

A NATURAL INFRAGENERIC CLASSIFICATION FOR CICER (LEGUMINOSAE, CICEREAE)

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SUMMARY

A comprehensive morphological survey and analysis of all taxonomically recognised wild species of *Cicer* L. (Leguminosae, Cicereae) is presented. The data (104 characters from 152 herbarium specimens representing 34 of the 44 recognised taxa in the genus *Cicer* with supplementary data for the remaining taxa taken from the literature) were analysed using multivariate statistics (cluster analysis, factor analysis and ordination techniques). The results are discussed in the context of extant classifications and the re-organisation of a novel infrageneric classification also incorporating information from published genetic data. A revised classification with 3 subgenera, 5 sections and 2 series is proposed.

Key words: Leguminosae, Cicereae, infrageneric classification, morphology, wild chickpeas.

INTRODUCTION

The genus *Cicer* (Leguminosae, Cicereae) comprises 44 species (*C. tragacanthoides* has two varieties), 9 annuals and 35 perennials (Van der Maesen et al., 2007), two more than Coles et al. were able to report (1998), which have a centre of diversity in south-western Asia, with remote, endemic species found in Morocco and the Canary Islands (Van der Maesen, 1987). The genus is the only member of the tribe Cicereae Alef., subfamily Papilionoideae, family Leguminosae. It was historically included in the legume tribe Viciae (Bronn) DC., but Kupicha (1977) presented detailed taxonomic evidence to support the tribal distinction of the genus from the other Viciae genera: *Vicia* L., *Pisum* L., *Lens* Adans., *Lathyrus* L. and *Vavilovia* Fed. To this end Kupicha (1977) reinstated the monogeneric tribe Cicereae originally proposed by Alefeld (1859) and provided a detailed generic description (Kupicha, 1981). The most widely known species is the cultivated chickpea, *Cicer arietinum* L. Much attention has focussed on the cultivated form and its subspecific taxa in the past. However, in more recent years the focus of interest has broadened to include all the annual species because of the search for various beneficial crop-related traits in wild *Cicer* species (Muehlbauer et al., 1994; Hannan et al., 2000). A consequence of this research bias is that the perennial species, largely located in remote Central Asia, have been under-collected and taxonomically neglected until recently. After the genus was revised by Van der Maesen (1972), several

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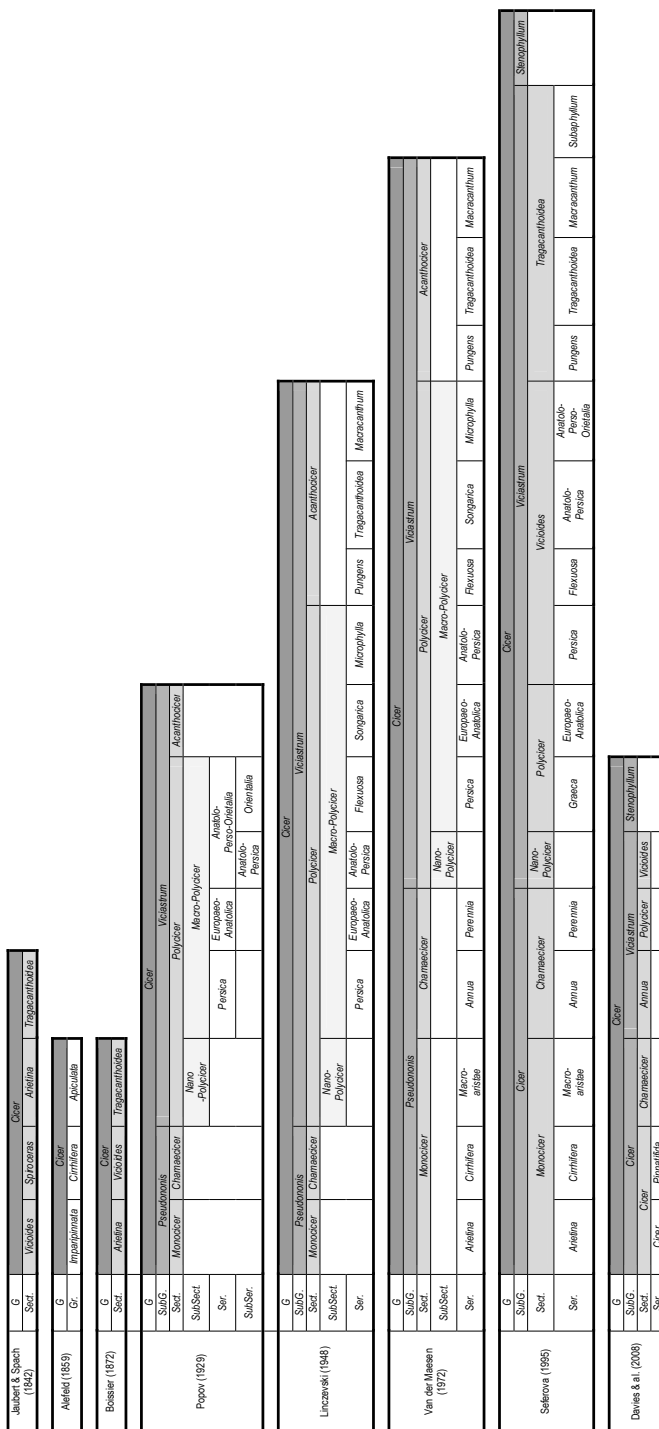


Fig. 1. Taxonomic history of the infrageneric hierarchies in *Cicer* L.

new *Cicer* species have been described. The current exploitation interest and addition of new taxa have resulted in the need for a revised classification of the genus. It has been increasingly clear that the traditionally defined infrageneric groupings result in non-monophyletic species, subgenera and sections (e.g., Rajesh et al., 2003; Frediani & Caputo, 2005). The general aim of this research was to clarify the relationships between *Cicer* taxa by combining multivariate analytical approaches with morphological data and the published genetic data and produce a revised natural classification that will aid future collection, conservation and utilisation of the genus. Interactive keys and short descriptions have been published by Van der Maesen et al. (2007), previous to the present paper of which publication was inadvertently delayed.

The genus *Cicer* was first studied in detail by Jaubert & Spach (1842), who described four sections, *Arietina*, *Vicioides*, *Spiroceras* and *Tragacanthoides* based on woodiness and terminal structure of the rachis (presence of a leaflet, spine or tendril). The infrageneric classification of *Cicer* over the last 165 years is illustrated in Fig. 1. Both formal and informal (Alefeld, 1859) hierarchies are included, as are the nomenclatural invalid series of Linczevski (1948). Boissier (1872) adopted this system but merged sections *Vicioides* and *Spiroceras*. Popov (1929) proposed a more detailed classification that subdivided the genus into 2 subgenera and 4 sections, also incorporating subsectional, series and subseries taxa. Linczevski (1948) revised Popov's classification streamlining the divisions within the sections.

The genus was comprehensively revised by Van der Maesen (1972), who extended the work of Popov (1929) and Linczevski (1948). The classification proposed by Van der Maesen contained 2 subgenera, *Pseudononis* Popov and *Viciastrum* Popov (distinguished by flower size and calyx morphology) and 4 sections distinguished as follows: *Monocicer*, annual, small-flowered species with firm, erect to inclined or prostrate stems and imparipinnate leaves, or the rachis terminating in a tendril; *Chamaecicer*, annual or perennial shrubby species with thin creeping branches and 3–7 leaflets per leaf; *Polycicer*, the large-flowered perennial species with imparipinnate leaves or tendrillous rachis; and *Acanthocicer*, large-flowered species with persistent spiny rachis and spinous calyx teeth. The sections are further subdivided into 2 subsections and 14 series. The characters used to divide the series included: standard length, number of pairs of leaflets on the rachis, apical structure of the rachis, number of flowers per inflorescence, bract and stipule characters, arista size and life cycle.

The *Cicer* taxa present within the former Soviet Union were reviewed by Seferova in 1995. As well as lectotypifying the supraspecific ranks, she replaced some illegitimate names, effectively publishing others and drew attention to several new Central Asian species. The amended classification includes 3 subgenera, 8 sections and 13 series. The characters she used to distinguish taxa are primarily the ones used previously by Van der Maesen (1972). The most significant difference between the classifications of Van der Maesen (1972) and Seferova (1995) is seen in the sections of subgenus *Cicer*, and sections *Polycicer* Popov, *Nanopolycicer* (Popov) Seferova and *Vicioides* Jaub. & Spach of subgenus *Viciastrum*, and in the series divisions of section *Tragacanthoidea* Jaub. & Spach.

Both the Van der Maesen (1972) and Seferova (1995) classifications were produced using non-numeric techniques. Seferova proposed several nomenclatural changes to the taxa accepted by Van der Maesen (1972), reducing several entities to synonyms

as follows: *C. macracanthum* Popov (= *C. incanum* Korotkova); *C. grande* (Popov) Korotkova (= *C. paucijugum* Nevski); *C. macracanthum* subsp. *acanthophyllum* (Boriss.) Seferova (= *C. acanthophyllum* Boriss. = *C. garanicum* Boriss.); *C. flexuosum* subsp. *mogoltavicum* Popov (= *C. mogoltavicum* Popov). In addition, several new *Cicer* species have been described since 1972: *C. canariense* A.G. Guerra & G.P. Lewis (Santos Guerra & Lewis, 1985); *C. heterophyllum* Contandr., Pamukç. & Quézel (Contandriopoulos et al., 1972); *C. reticulatum* Ladiz. (Ladizinsky, 1975); *C. luteum* Rassulova & Sharipova (Rassulova & Sharipova, 1992); *C. laetum* Rassulova & Sharipova (Rassulova & Sharipova, 1978) and *C. rassuloviae* Lincz. (Linczewski, 1948). The infrageneric structure of *Cicer* has become progressively more unwieldy over time. The complex hierarchy attempts to justify the perceived interspecific variation based on species whose infraspecific variation is often poorly understood.

New information from biochemistry, plant breeding and especially genetics have highlighted the weaknesses in the current infrageneric hierarchy, indicating that the existing perception of species relationships based on the congruence of a few characters cannot adequately explain true natural relationships in the genus.

Therefore, to clarify the relationships between taxa within the genus *Cicer* it is time to update and re-evaluate the infrageneric classification using objective techniques.

MATERIALS AND METHODS

Forty-one species and four varieties were included in the analysis. The characteristics of thirty-three species were recorded from 152 herbarium specimens and the remaining taxa were scored from literature sources. Herbarium specimens were loaned from BM, E, K and WAG (abbreviations follow Holmgren et al., 1990). Author names follow Brummitt & Powell (1992). A species citation list is given in the Identification List at the end of this article. The character set was compiled from the literature (Davis, 1970; Contandriopoulos et al., 1972; Van der Maesen, 1972, 1987; Kupicha, 1977; Coles, 1993; Macted, 1993) and personal observations of the specimens. The data matrix is provided in Table 1 and the characters and character states recognised are listed in Table 2. The final character list contained 104 characters, including: 14 habit and stem characters, 36 vegetative characters, 25 inflorescence characters, 16 pollen, anthers, pods and seeds characters and 13 characters covering features such as phenology, altitude and chromosome number. Many different types of character were recorded. Continuous data, usually considered to be intrinsically ordered when coded into 'discrete' states, were scored as numbered states accounting for the natural ranges of variation. E.g. rachis length (character 19; Table 2) was seen to vary in three natural clusters throughout the data set: those species whose rachis was persistently less than 40 mm long, those with rachis' between 40 and 70 mm long and those with long rachis' over 70 mm. All characters were scored as either binary or multistate but considered as unordered in the final analysis. The code of 9 was used to represent missing data. Where appropriate during the analyses non-variable characters, and characters for which there was a lot of missing data (e.g. characters 86–90, 93–104), were omitted.

Within *Cicer* there have been several non-morphologically-based investigations of species relationships, particularly among the annual species. Studies have covered molecular variation (Kazan & Muehlbauer, 1991; Ahmad & Slinkard, 1992; Ahmad et al.,

Table 1. Data matrix. The species names are indicated by the first four letters of the specific epithet, or in the case of varieties or subspecies the first letter of the specific epithet and the first 3 letters of the infraspecific epithet. There are 43 taxa and 106 characters, the codes of which can be found in Table 2. ‘9’ denotes missing values.

acan	0011019211	0221091100	0101120102	0021011000	0100102101	0111011100	3310010121	1222192001	1219921011	1199999999	9999
amat	0110202111	2221010111	0010100101	1321101000	0221011122	1211001901	3320101020	2202119011	0012011011	1199299999	9993
anre	1100020222	1211000111	2011020211	1121110100	0220001122	1201001111	1000100011	0001113010	0009901101	0100000901	0233
atla	1010209200	0210000100	0910200102	0101001111	1100191011	1200010111	3200101999	9900009009	1219920010	1199999999	9999
bale	1010021132	0119990121	0910001010	2921100111	0999091221	1121009911	9320111999	9902111001	0999910011	9999999999	9999
bald	0010020020	0229990122	0110010110	2331010111	0999011120	1121001111	4920001220	1009909999	9909910011	1299999999	9999
biju	0000123100	0020010061	2111020101	1121101011	0222121111	1231001111	3201011111	0001011111	1112001211	0111111012	2011
cana	1010110222	0112103200	2010100119	2011201000	1000111191	1000002111	2310001021	1002010110	1212200322	0299999999	9992
chor	0000012200	2120000002	2211020012	0200002111	1000110001	1100001100	3000001091	0011002010	1200111012	0091222929	9991
cune	1001112100	0211221011	2010010111	0210000100	0120111122	1200001100	3200000011	0001119210	0201101221	0123333939	9021
echi	1000222210	2020100101	2011020100	1121201100	0120121121	1221201111	3300000011	0210123109	1110301201	0100000100	2291
feet	0110210021	0100000101	0010000101	1221111100	0900011121	0210201101	1320010221	2020191001	1202021011	1199999999	9999
flex	0011021221	1111210111	0210010112	0102011110	0102011110	1111011011	4320101221	2210119011	1202001011	1299999999	9999
flor	1011003211	0110010111	2110000010	2321111000	0220021231	1011021011	3310011991	9200119211	1211100311	1299999999	9990
grae	1011012220	2110010111	2010010010	1241110000	0222012131	1031102101	3310010121	2390011211	0002010311	1299999999	9999
gran	0111011122	0219990222	0110010110	2321110001	0202021230	1121001111	0920110120	2202193000	1209910011	1199999999	9999
hete	1010000932	0119921129	9911020910	2221209999	9999991092	1099299999	9199999999	9999999999	9999900311	9999999999	9991
inea	0119003910	0129991101	9901120999	0201001111	1999191122	1199991111	1920101991	1299999999	9909920010	1199999999	9999
inci	0011210200	1010000000	2010200011	0121102101	1120101121	0201001110	1310000011	0209011011	0300111010	1199999999	9999
issu	0011020121	0112001112	2010200000	2321121111	1200021111	1021001101	1020001121	1409199909	9201000012	1299999999	9991
juda	1000120201	2020100100	2110201000	0121100110	1122101021	1200002110	3201010002	0110011120	1200000120	0111111110	1121
kern	1111120132	0211100221	0010100012	0100011110	0000111001	1221001110	9021000121	1391111001	1001020011	0199999999	9999
kors	0111011132	9229990111	0100000100	2321111100	0299011230	0299009911	1999999999	9902919999	9909911011	9999999999	9999
macr	0111020121	0021001201	0101200012	0131011100	0101122111	0211011101	3320000021	1021110111	1210211011	1199999999	9999
micr	0011211110	1211102211	0010000112	1221001100	0100021120	1110110111	1020010121	2002110010	0002021011	1199999999	9990
mege	0111020230	0219990222	0110101112	0200011101	0199101122	1121001111	3320010220	1002112010	1209900011	1299999999	9999
mont	1010011120	0111299011	2111020110	2341121101	1200021230	1021211001	3011011121	1302111021	2213001311	1299999999	9993
mult	0011211110	0011102021	0011020101	1121110000	0199011221	1121001101	2320000121	2029190021	1202030011	1199999999	9999
nuri	1100221210	0112000122	0010010010	1321100000	0299021120	1221011101	0301011221	2099912001	0212021319	1299999999	9999
oxyo	1110202222	1111200122	0010100000	1330111000	0202021021	1111011011	2010001120	1012112010	1211011010	1299999999	9999
pauc	1010211111	0029990011	2010201010	1221101111	0199101130	1210001101	0320011120	1001999999	9990921011	1299999999	9999
papa	1000121210	00290000101	2011020101	1021100111	1120211021	1201001110	3201010000	0011110020	1200101210	0111111112	1121
ppin	1000122200	2220000100	2011020101	0021101111	1100211122	1201001110	3201010000	0010010020	1200301212	0111111112	1121
pung	0111023211	01100001101	0201200110	1200011100	0000012111	1211001101	0310101121	1110112011	1200121011	1199999999	9990
rech	0111201210	0111201210	0201201210	1011111000	0000001111	1111001101	0310000121	1192019999	9910020011	1199999999	9999
reit	1000021212	0100000100	1141110000	1141110000	0100011190	1201001110	0310699999	9911013010	1099990911	0100000001	0201
song	0111021122	0101120211	0210000112	1220011100	0100021130	0111202101	2320110221	2022013000	2212011011	1299299999	9999
spir	0111020222	0112100122	0010100012	0230011110	0102020200	1111001111	3311010120	1512112011	1211010012	0299999999	9999
stap	0111020210	0119991101	2101121011	1030011100	0003002101	1111009111	3921100021	1121112001	1009930011	1199999999	9999
suba	0111029311	0112031122	2001121119	0011221100	0033002101	0111001101	3310001010	0011112001	1210010011	0299999999	9999
trag	0110212000	0111001101	0201120112	0000001100	0000002021	1211001101	1320110121	1012112010	0200210110	1199999999	9999
ttur	0011021200	0111011111	0201120112	0100001100	0000002021	1211000101	1320110121	1012119099	9900021010	1199999999	9999
yama	1100012201	2020100100	2911020011	2141101101	1120011011	1000011110	3200010001	0110021000	1211200011	0192229222	1191

Table 2. Description of characters and their states.

1	Woodiness	0 = woody; 1 = not woody
2	Stem robustness	0 = slender; 1 = sturdy
3	Growth cycle	0 = annual; 1 = perennial
4	Habit	0 = herb; 1 = shrub; 2 = climber
5	Form	0 = erect; 1 = semi-erect; 2 = procumbent
6	Branching	0 = simple; 1 = sparse; 2 = secondary
7	Stem hair density (hairs/mm ²)	0 = < 20; 1 = 20–30; 2 = 31–40; 3 = > 40
8	Stem hair type	0 = eglandular; 1 = glandular; 2 = both; 3 = glabrous
9	Stem height (mean cm)	0 = < 20; 1 = 20–30; 2 = 31–40; 3 = > 40
10	Stem height (range cm)	0 = < 10; 1 = 10–20; 2 = > 20
11	Pigmentation	0 = absent; 1 = sometimes; 2 = always
12	Stem orientation	0 = straight; 1 = flexuous; 2 = both
13	Stem surface ribbed	0 = prominently; 1 = ribbed; 2 = faintly
14	Internodal length (mean mm)	0 = < 20; 1 = 20–30; 2 = > 30
15	Internodal length (range mm)	0 = < 10; 1 = 10–20; 2 = > 20
16	Leaf hair length (mm)	0 = < 0.5; 1 = 0.5–0.89; 2 = > 0.9, 3 = no hairs
17	Leaf arrangement	0 = imparipinnate; 1 = paripinnate
18	Number of pairs of leaflets	0 = 1–4; 1 = 3–10; 2 = 7–15; 3 = > 20
19	Rachis length (mm)	0 = < 40; 1 = 40–70; 2 = > 70
20	Leaf spacing on rachis (character 18, 19)	0 = 1–5; 1 = 6–11; 2 = ≥ 12
21	Leaf shape outline	0 = decrescent; 1 = increscent; 2 = equal
22	Rachis rolled	0 = loosely; 1 = tightly; 2 = not
23	Rachis apex – spine	0 = present; 1 = absent
24	Rachis apex – tendril	0 = present; 1 = absent
25	Rachis apex – leaflet	0 = present; 1 = absent
26	Tendril structure	0 = simple; 1 = branched; 2 = none
27	Leaflet form	0 = laminate; 1 = spinose
28	Phyllotaxy	0 = opposite; 1 = ± opposite; 2 = alternate
29	Leaflet margins	0 = doubly incised; 1 = incised
30	Leaflet margin serrations	0 = entire –2/3; 1 = 1/2–2/3; 2 = apex –1/2
31	Leaflet length (mm)	0 = < 5; 1 = 5–10; 2 = > 10
32	Leaflet width (mm)	0 = 0–2; 1 = 2–4; 2 = 4–6; 3 = > 6
33	Leaflet shape	0 = cuneiform; 1 = linear; 2 = obovate; 3 = rotund; 4 = elliptic
34	Leaflets flabellate	0 = yes; 1 = no
35	Leaflet apex	0 = truncate; 1 = rounded; 2 = acute
36	Leaflet base	0 = cuneate; 1 = rounded-cuneate; 2 = truncate
37	Leaflet teeth shape	0 = acute; 1 = acuminate/triangular; 2 = rectangular/cuspidate
38	Terminal apical spine	0 = tendrillous; 1 = inflexed
39	Midrib tooth	0 = prominent; 1 = not
40	Midrib tooth	0 = spinose; 1 = not
41	Midrib tooth	0 = recurved; 1 = not
42	Number of teeth per leaflet	0 = 0–5; 1 = 6–11; 2 = ≥ 12
43	Leaflet surface ribbed	0 = U = L; 1 = U > L; 2 = U < L; 3 = smooth
44	Leaflet surface pubescent	0 = U = L; 1 = U > L; 2 = U < L; 3 = glabrous
45	Leaflet teeth apices	0 = spine; 1 = mucro; 2 = none
46	Leaflet petioles	0 = sessile (0–0.3); 1 = subsessile (0.4–0.6); 2 = petiolate (0.7–1.0)
47	Stipules	0 = spiny; 1 = laminate; 2 = both
48	Stipule length (mm)	0 = 0.0–2.9; 1 = 3.0–5.9; 2 = > 6.0
49	Nr. teeth on stipules	0 = 1 only; 1 = 1–3; 2 = 2–6; 3 = > 6
50	Stipule outline	0 = flabellate/oblique; 1 = ovate/lanceolate; 2 = triangular
51	Stipule (basal) v. leaflet size	0 = equal or bigger; 1 = smaller
52	Number of flowers / raceme	0 = some many flowered; 1 = none more than 2-flowered; 2 = always 1-flowered
53	Peduncle length (mm)	0 = 0–15; 1 = 16–30; 2 = 31–45; 3 = > 46
54	Pedicel length (mm)	0 = ≤ 5; 1 = ≥ 6
55	Arista form	0 = spine; 1 = leaflet; 2 = both

(Table 2 continued)

56	Arista length (mm)	0 = 0–10; 1 = 11–20; 2 = \geq 21
57	Bract shape	0 = spinose; 1 = triangular toothed; 2 = flabellate
58	Calyx teeth	0 = recurved; 1 = straight
59	Calyx dorsally gibbous	0 = strong; 1 = weak; 2 = not
60	Calyx length (mm)	0 = < 7; 1 = > 7
61	Calyx tooth shape	0 = triangular; 1 = broadly lanceolate; 2 = narrowly lanceolate; 3 = lanceolate acuminate; 4 = cuspidate
62	Corolla colour	0 = white; 1 = yellow; 2 = pink; 3 = blue; 4 = purple
63	Corolla length (mm)	0 = 5–10; 1 = 11–15; 2 = 16–27
64	Corolla shape	0 = obovate; 1 = ovate
65	Corolla pubescence	0 = pubescent; 1 = glabrous
66	Corolla apex	0 = marginate; 1 = emarginate
67	Corolla apex	0 = mucronate; 1 = not
68	Corolla width (mm)	0 = 4–9; 1 = 10–15; 2 = > 16
69	Filament length (mm)	0 = \leq 5; 1 = 6–10; 2 = \geq 11
70	Alae auriculate	0 = longly; 1 = shortly; 2 = not
71	Alae length (mm)	0 = < 10; 1 = 10–15; 2 = > 15
72	Alae shape	0 = obovate; 1 = oblong; 2 = both; 3 = clavate; 4 = pedicillate; 5 = triangular
73	Pod shape	0 = oblong; 1 = ovate; 2 = elliptic
74	Pod length (mm)	0 = small (0–10); 1 = medium (10–20); 2 = large (> 20)
75	Pod width (mm)	0 = < 6; 1 = > 6
76	Pod hair type	0 = eglandular; 1 = glandular; 2 = both; 3 = glabrous
77	Seed length mean (mm)	0 = 3; 1 = 4; 2 = 5; 3 = 6
78	Seeds beaked	0 = yes; 1 = no
79	Seed shape	0 = obovate; 1 = globular; 2 = angular
80	Chalazal tubercule	0 = prominent; 1 = not
81	Seed coat colour	0 = black; 1 = brown; 2 = purple
82	Seed coat surface	0 = wrinkled; 1 = echinate; 2 = tuberculate; 3 = smooth
83	Calyx teeth	0 = equal; 1 = unequal
84	Calyx hair length (mm)	0 = 0.0–0.5; 1 = 0.6–0.9; 2 = \geq 1.0
85	Calyx hair density (hairs/mm ²)	0 = < 20; 1 = 20–30; 2 = 31–40; 3 = > 40
86	Altitudinal range (m a.s.l.)	0 = < 1000; 1 = c. 2000; 2 = c. 3000; 3 = c. 4000
87	Endemic	0 = yes; 1 = no
88	Habitat	0 = rubble; 1 = cultivation; 2 = weedy; 3 = forest
89	Phenology	0 = Jan.–April; 1 = May–August; 2 = Sept.–Dec.
90	Soil type – Geology	0 = Basic, calcicole; 1 = indifferent; 2 = Acid, volcanic
91	Calyx tube length (mm)	0 = 0.0–2.9; 1 = 3.0–5.9; 2 = 6.0–8.9; 3 = > 9.0
92	Calyx teeth length (mm)	0 = 0.0–2.9; 1 = 3.0–5.9; 2 = 6.0–8.9; 3 = > 9.0
93	Crossability (Ladizinsky & Adler, 1976)	0 = I; 1 = II; 2 = III
94	Seed storage proteins (Ahmad & Slinkard, 1992)	0 = I; 1 = II; 2 = III; 3 = IV
95	Isozyme variation (Tayyar & Waines, 1996)	0 = I; 1 = II; 2 = III; 3 = IV
96	Isozyme polymorphism (Ahmad et al., 1992)	0 = I; 1 = II; 2 = III; 3 = IV
97	Seed proteins (Sammour, 1994)	0 = I; 1 = II; 2 = III; 3 = IV
98	Disease resistance (Robertson et al., 1996)	0 = greatest (> 5/7); 1 = average (3B4/7); 2 = least (0/7)
99	Allozyme variation and phylogeny (Kazan & Muehlbauer, 1991)	0 = I; 1 = II; 2 = III; 3 = IV
100	Pollen morphology (De Leonardis et al., 1994)	0 = primitive; 1 = middle; 2 = derived
101	Seed coat (De Leonardis et al., 1994)	0 = primitive; 1 = middle; 2 = derived
102	Pollen morphology (Ocampo, 1992)	0 = primitive; 1 = middle; 2 = derived
103	Karyotype morphology (Kabir & Singh, 1990)	0 = 7 pairs median; 1 = 5 pairs median; 2 = 1 subterminal
104	Chromosome numbers (Van der Maesen, 1987)	0 = 14; 1 = 16; 2 = 24; 3 = variable

1992, Sammour, 1994; Tayyar & Waines, 1996; Javadi, 2004; Javadi & Yamaguchi 2004a, b; Frediani & Caputo, 2005, Javadi et al., 2007), seed coat and plumule morphology (Javadi & Yamaguchi, 2004c), palynology (Ocampo et al., 1992; De Leonardis et al., 1994), cytology (Van der Maesen, 1987; Kabir & Singh, 1990), crossability groups (Ladizinsky & Adler, 1976) and disease resistance (Robertson et al., 1996). However, these studies have rarely attempted a genus-wide examination and have generally focussed on the annual species closely related to cultivated chickpeas. Where appropriate, their results are included in the taximetric analysis and in some cases they have been central in drawing overall conclusions for interspecific relationships.

The data set was initially analysed using the program NTSYS (Rohlf, 1995) – Cluster Analysis. The program used Sneath's Simple Matching Coefficient to calculate an Euclidean distance based similarity matrix and this was analysed using the UPGMA clustering method. Cophenetic correlation can be calculated and used as an indication of degree of fit between the similarity matrix and the cophenetic value matrix based on the UPGMA cluster file. Rohlf (1995) defines the goodness of fit as a correlation coefficient r , based on the Mantel statistic Z . A poor fit is deemed *a priori* to be in the region of $r = 0.7$ to 0.8 , good to very good being $r = 0.8$. Rohlf considers that for more than 12 OTUs (Operational Taxonomic Unit) a correlation greater than 0.5 will be statistically significant at the 99% level. The correlation is subjected to a Student's t -test to assess statistical significance. Note that the significance tests are biased because the matrices being compared are not fully independent.

Principle Components Analysis (PCA) is an ordination analysis technique that attempts to replace a large set of variables by selecting a smaller subset of variables which best summarizes the larger set. The two-fold advantage of this technique is the simplification of a large data set by highlighting significant sources of variance – in this case the characters, and the extraction of a relationship structure between the variables – in this study the species inter-relationships. The relationships between OTUs in low dimensional space (2-D or 3-D) and the efficiency of the true separation of points can be assessed by superimposing a Minimum Spanning Tree (MST) onto the first two principle component axes. Multiple methods of analysis were used because, as pointed out by Duncan & Baum (1981), different algorithms bias the results in different ways. The use of different methods of analysis allows the verification of the validity of the groups suggested by these analyses. Restricted PCA analyses on different subsets of the data allowed the selection of characters contributing the most variation separating the subgenera, sections and series. The ten most highly ranked characters (eigenvectors) for the first two components in three PCA runs (total data set, the *Cicer* annuals and the *Cicer* perennials) were selected and cross-referenced to the original data sets for systematic usefulness. These characters form the basis of the descriptions for the supraspecific ranks in the nomenclatural analysis.

RESULTS

Cluster analysis

The results of the cluster analysis are shown in Fig. 2. The species are divided into two clusters at the 46% level. One group, group A, contains all 9 annual species with 3 perennials: *C. canariense*, *C. incisum* and *C. atlanticum*. The second group, group B,

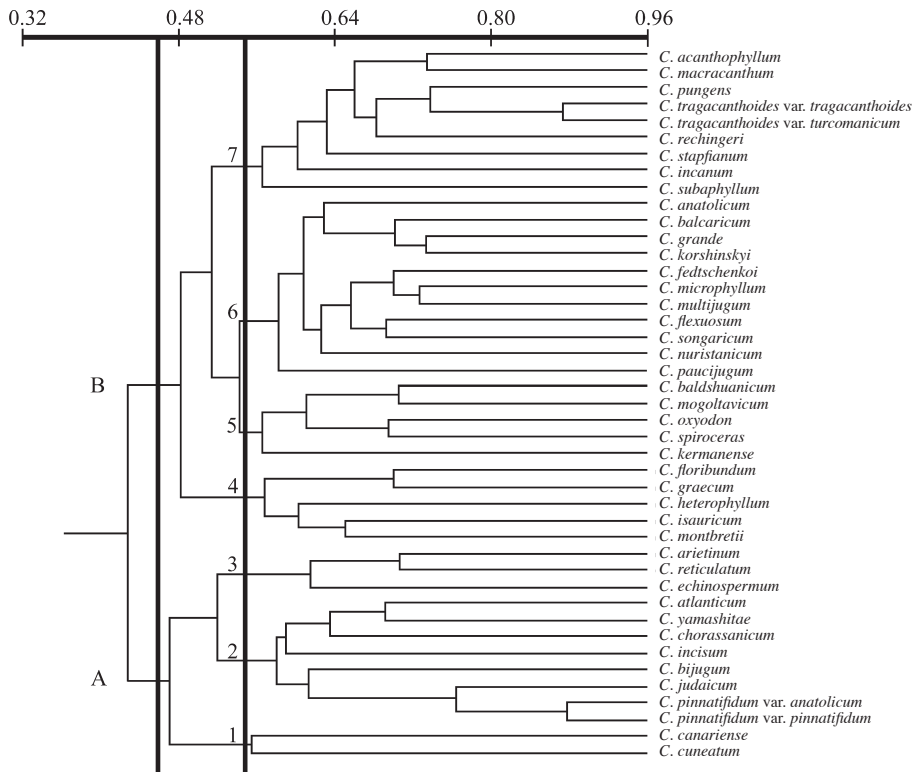


Fig. 2. Phenogram of all *Cicer* species based on 104 characters.

covers the remaining 29 species, which are all perennials. As similarity increases to 53% the taxa form 7 further clusters (numbered from 1 to 7 in Fig. 2). Three of these clusters fall under group A, and the remaining 4 into group B. The division of taxa into these clusters is as follows:

Cicer canariense and *C. cuneatum*.

The two varieties of *C. pinnatifidum* are most similar and these are most closely associated with *C. judaicum* and *C. bijugum*. The remaining species are *C. incisum*, *C. chorassanicum*, *C. yamashitae* and *C. atlanticum*.

Three closely related annual species: *C. arietinum*, *C. reticulatum* and *C. echinospermum*.

Cicer floribundum, *C. graecum*, *C. heterophyllum*, *C. isauricum* and *C. montbretii*.

Cicer baldshuanicum, *C. mogoltavicum*, *C. oxyodon*, *C. spiroceras* and *C. kermanense*.

Cicer paucijugum seems somewhat isolated from the other species in the cluster. *Cicer nuristanicum*, *C. songaricum*, *C. flexuosum*, *C. multijugum*, *C. microphyllum* and *C. fedtschenkoi*, and more remotely *C. korshinskyi*, *C. grande*, *C. balcaricum* and *C. anaticum*.

Cicer acanthophyllum, *C. macracanthum*, *C. pungens*, *C. tragacanthoides* (including the two varieties), *C. rechingeri*, *C. stapfianum*, *C. incanum* and *C. subaphyllum*.

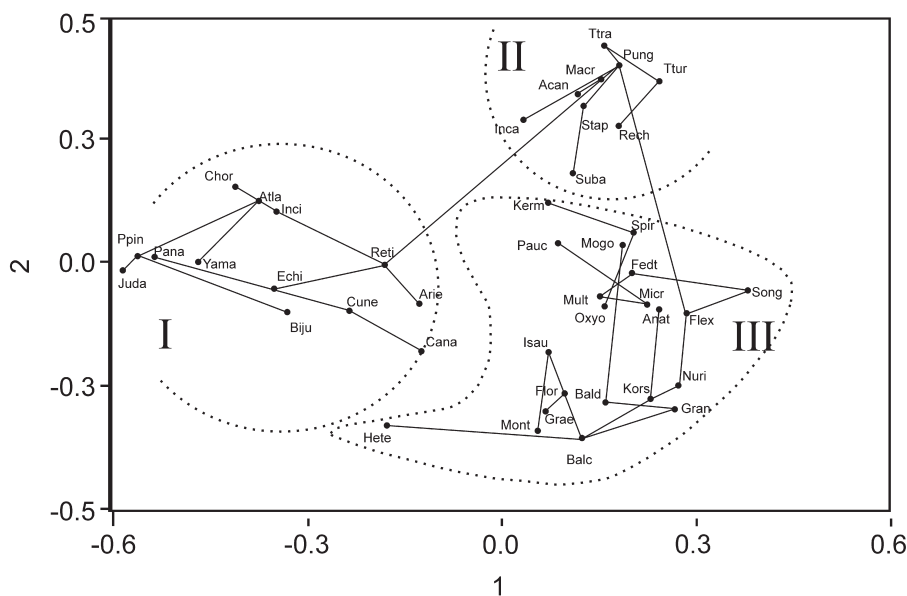


Fig. 3. PCA plot with MST superimposed. Clusters delineated by dotted lines and identified by I, II and III. Species names abbreviated to first four letters of the specific epithet, or in the case of subspecific epithets, the first letter of the specific name and the first three letters of the subspecific epithet, i.e. 'acan' = *C. acanthophyllum*; 'ttur' = *C. tragacanthoides* var. *turcomanicum* Popov.

Cophenetic correlation and principle coordinates analysis

The results of the multivariate techniques PCA and MST are shown in Fig. 3. The Mantel statistic Z gives $r = -0.81$, with the t -test giving $t = -19.37$ and $p < 0.000$, which indicates the result is a statistically reliable representation of the relationships between the OTUs. The PCA plot of the first two Principal Coordinates with a superimposed MST reinforces the preliminary groupings suggested by the cluster analysis. Three main clusters can be seen (identified in Fig. 3 by the roman numerals given here and delineated by a dotted line) and the membership of each is as follows:

Cluster I: *Cicer arietinum*, *C. atlanticum*, *C. bijugum*, *C. canariense*, *C. chorassanicum*, *C. cuneatum*, *C. echinospermum*, *C. incisum*, *C. judaicum*, *C. pinnatifidum* var. *anatolicum*, *C. pinnatifidum* var. *pinnatifidum*, *C. reticulatum* and *C. yamashitae*.

Cluster II: *Cicer acanthophyllum*, *C. incanum*, *C. macracanthum*, *C. pungens*, *C. rechingeri*, *C. stapfianum*, *C. subaphyllum*, *C. tragacanthoides* var. *turcomanicum* and *C. tragacanthoides* var. *tragacanthoides*.

Cluster III: *Cicer anatolicum*, *C. balcaricum*, *C. baldshuanicum*, *C. fedtschenkoi*, *C. flexuosum*, *C. floribundum*, *C. graecum*, *C. grande*, *C. heterophyllum*, *C. isauricum*, *C. kermanense*, *C. korshinskyi*, *C. microphyllum*, *C. mogoltavicum*, *C. montbretii*, *C. multijugum*, *C. nuristanicum*, *C. oxyodon*, *C. paucijugum*, *C. songaricum* and *C. spiroceras*.

Table 3. Eigenvalues, % variance and cumulative variance after PCA for the first 3 components in the analyses (PCA 1 ‘all taxa’ – 104 characters, 43 species; PCA 2 ‘*Cicer* annuals’ – 104 characters, 11 species; PCA 3 ‘*Cicer* perennials’ – 92 characters, 32 species).

	Component	Eigenvalue	%Variance	Cumulative Variance
All taxa	1	15.14	16.46	16.46
	2	10.51	11.42	27.88
	3	5.09	5.54	33.42
<i>Cicer</i> annuals	1	19.58	21.05	21.05
	2	16.55	17.79	38.84
	3	14.14	15.20	54.05
<i>Cicer</i> perennials	1	13.55	14.73	14.73
	2	9.14	9.93	24.67
	3	6.79	7.39	32.05

Character selection for supraspecific descriptions

The cumulative variance accounted for in the first two component axes was relatively low in all analyses (All taxa = 28%; Annuals = 38%; Perennials = 25%). This indicates that there is a lot of ‘noise’ in the data set, i.e., the characters are intrinsically variable (Table 3, 4).

Some characters in PCA 1 are principally important in defining the clusters among the perennials species such as leaflet characters and corolla size. Other characters are more important in circumscribing the annuals such as rachis apex or stem height. The remaining characters such as filament length, life cycle, habit, calyx tube length, presence of a terminal leaflet and leaflet shape could be considered as potential descriptors for subgeneric groups. Within the subgenera, the characters listed for PCA 2 and PCA 3 can be considered as potential descriptors for the sections and series.

DISCUSSION

Morphological analysis and extant taxonomy

Considering the results of the cluster and PCA analyses together, one overall picture of resemblance emerges which is compared and contrasted to previous classifications. Group A in Fig. 2 and Cluster I in Fig. 3 are identical and this grouping largely corresponds to subgenus *Pseudononis* Popov. This cluster contains all the annual and 3 perennial species and is composed of 3 or 4 subclusters which could be regarded as equivalent to sectional and series divisions within the subgenus.

The first subcluster of *C. arietinum* (the crop chickpea), *C. reticulatum* (the crop progenitor) and *C. echinospermum* are closely related species (see below) and this subcluster is directly referable to series *Arietina*. This grouping is supported by nearly all previous

Table 4. Character list of ten characters on the first two component axes with the highest \pm ranking eigenvectors for each PCA analysis.

PCA 1 'All taxa'		PCA 2 'Cicer annuals'		PCA 3 'Cicer perennials'	
cpt1	cpt 2	cpt1	cpt2	cpt1	cpt2
Growth cycle	Rachis apex spine	Phyllotaxy	Internodes length	Leaflet length	Leaf shape outline
Standard length	Leaflet length	Seed length	Calyx dorsally gibbous	Rachis apex spine	Midrib tooth recurved
Filament length	Number teeth per leaflet	Stem height	Tendrils structure	Leaflet petioles	Standard length
Leaf shape outline	Stipules laminate	Seed coat surface	Rachis apex tendril	Leaf arrangement	Standard width
Standard width	Leaf arrangement	Leaflet base	Habit	Leaflet width	Calyx hair density
Alae length	Rachis apex leaflet	Allozyme variation (Kazan & Muehlbauer, 1991)	Seed coat colour	Number teeth per leaflet	Branching
Calyx tube length	Leaflet margins serrations	Isozyme polymorphism (Ahmad et al., 1992)	Rachis length	Stipules laminate	Form
Habit	Leaflet petioles	Isozyme variation (Tayyar & Waines, 1996)	Seed storage proteins (Ahmad & Slinkard, 1992)	Leaflet margins serrations	Alae length
Stem height	Leaflet width	Midrib tooth spinous	Seed proteins (Sammour, 1994)	Calyx teeth length	Leaf spacing on rachis
Pigmentation	Leaflet shape	Calyx length	Crossability (Ladizinsky & Adler, 1976)	Calyx hair length	Peduncle length

studies and is reflected by results in crossing experiments (Ladizinsky & Adler, 1976), seed proteins (Sammour, 1994), seed storage proteins (Ahmad & Slinkard, 1992), isozyme polymorphism (Ahmad et al., 1992), isozyme polymorphism and genetic distance (Labdi et al., 1996) and karyotype analysis (Ocampo et al., 1992).

The second subcluster of *C. bijugum*, *C. judaicum* and *C. pinnatifidum* is also a well established natural grouping and biochemical and genetic research consistently confirms this association (Ladizinsky & Adler, 1976; Ahmad et al., 1992; Labdi et al., 1996; Tayyar & Waines, 1996). The taxa were divided into two series (*Macro-aristae* Maesen and *Pinnatifida* Seferova) by Seferova (1995) on the basis of the latter having more leaflets and a marginally smaller standard petal.

The third subcluster is composed of a less cohesive group of species. The close relationship between *C. chorassanicum* and *C. yamashitae* is also supported by the same biochemical and genetic data as the two clusters discussed above. Seed storage protein data (Ahmad & Slinkard, 1992; Sammour, 1994) singly place *C. chorassanicum* and *C. yamashitae* respectively within the secondary gene pool, i.e., towards series *Pinnatifida*, but isozyme polymorphism and calculated genetic distances place these two species together removed from the GP2 (Ahmad et al., 1992; Labdi et al., 1996). These two species also share the same plumule type (PII) distinct from many other species in *Cicer* (Javadi & Yamaguchi, 2004c). In contrast to the previously published supraspecific

hierarchies (Van der Maesen, 1972; Seferova, 1995) that placed both taxa in subgenus *Cicer* (= *Pseudononis*) molecular phylogenies based on nrITS, trnK/matK and trnS-trnG data (Van der Maesen et al., 2007) indicate that these two closely affiliated taxa should be placed in subgenus *Viciastrum*. It is also corroborated by ITS data (Frediani & Caputo, 2005). *Cicer chorassanicum* is spread over Persia and north/central Afghanistan while *C. yamashitae* is confined to Afghanistan.

An affinity between the two perennial species *C. atlanticum* and *C. incisum* is clearly indicated by this study. Although *C. atlanticum* is placed in subgenus *Viciastrum* by some molecular phylogenies (Van der Maesen et al., 2007), which tallies with Popov's allocation using his empirical-geographical system, the morphological data places *C. atlanticum* and *C. incisum* close together in subgenus *Cicer*. This is supported by ISSR (Sudupak, 2004), AFLP (Sudupak et al., 2004), allozyme (Sudupak & Kence, 2004) and RAPD (Sudupak et al., 2002) data based on *Cicer* species from Turkey. The close specific relationship between *C. atlanticum* and *C. incisum* has previously been noted by Van der Maesen (1972: 19) and Contandriopoulos et al. (1972). Although an African (Moroccan) species, *C. atlanticum* does not ally itself with the other African taxa in subgenus *Stenophylloma* (*C. canariense* and *C. cuneatum*) in the morphological or molecular analyses; it is placed much closer to *C. incisum* from the eastern Mediterranean / Persia.

Lastly, *C. canariense* and *C. cuneatum* are relatively remotely linked to each other and the other species of the cluster. Previous studies place *C. canariense* in a separate monospecific subgenus *Stenophyllum* A.G. Guerra & G.P. Lewis, on account of its geographical isolation from other *Cicer* species and distinctive characteristics. However, this study indicates a similarity to *C. cuneatum*. *Cicer cuneatum* has previously been loosely linked with the annual species, as the monospecific series *Cirrhifera* Maesen (1972) or as section *Cunecicer* Seferova (1995). The distinction of this species has also been indicated by genetic and biochemical studies (Ahmad & Slinkard, 1992; Ahmad et al., 1992; Sammour, 1994; Labdi et al., 1996; Tayyar & Waines, 1996). Seed and plumule analysis (Javadi & Yamaguchi, 2004c) also place these two species close together but at some distance from the other *Cicer* taxa. Van der Maesen (1987) described *C. canariense* as being "a vetch-like perennial" having the seedling morphology of *C. cuneatum*, this indicates close affinities with the tribe Viciae (Nozzolillo, 1985).

Group B in Fig. 2 and Clusters II and III in Fig. 3 are the same and correspond to the species of subgenus *Viciastrum*, Cluster II, with a few exceptions, is section *Tragacanthoides* Jaub. & Spach. The nine taxa included in the latter section are all high-altitude, xerophytic species from Central Asia. The analysis indicates four sub-clusters within Cluster II, although the organisation of species in these groups does not precisely follow previous classifications. The grouping of *C. subaphyllum* and *C. stapfianum* is recognised as series *Subaphylla* Seferova by Seferova (1995). *Cicer incanum*, cited as a synonym of *C. macracanthum* by Seferova (1995), was placed in section *Polycicer* by Van der Maesen although he notes its affinity to *C. macracanthum* (Van der Maesen, 1972: 23). Here it is a cluster outlier, but care must be taken when interpreting its placement here as the result may be partially due to a large quantity of missing data for this species. The remaining species, *C. pungens*, *C. tragacanthoides* and *C. rechingeri*, are grouped together. Two of the 3 species are given monospecific

status in series *Pungentia* and *Tragacanthoidea* by Seferova (1995), and she groups *C. rechingeri* with *C. macracanthum* on the basis of leaflet number, number of flowers on the inflorescences and leaflet shape. However, this distinction is not supported by the results presented here.

Groups 4, 5 and 6 (Fig. 2) and Cluster III (Fig. 3) represent the most complex and least resolved set of species in the genus *Cicer*. Many taxa have often switched taxonomic position and taxonomic rank. Popov (1929) defined series composition based on geographical distribution; but, as Coles et al. (1998) concluded, many *Cicer* species are seriously under-collected and their true pattern of distribution is incomplete. However, group B4 is geographically centred on the Greek and Turkish Aegean islands and is referable to section *Polycicer*. This grouping is supported by the cluster and ordination results as well as karyotype data; *C. graecum*, *C. heterophyllum*, *C. isauricum* and *C. montbretii* have $2n = 16$, while *C. floribundum* has $2n = 14$ (Contandriopoulos et al., 1972).

During the analyses certain taxa appeared to hold consistently stable key positions in the patterns of relationships (see Fig. 3) implying that they held closer affinities between subclusters than other taxa, while belonging quite clearly to independent subclusters (*C. balcaricum*, *C. flexuosum*, *C. grande* and *C. nuristanicum*). Closer study showed that these were among the species which had undergone the greatest taxonomic reclassification among previous classifications. *Cicer anatolicum* and *C. balcaricum* have been grouped together and referred to as series *Anatolo-Persica* (Popov) Lincz. in previous classifications, but appear quite separate in this analysis. Conversely, *C. grande* and *C. korshinskyi* are close in this analysis, which concurs with Van der Maesen's (1972) view that both are in series *Flexuosa*. Seferova keeps *C. grande* in series *Flexuosa* but moves *C. korshinskyi* to series *Anatolo-Persico-Orientalis*. Many of the species in this group appear to form small tight groups rather than larger clusters. So, while this analysis has clustered *C. kermanense*, *C. spiroceras* and *C. oxydon* with *C. baldshuanicum* and *C. mogoltavicum*, the former group of 3 species has been recognised as a distinct group (series *Persica*). *Cicer baldshuanicum* was placed with *C. mogoltavicum* in series *Flexuosa* Lincz. by Van der Maesen (1972). Seferova (1995) retained *C. baldshuanicum* in series *Flexuosa* Seferova and recombined *C. mogoltavicum* as *C. flexuosa* subsp. *mogoltavicum* Popov.

It is interesting to note that many species with similar geographical distribution are also linked by the results of the analyses. This either implies that the characters used here to segregate the taxa are heavily biased towards those influenced by geography or environment or they represent suites of characters which, when combined, are not independent within *Cicer*. *Cicer songaricum*, *C. microphyllum* and *C. anatolicum*, while appearing morphologically very similar, can be distinguished by their allopatric distribution: *C. songaricum* is confined to Central Asia, while *C. microphyllum* and *C. anatolicum* are from Kashmir and Turkey, respectively (Van der Maesen, 1987).

Character suites and novel taxonomic hierarchy

The multivariate analysis clearly indicated that the characters available for segregating taxa are very variable. Consequently, using only one or two features to delineate infrageneric groups will result in an indistinct, unstable hierarchy. This strongly argues

for groups defined using many more characters, to account for the intrinsic variation. It also implies that morphology alone cannot be used to define the species relationships. The morphometric analyses did not reveal any novel taxonomically useful characters. Instead, the morphometric analysis allowed the definition of taxonomically useful character suites, whose variation allowed the circumscription of distinct groups. Thus, in a departure from conventional descriptions that restrict supraspecific descriptions to a few minimal characters, the subgenera, sections and series are defined by comparatively many characters.

Homoplasy (similarity not as a direct result of common ancestry) or repeated evolution of certain character traits within the genus, is clearly a disrupting factor for the development of a monophyletic infrageneric structure. Traditionally favoured characters, e.g., life cycle (annual : perennial) or rachis terminal structure (tendrill : leaflet : spine) are particularly weak. By down-playing the importance of these characters in the definition of the infrageneric ranks of *Cicer*, and acknowledging the recent advances in molecular research of *Cicer*, it should be possible to construct a taxonomically useful infrageneric hierarchy that reflects interspecific relationships.

The revised classification proposed for *Cicer* is based on the morphometric analyses but take into account previously published hierarchies and the newly published molecular phylogenies.

The three subgenera *Cicer*, *Viciastrum* and *Stenophyllum* are distinguished on the basis of a suite of characters including habit (herbaceous : woody), life cycle (perennial : annual), terminal structure of rachis (tendrill : leaflet : spine), leaf shape (outline parallel : outline decrescent), corolla size (standard long and broad : short and narrow) and filament length (long : short). The broad geographical distribution (African : Aegean-Mediterranean : West and Central Asia) is also important.

The sections and series in the subgenus *Cicer* are defined by the following suite of characters. Phyllotaxy (nearly opposite : alternate), stem height (< 20 cm : > 20 cm), leaf base shape (rounded cuneate to cuneate), number of leaflet pairs on rachis (3–10 : 1–3(–7)), midrib tooth features (\pm spinous : recurved : prominent), calyx teeth length (< 7 mm : > 7 mm), seed length (c. 3–4 mm : c. 6 mm), seed coat surface features (wrinkled : echinate : tuberculate). The hierarchy of the primary and secondary gene pool is acknowledged by the nomenclatural series *Cicer* and *Pinnatifida* within section *Cicer*. Seed storage proteins (Ahmad & Slinkard, 1992, Sammour, 1994) and isozyme polymorphism data (Ahmad et al., 1992; Labdi et al., 1996; Tayyar & Waines, 1996) corroborate this grouping, as do RAPD DNA analyses (Ahmad, 1999; Sudupak et al., 2002). Section *Chamaecicer* includes the two perennial species in this subgenus: *C. atlanticum* and *C. incisum*.

Subgenus *Viciastrum* is divided into three monophyletic sections: *Annua*, *Polycicer* and *Vicioides* s. ampl. Section *Annua* groups *C. yamashitae* and *C. chorassanicum* together. Subgenus *Viciastrum* section *Polycicer* forms a unified morphological subset within section *Vicioides*. The character traits defining and uniting the five taxa in *Polycicer* are also frequently found in various combinations in section *Vicioides*. However, the following character traits are unique to *Polycicer*: Habit (always herbaceous, flexuous

stems); branching (mostly simple), leaf outline (always equal), leaflets (petiolate, always entirely dentate); raceme (1–many-flowered), arista (terminal clavate leaflet, not spinous); distribution (below 2000 m a.s.l. in Aegean-Mediterranean). The importance of the unique eco-geographic affiliation and the molecular phylogeny (Van der Maesen et al., 2007) of these species is recognised by the rank of section.

Subgenus *Viciastrum* section *Vicioides* s. ampl. indicates a significant shift in the supraspecific taxonomic hierarchy. Both the molecular data and several morphological analyses (e.g., Van der Maesen et al., 2007) indicate that the taxa within this group show a high degree of homoplasy, with parallel developments of character traits resulting in genetically distant (Van der Maesen et al., 2007) but morphologically similar taxa, i.e., *C. oxyodon* and *C. spiroceras*. These have ‘traditionally’ been the taxa whose precise taxonomic position has been most disputed and unstable. To avoid the persistent non-monophyletic artificial groupings that have characterised the description of these species’ relationships in the past, the section *Vicioides* has been emended and amplified, and the subsectional ranks have been abandoned.

Subgenus *Stenophyllum* is robustly supported by both the morphological and molecular studies, and includes both *C. canariense* and *C. cuneatum*. This nomenclatural relocation of *C. cuneatum* and acknowledgment of its phylogenetic origin as closer to *C. canariense* has already been suggested by several authors (viz. Frediani & Caputo, 2005; Javadi, 2004; Javadi & Yamaguchi, 2004 a, b; Van der Maesen et al., 2007).

INFRAGENERIC CLASSIFICATION OF CICER

Cicer

Cicer L. (1753).

= *Nochotta* S.G. Gmel.

= *Spiroceras* (Jaub. & Spach) Hutch., nom. invalid.

Subgenus Cicer

Cicer L. subg. *Cicer*. — *Cicer* L. subg. *Pseudononis* Popov (1929) 168, nom. illeg.; Maesen (1972) 18. — Type species: *Cicer arietinum* L.

Herbaceous (seldom woody at base) slender annual or perennials. Stems ± densely pubescent with eglandular to glandular hairs. Leaf outline is equal, not decrescent. Terminal leaflet on leaves. Stipules laminate, usually smaller than leaflets. Leaflets laminate; cuneiform, obovate or elliptic; rarely flabellate, always dentate but sometimes only at apex; midrib tooth ± prominent, ± spinous, ± recurved; petiolate, subsessile or sessile. Peduncles usually short (0–15 mm long) but some species with longer peduncles (> 30 mm L.) Pedicels short or long. Calyx teeth straight; calyx tube short, < 5 mm long. Standard small, 5–10(–15) mm long, and narrow, 5–10(–15) mm wide; obovate to ovate; marginate or emarginate; pubescent or rarely glabrous; blue, pink or white. Alae shortly to longly auriculate or not auriculate; alae oblong or obovate. Filaments short, < 10 mm long. Pods oblong, or ovate; pubescence glandular or eglandular; seeds angular, globular or obovate; seed coat surface tuberculate, echinate, wrinkled or smooth, ± prominent chalazal tubercle.

Section *Cicer*

Cicer L. sect. *Cicer*. — *Cicer* L. sect. *Arietaria* Jaub. & Spach (1842) 225, p.p. nom. illeg. — *Cicer* L. sect. *Monocicer* Popov (1929) 168, p.p. nom. illeg.; Maesen (1972) 18. — *Grex Imparipinnata* Alef. (1859) 357, p.p. — Type species: *Cicer arietinum* L.

Crop gene pools: primary and secondary.

Series *Cicer*

Cicer L. ser. *Cicer*. — *Cicer* L. ser. *Arietina* Lincz. ex Seferova (1995) 101, nom. illeg. — *Cicer* L. ser. *Arietina* Lincz. (1948) 296, nom. invalidum. — Type species: *Cicer arietinum* L.

Annual species, stem height 20–40 cm, leaves arranged nearly opposite or alternately, 3–10 pairs of leaflets on rachis, midrib tooth spinous, prominent, recurved; leaflet bases cuneate to rounded cuneate, calyx teeth < 7 mm (rarely more), Seed length c. 6 mm, seed coat wrinkled or echinate.

Species examined:

Cicer arietinum L.; *C. echinospermum* P.H. Davis; *C. reticulatum* Ladiz.

Series *Pinnatifida*

Cicer L. ser. *Pinnatifida* Seferova (1995) 102. — Type species: *Cicer pinnatifidum* Jaub. & Spach. *Cicer* L. ser. *Arietina* auct. non Lincz.: Maesen (1972) 18, p.p. nom. invalidum.

Annual species, stem height < 30 cm, leaves arranged nearly opposite, 2–10 pairs of leaflets on rachis, midrib tooth ± spinous, ± recurved, leaflet bases cuneate, calyx teeth < 7 mm (rarely more). Seed length c. 3–4 mm, seed coat echinate or tuberculate.

Note — These species represent the secondary gene pool for the crop species. This grouping is reinforced by isozyme polymorphism data (Ahmad et al., 1992; Labdi et al., 1996; Tayyar & Waines, 1996).

Species examined:

Cicer bijugum Rech.f.; *C. judaicum* Boiss.; *C. pinnatifidum* Jaub. & Spach.

Section *Chamaecicer*

Cicer L. sect. *Chamaecicer* Popov (1929) 168, p.p. — *Cicer* L. sect. *Nanopolycicer* (Popov) Seferova (1995) 98. — *Cicer* L. subsect. *Nanopolycicer* Popov (1929) 169. — *Cicer* L. ser. *Perennia* Lincz. ex Maesen (1972) 19. — *Cicer* L. ser. *Perennia* Lincz. (1948) 298, nom. invalidum. — *Grex Imparipinnata* Alef. (1859) 357, p.p. — Type species: *Cicer incisum* (Willd.) K. Malý. *Cicer* L. ser. *Arietina* auct. non Lincz.: Maesen (1972) 18, p.p. nom. invalidum.

Perennial creeping species, may be slightly woody at base, stem height < 20 cm, leaves arranged opposite, 1–3(–7) pairs of leaflets on rachis, midrib tooth not spinous but can be prominent, leaflet bases cuneate, calyx teeth < 7 mm (rarely more); seed length 3–4 mm, seed coat tuberculate.

Species examined:

Cicer atlanticum Coss. ex Maire; *C. incisum* (Willd.) K. Malý.

Subgenus *Viciastrum*

Cicer L. subg. *Viciastrum* Popov (1929) 168; Maesen (1972) 19. — Lectotype: *Cicer songaricum* Steph. ex DC. (designated by Seferova, 1995).

Herbaceous or woody perennial shrubs, seldom annual herbs. Terminal leaflet, spine or tendril on leaves. Stipules laminate or spiniferous, smaller or larger than leaflets. Leaf outline always decrescent. Leaflets laminate or spiniferous, cuneiform, obovate or rotund, occasionally flabellate, always dentate but sometimes only at apex, midrib tooth \pm prominent, \pm spinous, \pm recurved, petiolate, subsessile or sessile. Peduncles 16–45 mm long. Pedicels long (> 6 mm). Calyx teeth straight (rarely recurved), tube 6–8 mm long. Standard large (12–)15–17(–27) mm, and 10–16+ mm wide, obovate to ovate, marginate or emarginate, pubescent or glabrous, blue or white, seldom yellow. Alae shortly to longly auriculate, oblong, obovate or clavate. Filaments (6–)10–11+ mm long. Pods oblong, ovate or elliptic, glandular (seldom eglandular); seeds globular or obovate, tuberculate or wrinkled, \pm prominent chalazal tubercle.

Section Annuia

Cicer L. sect. *Annuia* (Maesen) Seferova (1995) 101. — *Cicer* L. ser. *Annuia* Maesen (1972) 19. — *Cicer* L. sect. *Chamaecicer* Popov (1929) 168, p.p. excl. typus. — *Cicer* L. ser. *Macro-aristatae* Maesen (1972) 18. — Grex *Imparipinnata* Alef. (1859) 357, p.p. — Type species: *Cicer chorassanicum* (Bunge) Popov.

Annual erect to creeping species, can be slightly woody at base, stem height < 20 cm, leaves arranged opposite, 1–3 pairs of leaflets on rachis, arista to 20 mm long, seed coat tuberculate.

Species examined:

Cicer chorassanicum (Bunge) Popov; *C. yamashitae* Kitam.

Section Polycicer

Cicer L. sect. *Polycicer* Popov (1929) 169. — *Cicer* L. ser. *Graeca* Seferova (1995) 97. — *Cicer* L. ser. *Anatolica* Seferova (1995) 97. — *Cicer* L. ser. *Europaeo-Anatolica* Popov (1929) 169. — Grex *Imparipinnata* Alef. (1859) 357, p.p. — *Cicer* L. sect. *Arietaria* Jaub. & Spach (1842) 230, p.p. — Lectotype: *Cicer montbretii* Jaub. & Spach (designated by Seferova, 1995).

Herbaceous, erect perennials. Flexuous stems with simple to rarely secondary branching. Leaf outline equal, leaflets evenly spaced on rachis (< 2 leaflets per cm), rachis laminate or tendrilous but never spiniferous, stipules laminate. Leaflets 3–10 pairs, petiolate, (6–10) > 11 by > 4 mm, margins entirely dentate, > 12 teeth per leaflet, midrib tooth \pm recurved. Raceme 1–many-flowered, arista with terminal clavate leaflet. Calyx strongly dorsally gibbous, medium to longish pubescent (hairs > 0.6 mm), calyx teeth > 9 mm long. Standard 12–15 mm long, seldom longer, 10–15 mm wide. Alae 11–15(>16) mm long. Occurs below 2000 m in the Aegean-Mediterranean.

Species examined:

Cicer floribundum Fenzl; *C. graecum* Orph.; *C. heterophyllum* Contandr., Pamukç. & Quézel; *C. isauricum* P.H. Davis; *C. montbretii* Jaub. & Spach.

Section Vicioides

Cicer L. sect. *Vicioides* Jaub. & Spach (1842) 230, s. ampl. emend. Davies, Maxted & Maesen. — *Cicer* L. sect. *Spiroceras* Jaub. & Spach (1842) 232. — *Cicer* L. sect. *Tragacanthoides* Jaub. & Spach (1842) 232. — *Cicer* L. sect. *Polycicer* subsect. *Macro-polycicer* Popov (1929) 169. — *Cicer* L. sect. *Acanthocicer* Popov (1929) 169. — *Cicer* L. ser. *Anatolo-Persica* (Popov) Lincz. (1948) 299. — *Cicer* L. ser. *Anatolo-Perso-Orientalia* Popov (1929) 169. — *Cicer* L. ser. *Flexuosa*

Lincz. (1948) 299, nom. invalidum. — *Cicer* L. ser. *Flexuosa* Lincz. ex Seferova (1995) 98. — *Cicer* L. ser. *Microphylla* Lincz. (1948) 304, nom. invalidum. — *Cicer* L. ser. *Macracantha* Lincz. (1948) 307, nom. invalidum. — *Cicer* L. ser. *Macracantha* Lincz. ex Seferova (1995) 99. — *Cicer* L. ser. *Persica* Popov (1929) 169. — *Cicer* L. ser. *Pungentia* Lincz. (1948) 306, nom. invalidum. — *Cicer* L. ser. *Pungentia* Lincz. ex Seferova (1995) 99. — *Cicer* L. ser. *Songorica* Lincz. (1948) 303, nom. invalidum. — *Cicer* L. ser. *Subaphylla* Seferova (1995) 100. — *Cicer* L. ser. *Tragacanthoidea* Lincz. (1948) 308, nom. invalidum. — *Cicer* L. ser. *Tragacanthoidea* Lincz. ex Seferova (1995) 100. — *Cicer* L. ser. *Anatolo-Perso-Orientalia* Popov subser. *Anatolo-Persica* Popov (1929) 170. — *Cicer* L. ser. *Anatolo-Perso-Orientalia* Popov subser. *Orientalia* Popov (1929) 170. — *Grex Apiculata* Alef. (1859) 357. — Lectotype: *Cicer songaricum* Steph. ex DC.: Jaub & Spach. (= *C. anatolicum* Alef.) (designated by Seferova, 1995).

Cicer L. ser. *Flexuosa* auct. non Lincz.: Maesen (1972) 19.

Cicer L. ser. *Macracantha* auct. non Lincz.: Maesen (1972) 20.

Cicer L. ser. *Pungentia* auct. non Lincz.: Maesen (1972) 20.

Cicer L. ser. *Songorica* auct. non Lincz.: Maesen (1972) 20.

Cicer L. ser. *Tragacanthoidea* auct. non Lincz.: Maesen (1972) 20.

Woody, erect to spreading perennials, straight to flexuous stems with secondary branching. Leaf outline decrescent, leaflets widely to evenly spaced along rachis (< 1 or 2 leaflets per cm), rachis laminate, tendrilous or spiniferous, stipules laminate or spiniferous. Leaflets (3–)10–15 pairs, subsessile to sessile, < 5– > 11 by < 6 mm, margins serrated to nearly entire, < 5–12 teeth per leaflet, midrib tooth always recurved. Raceme 1- or 2-flowered, arista spiniferous. Calyx strongly or weakly dorsally gibbous, glabrous to shortly pubescent (hairs < 0.5 mm long), calyx teeth 5–12 mm long. Standard 12–27 by 4–16 mm. Alae < 10–15 mm long. Occurs between 1000–4000 m a.s.l. in West and Central Asia.

Species examined:

Cicer acanthophyllum Boriss.; *C. anatolicum* Alef.; *C. balcaricum* Galushko; *C. baldshuanicum* (Popov) Lincz.; *C. fedtschenkoi* Lincz.; *C. flexuosum* Lipsky; *C. grande* (Popov) Korotkova; *C. incanum* Korotkova; *C. korshinskyi* Lincz.; *C. laetum* Rassulova & Sharipova; *C. luteum* Rassulova & Sharipova; *C. macracanthum* Popov; *C. microphyllum* Benth.; *C. multijugum* Maesen; *C. nuristanicum* Kitam.; *C. paucijugum* (Popov) Nevski; *C. pungens* Boiss.; *C. rassuloviae* Lincz.; *C. rechingeri* Podlech; *C. songaricum* Steph. ex DC.; *C. stapfianum* Rech.f.; *C. subaphyllum* Boiss.; *C. tragacanthoides* Jaub. & Spach.

Subgenus *Stenophylloma*

Cicer L. subg. *Stenophylloma* A.G. Guerra & G.P. Lewis (1985) 459. — *Cicer* L. sect. *Cuneicicer* Seferova (1995) 101. — *Cicer* L. ser. *Cirrhifera* Maesen (1972) 18. — *Grex Cirrhifera* Alef. (1859) 356. — Type species: *Cicer canariense* A.G. Guerra & G.P. Lewis.

Perennial or annual, slender, semi-erect to trailing or climbing herb or shrub. Terminal simple or branched tendril on upper leaves at least. Stipules laminate, smaller than leaflets. Leaf outline equal, rachis loosely rolled. Leaflets laminate, linear or obovate, margins dentate, midrib tooth prominent, spinous, ± recurved, pubescent, subsessile. Peduncles short or absent. Pedicels short. Calyx teeth straight, tube < 5 mm. Standard short, (5–)10–12(–15) mm long and narrow, 5–10 mm wide, obovate, emarginate, pubescent, blue or pink. Alae shortly auriculate, obovate. Filaments (6–)10–11+ mm long. Pods oblong, glandular; seeds globular, tuberculate, prominent chalazal tubercle. Occurs in Africa and the Canary Islands.

Species examined:

Cicer canariense A.G. Guerra & G.P. Lewis; *C. cuneatum* Hochst. ex A. Rich.

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IDENTIFICATION LIST

Cicer

1 = <i>anatolicum</i>	12 = <i>graecum</i>	23 = <i>pinnatifidum</i> var. <i>anatolicum</i>
2 = <i>arietinum</i>	13 = <i>incisum</i>	24 = <i>pinnatifidum</i> var. <i>pinnatifidum</i>
3 = <i>atlanticum</i>	14 = <i>isauricum</i>	25 = <i>pungens</i>
4 = <i>bijugum</i>	15 = <i>judaicum</i>	26 = <i>rechingeri</i>
5 = <i>canariense</i>	16 = <i>kermanense</i>	27 = <i>reticulatum</i>
6 = <i>chorassanicum</i>	17 = <i>macracanthum</i>	28 = <i>songaricum</i>
7 = <i>cuneatum</i>	18 = <i>microphyllum</i>	29 = <i>spiroceras</i>
8 = <i>echinospermum</i>	19 = <i>montbretii</i>	30 = <i>subaphyllum</i>
9 = <i>fedschenkoi</i>	20 = <i>multijugum</i>	31 = <i>tragacanthoides</i> var. <i>tragacanthoides</i>
10 = <i>flexuosum</i>	21 = <i>nuristanicum</i>	32 = <i>tragacanthoides</i> var. <i>turcomanicum</i>
11 = <i>floribundum</i>	22 = <i>oxyodon</i>	33 = <i>yamashitae</i>

- Aitchison 740: 18 — Akhtar 706/45: 6 — Alava 7067: 23; 10591: 6 — Alston & Sandwith 1642: 19 — Andrews R117: 5 — Archibald 2187: 1 — Aryavand, Edmondson & Miller 1420: 29 — Assadi, Edmondson & Miller 1681: 16 — Atchley 627: 12.
- A. Baytop 20127a: 4 — A. Baytop & T. Baytop 2583: 19 — Biggs 13153: 16 — J. Bormüller & A. Bormüller 6634: 22; 6635: 22 — Bowes 88: 17 — Brown & Rothera 15: 18.
- Carter 542: 20 — Clarke 28716B: 17 — Cosson 1873 (BM-type): 3; 1876 (BM-type x2): 3.
- Daly 1246: 31 — Davis 42876: 8; 43077: 24 — P.H. Davis 307: 13; 4339: 15; 18119: 13 — Davis & Hedge 27464: 24; 28545: 8; 29090: 23; 29179: 23; 29402: 1; 31201: 13; 31766: 1 — Davis & Polunin 24751: 1 — De Wilde 7041: 7.
- E00032291: 18 — Edmondson 1207: 32.
- Fouroughi, Sanii & Amini 12347: 29 — Furse 2568: 31; 2624: 22; 5692: 6; 8396: 6 — Furse & Syngé 427: 22.
- Gillet & Rawi 7669: 4.
- Hedge & Wendelbo 4202: 25; 4415: 25; 4525: 25; 5225: 26; 5348: 9; 8793: 31.
- Kerr 2422: 2 — Kie 2378: 25 — Kotschy 403: 30.
- Lempreg 434: 12 — Litinow 388: 32 — Ludlow 356: 18 — Ludlow & Sherriff 8399: 18; 8547: 18.
- Markova et al. 932: 19 — Massodegh 15: 29 — Maxted, Allkin & Khattab 4699: 19 — Maxted, Auricht & Kitiki 4843: 8; 5043: 8; 5230: 8 — Maxted, Ehrman, & Khattab 1870: 15; 1877: 15 — Maxted, Ladizinsky & Potokina 8045: 10; 8048: 10; 8062: 10 — Maxted & Sperling 8201: 28; 8234: 28 — Musselman 10329: 15.
- Noë 174: 19.
- Orphanides 495: 13.
- Pappi 138: 7; 6352: 7 — Polunin et al. 695: 2; 1197: 18 — Punjab Department of Agriculture Type 14: 2; Type 20: 2.
- Rabmanian 6321: 31 — Rechinger 10443: 22; 18720: 25; 37351: 20; 47970: 22; 53396: 32 — Roberts 566: 18 — Rowe & Sproul 34: 9.
- Schimper 270 (BM-isotype): 7; 810 (BM-isotype): 7; 1545 (BM-isotype): 7 — Siddiqui 4130: 18 — Southampton University 125: 18 — Stainton 2672: 21; 2691: 17 — Stapf 1294: 22.
- Van der Maesen 1347: 14; 2022: 33; 2023: 33; 2024: 33; 2058: 11; 2060: 11; 2100: 27; 2103: 4; 2105: 27; 2106B2: 27; 2211: 26; 2214: 26; 2765: 14; 3212: 12; Sdl. 1033-68: 10.
- Wheeler Haines W1544: 4.
- Zohary & Amdursky 345: 15.

From the literature: Contandriopoulos et al. (1972): *C. heterophyllum*; Van der Maesen 1972, 1987; Davis, 1970; Maxted, 1993; Kupicha, 1977; Coles, 1993: *C. acanthophyllum*; *C. balcaricum*; *C. baldshuanicum*; *C. grande*; *C. incanum*; *C. korshinskiyi*; *C. mogoltavicum*; *C. paucijugum*; *C. stapfanum*.