). Syn.: A. dulcis Miller, Gard. Dict. ed.8: no.2 (1768); Prunus amygdalus Batsch, Beytr. Entw. Pragm. Gesch. Nat.-Reiche 1: 30 (1801); P. communis (L.) Arcang., Comp. Fl. Ital.209 (1882) non Huds. (1778); P. dulcis (Miller) D.A. Webb in Feddes Rep. 74: 24.

Fig. 2. Characteristic morphological features of members of Sect. *Chamaeamygdalus* as seen in *A. nana* (after Jordanov, 1973). ×0.7.

Usually spineless shrubs or trees up to 10 m tall, with glabrous greenish twigs. Leaves oblong-lanceolate, ovate-lanceolate to oblong-elliptical, glaborous, with crenate-serrate margins and with 1–2 cm long petioles. Flowers campanulate, pinkish to white, 3–5 cm in dimension, nearly sessile. Fruits (in wild forms) ovoid to ellipsoidal, up to 4 cm long. (Some cultivated forms have bigger fruits). The stone is keeled and finely pitted, variable in shape and thickness, frequently somewhat compressed.

A. communis comprises a very variable "crop complex" containing the following, genetically interconnected, categories: (a) Genuinely wild forms occupying primary habitats. (b) Domesticated forms (cultivars) growing under cultivation. (c) Spontaneous feral derivatives and products of hybridization between cultivars and wild forms which usually colonize disturbed habitats within the general area of almond cultivation. The situation in *A. communis* is further complicated by the fact that the wild forms are variable: Relatively large wild almonds, very similar in their morphology to the cultivars and feral forms, grow in the more mesic Mediterranean environments. Much smaller, xerophyllous forms (deserving subspecific ranking) occur in drier environments; and a whole range of intermediate forms interconnect these two ecological races. The following three subspecies are recognized by us in this variable species:

(i) *A. communis* L. subsp. *communis*.

Cultivated fruit trees with unarmed branches, big (1–2 × 4–8 cm) leaves and large (up to 5 cm long) fruits. Most forms have non-bitter seeds. Some are characterized by relatively soft shells. Most almond cultivars are self incompatible; yet few cultivated forms (particularly in Puglia district, Italy) were found to be self-fertile (Dicenda & Garcia, 1993b). (For descriptors of the morphological variation among the cultivars see Gülcan, 1985).

The cultivated almond is a Mediterranean crop. The ideal conditions for its cultivation are mild (but cool) rainy winters, and hot, dry summers. The Mediterranean basin and southwest Asian constitute the tra-

Fig. 3. Characteristic morphological features of members of Sect. *Spartioides* as seen in *A. arabica* (after M. Zohary, 1972). ×0.5.

Fig. 4. Characteristic morphological features of members of Sect. *Dodecandra* as seen in *A. spinosissima* (after Zapryagaeva, 1964). Branches ×0.5; fruits ×1.0.

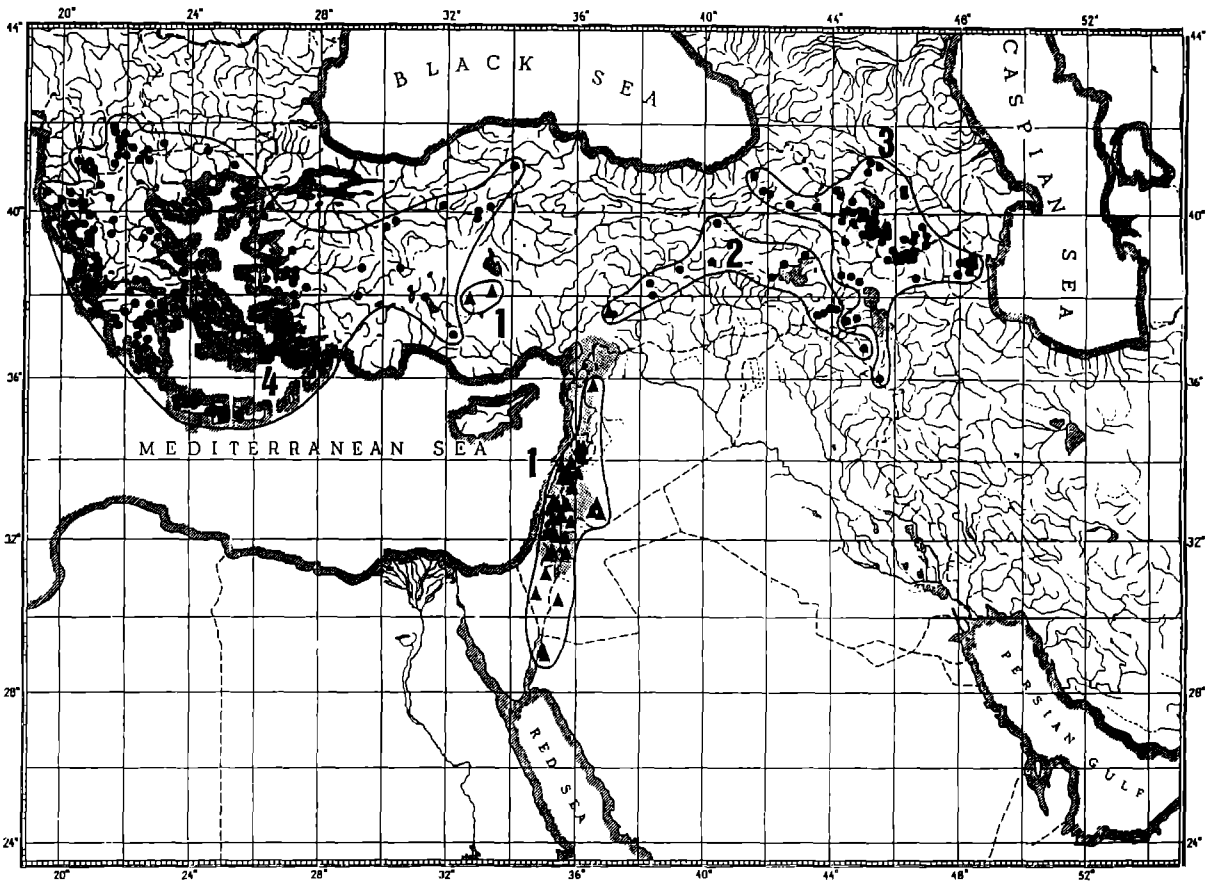
ditional belt of almond cultivation which also extends to middle Asia and some areas in temperate Europe (Grasselly & Crossa-Raynaud, 1980; Kester et al., 1991). More recently almond cultivation was introduced also into areas with Mediterranean-type climate in North and South America, South Africa, and Australia. Today California is the largest almond producer.

(ii) *A. communis* L. subsp. *spontanea* (Korsh.) Browicz & D. Zohary comb. nov. [Basonym: var. *spontanea* Korsh., Izv. Imp. Akad. Nauk. 5th series, 14: 90, 1901].

Spontaneously growing, unarmed, relatively large almonds (mostly trees) with large leaves (similar to those of cultivars), and with bitter, hard-shelled fruits. This subspecies includes the relatively large mesic wild forms and the spontaneous "weedy" forms. Morphologically they are indistinguishable from one another.

Wild forms of subsp. *spontanea* are known definitely only from the Mediterranean parts of Syria, Lebanon, Israel and Jordan (Map 2). In these territories they are common constituents of the Mediterranean maquis formations, thriving mainly on rocky slopes, at elevations ranging between 50–1200 m. Claims were also made that wild forms of *A. communis* occur in Turkmeniya, Kirgiziya and Uzbekistan (Popov, 1929; Zaprjagaeva, 1964; Denisov, 1988; Kester et al., 1991). Yet it is questionable whether the *A. communis* populations that grow spontaneously in these areas are native, or whether they are only naturalized, i.e. the outcome of the introduction of almond cultivation into Middle Asia. For several reasons (see p. 17) we regard them as feral.

Feral and "weedy" forms of subsp. *spontanea* are more widely distributed than the wild forms. They are common in the Levant and extend to several other parts of the Mediterranean basin, southwest Asia and middle Asia. In the Levant they grow mostly in areas of almond cultivation. In contrast with the genuinely wild forms they occupy roadsides, edges of orchards, abandoned cultivation and similar man-made habitats. They frequently grow in close proximity to almond



Map 2. Distribution of the western members of the *Communis* species group: 1. Wild forms of *A. communis* L. (excluding feral populations): Triangles show known sites of subsp. *micophylla*. The shaded area indicates the known territory of wild forms of subsp. *spontanea*. 2. *A. trichamygdalus* (Hand.-Mazz) Woronow. 3. *A. fenzliana* (Fritch) Lipsky. 4. *A. webbii* Spach. Note that toward west *A. webbii* extends, beyond the boundaries of this map, into south Italy. Since it is the only wild almond native to Italy, its distribution in this country is shown in map 1.

plantations and to the wild stands, and they occasionaly hybridize with them and form variable aggregates of wild forms, "weedy" derivatives and cultivars (Zohary, 1983). Outside the Levant, feral forms of *A. communis* can also be common; and again they occupy mainly disturbed, man-made habitats.

(iii) *A. communis* L. subsp. *microphylla* (Post) Browicz & D. Zohary comb. nov. [Syn.: *A. communis* L. var. *microphylla* Post, Fl. Syria 302 (1898); *A. korshinskyi* (Hand.-Mazz.) Bornm., Beih. Bot. Centrbl. 31(2): 212 (1914)].

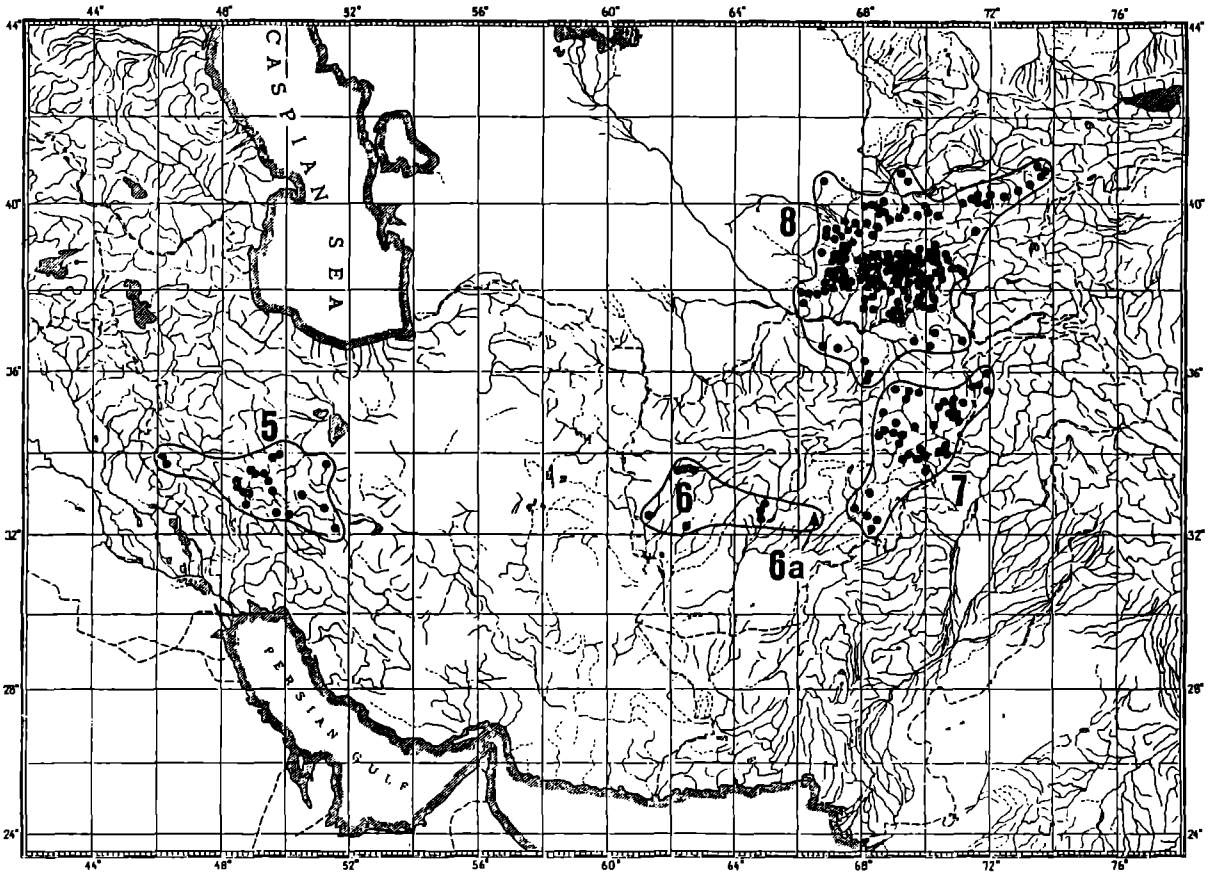
Smaller wild almonds, usually shrubs or small trees (up to 3–4 m tall), sometimes with slightly spinescent ultimate branches. The leaves, flowers and fruits are usually smaller than those at the two previous subspecies.

This is the more xeric subspecies of *A. communis* occupying steppe forest and steppe-like habitats in the Levant countries (Map 2), frequently together with *Pistacia atlantica* Desf. and *Crataegus aronia* (L.) Bosc. It thrives in areas where the total annual percipitation is usually only 150–300 mm, in elevations ranging from 100 to 180 m. Also the wild forms native to Israel's central Negev, described by Danin (1980) as *A. ramonensis* belong to this subspecies.

A whole gradient of intermediate plants bridges and xeric subsp. *microphylla* with the more mesic Mediterranean wild forms of subsp. *spontanea*.

2. *Amygdalus trichamygdalus* (Hand.-Mazz.) Woronow, Bull. Appl. Bot. Pl. Breed. (Leningrad) 14: 49 (1925). Syn.: *Prunus trichamygdalus* Hand.-Mazz., Ann. K. K. Naturhist. Hofmus. Wien 27: 70 (1913).

Spineless shrubs up to 3 m tall (sometimes small trees) closely resembling *A. communis* but with characteristic short-petioled leaves, bearing relatively large



Map 3. Distribution of the eastern members of the *Communis* species group (excluding *A. tangutica*): 5. *A. haussknechtii* (C. Schneider) Bornm.; 6. *A. browiczii* Freitag and 6a. *A. zabulica* Seraf.; 7. *A. kuramica* Korsch.; 8. *A. bucharica* Korsch.

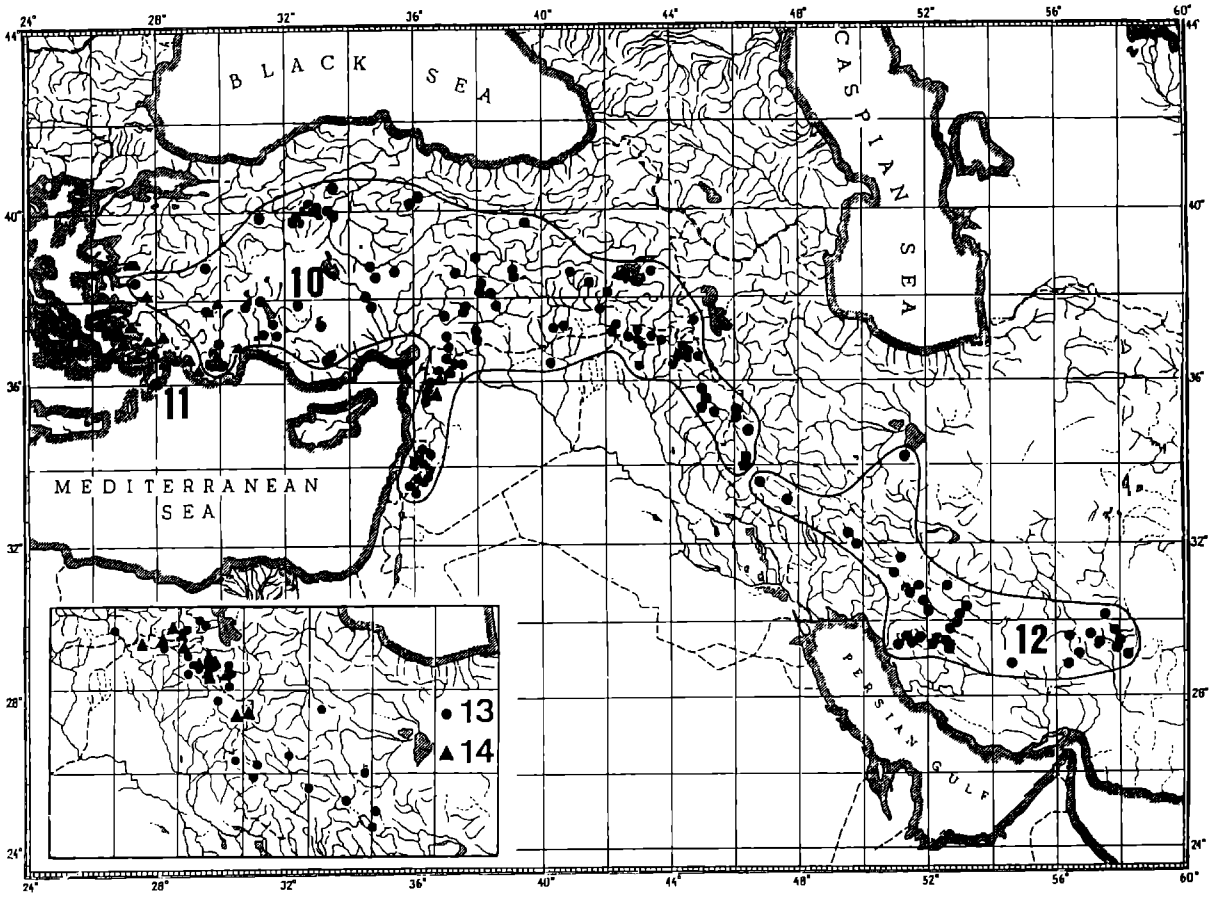
(3.0 × 2.0 cm) compressed fruits. A narrowly distributed East Anatolian species (Map 2), and one of the least known members of the *Communis* group. Only a few scattered stands of this wild almond have been discovered up to date in eastern Turkey and in adjacent areas in Iran. They grow on limestone slopes and in rock gorges at 1250–1900 (–2100) m elevation (Browicz & Zieliński, 1984).

3. *Amygdalus fenzliana* (Fritsch) Lipsky, Acta Horti Petrop. 14: 263 (1897). Syn.: *Prunus fenzliana* Fritsch, Sitzungsber, Kaiserl. Akad. Wiss. Math. Naturwiss. Wien 101: 632 (1892).

A subspinescent shrub usually 2–3 m tall (and more rarely a small tree up to 4 m height), with rather large (2.5 × 1.5 cm) tomentose fruits. A Caucasian element extending to northeast Turkey and northwest Iran (Map 2), growing mainly in stony or rocky slopes occupied by sparse xerophytic woody vegetation or in open steppe communities, mostly between 700–1800 m altitude (Browicz & Zieliński, 1984).

4. *Amygdalus webbii* Spach, Ann. Sci. Nat. (Paris) ser. 2, 19: 117 (1843). Syn.: *A. salicifolia* Boiss. & Bal., in Boiss Diagn. ser.2: 71 (1859); *Prunus webbii* (Spach) Vierh., Öst. Bot. Zeitschr. 65: 21, (1915).

Much branched spinose shrubs or small trees usually attaining the height of 2–3 m. A very variable wild almond in terms of leaf size and fruit shape, with linear-oblong to lanceolate 3.0–4.0 × 0.6–0.9 cm leaves and relatively small fruits. A Balkano-Anatolian species (Map 2), extending to Puglia district in south Italy and to Sicily. It was also reported growing spontaneously in Spain (Felipe & Socias i Company, 1977). Judging by its bushy spinescent habit, it is apparently the wild member of the *Communis* group most distant from the crop.



Map 4. Distribution of the eastern members of the *Orientalis* species group (excluding *A. mongolica*): 10. *A. orientalis* Duhamel; 11. *A. graeca* Lindley; 12. *A. elaeagnifolia* Spach; 13. *A. kotchyi* Boiss. & Hohen.; 14. *A. carduchorum* Bornm.

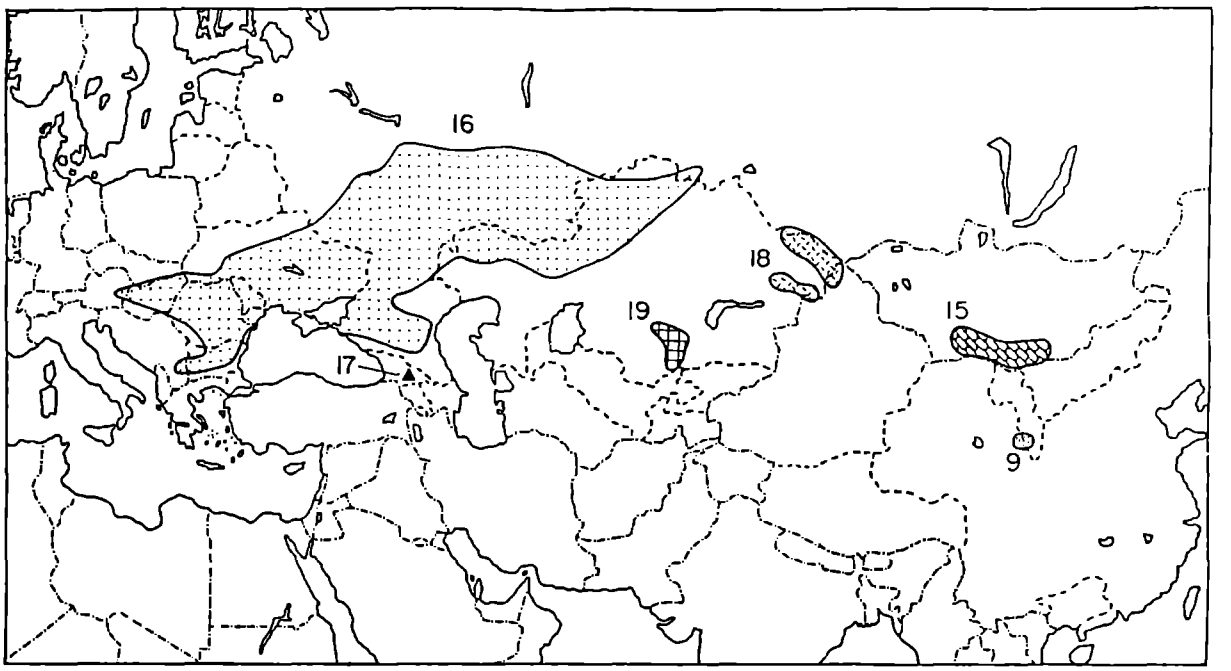
A. webbii grows in open sunny places in limestone rocks or gravelly slopes from sea level up to 900 m altitude. Few stands were recorded up to 1200–1600 m. It thrives in degraded oakwoods and in opened Mediterranean bush (phrygana) formations (Browicz & Zieliński, 1984).

In contrast with most other almond species (which, as far as we know, are self-incompatible), at least some populations (or individuals) of *A. webbii* are self-fertile (Socias i Company, 1990). It was suggested that also the rare self-compatible almond cultivars (particularly those discovered in Puglia district, Italy) acquired their self-fertility through hybridization with local *A. webbii*. (For a review of the origin of self-fertility in these cultivars see Socias i Company, 1990).

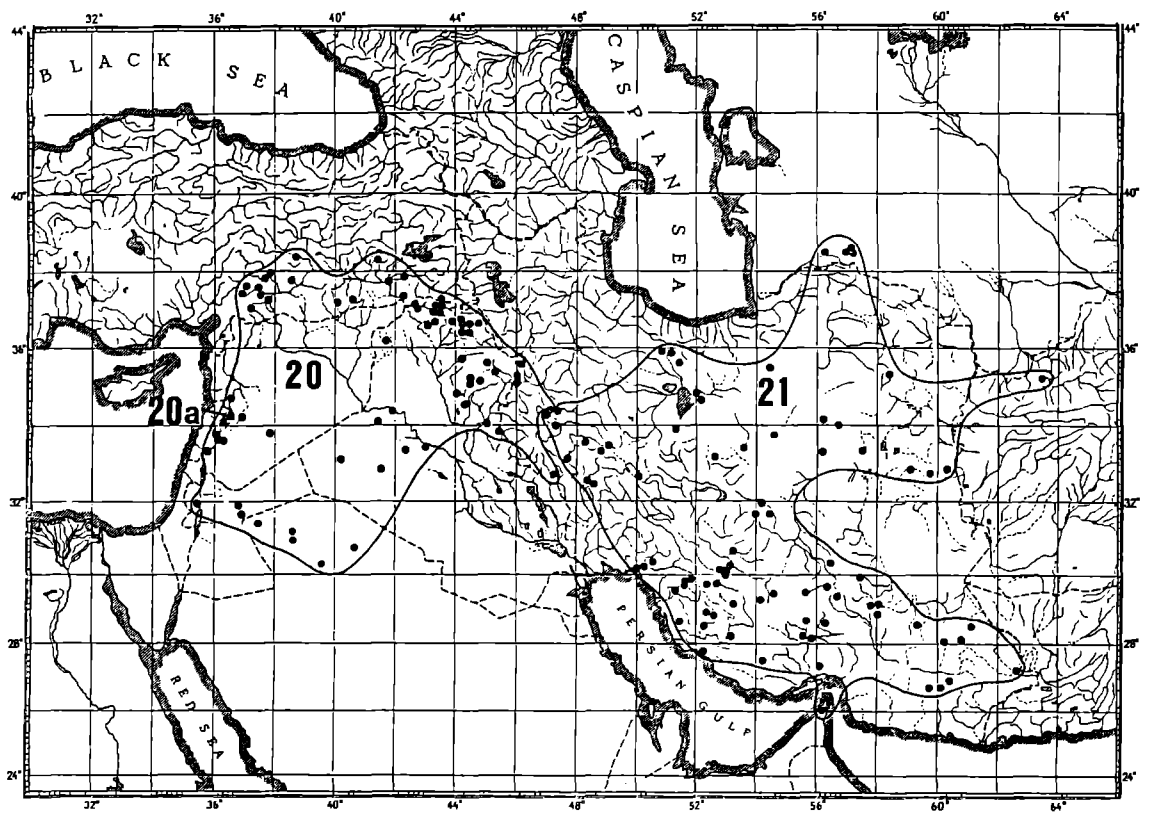
5. *Amygdalus haussknechtii* (C. Schneider) Bornm., Beih. Bot. Centralbl. 28(2): 226 (1911). Syn.: *Prunus haussknechtii* C. Schneider, Ill. Handb. Laubholzk.1: 592 (1905).

Widely branched, dense, spinescent shrubs or small tree, with narrowly elliptical up to obovate leaves. The fruits are about 2.5 × 1.8 cm, puberulent and distinctively compressed. A montane, west Iranian endemic (Map 3), growing mostly at the altitude range of 1600–2800 m. Its ecology is still poorly known. It seems to grow on limestone bedrock in the degraded *Quercus brantii* Lindl. park-forest, at the upper level of this formation (Browicz & Zieliński, 1984).

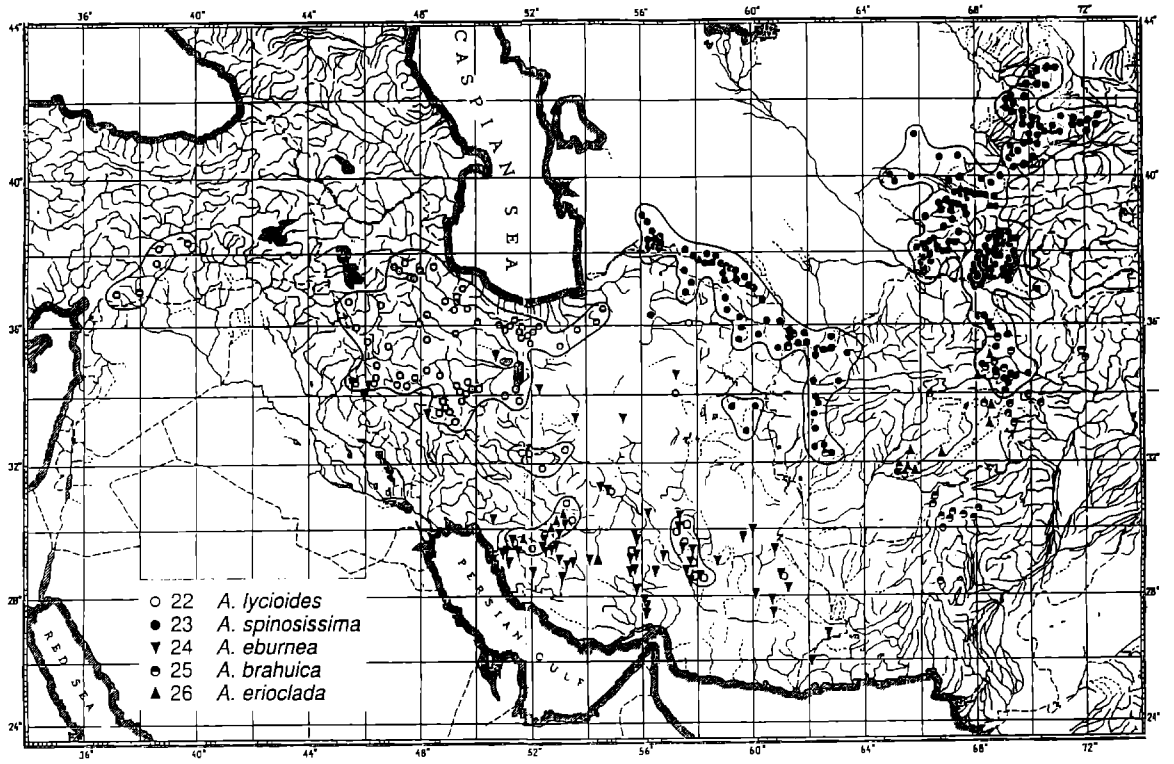
6. *Amygdalus browiczii* Freitag, Bot. Jahrb. Syst. 91(4): 470 (1972). A montane non-spiny small (up to 5 m) tree closely resembling *A. communis* restricted to south Afghanistan (Map 3). Only few stands of this wild almond have been discovered until now in Farah and Hilmand provinces, growing together with *Pistacia atlantica* Desf. Both form a loose park-type



Map 5. Distribution of the members of Sect. *Chamaeamygdalus*: 16. *A. nana* L.; 17. *A. georgica* Desf.; 18. *A. ledebourina* Schlecht.; 19. *A. petunnikovii* Litv.; as well as distribution of the two east-most *Amygdalus* species: 9. *A. tangutica* (Batalin) Korsch.; 15. *A. mongolica* Maxim.



Map 6. Distribution of the members of Sect. *Spartioides*: 20. *A. arabica* Olivier; 20a. *A. agrestis* Boiss.; 21. *A. scoparia* Spach.



Map 7. Distribution of the members of Sect. *Dodecandra*: 22. *A. lycioides* Spach; 23. *A. spinosissima* Bunge; 24. *A. eburnea* Spach; 25. *A. brahuica* Boiss.; 26. *A. erioclada* Bornm.

vegetation, mainly between 1300 and 1900 m altitude (Browicz & Zieliński, 1984). *A. browiczii* was described only in 1972, and it is not yet sufficiently known.

An additional poorly known almond, *A. zabulica* Seraf., Novosti Sist. Vyss. Rast. 8: 173 (1971), described from more eastern parts of Afghanistan (Map 3), is probably conspecific with *A. browiczii*.

7. *Amygdalus kuramica* Korsh., Bull. Acad. Imp. Sci. Saint-Petersbourg, ser. 5, 14: 93 (1901). Syn.: *Prunus kuramica* (Korsh.) Kitam., Fl. Afgh. 179 (1960).

An erect shrub or small tree up to 4–5 m tall, resembling *A. communis* from which it differs by having small (up to 2.0 cm long) subspherical fruits and usually also deeply sulcate stones. *A. kuramica* is restricted in its distribution to eastern Afghanistan and its border with Pakistan (Map 3). It grows in river valleys and on steep rocky or gravelly slopes in open sunny places, as well as in degraded *Quercus baloot* Griffith oak woods, at altitudes ranging between 1000–1600 m (Browicz & Zieliński, 1984).

8. *Amygdalus bucharica* Korsh., Bull. Acad. Imp. Sci. Saint-Petersbourg, ser. 5, 14: 92 (1901). Syn.: *Prunus bucharica* (Korsh.) Hand.-Mazz., Ann. Naturhist. Hofmus. Wien 27: 70 (1913).

An erect shrub 1.5–4.0 m high, or more rarely a small tree with several trunks up to 6.0-7.0 m tall, resembling *A. communis* in general form but with tomentose twigs and tomentose lower side of the leaves. The fruits are relatively large (4.0 × 2.5 cm) and slightly asymetric. This almond varies considerably in the pubescence of the twigs and the leaves, and in the sculpturing of the shell. Very hairy forms appear to be more common in Tadzhikistan and Afghanistan; less hairy plants occur in the northern part of its range. As in other wild almonds, the seeds are bitter; but occasional individuals bearing sweet fruits were also detected.

A. bucharica is distributed over the mountainous parts of Tadzhikistan and Uzbekistan and it extends to south Afghanistan (Map 3). This wild almond grows scattered or in small groups mainly on stony, sandy or loessy slopes, on rocks and also in dry valleys. It usually occurs together with other xerothermic trees

and shrubs. It is common in the 1000–1800 m altitude range and rarer in lower (600-1000 m) and in higher (up to 2500 m) altitudes (Pachomova, 1961, pp. 90–130; Zaprjagaeva, 1964, pp. 209–289; Browicz & Zieliński, 1984).

9. *Amygdalus tangutica* (Batalin) Korsh., Bull. Acad. Imp. Sci. Saint-Petersbourg, ser.5, 14: 94 (1901). Syn.: *Prunus tanguitica* (Batalin) Koehne, in Sargent Pl. Wilson. 1: 276 (1912).

Shrubs or small trees up to 4 m tall with spreading branches, small oblong (3.0 × 1.0 cm) leaves, and subsessile, 2.0 cm long densely tomentose fruits. An insufficiently known wild almond restricted to east Kansu and Szechwan provinces of China (Map 5). It is widely separated geographically from the other members of the *Communis* group.

(b) Orientalis species group

10. *Amygdalus orientalis* Duhamel, Trait. Arb. Arbust. 1: 48 (1755). Syn.: *A. argentea* Lam., Encycl. Meth. Bot. 1: 103 (1783); *Prunus argentea* (Lam.) Rehder, J. Arnold Arbor. 3: 27 (1922).

A subspinescent shrub 1–2(3) m tall, characterized by white tomentose shoots, leaves and fruits, particularly when of young age. The fruits are very variable in size and shape. *A. orientalis* is a Near East species (Map 4). In northeast Iraq and in south and central Anatolia it is one of the most common wild almond species. Specimens with large (up to 3.0 cm) and much flattened fruits occur in the southern part of its distribution range. *A. orientalis* mainly occupies open, sunny niches such as sandy hills covered with steppe or steppe forest vegetation, loose gravel and limestone cliffs or rock slopes. *A. orientalis* is a low altitude plant, growing mainly in altitudes between 600 and 1200 m (Browicz & Zieliński, 1984).

11. *Amygdalus graeca* Lindley, in Sibth. & Smith. Fl. Graeca 10: 71 (1840). Syn.: *A. discolor* (Spach) Roemer, Syn. Monogr. 3: 12 (1847); *Prunus discolor* (Spach) C. Schneider, Ill. Handb. Laubholzk. 1: 591 (1905).

A shrub or small tree 1–4 m tall, resembling *A. orientalis* in its growth form but more spinescent and with glabrous dorsal leaf surface. The main range of *A. graeca* is in southwest Anatolia and in some of the adjacent Greek Islands, particularly Rhodos (Map 4). *A. graeca* reappears in Aleppo district, Syria and near Ankara, Turkey, but in these localities it is represented only by few stands.

A. graeca is a xerophylous shrub growing on rocky calcareous slopes mainly in phrygana-type vegetation. In few places (in Anatolia) it occurs side by side with *A. orientalis*. However such contacts are relatively rare since *A. graeca* is distinctly a low altitude plant, growing mainly at altitudes ranging from 10 to 500 m (Browicz & Zieliński, 1984).

12. *Amygdalus elaeagnifolia* Spach, Ann. Sci. Nat. (Paris) ser.2 19: 123 (1843). Syn.: *A. kermanensis* Bornm., Beih. Bot. Centralbl. 58B: 256 (1938); *Prunus elaeagnifolia* (Spach) E. Murray, Kalmia 1(7): 30 (1969).

A densely branched shrub or small tree up to 3–4 m tall, with yellowish-brown or even grey bark on the older twigs. The leaves are up to 2 cm long, almost sessile and with entire or only slightly crenate margins. The flowers are white and the fruits can attain 2 cm in length. This wild almond varies considerably in leaf shape and in the degree of pubescence on the shoots, leaves and fruits. The pubescent forms are placeded in subsp. *elaeagnifolia* while the glabrous ones are named subsp. *leiocarpa* (Boiss.) Browicz.

A. elaeagnifolia is an Iranian endemic (Map 4). It is xeric, thermophylous and light demanding almond, growing on marly limestone, clay and stony bedrocks in sparcely covered or degraded steppe-forests (Browicz & Zieliński, 1990).

13. *Amygdalus kotschyi* Boiss. & Hohen., in sched. Kotschy, Pl. Alepp. Kurd. Mossul 338 (1843). Syn.: *Prunus kotschyi* (Boiss. & Hohen.) Náb., Publ. Fac. Sci. Univ. Masaryk (Brno) 35: 105 (1923).

A small subspinescent shrub scarcely 30–45 cm tall, characterized by very dense, soft, long, yellowish-grey hairy cover on the shoots, leaves and fruits. A montane species confined mostly to the Zagros mountain range of west Iran and north Iraq as well as few sites in southeast Anatolia (Map 4). It grows on limestone rocks, bolders and screes and in dry and open places in the upper margins of the oak and pistachio park-forest zone, and also in the thorny cushion-type vegetation above the forest belt, in altitudes between 1800 and 2500 m (Browicz & Zieliński, 1984).

14. *Amygdalus carduchorum* Bornm., Bot. Centralbl. 58B: 257 (1938). Syn.: *Prunus carduchorum* (Bornm.) Meikle, Kew Bull. 19(2): 229 (1965).

A small subspinescent shrub 0.5–1.0 m high with narrow, lanceolate or linear leaves and with globose or ovate-globose slightly compressed upto 15 mm long fruits. A narrowly distributed montane species, restricted to a small area in Kurdistan on the border between Turkey, Iraq and Iran (Map 4). It occurs mainly close to the upper limits of the oak park-forest belt, and in the zone of the thorny cushion-type vegetation above it, growing on rock slopes and screes, in open places or in degraded oak forests in altitudes between 1500 and 3000 m (Browicz & Zieliński, 1984).

15. *Amygdalus mongolica* (Maxim.) Ricker, Proc. Biol. Soc. Wash. 30: 17 (1917). Syn.: *Prunus mongolica* Maxim. Bull. Soc. Nat. Mosc. 45: 16 (1879).

This is a very spiny shrub up to 1.8 m high, with thin, acute spines. The leaves are ovate to broadly-ovate, sometimes obovate, 9–15(25) mm long and 5–10(14) m broad, serrulate or crenulate, and glabrous (even in the young state). Petioles are 2–6(10) mm long. The flower is campanulate, saucer shaped, with 20–24 stamens. Fruits are 2 cm long and 1 cm broad.

A. mongolica grows on sunny, rocky slopes in south Mongolia (Map 5), and it is geographically separated from all other members of the genus. Taxonomically this wild almond is as yet insufficiently studied. It flower shape resembles that found in the *Orientalis* species group. Therefore, it is tentatively placed by us in Sect. *Amygdalus*. Yet in several other morphological traits *A. mongolica* stands by itself, and it may represent a separate, fully diverged section within the genus *Amygdalus*.

(ii) Section Chamaeamygdalus Spach

16. *Amygdalus nana* L., Sp. Pl. 473 (1753). Syn.: *Prunus tenella* Batsch, Beytr, Entw. Pragm. Gesch. Natur-Reiche 29 (1801); *P. nana* (L.) Stokes, Bot. Mat. Med. 3: 103 (1812).

Low, suckering, spineless shrubs 1.0–1.5 m tall with large lanceolate to ovate leaves (up to 6.0 cm long and up to 2.5 cm broad), and ovate, relatively small (1–2 cm long) fruits (Fig. 3). A very variable wild almond and the north-most species of *Amygdalus*. Widely distributed over the steppes and oak forest edges of Ukraine and south Russia; extending eastward to north Kazakhstan; and westward to the north Balkan, Czechoslovakia, Austria and Hungary (Map 5).

17. *Amygdalus georgica* Desf., Hist. Arbr. Arbriss. 2: 221 (1908). A shrub up to 1.0 m tall and closely resembling *A. nana* but with smaller (1.7–2.00 cm long) broadly ovate fruits. Endemic to a small area of central Georgia (Map 5), where it grows on south facing rocky slopes and at the edge of broad-leaved forests at 400–700 m altitude. Regarded by Russian botanists (Svjazeva, 1980) as an separate species, but very probably it represents only an isolated southern extension of the widely distributed and variable *A. nana*.

18. *Amygdalus ledebuoriana* Schlecht., Abh. Naturf. Ges. Halle 2: 21 (1854). A wild almond closely resembling *A. nana* but taller (up to 2 m), and with larger leaves and fruits. Restricted to the Tarbagatay range of east Kazakhstan and to the southwestern part of the Altai range (Map 5). Growing on mountain slopes and along river valleys at 500–1100 m altitude. Regarded by Russian botanists (see Svjazeva, 1980) as an independent species, but probably it represents only an isolated eastern extension of the widely distributed and variable *A. nana*.

19. *Amygdalus petunnikovii* Litv., Trudy Bot. Muz. Imp. Akad. Nauk 1:16 (1902). Syn.: *Prunus petunnikovii* (Litv.) Rehder, J. Arnold Arbor. 7: 29 (1926).

Shrubs up to 1.0 m tall resembling *A. nana* in their general habit but with oblanceolate to almost linear leaves which have distinct serrate margins (the narrowest leaves in Sect. *Chamaeamydalus*). The fruits are relatively large (1.5–2.8 cm long), and the stone is constricted or beak-like at its base. Endemic to west Tien-Shan range (Map 5). A montane species growing on skeletal soils and rocky mountain slopes in shrubby thickets and in open formations of juniper, between 1400 and 1800 m altitude (Pachomova 1961, pp. 172–184; Svjazeva, 1980).

(iii) Section Spartioides Spach

20. *Amygdalus arabica* Olivier, Voy. Emp. Othoman 3: 460 (1804). Syn.: *A. spartioides* Spach, in Ann. Sci. Nat. (Paris) ser.2, 19: 108 (1905); *Prunus spartioides* (Spach) C. Schneider Ill. Handb. Laubholzk. 1: 590 (1905). *P. arabica* (Olivier) Meikle, Kew Bull. 19(2): 229 (1967).

An erect, broom-like shrub up to 1.5–2.5 m tall, characterized by stiff, long, permanently green, glaborous, angled branches. Throughout most of the year the shrubs are leafless since they shed their leaves

at the beginning of the dry season (Fig. 3). *A. arabica* is a Near Eastern plant. Its range covers southeastern Anatolia, Iraq and Syria (Map 6). Single stands are known also from western Iran, Israel, Jordan and northwest Saudi Arabia. This almond grows on dry bare limestone rocks and sandstone cliffs, both in lowland and in hilly terrains. In the northern parts of its distribution it occurs in degraded oakwoods, while in the more arid south it enters forest-steppe, steppe and semi-desert formations. *A. arabica* is also found in sandy places and in wadi beds. Its altitude range is between 150–1200 m, rarely up to 1500 m (Browicz & Zieliński, 1984).

A. agrestis Boiss., a small spartioid shrub about 60 cm tall, described from near Baalbeck, Lebanon, could be a miniaturized form of *A. arabica* or an isolated endemic almond closely related to this species (Map 6).

21. *Amygdalus scoparia* Spach, Ann. Sci. Nat. (Paris) ser.2, 19: 109 (1843). Syn.: *Prunus scoparia* (Spach) C. Schneider, Ill. Handb. Laubholzk. 1: 590 (1905).

An upright broom-like shrub up to 3–4 m tall, resembling *A. arabica* but with non-angled branches. The trunks of well developed individuals can be as thick as an arm. Essentially an Iranian species (Map 6), replacing *A. arabica* in this regions. *A. scoparia* is a distinct xerophyte distributed over dry and hot areas, growing on loose conglomerates and limestone cliffs, loose vulcanic rocks, crevices in rock slopes and in clay and sandy soils. It frequently colonizes degraded steppe-forest communities. In some localities *A. scoparia* is the dominant element in the plant cover. In contrast to *A. arabica*, it occurs most commonly above 1200 m altitude. The most elevated stands reach 2700 m (Browicz & Zieliński, 1984).

II. Subgenus Dodecandra *(Spach) Browicz [Syn.: Sect.* Lycioides *Spach]*

22. *Amygdalus lycioides* Spach. Ann. Sci. Nat. (Paris) ser.2, 19: 120 (1843). Syn.: *Prunus lycioides* (Spach) C. Schneider, Ill. Handb. Laubholzk. 1: 600 (1906).

A very spiny, much branched, dense shrub about 1 m tall, with linear-lanceolate 1.5–3.0 cm long leaves which have sharp pointed apex and crenate-dentate margins. The flowers are sessile; and the fruits are flattened and velutinous, up to 1.5 cm long. An Iranian species extending (in few localities) into south Anatolia (Map 7). *A. lycioides* grows on steep dry slopes made of limestone, sandstone or even granite, as well as in clayish or gravelly habitats — both in steppe areas and in degraded oak-pistachio woodlands. It covers a wide altitude range — from 200 to 2900 m. Its optimal conditions are, however, at 600–1200 m (Browicz & Zieliński, 1990). Two varieties are recognized within this species: (i) var. *lycioides*. and (ii) var. *horrida* (Spach) Browicz (Syn.: *Amygdalus horrida* Spach). The latter is characterized by smaller and more rounded fruits.

23. *Amygdalus spinosissima* Bunge. Beitr. Kenntn. Fl. Russl. u. Stepp. Centr.-As. 106: (1852). Syn.: *Prunus spinosissima* (Bunge) Franchet, Ann. Sci. Nat. (Paris) ser.6, 16: 281 (1883).

A very prickly shrub, 1.5–2.0 m tall or rarely a small tree. The first year twigs are purple-red and lustrous, the older twigs are grey while the bark of well developed trunks is almost black. The fruits are variable, up to 2 cm long. Two subspecies have been recognized in this almond: Relatively taller forms (subsp. *spinosissima*), with long-ovate to ovate lanceolate and more or less flattened drupes occur in the eastern part of this species range. Somewhat lower forms (subsp. *turcomanica* (O. Lincz.) Browicz.), with smaller and globular fruits grow in the west part of the range. Transitional forms interconnect the two subspecies.

A. spinosissima is a middle Asiatic element (Map 7), distributed over northeast Iran and Afghanistan, extending to south Kazakhstan. It occupies dry and warm habitats such as open sunny slopes and escarpments, steppes, and degraded or eroded lands (Pachomova, 1961; Zaprjagaeva, 1964; Browicz & Zieliński, 1990). Its optimal vertical range is between 300 and 1800 m. Some individuals climb as high as 2700 m.

24. *Amygdalus eburnea* Spach, Ann. Sci. Nat. (Paris) ser.2, 19: 123 (1843). Syn.: *A. spathulata* Boiss., Diagn. ser.1, 6: 52 (1845); *Prunus eburnea* (Spach) C. Schneider, in Ill. Handb. Laubholzk. 1: 599 (1906).

A very prickly shrub up to 1.5 m tall; with strong, smooth, whitish thorns protruding at right angle to the stem. Characterized by sessile, narrowly spatulate, glaucous, small leaves (not longer than 1.2 cm), by pubescent flowers, and by small ovate to ovate-globular (1.0–1.5 cm long) fruits. *A. eburnea* is a south Iranian species with few penetrations to central and north Iran (Map 7). It grows in steppes and in degraded steppe-forests on sandy and stony substrates, particularly limestone, mostly at 1000-2000 m altitude (Browicz & Zieliński, 1990).

25. *Amygdalus brahuica* Boiss., Fl. Orint. 2: 645 (1872). Syn.: *Prunus brahuica* (Boiss.) Aitch. & Hemsley, Trans. Linn. Soc. ser.2, 3: 62 (1986).

A low, prostrate, prickly shrub with small (up to 1.5 (2.0) cm long), elliptical to elongate-obovate leaves; and subsessile, short (up to 5 mm) glabrous hypanthium. The fruits are small (up to 1.5 cm), and the shells are distinctly reticulate-sulcate. A montane species native to Afghanistan, extending to southeast Turkmeniya and to west-most Pakistan (Map 7), growing on exposed sandy or granite slopes at elevations ranging between 1800 and 3000 m (Browicz & Zieliński, 1990).

26. *Amygdalus erioclada* Bornm., in Bornm. & Gauba. Feddes Repert. 49: 256 (1940). A spiny, spreading, low shrub, 0.5–1.0 m tall; with characteristic tomentose, white or whitish-grey young spines, leaves and fruit. An insufficiently known montane species, with disjunt distribution. It occurs in southwest Iran, and it reappears in east Afghanistan (Map 7). It grows on dry stony slopes and actually above 1700 m, reaching 2050 m in Iran and 2560 m in Afghanistan (Browicz, 1991).

Spontaneous interspecific hybrids

Numerous spontaneous interspecific hybrids have been detected in *Amygdalus*, and about 20 different combinations have been described (Table 2). All are rare, sporadic individuals in places where their parental species come in contact. In most cases spontaneous hybrids can easily be detected in the field since they appear intermediate between their two parental stocks. The known spontaneous hybrids fall into the following two categories:

(i) *Hybrids between wild species:* These are mostly products of hybridization between relatively distant species, i.e. members of different sections or different subgenera of *Amygdalus*. Intra-group or intra-section hybrids are largely missing, because closely related species are, as a rule, allopatrically distributed. The hybrid combinations encountered up to date are listed in Table 2. Significantly, many of the spontaneous hybrids between such distant species set fruits, and appear to be at least partly fertile.

(ii) *Hybrids between the cultivated almond and wild species:* As a result of the spread of almond cultivation over large parts of southwest Asia, Middle Asia and the Mediterranean basin, *A. communis* grows today side by side with numerous wild almond species. Most conspicuous are the contacts with some of its close wild relatives (members of the *Communis* group). In the Caucasus a whole array of intermediate and recombinant individuals bridging *A. fenzliana* with cultivated *A. communis* were detected in areas in which these two almonds grow in close proximity (Denisov et al., 1978). In Crete rare individuals intermediate between *A. webbii* and *A. communis* and bearing numerous fruits, were encountered at edges of almond cultivation (Browicz, field observations). Spontaneous crossing between the cultivated almond and *A. webbii* is reported also from south Yugoslavia (Vlasic, 1977) and from south Italy. Similar hybridization patterns at contact places were detected between *A. communis* and *A. kuramica* in Afghanistan (Serafimov, 1971; Grasselly, 1976). In Tadzhikistan the occurrence of intermediate individuals (Popov, 1929; Denisov, 1988) indicate that such spontaneous hybridization takes place also between *A. communis* and *A. bucharica*. Finally, spontaneous interspecific hybrids have been detected not only between culitivated *A. communis* and members of the *Communis* group, but also with several more distant species: *A. orientalis*, *A. graeca*, *A. kotschyi* and *A. spinosissima* (see Table 2).

Artificial interspecific hybridization

Three centres of almond breeding (C. Grasselly and his colleagues in France; A.A. Richter's group in the Nikitski Botanical Garden, Yalta, Krym; E. Kester and his team in California) experimented with interspecific crossing in *Amygdalus*. Their results complement the information available on spontaneous hybridization and show that in *Amygdalus* crosses can be made between very distant species. The majority of the attempted interspecific pollinations resulted in viable F_1 hybrids — morphologically intermediate between the parental species.

(i) *Crosses within Section Amygdalus*: Cultivars of *A. communis* were crossed with wild forms of *A. communis* as well as with five other wild members of the *Communis* species group: *A. fenzliana*, *A. webbii*, *A. kuramica*, *A. bucharica* and *A. tangutica* (= *A. dehiscens*). They were also crossed with the somewhat more distant *A. orientalis* (= *A. argentea*). In all these cross-combinations hybrids were easily obtained, and they proved to be fully fertile (Kester & Asay, 1977; Grasselly, 1977; Grasselly & Crossa-Raynaud, 1980; Denisov, 1988).

(ii) *Crosses between members of different sections or subgenera*: Hybrids were readily obtained also between *A. communis* and some more distant species: *A. nana* of Sect. *Chamaeamygdalus, A. scoparia* of Sect. *Spartioides* and *A. spinosissima* of Subgenus *Dodecandra* (Richter, 1969, 1983; Grasselly & Crossa-Raynaud, 1980; Denisov, 1988). There are no detailed accounts on pollen or seed fertility in these distant hybrids. Yet it is clear that all were at least somewhat fertile.

(iii) *Crosses with peach and with other allied genera*: The cultivated almond crosses readily also with the peach *Persica vulgaris* Miller (Kester & Asay, 1975). The peach × almond F_1 hybrids were found to be partly fertile. Their progeny segregated widely and bridged morphologically the two parental fruit trees.

The cultivated almonds will cross — although with much greater difficulty — also with apricot *Armeniaca vulgaris* L., with some plums, and with several other *Prunus* species (Kester & Asay, 1975). Many of the recovered F_1 hybrid seedlings from these distant crosses failed to develop normally. Also those that reached the flowering stage proved to be largely sterile.

Wild genetic resources for almond breeding

The occurrence of numerous spontaneous interspecific hybrids and the results obtained from crossing experiments show that species in the genus *Amygdalus* L. are not fully isolated from one another by lack of crossability or by hybrid sterility. This is true not only within sections, but also for members of different sections or subgenera. Very probably the cultivated almond is at least partly inter-fertile with most (may be all) *Amygdalus* species. Similar to the situation in *Malus* Miller and *Pryus* L. (Watkins, 1981), or in *Vitis* L. (Olmo, 1976), the whole genus constitutes an immense wild gene-pool available for the breeding work in this crop. As already stressed by Kester et al. (1991), the 9 closely related wild members of the *Communis* group (Table 1) comprise the most attractive and easy-to-tap potential. But even a wider range of species (including peach) seems to be promising, particularly for rootstock development.

Evolution under domestication

Place of origin. Wild-growing *communis* populations (conforming in their morphology to subsp. *spontanea*) were reported from middle Asia by various Russian botanists (Popov, 1929; Pachomova, 1961; Zaprjagaeva, 1964). These almonds have been regarded by most almond workers (see reviews by Grassely & Crossa-Raynaud, 1980; Denisov, 1988; Kester et al., 1991) as the wild stock from which the cultivated almond originated. Most of the proponents of such a middle Asian place of origin ignored the fact that wild growing populations of *A. communis* are not restricted to middle Asia. They thrive also in the countries bordering the east shore of the Mediterranean Sea.

We are impressed by the abundance of wild forms of *A. communis* in the Levant countries, and the role they play as constituents of the natural vegetation in this part of the World. They seem to be truly wild here. The nature of *A. communis* in middle Asia is more problematic. We suspect that the spontaneous *communis* almonds growing in this area are feral forms, which established themselves after the introduction of the cultivated almond into middle Asia. One of the facts that led us to question the nature of the spontaneous *communis* populations in middle Asia are the distribution patterns displayed by other *Amygdalus* species, particularly the wild members of the *Communis* species group. All these closely related species (Maps 2,3) show strict allopatric distribution. The only exception is *A. communis*. Wild-growing populations of this species occur (alone) in the Levant countries. In contrast to all other species, they reappear in middle Asia — where they frequently occur sympatrically with other members of the *Communis* group. It is hard to imagine how wild *A. communis* could have co-existed (for a long time) in middle Asia, side by side with its close relatives (*A. bucharica* and *A. kuramica*), without fusing with them. Also the parallel variation (to almond cultivars) in fruit traits reported to occur in middle Asia in the spontaneous *communis* populations (Denisov, 1988; Kester et al., 1991) seems suspicious. We are therefore led to the conclusion, that prior to the advent of agriculture *A. communis* was very likely confined to the Levant, and it is only naturalized in middle Asia. For these reasons we also decided not to record the middle Asian *A. communis* populations in Map 2, which represents the distribution of wild taxa.

The available archaeological evidence further supports this assumption. The first convincing signs of almond domestication come from Bronze Age sites in

the Levant, dated to the late part of the 3rd millennium bc (non-calibrated radiocarbon time) and to the first half of the 2nd millennium bc (Zohary & Hopf, 1993, p. 175). Exceptionally well preserved almond fruits were found somewhat later in Egypt — in the tomb of Tutankhamum dated to 1327 BC (Hepper, 1990, p. 62). As argued by Zohary & Hopf (1993) the almond seems to have been a member of a small group of fruit trees that founded horticulture in the Near East. (The main founders were the olive, grape-vine, fig and date-palm).

All in all, the evidence from the living plants and the archaeological finds complement each other. Wild forms of *Amygdalus communis* morphologically similar to the cultivated varieties and growing in primary habitats, abound in the Levant (Map 2). Also the earliest archaeological signs of almond cultivation come from this area. This seems to implicate the lands bordering the east shore of the Mediterranean Sea as the place of origin of the cultivated almond. In comparison, a middle Asian origin seems much less probable.

Main developments under cultivation. The main changes in *A. communis* under domestication were: (i) A shift from bitter, poisonous, amygdalin-containing seeds to non-poisonous sweet seeds. The loss of this wild-type chemical defence is caused by a single dominant mutation (Spiegel-Roy & Kochba, 1981; Dicenta & Garcia, 1993a). (ii) Increase in the size of the drupes. (iii) Emergence of forms with softer and thinner shells.

Another major development under domestication was the establishment of genetic contacts between *A. communis* and numerous other almond species. The spread of almond cultivation over the Mediterranean basin, southwest Asia and middle Asia brought the cultivated *A. communis* in contact with several wild *Amygdalus* species which were previously geographically separated from it. As evident from spontaneous hybrids encountered in places of contact, the superimposition of almond cultivation initiated hybridization between the cultivated almond and its wild relatives, particulary the more closely related wild species (*A. fenzliana, A. webbii, A. kuramica* and *A. bucharica*). How extensive has been the spontaneous gene-flow between the crop and these cross-fertile wild relatives is hard to assess. Yet the presence of intermediate and recombinant individuals indicates that introgression from wild species could have facilitated the development of locally adapted *A. communis* cultivars, or helped in the establishment of local feral *communis* populations.

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