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Morphological variation of the *Oncocyclus* irises (*Iris*: Iridaceae) in the southern Levant

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Morphological traits of *Iris* section *Oncocyclus* (Siems.) Baker in the southern Levant (Israel, Jordan, The Palestinian Authority and Sinai/Egypt) were analysed in order to clarify taxonomic relationships among taxa and the validity of diagnostic characters. Floral and vegetative characters were measured in 42 populations belonging to nine species during the peak of the flowering season in 1998–2000. Pearson's Coefficient of Racial Likelihood (CRL) was used to calculate morphological distances between populations. Twelve of the measured populations, distributed along the north-south aridity gradient in Israel, were further explored for morphological changes along the gradient. Cluster analysis revealed two major clusters: the first includes most of the dark-coloured *Iris* populations, with populations of *I. petrana* Dinsmore and *I. mariae* W. Barbey forming a subcluster; the second consists of all the light-coloured populations but also some dark-coloured populations. Pearson's CRL and geographical distance were significantly correlated among the dark-coloured populations. Along the geographical gradient, flower, stem and leaf size traits decrease towards the south, probably as an adaptation to aridity. This suggests that natural selection promoted the differences between populations. Almost no discrete phenotypic groups exist within the *Oncocyclus* species of the southern Levant except for variation in the floral colours. Most of the suggested diagnostic characters proved unreliable in that they varied continuously across populations. The taxonomical difficulties encountered in this study reflect the special evolutionary state of the *Oncocyclus* irises as a group in the course of speciation. © 2002 The Linnean Society of London. *Botanical Journal of the Linnean Society*, 2002, 139, 369–382.

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INTRODUCTION

IRIS SECTION *ONCOCYCLUS*

The species of *Iris* section *Oncocyclus* (Siems.) Baker are best characterized by a solitary large flower on the stem, a dark signal patch at the entrance of the pollination tunnel, and an elaiosome on the seed (Dykes, 1913; Avishai, 1977; Avishai & Zohary, 1980; Rix, 1997). These irises grow in the Middle East in an area extending from Edom and the Negev desert in the south to the high mountains of Transcaucasia in the

north-east (Avishai & Zohary, 1980). Seven aggregates have been described within section *Oncocyclus* on the basis of the floral morphology, flower colour and the micromorphology of hairs at the entrance of the pollination tunnel (Avishai & Zohary, 1980). The number of *Oncocyclus* species currently recognized is 60 (Avishai, 1977), 41 (Mathew, 1989) or 33 (Rix, 1997).

Ten species of the section were recorded in Israel and adjacent areas (Jordan, The Palestinian Authority and Sinai/Egypt) henceforth referred to as the southern Levant (Feinbrun-Dothan, 1986; Rix, 1997). Three of these species have light-coloured standards, namely *Iris lortetii* W. Barbey of the Lortetii aggregate, and *I. bismarckiana* Regel and *I. hermona* Dinsmore of the Iberica aggregate. In the other seven

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species the standard (and whole appearance of the flower) is dark-coloured. The latter group includes *I. haynei* Baker, *I. atrofusca* Baker, *I. bostrensis* Mouterde, *I. nigricans* Dinsmore, *I. petrana* Dinsmore, *I. mariae* W. Barbey and *I. atropurpurea* Baker, all of which belong to the Haynei aggregate (Avishai, 1977; Avishai & Zohary, 1980). In the past, many more species and microspecies had been described in the southern Levant (Davis, 1946; Dinsmore, 1934), but all were regarded later as synonyms (Feinbrun-Dothan, 1986; Mathew, 1989; Rix, 1997).

Most of the *Oncocyclus* species in the southern Levant grow in the semiarid zones and in the transition belt between the Mediterranean and the desert. A few species, however, also occur in the montane regions of the Mediterranean zone, i.e. towards the ridges of the Lebanon Mountains and the Golan Heights. Populations occupy open low-herbaceous or open shrub communities, composed mostly of perennial herbs and annuals. The dominant species composition in each location changes locally, but generally the plant association is of the semisteppe batha types (Danin & Orshan, 1999). *Oncocyclus* irises usually grow in a patchy, disjunct pattern. The populations are relatively dense (up to two clones per m²), ranging between a few dozen to several thousand clones. The boundaries of the populations are clearly recognizable while sampling in the field.

Although clear-cut diagnostic characters were given in the taxonomy of the *Oncocyclus* irises in the southern Levant (Feinbrun-Dothan, 1986; Mathew, 1989; Rix, 1997), extensive morphological variation and intermediate populations have been observed in the field. Transition forms between species are known in which the diagnostic characters fit more than one species. While the above aggregates are easily distinguished, accurate species identification is often problematical. The continuous nature of morphological variation in these irises has led to much confusion in attempts to distinguish species by using morphological criteria.

Given this taxonomic confusion, along with the high variation observed in natural populations and transitional populations frequently encountered in the field, more detailed research is required on patterns of morphological variation. In this paper we report on a detailed morphometric study of nine species of section *Oncocyclus* from the southern Levant, aiming to clarify taxonomic boundaries and species relationships.

MORPHOLOGICAL CHANGES ALONG AN ENVIRONMENTAL GRADIENT

The differentiation of geographical races into new species is promoted by two major processes: random

genetic drift and natural selection (Grant, 1981). When natural selection is predominant, we may expect populations in close proximity to be morphologically more similar than those far apart because the macroenvironments (and therefore selective forces) are likely to be more similar over short than over long distances (Endler, 1977). When genetic drift is the main mechanism, such a relationship between phenotypic similarity and geographical distance is less likely. In plants, morphological characters have been investigated along various environmental gradients, such as latitude/longitude (Small & Fawzy, 1992; Passioura & Ash, 1993; Allen *et al.*, 1996), climate (Emery, Chinnappa & Chmielewski, 1994; Montagnes & Vitt, 1991; Passioura & Ash, 1993), rainfall (Sandquist & Ehleringer, 1998), soil and nutrients (Wilson, 1991; van Tienderen, 1992).

In Israel and Jordan, extreme aridity gradients exist over relatively short distances in both the west-east and north-south directions. Such gradients may be the main factor promoting clinal/spatial differentiation in morphological traits among plant populations (Nevo, 1988; Parsons, 1988). Annual precipitation, as well as maximum and minimum temperatures, change accordingly from the Mediterranean region southwards to the Saharo-Arabian deserts, eastwards in Israel and westwards in Jordan towards the regional rain-shadow desert in the Dead-Sea Rift Valley. Three dark-coloured *Oncocyclus* species (*viz.* *I. haynei*, *I. atrofusca* and *I. petrana*) are distributed along the north-south climato-geographical gradient, and provide an ideal model system for the study of adaptation. In the second part of this paper, we test whether there is a significant association between the morphological characters measured in these irises and the environment (i.e. latitude).

MATERIAL AND METHODS

MORPHOLOGICAL MEASUREMENTS

Forty-two wild populations were measured in this study (Table 1), totalling 995 plants. These populations represent nine of the 10 species recorded in the southern Levant, whereby at least one population of each species was measured. *Iris bostrensis* from north Jordan was only observed in the field but not measured. Measurements were taken during the peak of flowering season (mid-February to early April) in 1998–2000. Clones were determined as clumps (ramets) of leaf-fans separated by more than 20 cm from each other. Only one individual leaf-fan with flowering stem was measured from each clone (Tucic *et al.*, 1990). The measured plants were chosen randomly within each clone, which were also chosen randomly within each population.

Table 1. Locations of *Oncocyclus* iris populations measured for morphological traits. Altitude is metres above sea level

Species	Code	Location	Region	Latitude	Longitude	Altitude (m)	Sample size
<i>I. atrofusca</i>	BNA	Bani-Naim	Judean mts.	31°31'N	35°10'E	900	16
<i>I. atrofusca</i>	GRL	Goral hills	Northern Negev	31°19'N	34°47'E	320	30
<i>I. atrofusca</i>	KNJ	Kubet-Najme	Shomron mts.	31°56'N	35°20'E	580	23
<i>I. atrofusca</i>	MRT	Mar'it wadi	Northern Negev	31°15'N	35°02'E	450	30
<i>I. atrofusca</i>	RJB	Rajib	Gilead (Jordan)	32°14'N	35°41'E	350	8
<i>I. atrofusca</i>	RMN	Rimonim	Shomron mts.	31°54'N	35°20'E	550	30
<i>I. atrofusca</i>	TKO	Tekoa	Judean mts.	31°38'N	35°14'E	620	30
<i>I. atrofusca</i>	ARD	Tel Arad	Northern Negev	31°16'N	35°06'E	535	30
<i>I. atrofusca</i>	UMK	Um-Keiss	Gilead (Jordan)	32°39'N	35°39'E	265	9
<i>I. atrofusca</i>	WHD	Wahadna	Gilead (Jordan)	32°19'N	35°37'E	290	15
<i>I. atropurpurea</i>	ASD	Ashdod	Coastal plain	31°49'N	34°40'E	30	15
<i>I. atropurpurea</i>	BOV	Beit oved	Coastal plain	31°55'N	34°47'E	70	30
<i>I. atropurpurea</i>	NTN	Netania	Coastal plain	32°17'N	34°50'E	30	30
<i>I. atropurpurea</i>	PLM	Palmahim	Coastal plain	31°55'N	34°44'E	20	30
<i>I. atropurpurea</i>	PLG	Poleg	Coastal plain	32°16'N	34°50'E	30	30
<i>I. atropurpurea</i>	SHD	Shdema	Coastal plain	31°49'N	34°44'E	45	30
<i>I. bismarckiana</i>	DSN	Dishon Wadi	Upper Galilee	33°04'N	35°29'E	400	11
<i>I. bismarckiana</i>	GHM	Givat hamore	Lower Galilee	32°36'N	35°25'E	480	30
<i>I. bismarckiana</i>	NZR	Nazareth	Lower Galilee	32°43'N	35°20'E	560	26
<i>I. bismarckiana</i>	RJW	Rajib	Gilead (Jordan)	32°14'N	35°41'E	350	17
<i>I. bismarckiana</i>	YFT	Yiftach	Upper Galilee	33°07'N	35°33'E	430	18
<i>I. haynei</i>	GLB	Gilboa	Lower Galilee	32°30'N	35°24'E	450	36
<i>I. haynei</i>	SGL	South Golan	Golan Heights	32°44'N	35°39'E	225	36
<i>I. haynei</i>	UMZ	Um-Zuka	Shomron mts.	32°18'N	35°31'E	70	27
<i>I. hermona</i>	KST	Keshet	Golan Heights	32°58'N	35°48'E	700	30
<i>I. hermona</i>	MJS	Majdal Shams	Hermon mts.	33°16'N	35°46'E	1300	20
<i>I. hermona</i>	MPL	Mapalim	Golan Heights	32°59'N	35°45'E	550	30
<i>I. lortetii</i>	BDJ	Beit-Dajan	Shomron mts.	32°11'N	35°24'E	630	30
<i>I. lortetii</i>	DUM	Duma	Shomron mts.	32°04'N	35°21'E	550	9
<i>I. lortetii</i>	ITM	Itamar	Shomron mts.	32°10'N	35°18'E	600	15
<i>I. lortetii</i>	KSH	Kiriat Shmona	Upper Galilee	33°12'N	35°33'E	340	10
<i>I. lortetii</i>	MLK	Malkia	Upper Galilee	33°05'N	35°29'E	670	30
<i>I. lortetii</i>	UZR	Uzarin	Shomron mts.	32°07'N	35°18'E	600	10
<i>I. lortetii</i>	WAH	W. Ahmar	Shomron mts.	32°07'N	35°22'E	370	15
<i>I. mariae</i>	GVL	Gevulot	Western Negev	31°12'N	34°27'E	130	20
<i>I. mariae</i>	KRN	Keren mt.	Western Negev	31°01'N	34°31'E	310	30
<i>I. mariae</i>	MGN	Magen	Western Negev	31°17'N	34°25'E	135	20
<i>I. mariae</i>	SVT	Shivta	Western Negev	30°57'N	34°36'E	330	30
<i>I. nigricans</i>	KRK	Kerak	Moav (Jordan)	31°11'N	35°42'E	870	25
<i>I. petrana</i>	EIS	El-Is	Edom (Jordan)	30°50'N	35°38'E	1150	20
<i>I. petrana</i>	RTM	Rotem plain	Northern Negev	31°03'N	35°08'E	390	31
<i>I. petrana</i>	YER	Yeruham	Northern Negev	31°01'N	34°58'E	560	30

The populations were scored for 16 characters (Table 2). Ten of the characters are descriptors of floral morphology, while three describe shape and size of leaves (one leaf, the second from the centre of the leaf-fan, was measured in each individual). The remaining three characters are descriptors of stem structure. All the characters chosen have previously been considered diagnostic for the taxonomy of *Oncocyclus* irises of the southern Levant

(Feinbrun-Dothan, 1986). Although flower colours were used as diagnostic characters in the past (Dinsmore, 1934; Feinbrun-Dothan, 1986), we preferred not to use them due to difficulties in objectively quantifying colour shades. Flower colours are particularly problematic in the dark-coloured species, where colours might vary to a great degree from pink to black or blue to deep purple, even within the same population.

Table 2. Description of morphological characters recorded in *Oncocyclus* iris populations

No.	Character	Description
1	Flower height	From fall bottom to standard top (in cm)
2	Flower diameter	At the height of the pollination tunnel (in cm)
3	Flower diameter/height	Ratio determines the flower shape (Feinbrun-Dothan, 1986)
4	Flower surface	Flower diameter \times flower height (in cm ²)
5	Fall width	In its broadest place (in cm)
6	Standard width	In its broadest place (in cm)
7	Signal patch length	In its broadest place (in cm)
8	Signal patch width	In its broadest place (in cm)
9	Signal patch surface	Signal patch length \times width (in cm ²)
10	Patch surface/fall width	Ratio determines the projection of the signal patch over the fall
11	Leaf arch	Categorical character, coded by 1 = erect, 2 = semi curved and 3 = curved.
12	Leaf width	In the point of deviation from stem (in cm)
13	Leaf height	From ground to the highest point (could be the peak of the curve) (in cm)
14	Stem height	From ground to fall bottom (in cm)
15	Stem gap	The ratio of the gap between leaves and flower, and stem height. (stem height – leaf height)/stem height
16	Flower/stem height	Ratio determines the size of the flower compared with stem height

STATISTICAL ANALYSIS

Morphological distances between pairs of populations were calculated using Pearson's Coefficient of Racial Likelihood (CRL) (Sneath & Sokal, 1973; Ariyo, 1990), selected because it takes into account the variation and size of each population. Cluster Analysis (CA), with the clustering method of Unweighted Pair Group Average (UPGMA), as well as Principal Coordinate Analysis (PCO) were performed on the CRL matrix, using the program MVSP v. 3.12a (Kovach, 2000). PCO was preferred over the more commonly used Principal Component Analysis (PCA) because we could not assume a normal distribution for all characters.

Geographical distances between each pair of populations were calculated as the geometrical mean of coordinates, i.e. the square root for the sum of squared differences between latitude and longitude for each pair of populations. Coordinates were recorded for all populations in 1 km² resolution.

For the morphological north-south gradient study, 12 populations were chosen for analysis, encompassing populations of (i) *Iris haynei* from south Golan, Gilboa and Um-Zuka (ii) *I. atrofusca* from Kubet-Najme, Rimonim, Tekoa, Bani-Naim, Goral, Tel Arad and Mar'it, and (iii) *I. petrana* from Rotem plain and Yeruham. Population means of each of the 16 characters measured were linearly regressed against the latitude of each locality.

RESULTS

Population means and standard deviations for each character are given in Table 3. The raw data matrix is

available from the first author upon request. The largest morphological distance (CRL = 14.7) was found between Keshet (*I. hermona*) and Rotem (*I. petrana*) populations, separated by 222 km, while the smallest distance (CRL = 1.0) was found between Wahadna and the neighbouring (10 km) Rajib population, both of *I. atrofusca*. The largest geographical distance between populations measured is 280 km, between Shivta (*I. mariae*) and Majdal-Shams (*I. hermona*), which are morphologically rather different (CRL = 9.9). The second smallest morphological distance (CRL = 1.01) was found between the Rajib and Dishon populations of *I. bismarckiana*, despite their relatively large geographical distance (93 km).

CLUSTER AND MULTIVARIATE ANALYSES

Cluster analysis (CA) based on the UPGMA method revealed two major clusters (Fig. 1). The differences between these two clusters are highly significant (MANOVA; $p < 0.001$). The first cluster includes most of the dark-coloured *Iris* populations, with the populations of *I. petrana* and *I. mariae* forming a small sub-cluster, which is significantly different (MANOVA; $p < 0.001$) from all the remaining populations of this 'dark-coloured cluster'. There is no clear separation between populations of this latter group, comprising *I. atropurpurea* from the coastal plain, *I. atrofusca* (Gilead, northern Negev and Judean Mountains) and *I. nigricans* (Kerak, Moab), and despite their geographical separation. The second major cluster consists largely of the light-coloured populations of *I. lortetii*, *I. bismarckiana* and *I. hermona*, but also

Table 3. Average (and standard deviation) of morphological characters measured in *Oncocylus* iris populations. Character numbers are according to the numbers given in Table 2. In few populations no data were available for a small number of leaf traits due to high grazing pressure. In those cases, n.d. denotes No Data

Location	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Bani-Naim	<i>I. atrofusca</i>	8.0 (1.24)	7.4 (0.68)	0.95 (0.2)	58.2 (11.28)	3.9 (1.03)	5.2 (0.65)	1.13 (0.23)	1.01 (0.22)	1.18 (0.45)	0.32 (0.12)	1.7 (0.48)	0.9 (0.19)	18.3 (6.8)	22.2 (5.73)	0.13 (0.21)	0.27 (0.19)
Goral	<i>I. atrofusca</i>	7.7 (0.87)	7.2 (0.7)	0.95 (0.11)	54.9 (9.52)	3.9 (0.46)	5.6 (0.67)	1.3 (0.16)	1.26 (0.17)	1.65 (0.37)	0.43 (0.08)	1.3 (0.45)	0.8 (0.13)	21.8 (4.36)	22.4 (3.92)	0.03 (0.14)	0.36 (0.08)
Kubet-Najme	<i>I. atrofusca</i>	10.0 (1.37)	8.8 (0.99)	0.9 (0.09)	88.4 (19.34)	4.8 (0.75)	7.1 (0.83)	1.43 (0.27)	1.28 (0.22)	1.85 (0.56)	0.39 (0.1)	1.4 (0.48)	1.2 (0.22)	24.5 (5.94)	30.5 (8.24)	0.17 (0.2)	0.35 (0.11)
Mar'it	<i>I. atrofusca</i>	7.7 (0.94)	7.3 (0.75)	0.96 (0.08)	55.7 (11.88)	3.6 (0.53)	5.1 (0.74)	1.32 (0.26)	1.26 (0.2)	1.68 (0.52)	0.47 (0.13)	1.7 (0.56)	1.0 (0.2)	17.7 (5.5)	21.6 (6.58)	0.17 (0.18)	0.39 (0.13)
Rajib	<i>I. atrofusca</i>	7.7 (1.17)	7.1 (0.61)	0.94 (0.09)	54 (12.32)	3.7 (0.55)	5.4 (1.04)	1.45 (0.2)	1.22 (0.21)	1.8 (0.5)	0.5 (0.12)	1.6 (0.5)	1.4 (0.22)	26.8 (6.68)	26 (2.73)	-0.02 (0.2)	0.3 (0.06)
Rimonim	<i>I. atrofusca</i>	8.8 (0.94)	7.6 (0.81)	0.86 (0.08)	66.5 (12.78)	4.1 (0.6)	6.4 (0.69)	1.28 (0.32)	1.28 (0.34)	1.72 (0.61)	0.42 (0.14)	1.2 (0.41)	1.1 (0.19)	22.7 (6.39)	25.1 (7.49)	0.08 (0.16)	0.38 (0.11)
Tekoa	<i>I. atrofusca</i>	8.4 (0.72)	8.3 (0.66)	1.01 (0.09)	69.2 (9.31)	4.0 (0.5)	6.0 (0.54)	1.44 (0.26)	1.49 (0.35)	2.21 (0.95)	0.55 (0.19)	1.4 (0.5)	1.6 (0.4)	n.d.	34.7 (9.92)	n.d.	0.27 (0.09)
Tel Arad	<i>I. atrofusca</i>	8.6 (0.91)	7.6 (0.72)	0.9 (0.09)	64.8 (11.5)	3.9 (0.51)	6.0 (0.82)	1.48 (0.26)	1.4 (0.22)	2.1 (0.63)	0.54 (0.13)	1.9 (0.51)	1.0 (0.13)	14.1 (3.59)	20.0 (3.7)	0.3 (0.15)	0.44 (0.08)
Um Keiss	<i>I. atrofusca</i>	8.3 (0.29)	7.7 (0.59)	0.94 (0.08)	63 (5.69)	4.0 (0.35)	6.2 (0.73)	1.68 (0.28)	1.53 (0.25)	2.58 (0.73)	0.66 (0.19)	1.3 (0.45)	1.4 (0.18)	35.5 (6.25)	34.2 (5.8)	-0.04 (0.12)	0.25 (0.05)
Wahadna	<i>I. atrofusca</i>	8.0 (1.42)	7.3 (0.77)	0.92 (0.09)	58.4 (16.7)	3.4 (0.47)	5.4 (0.74)	1.46 (0.29)	1.4 (0.17)	2.06 (0.59)	0.61 (0.12)	1.3 (0.32)	1.3 (0.22)	25.4 (5.59)	24.5 (3.61)	0.02 (0.33)	0.34 (0.09)
Ashdod	<i>I. atropurpurea</i>	8.0 (1.1)	6.4 (0.81)	0.82 (0.11)	51.1 (11.47)	3.3 (0.33)	5.5 (0.82)	1.35 (0.28)	1.22 (0.21)	1.69 (0.59)	0.51 (0.15)	1.9 (0.75)	0.8 (0.13)	22.6 (9.68)	34.1 (8.36)	0.37 (0.16)	0.25 (0.08)
Beit-Oved	<i>I. atropurpurea</i>	6.9 (1.01)	6.2 (0.76)	0.9 (0.09)	42.7 (10.93)	3.2 (0.34)	5.2 (0.53)	1.2 (0.21)	0.98 (0.2)	1.2 (0.39)	0.38 (0.11)	1.4 (0.5)	0.9 (0.16)	21.1 (5.96)	30.7 (7.31)	0.31 (0.1)	0.24 (0.07)
Netania	<i>I. atropurpurea</i>	8.9 (1.03)	7.1 (0.66)	0.81 (0.08)	63.6 (12.02)	4.1 (0.51)	6.1 (0.7)	1.53 (0.21)	1.25 (0.16)	1.92 (0.44)	0.49 (0.11)	1.7 (0.56)	1.1 (0.18)	21.5 (4.23)	28.8 (6.66)	0.24 (0.13)	0.33 (0.09)
Palmahim	<i>I. atropurpurea</i>	7.5 (1.09)	7.4 (0.78)	1.0 (0.12)	56.0 (12.99)	3.5 (0.54)	5.3 (0.71)	1.49 (0.31)	1.27 (0.3)	1.93 (0.76)	0.56 (0.19)	1.7 (0.55)	0.8 (0.12)	11.9 (3.46)	34.2 (6.05)	0.65 (0.1)	0.23 (0.05)
Poleg	<i>I. atropurpurea</i>	8.6 (1.05)	6.9 (0.64)	0.82 (0.09)	59.3 (11.42)	3.8 (0.54)	6.1 (0.72)	1.48 (0.24)	1.23 (0.2)	1.84 (0.52)	0.49 (0.1)	1.4 (0.48)	1.0 (0.19)	17.0 (6.82)	30.9 (6.95)	0.45 (0.21)	0.29 (0.08)
Shdema	<i>I. atropurpurea</i>	8.3 (0.82)	7.0 (0.5)	0.85 (0.08)	57.6 (8.43)	3.9 (0.33)	5.8 (0.55)	1.5 (0.29)	1.3 (0.21)	1.98 (0.62)	0.51 (0.14)	1.2 (0.41)	0.9 (0.09)	28.6 (6.18)	39.8 (7.1)	0.29 (0.09)	0.22 (0.05)
Dishon	<i>I. bismarckiana</i>	9.1 (1.54)	8.5 (1.02)	0.96 (0.13)	77.7 (20.84)	5.2 (0.72)	5.6 (0.99)	1.59 (0.34)	1.5 (0.31)	2.45 (0.95)	0.47 (0.15)	1.3 (0.47)	1.8 (0.36)	23.7 (4.95)	26.2 (7.05)	0.08 (0.16)	0.36 (0.08)
Givat-Hamore	<i>I. bismarckiana</i>	11.8 (1.78)	9.7 (0.91)	0.84 (0.13)	113.4 (23.51)	6.8 (0.88)	7.6 (0.58)	1.69 (0.17)	1.53 (0.28)	2.6 (0.6)	0.39 (0.09)	1.7 (0.67)	1.6 (0.23)	27.9 (7.68)	36.1 (7.87)	0.23 (0.15)	0.34 (0.09)
Nazareth	<i>I. bismarckiana</i>	10.6 (1.14)	8.8 (1.31)	0.84 (0.09)	92.9 (22.45)	5.9 (0.87)	6.4 (1.08)	1.45 (0.24)	1.23 (0.24)	1.81 (0.64)	0.31 (0.09)	1.4 (0.48)	1.7 (0.3)	26.5 (6.43)	32.2 (6.57)	0.18 (0.14)	0.35 (0.09)
Rajib	<i>I. bismarckiana</i>	9.6 (1.43)	8.4 (1.25)	0.88 (0.06)	82.1 (23.68)	5.4 (0.85)	6.2 (1.25)	1.4 (0.37)	1.45 (0.32)	2.1 (0.94)	0.39 (0.16)	1.4 (0.49)	1.8 (0.36)	24.5 (7.94)	23.4 (6.62)	-0.05 (0.26)	0.44 (0.13)
Yiftach	<i>I. bismarckiana</i>	11.3 (1.76)	9.7 (1.09)	0.88 (0.12)	108.3 (30.18)	6.4 (0.73)	7.5 (0.87)	2.01 (0.31)	1.64 (0.25)	3.36 (0.95)	0.53 (0.11)	1.1 (0.24)	2.0 (0.45)	36.7 (7.54)	41.9 (7.8)	0.13 (0.06)	0.27 (0.05)

Table 3. Continued

Location	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Gilboa	<i>I. haynei</i>	11.4	9.1	0.8	103.7	5.4	8.0	1.9	1.57	3.04	0.57	1.4	1.5	32.2	37.8	0.14	0.33
		(1.51)	(0.78)	(0.08)	(20.64)	(0.82)	(1.14)	(0.29)	(0.32)	(0.98)	(0.16)	(0.47)	(0.23)	(7.39)	(9.27)	(0.13)	(0.1)
South-Golan	<i>I. haynei</i>	9.4	8.1	0.86	75.7	4.4	6.9	1.7	1.76	3.0	0.69	1.2	1.7	38.2	42.9	0.1	0.23
		(1.12)	(0.88)	(0.1)	(15.72)	(0.57)	(0.74)	(0.28)	(0.29)	(0.8)	(0.16)	(0.32)	(0.25)	(5.47)	(7.58)	(0.14)	(0.05)
Um-Zuka	<i>I. haynei</i>	10.1	8.5	0.85	84.8	4.9	7.5	1.93	1.66	3.27	0.68	1.4	1.3	31.3	39.7	0.21	0.27
		(0.9)	(0.68)	(0.08)	(12.32)	(0.59)	(0.73)	(0.31)	(0.31)	(1.02)	(0.21)	(0.5)	(0.16)	(6.73)	(8.6)	(0.1)	(0.06)
Keshet	<i>I. hermona</i>	12.6	10.3	0.83	130.1	6.7	9.2	1.52	1.61	2.51	0.38	1.6	1.6	33.7	47.2	0.28	0.28
		(1.6)	(0.83)	(0.1)	(23.77)	(0.84)	(0.87)	(0.37)	(0.28)	(1.06)	(0.14)	(0.51)	(0.31)	(7.15)	(9.69)	(0.11)	(0.07)
Majdal-Shams	<i>I. hermona</i>	10.4	9.4	0.92	97.3	5.9	6.4	1.73	1.6	2.84	0.49	1.4	1.5	18	22.8	0.21	0.48
		(1.01)	(0.95)	(0.11)	(15.32)	(0.9)	(0.8)	(0.41)	(0.27)	(1.02)	(0.17)	(0.41)	(0.19)	(4.22)	(5.32)	(0.1)	(0.1)
Mapalim	<i>I. hermona</i>	11.2	9.8	0.89	109.9	6.4	7.8	1.52	1.53	2.38	0.38	1.2	1.8	34.3	54.8	0.37	0.21
		(1.61)	(1.1)	(0.09)	(25.97)	(0.94)	(0.94)	(0.33)	(0.26)	(0.86)	(0.11)	(0.38)	(0.32)	(4.99)	(10.18)	(0.1)	(0.05)
Beit-Dajan	<i>I. lortetii</i>	9.9	8.0	0.82	78.8	5.4	8.0	1.54	1.52	2.39	0.45	1.7	1.5	20.1	20.5	0.56	0.47
		(1.27)	(0.65)	(0.13)	(12.2)	(0.75)	(0.94)	(0.28)	(0.41)	(0.86)	(0.15)	(0.51)	(0.36)	(3.7)	(4.17)	(0.51)	(0.16)
Duma	<i>I. lortetii</i>	9.1	8.2	0.92	74.3	4.4	6.6	1.59	1.66	2.66	0.61	1.4	1.5	24.1	24.9	0.05	0.31
		(0.85)	(0.88)	(0.1)	(12.39)	(0.67)	(0.72)	(0.19)	(0.24)	(0.64)	(0.15)	(0.51)	(0.38)	(5.25)	(3.35)	(0.12)	(0.16)
Itamar	<i>I. lortetii</i>	12.1	8.1	0.68	97.4	5.9	8.6	1.35	1.26	1.75	0.3	1.2	1.5	27	29.8	0.06	0.43
		(1.42)	(0.79)	(0.07)	(19.3)	(0.49)	(0.85)	(0.28)	(0.28)	(0.7)	(0.12)	(0.42)	(0.21)	(4.52)	(8.78)	(0.19)	(0.11)
Kiriati-Shmona	<i>I. lortetii</i>	10.2	6.5	0.65	66.5	5.7	7.2	1.13	0.97	1.1	0.2	1.1	1.1	36.9	30.8	-0.21	0.35
		(1.1)	(0.56)	(0.06)	(11.67)	(0.49)	(0.74)	(0.07)	(0.07)	(0.12)	(0.03)	(0.16)	(0.16)	(8.36)	(7.04)	(0.15)	(0.1)
Malkia	<i>I. lortetii</i>	10.9	7.8	0.73	84.1	5.4	7.4	1.08	0.98	1.07	0.2	1.6	1.5	n.d.	36.7	n.d.	0.31
		(1.06)	(0.63)	(0.09)	(10.62)	(0.72)	(0.57)	(0.24)	(0.17)	(0.34)	(0.06)	(0.51)	(0.28)	(6.56)	(6.56)	(0.13)	(0.07)
Uzarin	<i>I. lortetii</i>	10.5	7.8	0.75	81.9	5.2	7.8	1.22	1.02	1.26	0.25	1.4	1.3	26.5	30.7	0.13	0.37
		(1.28)	(1.23)	(0.1)	(20.44)	(0.88)	(1.2)	(0.21)	(0.13)	(0.34)	(0.05)	(0.52)	(0.23)	(7.82)	(8.93)	(0.17)	(0.1)
Wadi Ahmar	<i>I. lortetii</i>	10.9	8.2	0.76	89	5.6	7.8	1.32	1.2	1.6	0.29	1.6	1.6	25.2	24.8	-0.03	0.48
		(1.21)	(0.89)	(0.08)	(16.87)	(0.71)	(0.78)	(0.26)	(0.21)	(0.53)	(0.09)	(0.55)	(0.29)	(8.44)	(7.96)	(0.16)	(0.13)
Gevulot	<i>I. mariae</i>	7.0	6.3	0.9	44.3	3.8	4.9	1.29	1.09	1.42	0.38	2.9	0.6	7.5	17.8	0.59	0.41
		(1.08)	(0.9)	(0.09)	(12.56)	(0.5)	(0.57)	(0.22)	(0.19)	(0.44)	(0.09)	(0.37)	(0.11)	(2.37)	(3.63)	(0.1)	(0.09)
Keren	<i>I. mariae</i>	7.8	6.7	0.87	52.7	4.0	5.2	1.27	1.17	1.49	0.38	2.9	0.6	7.4	21.2	0.66	0.38
		(0.92)	(0.74)	(0.08)	(11.27)	(0.46)	(0.63)	(0.19)	(0.16)	(0.33)	(0.07)	(0.35)	(0.08)	(3.86)	(3.48)	(0.16)	(0.07)
Magen	<i>I. mariae</i>	6.7	5.9	0.88	38.8	3.4	4.4	1.39	1.09	1.55	0.47	2.8	0.6	9.5	22.2	0.58	0.31
		(0.75)	(0.41)	(0.08)	(6.39)	(0.5)	(0.67)	(0.22)	(0.18)	(0.48)	(0.13)	(0.42)	(0.11)	(3.36)	(4.11)	(0.14)	(0.05)
Shivta	<i>I. mariae</i>	7.7	6.5	0.85	49.5	3.7	4.9	1.25	1.21	1.55	0.43	3.0	0.7	6.8	20.1	0.66	0.41
		(0.85)	(0.62)	(0.08)	(8.95)	(0.48)	(0.61)	(0.22)	(0.23)	(0.53)	(0.13)	(0.19)	(0.14)	(2.36)	(5.28)	(0.12)	(0.11)
Kerak	<i>I. nigricans</i>	7.8	6.9	0.9	53.5	3.4	5.3	1.23	1.17	1.45	0.44	n.d.	0.8	16	18.8	0.13	0.44
		(1.09)	(0.74)	(0.09)	(12.43)	(0.35)	(0.61)	(0.19)	(0.22)	(0.38)	(0.09)	(0.16)	(0.16)	(4.7)	(4.9)	(0.24)	(0.13)
EI-Is	<i>I. petrana</i>	7.7	6.8	0.9	51.7	3.6	5.1	1.14	1.36	1.57	0.45	2.5	0.9	7.8	16.3	0.52	0.49
		(1.25)	(0.89)	(0.13)	(12.57)	(0.57)	(0.93)	(0.2)	(0.17)	(0.41)	(0.08)	(0.52)	(0.13)	(2.26)	(3.18)	(0.14)	(0.13)
Rotem	<i>I. petrana</i>	5.7	5.9	1.05	33.9	2.9	3.9	1.03	1.06	1.12	0.38	2.0	0.6	10.2	15.3	0.34	0.4
		(1.0)	(0.73)	(0.11)	(9.82)	(0.5)	(0.67)	(0.27)	(0.22)	(0.51)	(0.12)	(0.74)	(0.13)	(4.59)	(4.64)	(0.25)	(0.11)
Yerusham	<i>I. petrana</i>	6.8	6.6	0.98	44.4	3.4	4.9	1.04	1.0	1.06	0.32	2.7	0.7	10	24.6	0.59	0.29
		(0.9)	(0.73)	(0.08)	(10.41)	(0.57)	(0.77)	(0.25)	(0.15)	(0.37)	(0.1)	(0.56)	(0.13)	(3.22)	(4.23)	(0.13)	(0.07)

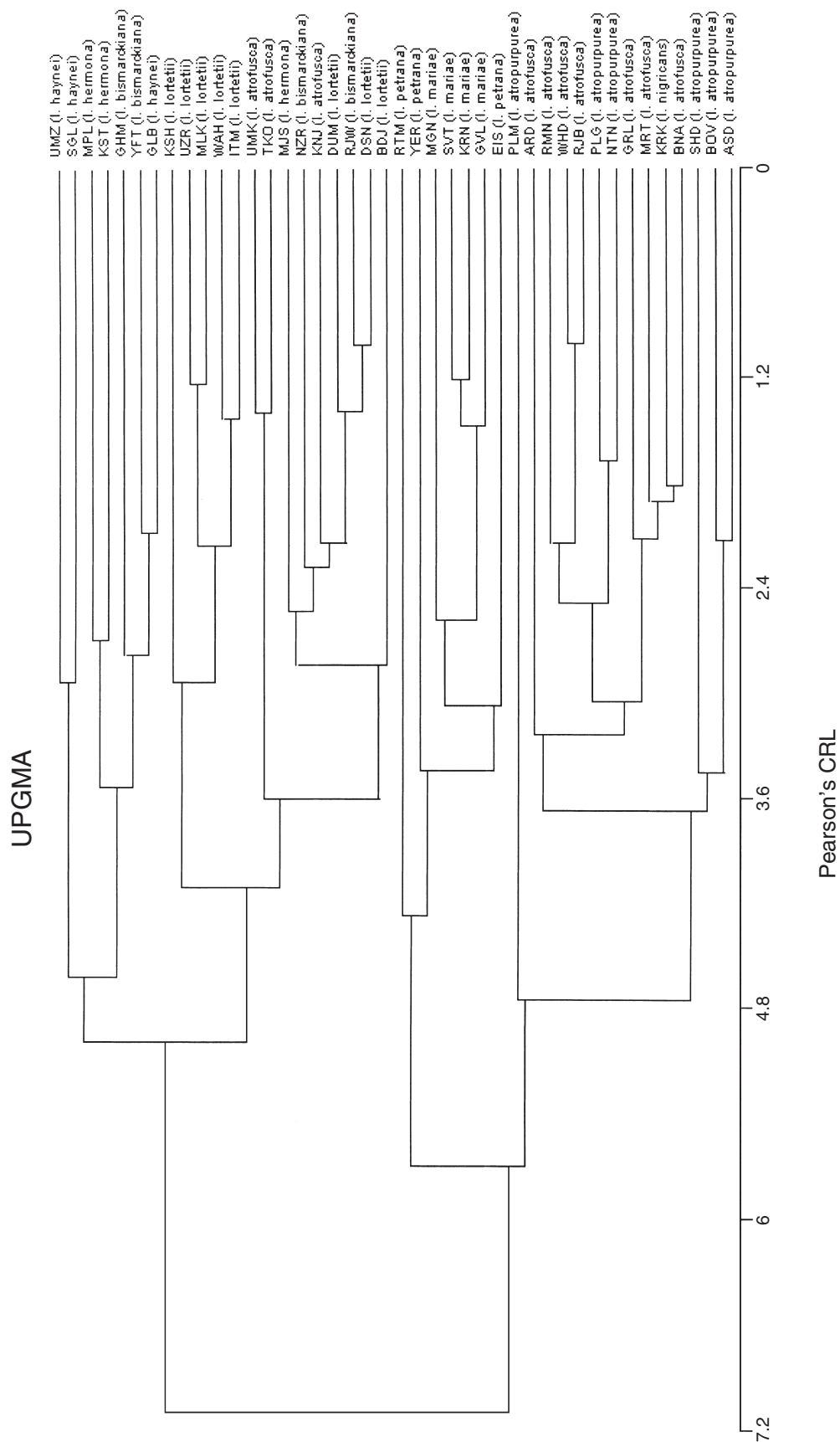


Figure 1. UPGMA dendrogram based on Pearson's Coefficient of Racial Likelihood among *Oncocyclus iris* populations in the southern Levant. Populations are represented by their code (see Table 1).

includes the dark-coloured populations of both *I. haynei* (Um-Zuka, south Golan and Gilboa) and *I. atrofusca* (Tekoa, Um-Keiss and Kubet-Najme). Most of the populations of *I. lortetii* form a somewhat distinct cluster within this 'light-coloured cluster' despite their sympatric distribution with *I. bismarckiana* in the Upper Galilee.

The two main clusters identified in the CA differed significantly for all characters except the ratios 'patch area/fall width' and 'flower/stem height' (Table 4). Within the 'dark-coloured cluster', the subcluster of *I. petrana* and *I. mariae* differed from the other dark-coloured populations in all characters except 'fall width', 'signal patch length' and the ratio 'flower diameter/height' (Table 5). *Iris petrana* and *I. mariae* only differed in 'signal patch width' (mean diff. = 0.2 cm; $P = 0.005$), 'leaf arch' (mean diff. = -0.51; $P = 0.024$) and the ratio 'flower height/diameter' (mean diff. = 0.1; $P = 0.039$).

Principal Coordinate Analysis (PCO) explained 67.7% and 14.5% of the total phenotypic variance along the 1st and 2nd axes, respectively, although it failed to identify two separate groups, as in the CA (Fig. 2). Instead, a major group comprising most of the light-coloured populations and part of the dark-coloured populations was formed. Similar to the CA, a slightly distinct group was formed by populations of *I. petrana*-*I. mariae* populations, while those of *I. lortetii* were not as clearly separated as in the CA. Two populations of the dark-coloured *I. haynei* (Gilboa,

Um-Zuka), together with one population of each the light-coloured *I. hermona* (Mapalim) and *I. bismarckiana* (Yiftah) were slightly separated from the main cluster, while the remaining *I. haynei* population (south Golan) unexpectedly stands alone when compared with the CA results. Thus, while in the CA all populations of *I. haynei* grouped with the light-coloured populations, in the PCO analysis they were separated from most of the populations, including other dark-coloured populations (i.e. Um-Keiss, Tekoa and Kubet-Najme of *I. atrofusca*) that were grouped with them in the same UPGMA cluster. However, a subsequent MANOVA revealed no significant differences between populations of *I. haynei* and *I. atrofusca* ($P = 0.213$).

For the light-coloured populations, Pearson's CRL was not significantly correlated with geographical distance (Spearman's rho = 0.06; $N = 105$; $P = 0.54$), whereas a significant relationship was found for the dark-coloured populations (Spearman's rho = 0.32; $N = 351$; $P = 0.001$).

MORPHOLOGICAL VARIATION ALONG THE NORTH-SOUTH ARIDITY GRADIENT

Most of the characters measured in the 12 populations occurring along the North-South aridity gradient were significantly associated with latitude (Fig. 3, Table 6). Only 'stem gap' and the ratio 'flower/stem height' were not significantly associated with latitude.

Table 4. Summary of MANOVA pairwise comparisons between two clusters revealed in the CA (Fig. 1), for all characters. Cluster 1 includes populations of all the light-coloured taxa together with *I. haynei* and few *I. atrofusca* populations. Cluster 2 includes all of the remaining dark-coloured populations. *Significant difference ($P < 0.05$) between clusters

Character	Cluster 1 mean value	Cluster 2 mean value	Mean diff. (cl. 1-cl. 2)	SE	<i>P</i>
Flower height (cm)	10.4	7.6	2.73*	0.309	$P < 0.001$
Flower diameter (cm)	8.5	6.8	1.76*	0.237	$P < 0.001$
Flower diameter/height	0.83	0.9	-0.06*	0.024	$P = 0.009$
Flower surface (cm ²)	90.2	52.8	37.3*	4.33	$P < 0.001$
Fall width (cm)	5.4	3.6	1.84*	0.188	$P < 0.001$
Standard width (cm)	7.2	5.2	1.97*	0.243	$P < 0.001$
Signal patch length (cm)	1.4	1.2	0.24*	0.058	$P < 0.001$
Signal patch width (cm)	1.5	0.8	0.24*	0.064	$P < 0.001$
Signal patch surface (cm ²)	2.3	1.6	0.72*	0.164	$P < 0.001$
Patch surface/fall width	0.43	0.44	-0.007	0.038	$P = 0.84$
Leaf arch (see Table 2)	1.3	1.9	-0.56*	0.150	$P = 0.001$
Leaf width (cm)	1.5	0.8	0.66*	0.070	$P < 0.001$
Leaf height (cm)	28.7	16.3	12.3*	2.11	$P < 0.001$
Stem height (cm)	33.1	24.8	8.3*	2.51	$P = 0.002$
Stem gap (cm)	0.13	0.34	-0.21*	0.065	$P = 0.002$
Flower/stem height	0.34	0.33	0.009	0.025	$P = 0.7$

Table 5. Summary of MANOVA pairwise comparisons between the majority of dark-coloured populations (cluster 1) and the subcluster of *I. petrana*–*I. mariae* (cluster 2), as revealed in CA for all characters. *Significant difference ($P < 0.05$) between clusters

Character	Cluster 1 mean value	Cluster 2 mean value	Mean diff. (cl. 1–cl. 2)	SE	<i>P</i>
Flower height (cm)	8.0	7.0	0.98*	0.301	$P = 0.004$
Flower diameter (cm)	7.0	6.3	0.75*	0.189	$P = 0.001$
Flower diameter/height	0.89	0.91	0.01	0.031	$P = 0.53$
Flower surface (cm ²)	57.0	45.0	12.0*	3.02	$P = 0.001$
Fall width (cm)	3.6	3.4	0.19	0.141	$P = 0.19$
Standard width (cm)	5.5	4.6	0.88*	0.202	$P < 0.001$
Signal patch length (cm)	1.2	1.1	0.09	0.057	$P = 0.11$
Signal patch width (cm)	1.3	1.1	0.18*	0.061	$P = 0.006$
Signal patch surface (cm ²)	1.7	1.3	0.35*	0.124	$P = 0.011$
Patch surface/fall width	0.47	0.39	0.07*	0.033	$P = 0.03$
Leaf arch (see Table 2)	1.5	2.6	–1.14*	0.131	$P < 0.001$
Leaf width (cm)	0.95	0.63	0.32*	0.075	$P = 0.001$
Leaf height (cm)	20.6	8.4	12.3*	1.89	$P < 0.001$
Stem height (cm)	27.6	19.6	8.0*	2.45	$P = 0.004$
Stem gap (cm)	0.22	0.55	–0.33*	0.079	$P = 0.001$
Flower/Stem height	0.30	0.37	–0.07*	0.032	$P = 0.037$

DISCUSSION

CLINAL VARIATION ALONG THE NORTH-SOUTH ARIDITY GRADIENT

The results in Figure 3 show directional change in most of the morphological characters along the north-south aridity gradient of Israel. This suggests that natural selection, rather than random processes, plays a dominant role in shaping these characters (Endler, 1977; Davis & Gilmartin, 1985), thus likely representing an adaptation of the *Oncocyclus* species to this environmental gradient in the southern Levant. Similar phenotypic gradients were also found in other plant and animal groups of this region (Endler, 1977; Nevo, 1988).

Shmida *et al.* (1986) suggested that a decrease in size and organ dimensions is a general rule for plants distributed along a climatic gradient towards the desert. We found that along the gradient, flower traits as well as stem and leaf size generally decrease towards the south (Fig. 3). This could be an adaptation to aridity, presumably for reasons of reducing water loss through reduction of the area exposed to radiation (Shmida *et al.*, 1986).

The ratio 'flower diameter : flower height' has been used as a diagnostic trait for differentiating *I. haynei* and *I. atrofusca*. According to Feinbrun-Dothan (1986), flower diameter is smaller than flower height in *I. haynei* but similar to flower height in *I. atrofusca*. Our results, however, show that this ratio changes continuously along the gradient. Northern populations

exhibit a low ratio (<1), and in southern populations the average value is nearly one (Fig. 3). We suggest that this ratio is not critical in separating *I. haynei* and *I. atrofusca*. A decrease of this ratio and, hence, of flower surface towards the south suggests that natural selection favours different flower dimensions along the gradient. The trend of smaller flower size in more arid habitats might reflect pollinator-mediated selection (Shmida & Ivri, 1996), or might serve as an adaptive mechanism for reducing water loss (see above).

The observed decrease of overall vegetative biomass in *Oncocyclus* irises might be a response to the increase of radiation towards the desert (Wanli, 1996; Wanli & Zhangcheng, 1998). Leaf falcation has been considered by various authors to be a diagnostic character for some *Oncocyclus* species (Dinsmore, 1934; Feinbrun-Dothan, 1986; Mathew, 1989; Rix, 1997), although Dykes (1913) had already emphasized the unreliability of this trait. An increase of leaf falcation and an associated decrease of leaf height towards the desert, as found in the present study, has also been recorded in other geophytes in Israel (Fragman & Shmida, 1995). Our field observations suggest that variation in leaf falcation also depends on the microhabitat. In shady, more favourable microhabitats, leaves tend to be straighter, while in dry exposed microhabitats they are more falcate. Leaf height seems to show a similar tendency. Thus our impression is that the importance of leaf falcation as a diagnostic character has been overemphasized in *Oncocyclus* taxonomy.

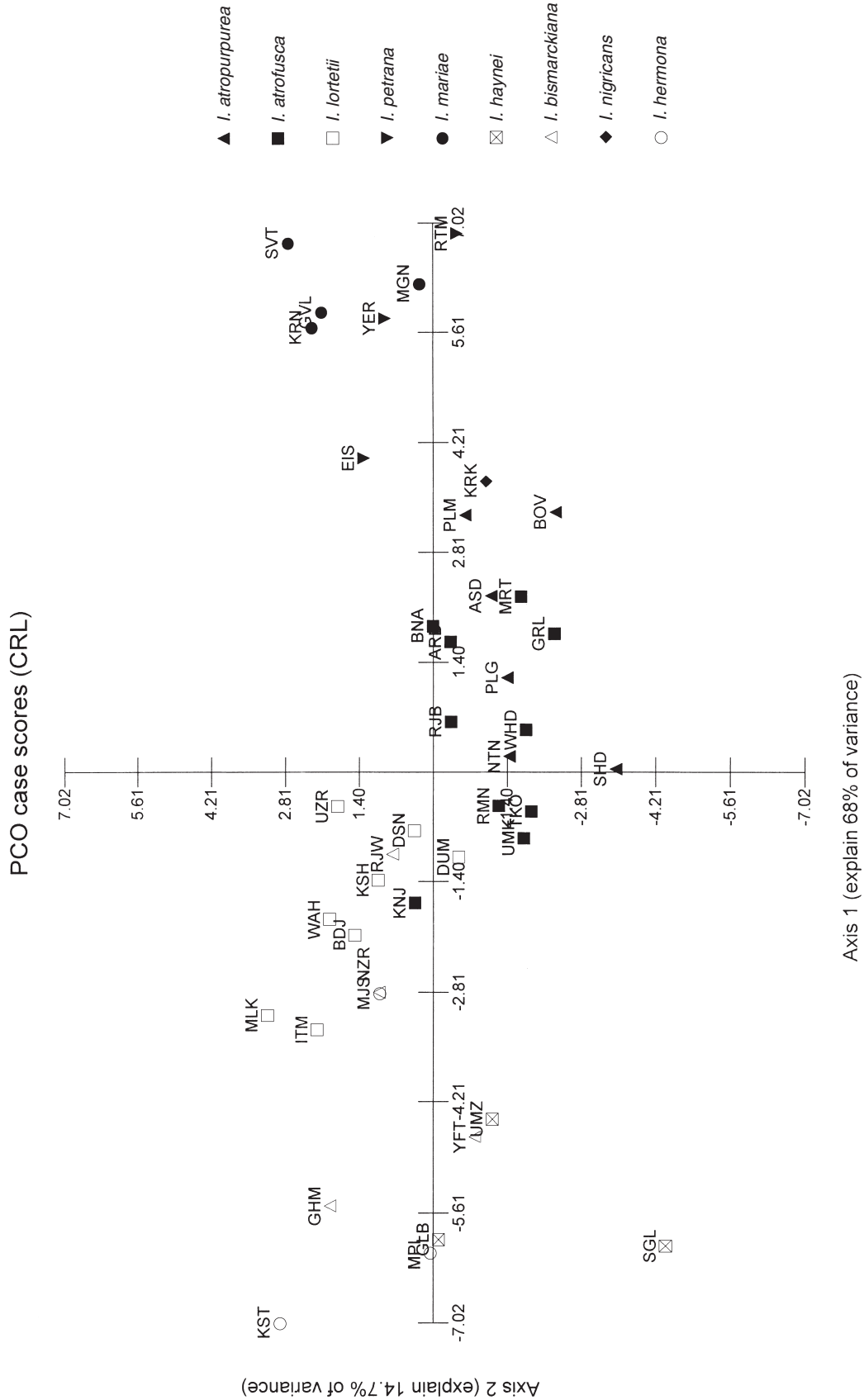


Figure 2. Principal Coordinate Analysis based on Pearson's Coefficient of Racial Likelihood among *Oncocycclus* iris populations in the southern Levant. Note that populations of the dark-/light-coloured taxa are indicated by dark and open symbols, respectively. Populations are represented by their code (see Table 1).

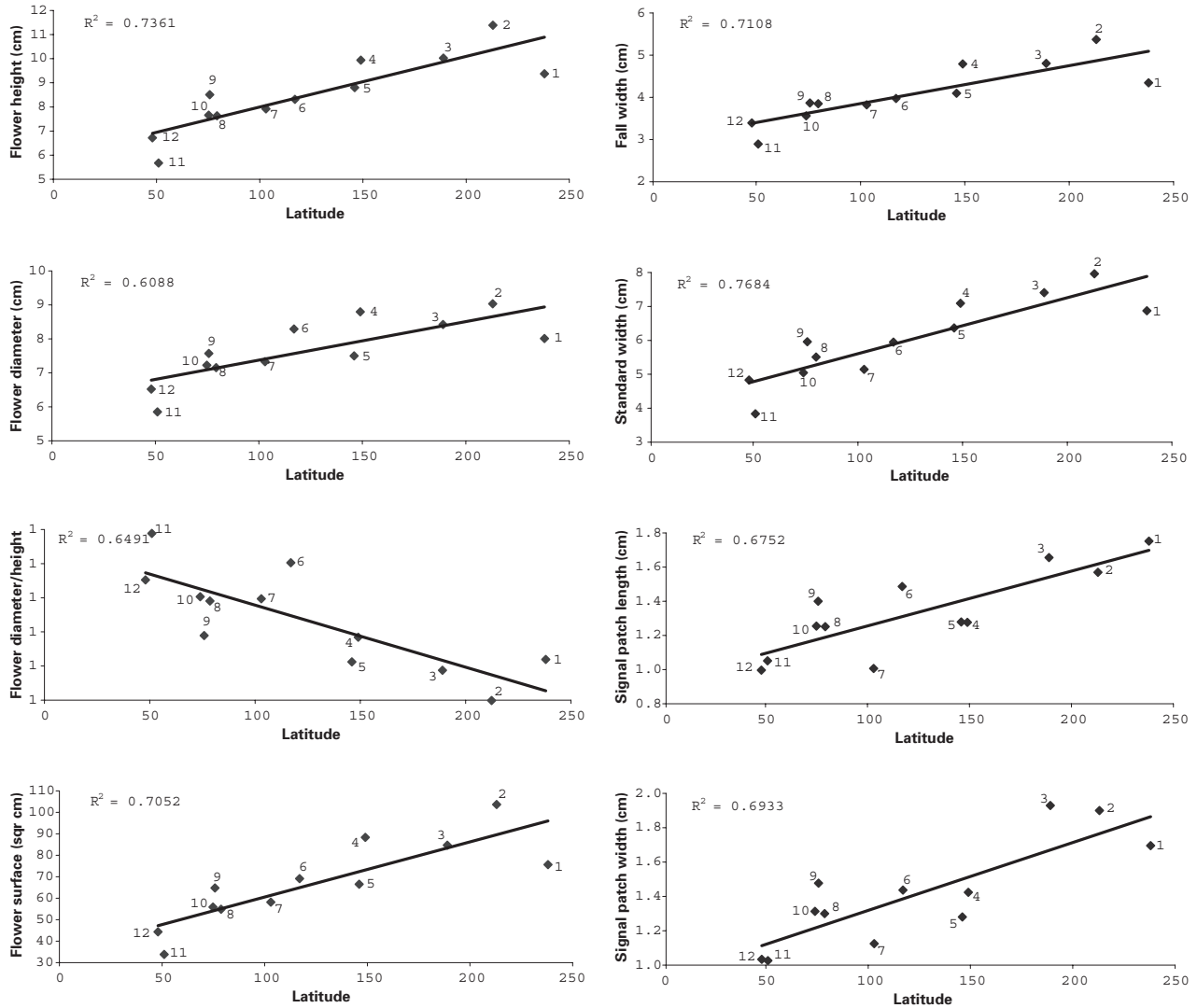


Figure 3. Population mean values of characters plotted against the latitude of locations along the north-south gradient in Israel. Latitude is according to the Israel map grid, but see Table 1 for coordinates according to the international system. Population numbers are ordered from north to south: 1. South Golan; 2. Gilboa; 3. Um-Zuka; 4. Kubet-Najme; 5. Rimonim; 6. Tekoa; 7. Bani-Naim; 8. Goral; 9. Tel Arad; 10. Mar'it; 11. Rotem plain; 12. Yeruham.

Leaf width was found in the past to be affected by local conditions (Dykes, 1913; Davis & Jury, 1990). Along the north-south gradient, the *I. atrofusca* population at Tekoa is an exception by having wider leaves than would be expected on the basis of the regression analysis (see Table 3 and 'leaf width' graph in Fig. 3). All the other characters of this population fit their expected values along the gradient (Fig. 3). The exceptionally broad leaves of the Tekoa population are probably due to a key difference in their local habitat conditions, i.e. cliff fissures, which characteristically have greater water availability because of the greater runoff received (Danin, 1999).

TAXONOMIC AND EVOLUTIONARY IMPLICATIONS

The main taxonomic conclusion arising from the morphometric analysis is that only a few discrete groups are recognizable among the *Oncocylus* irises of the southern Levant, not considering their overall differentiation in floral colour ('light' vs. 'dark'). Most of the suggested diagnostic characters are continuously distributed among populations and probably adapted to local environmental conditions to some extent, as exemplified by the chosen populations along the north-south gradient (see above). The observed correlation between morphological (CRL) and

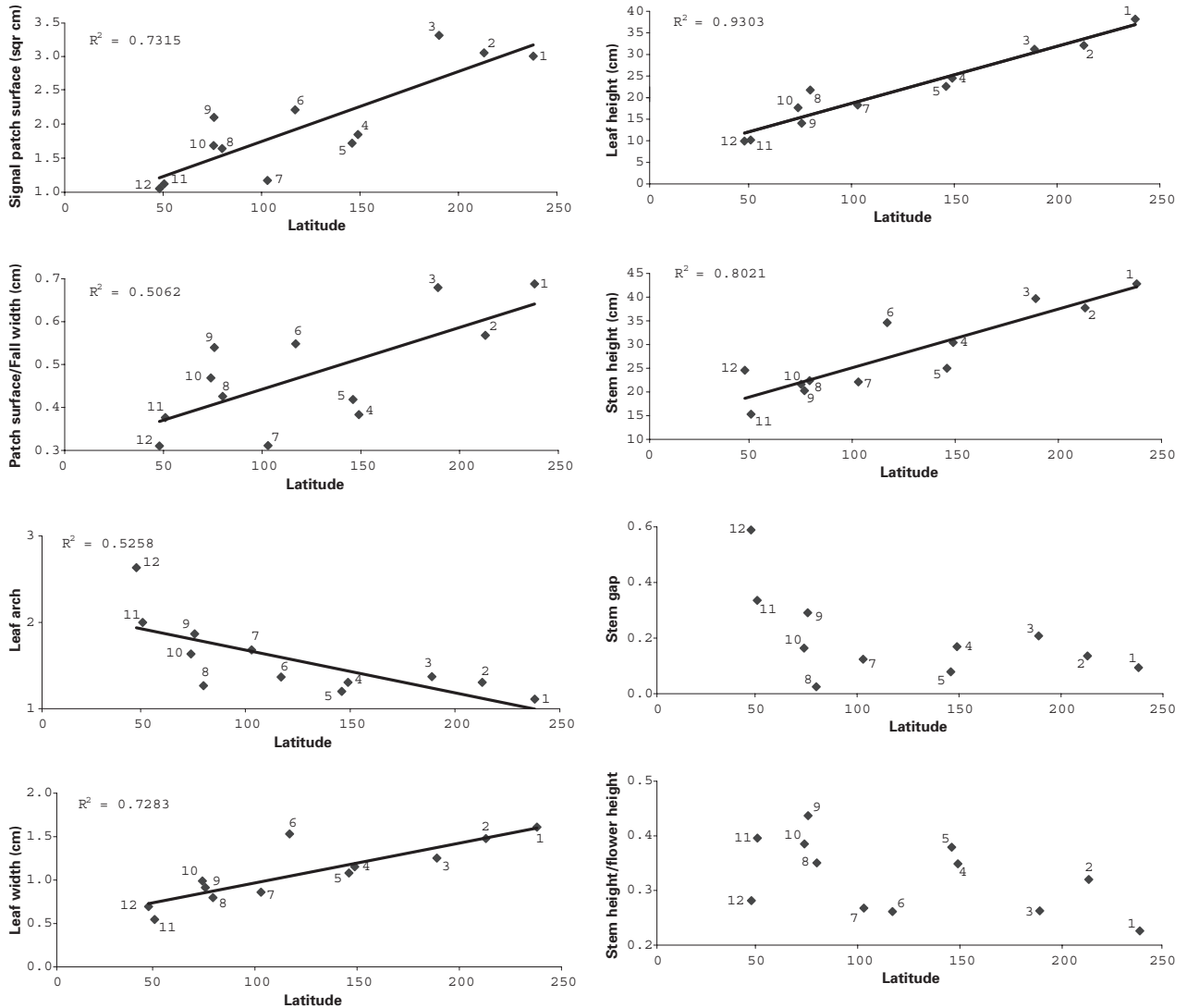


Figure 3. Continued.

geographical distance in the entire group of dark-coloured populations is also suggestive of restricted dispersal in the group, i.e. gradual dispersal of plants from the source area and simultaneous adaptation to local conditions.

Dykes (1913) claimed that some (or most) of the dark-coloured *Oncocyclus* species described at Kew by Baker or others at the end of the 19th century were cultivated forms. These plants, of unknown origin, were brought by the assistants of Messrs Dammann (the main commercial traders in irises), who 'seem to have been in the habit of setting up for themselves and then importing plants from the same neighbourhood' (Dykes, 1913: 122). The 'iris-mania' at the end of the 19th century resulted in ambiguously labelled origins

of plants from the southern Levant, which were cultivated in Europe and classified as 'species' without referring to the natural entities and the wide range of variation observed in nature. Some of the *Oncocyclus* species in the southern Levant were regarded as microspecies or doubtful taxa (Dinsmore, 1934; Davis, 1946), but nevertheless included in floras (Feinbrun-Dothan, 1986).

With regard to the dark-coloured populations, only two groups are clearly recognizable from the results of the CA: the *I. petrana-I. mariae* subcluster and all the remaining populations, with the exception of *I. haynei* and three populations of *I. atrofusca*, which were assigned to the 'light-coloured' cluster (Fig. 1). In the PCO these 'deviant' *I. atrofusca* popu-

Table 6. Summary of regression models for morphological characters against latitude. *F*-values and significance levels are based on a one-way ANOVA

No.	Character	R ²	<i>F</i>	<i>P</i>
1	Flower height	0.736	27.8	<i>P</i> < 0.001
2	Flower diameter	0.609	15.5	<i>P</i> = 0.003
3	Flower diameter/height	0.649	18.4	<i>P</i> = 0.002
4	Flower surface	0.705	23.9	<i>P</i> = 0.001
5	Fall width	0.711	24.5	<i>P</i> = 0.001
6	Standard width	0.768	33.1	<i>P</i> < 0.001
7	Signal patch length	0.675	20.7	<i>P</i> = 0.001
8	Signal patch width	0.693	22.6	<i>P</i> = 0.001
9	Signal patch surface	0.732	27.2	<i>P</i> < 0.001
10	Patch surface/fall width	0.506	10.2	<i>P</i> = 0.009
11	Leaf arch	0.526	11.0	<i>P</i> = 0.008
12	Leaf width	0.728	26.8	<i>P</i> < 0.001
13	Leaf height	0.930	120.0	<i>P</i> < 0.001
14	Stem height	0.802	40.5	<i>P</i> < 0.001
15	Stem gap	0.261	3.1	<i>P</i> = 0.1
16	Flower/Stem height	0.260	3.5	<i>P</i> = 0.09

lations grouped together with the majority, whereas the *I. haynei* populations still formed a separate (albeit scattered) group, with clear affinities towards the light-coloured populations of *I. hermona* and *I. bismarckiana* (Fig. 2). Given that *I. haynei* and these light-coloured taxa have a northern distribution, it seems feasible that their morphological similarities reflect an adaptive response to shared selective pressures in similar (i.e. northern) environments rather than common ancestry. The overall conclusion is that only two groups are recognizable among the dark-coloured populations: the *I. petrana*-*I. mariae* subcluster and the others. Most of the characters that differentiate the subcluster accord with their location along the north-south gradient (Fig. 3). This raises doubts concerning the separate clustering of *I. petrana*-*I. mariae* in both the CA and PCO, unless the notion of a step cline (*sensu* Endler, 1977) is invoked.

I. mariae populations are additionally distinguished by the dark purple coloration of the hairs within the pollination tunnel. In general, these vary between white, cream and yellow within the dark-coloured group. Also leaf falcation (character 'leaf arch') is much more convex in *I. mariae*, and thus appears as a reliable diagnostic character for this taxon (Feinbrun-Dothan, 1986; Mathew, 1989; Rix, 1997). Hair colours and leaf falcation therefore support a separation of *I. mariae* from *I. petrana* and the remainder of the dark-coloured *Oncocylus* irises in the southern Levant.

With regard to the light-coloured populations, no clear pattern could be detected in either the CA or the PCO analysis, except that five out of seven populations of *I. lortetii*, grouped into a subcluster. Its distinct flower colours might further support this slight morphometrical separation of *I. lortetii* from the other light-coloured populations. *Iris bismarckiana* and *I. hermona* flowers are dotted heavily with brown-purple spots on the fall and the hairs within the pollination tunnel are dark purple, while in *I. lortetii* the spots are small and fine, pink or light brown, and the hairs are in a wide range of light colours. Overall, this would argue for taxonomic separation of *I. lortetii* from the other light-coloured populations in the southern Levant.

We conclude that due to the continuous morphological changes, alongside their complete interfertility (Avishai, 1977; Avishai & Zohary, 1980), the *Oncocylus* populations in the southern Levant do not fit properly into the previously established taxa. In our results most of the diagnostic characters were unreliable, except for the colours of the flower. Thus, a few complexes are recognizable:

1 *I. maria*-*I. petrana*, with an emphasis on the unique characters of hair colour in the former, suggesting a divergence of the western Negev populations.

2 *I. atrofusca*-*I. atropurpurea*, which are similar in morphology and grouped together in the CA and PCO, in spite of their disjunct distribution along the central mountain range and the coastal plain, respectively. Such similarity might reflect common ancestry or parallel evolution due to similar environmental conditions.

3 *I. bismarckiana*/*I. hermona*-*I. lortetii*, with an emphasis on the latter's slight separation in the CA and its differing floral colours.

4 *I. haynei*, alongside with few populations of *I. atrofusca* (according to the CA; Fig. 1), with affinities to the third, light-coloured group. However, similar to its clear separation from the majority of *I. atrofusca* populations in the CA, the PCO identified *I. haynei* as a divergent and highly variable taxon. On the other hand, regarding the gradient regressions, there was no evidence of a 'step cline' for most of the characters analysed (Fig. 3) and a MANOVA failed to distinguish the two taxa. The phenotypic and genetic relationships among *I. haynei* and *I. atrofusca* are more fully discussed elsewhere (Arafeh *et al.*, 2002).

In summary, the morphometric study of the *Oncocylus* irises revealed more complicated relationships between taxa than suggested by current taxonomy. The results of the study reflect the special evolutionary state of the *Oncocylus* irises in the southern Levant as a plant group in the course of speciation.

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