

Chapter 2

The Annual Species of the *Cicer* Genus

Chickpea, after common bean the second most important pulse crop worldwide, has been a traditional crop in the Indian subcontinent, in the Middle East, the Mediterranean countries, and Ethiopia. In modern times, it has also become an important crop in North and South America and Australia.

Chickpea belongs to the genus *Cicer*, which comprises 43 species of which 8 are annuals and the rest perennials (van der Maesen 1987). We assumed that the chickpea originated from the annual *Cicer* species and might also be a part of the wild genetic resources of this crop. When we began our study of *Cicer* in the late 1960, neither the progenitor nor any other genetically related species of that crop was known. Since then, much knowledge has accumulated on genetic relationships among the annual *Cicer* species, but the perennial species have hardly been investigated.

2.1 Taxonomy of Annual *Cicer* Species

Leaves imparipinnate or paripinnate with dentate stipules mostly adnate to the stem and with denticulate leaflets. Peduncle up to a few flowered. Arista usually 1–2 mm in length but in some species may reach 20 mm. Calyx deeply 5-toothed; calyx tube sometimes gibbous, rim of calyx tube often oblique. Corolla as long as the calyx or somewhat longer; standard ovate to orbicular; wings obliquely obovate. Pod turgid, dehiscent, 2-valved, 1–4 seeds. Seeds globular, angular, or obvoid.

The annual species of *Cicer* comprises:

C. arietinum L., ssp. *arietinum* (domesticated chickpea) and ssp. *reticulatum* Ladizinsky (the chickpea's wild progenitor).

C. bijugum K.H. Rech

C. chorassanicum (Bge) M. Pop

C. cuneatum Hochst. Rich

C. echinospermum P.H. Davis

C. judaicum Boiss.
C. pinnatifidum Jaub. et Spach
C. yamashitae Kitamura

2.1.1 Key to the Annual *Cicer* Species

1. Leaves trifoliate. *C. chorassanicum*
 - Leaflets, more than 3 per leaf (2)
2. Leaves terminating in tendrils. *C. cuneatum*
 - Leaves terminating in leaflet (3)
3. Leaves 2–3 paired, arista up to 20 mm. *C. yamashitae*
 - Arista shorter (4)
4. Leaflets 2–3 pairs per leaf, seed densely papillose-echinulate. *C. bijugum*
 - Leaflets more numerous (5)
5. Leaflets 3–5 pairs per leaf, seeds 4–6 mm, tuberculate (6)
 - Seeds larger (7)
6. Leaflets 2–4 pairs per leaf, petioles 10–17 mm. *C. pinnatifidum*
 - Leaflets 3–5 pairs per leaf, petioles 5–12 mm. *C. judaicum*
7. Leaflets 3–7 pairs per leaf, stem erect or semispreading.
 - Seeds of different sizes, shapes, and colors, cultivated. *C. arietinum* ssp. *arietinum*
 - Stem prostrate, rarely ascending. Seed reticulate. ssp. *reticulatum*
 - Seed echinate with short setae with whitish end. *C. echinospermum*

2.2 Morphology of Annual *Cicer* Species

2.2.1 *Cicer arietinum* ssp. *arietinum*

Stems ascending, erect, 15–35 cm. Leaves imparipinnate; leaflets 5–7 paired, obovate-oblong, 7–15 mm, sharply and more or less doubly serrate, pubescent with glandular and eglandular hairs. Peduncle and pedicel longer than petiole. Arista 1–2.5 mm. Flowers solitary, 10–12 mm, usually white or mauve. Calyx sub-gibbous. Legume ellipsoid, 17–25 mm, glandular-pilose, 1–2 seeded. Seeds ovate-globular or angular, beaked; seed-coat warty or rugose; various colors. Cultivated.

2.2.2 *Cicer arietinum* ssp. *reticulatum*

Stems prostrate, 15–30 cm. Leaves imparipinnate; leaflets 3–5 paired, obovate-oblong, 5–10 mm, pubescent with a few glandular and numerous eglandular hairs. Stipules incised-dentate. Peduncle and pedicel longer than petiole. Arista usually less than 1 mm. Flowers solitary, 10–12 mm, dusky mauve. Calyx subgibbous. Legume ellipsoid, 17–22 mm, glandular or pilose, 1–2 seeded. Seeds angular, markedly reticulate, occasionally with whitish ridges.

2.2.3 *Cicer bijugum*

Stems prostrate to semierect, 10–20 cm. Leaves imparipinnate; leaflets 1–2 paired, narrow obovate-oblong, 8–15 mm, with glandular hairs. Stipule incised. Peduncle and pedicel usually shorter than petiole. Arista up to 1.75 mm flowers solitary, 7–9 mm. Calyx subgibbous. Legume ellipsoid, 14–16 mm, glandular-villous, 1–2 seeded. Seeds globular, densely papillose-echinate.

2.2.4 *Cicer chorassanicum*

Stems erect to semierect, up to 10 cm. Leaves trifoliate, petiole 10–23 mm, leaflets cuneate-flabellate, 6–10 mm long, 3–9 mm wide; base cuneate, top rounded or truncate and dentate. Stipules minute up to 1 mm. Flowers in single-flowered racemes; peduncles 3–6 mm, ending in arista 2–9 mm. Pod ovoid, 8–10 mm long, 5–6 mm wide, 1 seeded. Seeds ovate-globular, roughly tuberculate.

2.2.5 *Cicer cuneatum*

Erect to semierect with more or less climbing habit. Stems flexuous, 40–60 cm. Lower leaves with 8–10 leaflets, ending in a leaflet, upper leaves with up to 22 leaflets, ending in branched tendrils. Leaflets fairly close, cuneate, top oval-dentate, 5–10 mm long, 2–5 mm wide. Stipules incised, fan-shaped, up to 7 mm. Peduncle 1–3 flowered, up to 30 mm long, ending in slender arista, 4–12 mm long. Pods elliptic-obtuse, 15–23 mm long, 7–10 mm wide, 2–4 seeded. Seeds globular, diameter 3–4 mm, fine tuberculate.

2.2.6 *Cicer echinospermum*

Stems prostrate, 20–35 cm. Leaves imparipinnate; leaflets 3–5 paired, obovate-oblong, 5–10 mm, pubescent with a few glandular and numerous eglandular hairs. Stipules incised dentate. Peduncles and pedicels much longer than petioles. Arista not longer than 1 mm. Flowers solitary, 10–12 mm; corolla dusky mauve. Legumes

broadly ellipsoid, glandular pilose. Seeds angular, conspicuously echinated by short setae with whitish end.

2.2.7 *Cicer judaicum*

Stems prostrate or slightly ascending, 10–40 cm. Leaves imparipinnate, 7–11 leaflets; rachis 15–40 mm, petiole 5–12 mm. Leaflets 3–5 pairs, rather close, obovate or rounded-obovate, 4–7 mm long, 2–5 mm wide. Stipules ovate or ovate-lanceolate, 2–3 mm with 2–5 unequal teeth. Peduncle 10–20 mm, ending in arista, 0–3 mm, pedicel 5–7 mm. Pods rectangular ovate, 10–13 mm long, 5–6 mm wide, 1–3 seeded. Seeds triangular, partially bilobular, beaked, 3–4 mm long, 3–4 mm wide. Seed coat unevenly tuberculated.

C. judaicum may be confused with *C. pinnatifidum* and even regarded as conspecific with the latter (Zohary 1972a). It can be distinguished, however, by the longer petioles and larger number of leaflets per leaf that are less deeply toothed (Figs. 2.1, 2.2). We have confirmed the distinct genetic identity of these two species by hybridization experiments (below) as well as by DNA-marker profiling (Peleg et al. 2015).

Fig. 2.1 *Cicer judaicum*:
1 plant, 2 leaflet, 3 flower,
4 flag, 5 keel, 6 wing,
7 anthers, 8 pistil, 9 pod,
10 seed. (Courtesy LJG van
der Maesen)



Fig. 2.2 *Cicer pinnatifidum*:
 1 plant, 2 leaflet, 3 flower,
 4 flag, 5 keel, 6 wing, 7
 anthers, 8 pistil, 9 pod, 10
 seed. (Courtesy LJG van der
 Maesen)



2.2.8 *Cicer pinnatifidum*

Stems semierect or prostrate. Leaves imparipinnate; rachis 2–5 cm ending in 1 or 2 leaflets; petioles 10–17 mm. Leaflets 2–4 pairs, obovate or obovate-cuneate, 4–11 mm long, 2–5 mm wide. Stipules ovate-fanshaped, 2–3 unequal lanceolate teeth. Peduncle 5–25 mm long 1–2 flowered, ending in arista, 1–5 mm long. Pods ovate, 6–8 mm wide. Seeds angular, ovoid, bilobular, curved beak, 4–6 mm long, 6–8 mm wide, strongly and unevenly tuberculated.

2.2.9 *Cicer yamashitae*

Stems erect or procumbent, 10–30 cm long. Leaves imparipinnate, 5–7 leaflets; rachis 1–3 cm. Leaflets fairly close, opposite or not, lanceolate or elliptic-oblong, 10–15 mm long, 1–5 mm wide. Stipules dentate perulate. Peduncles 9–15 mm

ending in long slender arista, 5–20 mm; pedicels 2–5 mm. Pods ovate-oblong, 10–12 mm long, ca. 3 mm wide, 1–2 seeded. Seeds rather flat, arietinoid-shaped, beak curved, 5 mm long, 4 mm wide; seed coat irregularly tuberculated.

2.3 The Search for the Wild Progenitor of Chickpea

When we began our search for the chickpea wild progenitor we started from scratch. Suggested candidates ranged from “unknown” to “extinct.” There were some opinions about the possible candidature of *C. judaicum* or *C. echinospermum*, at that time known only as a herbarium sheet. One of the problems was the lack of seeds of the annual *Cicer* species that were known at that time and were needed in order to test their cytogenetic relationships with the domesticated chickpea. Our attempts to hybridize the domesticated chickpea with *C. judaicum* (a *Cicer* species native to Israel) were unsuccessful, indicating that this taxon could not be regarded as the wild progenitor.

We wanted to see if the chickpea’s seed protein profile could tell us something about its wild progenitor. To this end, we studied the seed protein profile obtained by electrophoresis as a possible means of portraying species identity. The advantage of utilizing the seed protein profile for this purpose is that this characteristic can be detected only by means of experimentation and apparently was not selected, for or against, either during or after chickpea domestication.

We tested the seed protein profiles of 88 chickpea accessions, which represented wide morphological ranges and the main geographic areas where chickpea is grown. Almost invariably they all shared the same profile. The seed protein profile of *C. judaicum* differed from that of *C. arietinum* by the number and position of its bands (Ladizinsky and Adler 1975). Whereas the profile of *C. arietinum* was composed of seven bands, the profile of *C. judaicum* had nine, of which only six were comparable to the chickpea protein profile. The unique and stable seed protein profile of *C. arietinum* was taken as an indication that its profile is probably shared by the chickpea wild progenitor.

The quandary, however, was where to look for it. Southeastern Turkey was finally selected for two reasons. First, three annual *Cicer* species from that territory (*C. pinnatifidum*, *C. bijugum*, and *C. echinospermum*) had been reported in the botanical literature (Davis 1970a). No seeds were available, but we hoped to obtain them for future studies. Second, that region is part of the Fertile Crescent where several cereals and pulses were domesticated.

The field study was initiated in the area between Urfa and Diyarbakir, where *C. echinospermum* had been reported to occur. The soil there is of basalt origin and most of it is covered by stones and boulders, with extensive cultivation in places where boulders had been removed. We found that most of that area had been exploited for grazing. The natural vegetation, mainly annuals, had been overgrazed and no wild *Cicer* plants were detected, so we looked for uncultivated patches in fields where goats and sheep had been kept out until the end of harvest. Here much



Fig. 2.3 Seeds of *C. arietinum* ssp. *reticulatum* (left) and *C. echinospermum* (right)

more of the natural vegetation could be observed and after examining such habitats near the town of Siverek, we soon found several plants of *C. echinospermum* with ripened seeds. These seeds were markedly echinate with whitish setae (Fig. 2.3). The mature pods had been shed onto the ground and only later had burst and released their seeds. Other pods had fallen intact into the soil cracks.

Davis (1970 a) reported that *C. echinospermum* occurs also in the province of Mardin and we checked this area as well. That habitat, however, appeared to differ markedly from the one in Diyarbakir/Siverek. The bedrock was chalk with no traces of basalt and the natural vegetation, although severely depressed, was of oak park-forest. Besides the cultivated area where cereals and legumes were raised, vineyards were also common. We followed the road from Savur to Midyat and stopped about 500 m from a village called Dereici. Next to a vineyard on a pile of stones we observed a few chickpea plants in an advanced stage of maturity. Some of the pods had already fallen, burst, and released their seeds, while others were intact. The seed color was gray-brown and the seed coat structure was markedly reticulate (Fig. 2.3) and differed completely from that of *C. echinospermum* seeds. We had not come across a seed coat like that in the domesticated chickpea and wondered whether it was feral or genuinely wild.

Back home, the seeds from Siverek and Dereici were tested for their protein profile. The profile of the Siverek accession comprised eight bands, of which only four were comparable to *C. arietinum*. Surprisingly, the profile of the Dereici accession had six bands, but all were comparable to those of the domesticated chickpea (Ladizinsky and Adler 1975). The tentative conclusion was that *C. echinospermum* is more distantly related than the Dereici accession to the domesticated chickpea. The definitive test, however, was a breeding experiment.

The domesticated chickpea *C. echinospermum* and the Dereici accession had the same chromosome number, $2n=16$. At meiosis, two pairs of chromosomes appeared to be larger than others in each of the examined accessions and were always in the form of rod bivalents with a single chiasma. The smaller chromosomes occasionally paired as ring bivalents with two chiasmata.

The *C. echinospermum* from Siverek and the accession from Dereici were crossed with one another and with five accessions of *C. arietinum*. Of the 230 crosses between *C. echinospermum* and the Dereici accession, only one hybrid seed was obtained. A total of 2 hybrid seeds resulted from 54 crosses in *C. arietinum* \times *C. echinospermum* combinations and 7 hybrid seeds from 88 crosses in cross combinations of *C. arietinum* \times Dereici accession.

Chromosome pairing at meiosis of the hybrid between *C. echinospermum* and the Dereici accession was characterized by the formation of a quadrivalent or a trivalent and univalent per cell. At telophase II, the pollen mother cells divided into five and eight cells instead of the normal four. Pollen fertility was only 20% and no seeds were formed.

The meiosis of hybrids between *C. echinospermum* and two accessions of the domesticated chickpea, one from Greece (no.77) and the other one from Ethiopia (no.58F), revealed complex cytogenetic relationships. The hybrid involving accession no.77 revealed difference of one chromosome translocation between the parents, as indicated by the formation of a quadrivalent or of a trivalent and univalent, whereas in the hybrid involving the no.58F accession indicated two paracentric inversions difference between the parents, as indicated by two bridges and two fragments in anaphase I. No seeds were set on the hybrids with the Ethiopian accession and only about 2% with those from Greece.

Chromosome pairing at meiosis was normal in four of the five hybrid combinations between *C. arietinum* and the Dereici accession, and the hybrids were as fertile as their parents. The hybrid involving the Ethiopian accession, no.58F, was characterized by the formation of a quadrivalent in metaphase I and a bridge and fragment in anaphase I, and was completely sterile (Ladizinsky and Adler 1976a).

While the cytogenetic evidence clearly indicated that *C. echinospermum* differs from the domesticated chickpea, it appeared that the Dereici accession was much closer to the domesticated species and that some chromosome repatterning had occurred in *C. arietinum*.

Although the Dereici accession complied with the requirements for its consideration as the wild progenitor of the domesticated chickpea, it was derived from a tiny population and we therefore needed to obtain more information on its distribution before this could be confirmed. In a subsequent visit to the Mardin province we detected two more populations of the Dereici type, one on the outskirts of Mardin and the other 7 km south of Gercus on the road to Midyat. In both places, it was part of the natural vegetation and occurred among annual legumes such as *Lens*, *Pisum*, *Medicago*, *Vicia*, and *Trifolium* species.

Accordingly, the Dereici accession was declared a new taxon, *C. reticulatum* (Ladizinsky 1975b), and confirmed as the wild progenitor of the domesticated

chickpea (Ladizinsky and Adler 1976b). Although it was considered at that time to be a new species, from the genetic point of view it should be viewed as *C. arietinum* ssp. *reticulatum*.

2.4 Distribution and Ecology of Other Annual Wild Chickpea Species

2.4.1 *Cicer bijugum*

This species was repeatedly observed by us on basalt soil along the roads from Urfa to Diyarbakir and the roads from Diyarbakir to Ergani, all in southeastern Turkey, as well as in field edges along the road from Savur to Senkoy in Mardin province, where it was growing on soil derived from limestone. It is a common weed in dry-land cultivation and is often harvested with lentil and chickpea crops, but not when it infests flax fields. In uncultivated patches it was rarely observed. This species has also been found in northern Syria and northern Iraq (van der Maesen 1972). Like pods of mature *C. echinospermum*, those of *C. bijugum* fall intact and burst on the ground, releasing their seeds.

2.4.2 *Cicer chorassanicum*

This species is unique in having small stature and trifoliate leaves. It is confined to northeastern Iran and Afghanistan, and apparently is quite common in the Kabul area. It occurs in rocky habitats and scree slopes.

2.4.3 *Cicer cuneatum*

This wild chickpea is restricted to northern Ethiopia, Eritrea, and southeastern Egypt. It is characterized by its tendrils and climbing habit. It is a weed in cultivation, mainly in sorghum fields but also in wheat fields, where it is more difficult to detect because of the high density of wheat compared to that of the spaced sorghum.

2.4.4 *Cicer judaicum*

This species has a somewhat restricted distribution range. It is found in Israel, Lebanon, Jordan, and probably near Damascus in Syria. It is usually confined to stony habitats together with other annual legumes such as *Trifolium*, *Lathyrus*, *Pisum*, and

Vicia species. Because this species is native to Israel we have studied its ecology in greater detail than those of the other *Cicer* taxa.

Wild annual *Cicer* species have a relatively narrow geographic range (van der Maesen 1972), and some even have specific soil preferences (e.g., *C. echinospermum*, known only from basaltic regions). It therefore seems that the scope for identifying unique ecotypes among populations of any single species of wild annual *Cicer* is somewhat limited. Prior to our work on the ecogeography of annual wild chickpeas, most wild *Cicer* accessions in gene banks were individual samples from their collection sites (Berger et al. 2003), and hardly any information was available on the spatial structures of the different wild populations nor on the genetic variation within such populations.

We first reviewed the records and the specimens deposited in the herbarium of the Hebrew University of Jerusalem, and later went to inspect the collection sites of these specimens and their adjacent environs. We continued to screen many habitats across the Mediterranean regions of Israel which, in our view, matched the characteristics of *C. judaicum* habitats that were already known. New populations were observed in many cases, but in many others no *C. judaicum* plants were identified (Ben-David et al. 2006). Using the ecogeographic parameters of sites that harbor *C. judaicum* populations, we employed a correlative predictive model in an attempt to identify sites in which additional populations could be found. In some of the flagged sites, however, we were unable to find *Cicer* populations despite intense efforts. This failure highlights some of the problems associated with procedures that rely in part on extrapolation errors and on the scatter of meteorological stations, precluding exposure of the full relevant local climatic spectrum.

With respect to the spatial structure of the populations, we noticed that throughout the surveyed area in Israel (and several Jordanian populations that we inspected) *C. judaicum* is confined mostly to stony and rocky niches, where there is little competition with more aggressive annuals. This habitat preference dictates a patchy distribution pattern from local niches throughout the geographic range of the species. In a detailed demographic survey conducted in two sites in the Judean foothills, the average size of a populated niche ranged from 1.5 m² to 10 m², the mean number of individuals in such an area ranged between 13.1 and 4.8, and the average plant density was 3.5–2.2 plants/m² (Ben-David et al. 2006).

To obtain estimates of intrapopulation genetic variations in wild *C. judaicum*, we used the vernalization-response phenotype as a test case (Ben-David and Abbo 2005). The morphological vernalization responses and flowering times of accessions sampled from a range of Israeli populations of *C. judaicum* were quantified in a replicated field nursery alongside domesticated cultivars and two accessions of *C. reticulatum*, the wild progenitor, as checks. Development of the main shoot and the number of days to first flowering were recorded in both the control and the vernalized experimental units. Vernalization treatment for 4 weeks (at 4°C) led to a similar advance (ranging from 14 to 30 days) in flowering time in both Israeli *C. judaicum* and in two accessions of Turkish *C. reticulatum*. The two wild taxa, however, showed a differential response in their main shoot development following the vernalization treatment: in Turkish *C. reticulatum* nonvernalized (control) plants,

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