Species concepts and ecogeographical divergence of *Oncocyclus* irises

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ABSTRACT

Several species concepts (SC) have been suggested as ways to view species, most of them based on Mayr’s Biological SC. Recent research has raised the debate on the application of the species concepts to *Oncocyclus* irises. All the *Oncocyclus* species are able to produce viable progenies when crossed, thus, according to the Biological SC, they are a single biological species. Quantitative morphological characters are continuous among populations and also correlate with environmental conditions, preventing species delimitation according to Phenetic and Ecological SC. Genetic studies revealed high genetic diversity within the populations, thus, obscure delimitation by Phylogenetic SC. Pollination of the *Oncocyclus* irises is not species-specific, yet no transitional forms exist on the rare occasions of sympatric/parapatric distribution, roughly supporting delimitation according to the Recognition SC. The conclusion is that *Oncocyclus* populations do not clearly fit into species boundaries according to the relevant species concepts.

*Oncocyclus* irises are distributed along an Ecogeographical Speciation Cline that could lead to one of three patterns of divergence, that is, discrete, ecotonal, or continuous, along the spatial dimension. Nonetheless, the exact variation pattern is not clear because of the patchy distribution. The taxonomic status of the *Oncocyclus* irises is viewed in light of the evolutionary processes in this highly variable group.

INTRODUCTION: SPECIES CONCEPTS—THEORY AND PRACTICE

The term “species” was derived from the Greek Aristotelian system of a natural logic, where “species” is the particular (=specific) that differs from the others in the general (=genus) by the “differential” (Cain, 1958). Several species concepts (SC) have been suggested as ways to view species (Luckow, 1995; Mallet, 1995; Claridge et al., 1997; Goldstein and DeSalle, 2000; Mallet, 2001). The most commonly accepted definition is the Biological SC (Mayr, 1942), which considers a species to be an isolated reproductive group of organisms. From this original definition, several other concepts have been developed (Luckow, 1995; Claridge et al., 1997; Mayden, 1997; Levin, 2000). Recent research on the irises (Young, 1998; Reeves et al., 2001a, 2001b; Sapir et al. 2001a, 2001b, 2002; Tillie et al., 2001) has raised the debate on the application of the species concept to plants in general and to *Oncocyclus* irises in particular.

All the species concepts mentioned above consider the species as an evolutionary unit that (i) is able to undergo speciation; (ii) occupies an adaptive peak due to a genetic combination; and (iii) performs isolation mechanisms and is independent in its speciation avenues (Waddington, 1957; Levin, 1979). Thus, species can be viewed either as current participants in the ongoing evolutionary process of speciation, or as the terminal...

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end of past processes (Luckow, 1995). The diverse species concepts can be categorized into two groups (Goldstein and De Salle, 2000; Levin, 2000):

1. Functional concepts, which emphasize the mechanisms for maintaining the persistence of the species (e.g., Biological SC, Recognition SC, and Ecological SC). These concepts consider the role of speciation mechanisms as the force that prevents hybridizations (present processes).

2. Theoretical concepts, which emphasize the evolutionary process and origin (e.g., Evolutionary SC, Phylogenetic SC, and Phenetic SC). These concepts view species as the results of genetic differentiation (past processes).

The Biological SC has been widely accepted among animal systematists, yet several characteristics of plant populations render it more difficult to apply in the context of plants. Phenomena such as hybridization, introgression, autoploidy, vegetative reproduction, and ecological niche shifting, just to name a few, are problematic when applying species concepts to plants (Levin, 1979, 2000).

An alternative way to tackle the species concept is to approach it from the anthropocentric angle. As species delimitation may be a convenient human-based way of organizing diversity into distinctive packages (Levin, 2000), it is important to make the task of identification feasible. The process of identification of species should be made “as practical and functional as possible” (Heywood, 1998). The Phenetic SC suggests considering phenetic or genetic gaps between species as a way of categorization (Michener, 1970; Mallet, 1995). Qualitative differentiation between species, based on natural gaps or discontinuity of character values, provides a practical approach for handling the taxonomy of natural organisms. When facing a field with plants, characters with discrete ranges of values are best suited for assigning the taxonomic names to the different groups and hence making species a feasible feature to handle.

It is important to emphasize that species delimitation generally applies in taxonomy when there are no overlapping values (quantitative) or transitional state(s) (qualitative) between the different taxa. The challenge is to decide whether the distribution of the values represents two distinct groups with clear borders or they are the centroid values that represent the central tendency measurement (average, median, or mode) of the value distribution (Fig. 1). The problem is increased when there is an overlap between the distributions of the character values. It is usually solved by numerical taxonomy and statistics.

When two populations are allopatric, any overlap in character values does not hinder the identification of each population as a species. In sympatric populations, the same overlap can now be interpreted as a single species with morphotypes (dashed lines in Fig. 1), or it can represent two species that are separated in different ecological niches. “Typical” or “representative” specimens that differ significantly and seem to belong to different species, may derive from a large, highly variable population.

We suggest applying a practical approach to species delimitation in plants. Irrespective of which species concept is used, species may be defined as a group of organisms that share similar characters, or character range, and in which a clear gap or discontinuity exists between them and other groups. Gaps can be found in any of the methods used, e.g., morphologically discrete value ranges, reproductive isolation in the wild, or ecological divergence. The only requirement is recognizing practical and functional units, regardless of the procedure used. Of course, a single apomorphy (morphological or genetic or any other) is not enough to recognize a separate species (and detailed techniques will find apomorphies or uniqueness for almost any individual.

![Fig. 1. Two ways of species delimitation based on differences in character's values. Values may represent two different groups with clear limits (1 and 2), or they may be the centroid values that represent the central tendency measurement (average, median, or mode) of the value distribution (2 and 3). The overlap between 2 and 3 in character values may be an interpretation (dashed lines) in sympatric species.](image-url)
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(Mallet, 1995)), thus, a set of characters should be chosen (see Sneath and Sokal, 1973 for the requisite number of characters).

Using characters that can be measured in the field has the advantage of providing a tool for diversity measurement in-situ. The practical use of SC is valid mainly at the phenotypic level, but may be strengthened by the genotype level or by the mating system. Genetic differentiation alone, not accompanied by phenotypic outcome, may form genetic races that do not play a part in the speciation process until reproductive isolation is attained (Endler, 1977; Grant, 1981; Futuyma, 1986; Niklas, 1997; Maynard Smith, 1998; Levin, 2000). Phylogeographic patterns of populations within a morphospecies may give an insight into the evolutionary process (Templeton, 1998), but may not provide a framework for species delimitation. Genetic markers on the DNA sequences, as well as biochemical or physiological differences, are impractical to differentiate species outside the laboratory, unless detectable characters accompany them. In other words, genotype can contribute to species delimitation only when a phenotypic character does.

**SPECIES CONCEPT APPLICATIONS IN ONCOCYCLUS IRISES**

The section Oncocyclus in the genus Iris is defined mainly by the single flower on the stem and by the aril appendix on the seed (Mathew, 1989; Rix, 1997; Sapir et al., 2002). The section comprises 33 entities or “taxa”, 10 of which grow in Israel and Jordan; the rest are distributed from Lebanon and Syria to Turkey and Iran (Avishai and Zohary, 1980; Rix, 1997). Here we evaluate the taxonomic status of the current taxa in the section Oncocyclus in light of the existing species concepts.

**Oncocyclus irises under Biological SC**

The breeding system in Oncocyclus irises is obligatory cross-fertilization, with self-incompatibility. The natural fruit set obtained from cross-fertilization in the Oncocyclus irises is 30% to 40%, whereas insect-proof covered flowers bore no fruits (Y. Sapir, unpublished data). The number of chromosomes in all Oncocyclus taxa is 2n = 20, all similar in shape and size, whereas in the nearest section Regelia, chromosome number is 2n = 22 (Avishai and Zohary, 1977). Biologically, all the Oncocyclus species can interbreed, and produce vital progenies, with hybrids (F1 and F2 generations) that also are fertile (Avishai and Zohary, 1980). The criterion of free gene-flow is met, thus according to the Biological SC (Mayr, 1942), all Oncocyclus irises may be considered as a single biological species (Avishai and Zohary, 1980).

**Oncocyclus irises under Phenetic SC**

In Oncocyclus irises, quantitative characters for species delimitation include, for example, stem height, leaf width, and the ratio between flower diameter and flower height. An example is the difference between Iris haynei Baker, in which the ratio between flower height and flower diameter is greater than 1, compared with Iris atrofusca Baker, in which the flower’s diameter is equal to the flower height (Feinbrun-Dothan, 1986). Qualitative characters include colors of the petals and hairs and rhizome form (Dinsmore, 1934; Feinbrun-Dothan, 1986; Mathew 1989; Rix, 1997). An example is the light-colored petals of Iris lortetii W. Barbey as compared to the dark-colored petals of Iris atrofusca (Dinsmore, 1934; Feinbrun-Dothan, 1986; Mathew, 1989; Rix, 1997). Qualitative characters of colors form detectable gaps between groups within the Oncocyclus irises, but only four morphs are recognized in Israel (Sapir et al., 2002). Three of these morphs are also in concordance with the aggregates within the section, namely Iberica, Lortetii, and Haynei (Avishai and Zohary, 1980). Iris mariae W. Barbey is considered part of the Haynei aggregate, but differs in the colors of the hairs in the pollination tunnel (Sapir et al., 2002). On the other hand, most of the quantitative characters in the Oncocyclus irises are continuous between species, while gaps, if any, are small and not clear-cut (Sapir et al., 2002). For example, measured values of diagnostic characters, such as leaf width, stem height, and flower shape, overlap across species (Fig. 2).

**Oncocyclus irises under Ecological and Phylogenetic SC**

The distribution of morphological characters of the Oncocyclus irises in Israel was found to be correlated with latitude in populations of three taxa (Iris haynei, L. atrofusca, and L. petrana Dinsmore), that are distributed along the geo-climatological North–South gradient in Israel (Sapir et al., 2001b; Arafeth et al., 2002). Applying the Ecological SC (van Valen, 1976) revealed an ambiguity with respect to these three species. On the one hand, the continuous morphological/genetic and geographical gradients create no discrete pattern. On the other hand, each population may be at a morphological adaptive peak for the local conditions. These clusters of populations could be viewed as separate ecological species or ecotypes, while the change along the gradient might be actually in steps through ecotonal zones. While an ecotype is a genetic entity reflecting environmental selection (Turesson, 1922), an ecotone is the geographical boundary between adjacent ecosystems (or biotopes) where a (gradual) change in the species'
character forms a "step" in the character's distribution (Endler, 1977).

The problem arises whether differences revealed between sampling locations along a gradient are reflecting differences between discrete groups or are due to ecotonal change (Fig. 3). Variability is expected whenever the ecological conditions and the selection pressures change gradually along a spatial scale (Boyko, 1947; Endler, 1977), thus creating an Ecogeographical Speciation Cline. The Ecogeographical Cline may lead to each of the three patterns, i.e., discrete, ecotonal, or continuous, along the spatial dimension.

Spatial distribution of the Oncocycles populations in Israel and Jordan is patchy, i.e., between each two loca-

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**Fig. 2.** Normal frequency distribution of (A) leaf width, (B) stem height, and (C) the ratio flower diameter/flower height, in eight Iris species.
tions with relatively dense populations there are distances of up to thirty kilometers (Y. Sapir and A. Shmida, unpublished data), but populations are usually clustered geographically. The continuous distribution of characters in correlation with geographical scale (Sapir et al., 2001b; Arafah et al., 2002) suggests that the Oncocyclus populations form an Ecogeographical Speciation Cline.

Genetic study of populations of two relatively widely distributed species (I. hayniei and I. atrofusca) in Israel and the West Bank revealed high levels of RAPD diversity (Arafah et al., 2002). Most population pairs were significantly different, based on marker frequencies (Arafah et al., 2002), implying that according to the Phylogenetic SC (Nixon and Wheeler, 1990), each population may be considered a separate taxon (but not necessarily a species).

**Oncocyclus irises under Recognition SC**

Specification of pollinator–flower relationships is one of the isolating mechanisms in sympatric speciation (Grant, 1981; Waser et al., 1996; Waser, 1998; Johnson and Steiner, 2000). The pollinators of the Oncocyclus irises are male solitary bees, mainly of the genus Euceria, that spend the night within the pollination tunnels (Shmida and Ivri, 1996). Species-specific pollination does not occur in Oncocyclus Irises, as each Iris species is visited by more than one species of subfamily Eucerini (Table 1). In addition, males of the Eucerini group are also found in other flowering species, namely Acanthus syriacus Boiss., Ranunculus asiaticus L., Anemone coronaria L., and Echium spp. In spite of this nonspecificity, no hybrids were found in three rare cases of sympatric/parapatric distribution. In the Upper Galilee, I. bismarkiana and I. lortetii share the same site in Naftali Ridge (33°7'N/35°33'E); midway between Yeruham and Beer-Sheva (31°5'N/34°51'E), I. petrae and I. mariae populations grow at a distance of less than five kilometers apart; in Rajib, Jordan, I. bismarkiana is 800 meters away from I. atrofusca (32°14'N/35°41'E).

In spite of the pollinators’ ability to fly over distances between populations (Levin, 1981; Proctor et al., 1996), no intermediate transitional forms exist in those three instances. This raises the possibility of individual insects learning and imprinting a certain flower pattern, without reward difference between the different patterns (Keasar et al., 1997). In the case of the irises, it is possible that imprinting shaped the individual male’s preference, thus, sheltering occurs in only one type of flower, and no cross-pollination occurs between the two types. The Recognition SC (Paterson, 1985), which emphasizes existence of ethological pre-mating barriers, can be used for species differentiation in these instances. However, more experimental work is needed to confirm this hypothesis.

**DISCUSSION AND CONCLUSIONS**

**Species delimitation**

To summarize the evidences, Oncocyclus populations in Israel and Jordan generally do not fit clearly into species boundaries according to the relevant species concepts. Species delimitation in this group was made following herbarium sheets, representing only the “typical” form of each group, and did not consider the natural

* Sapir and Shmida / Species concept for Oncocyclus irises
Table 1

Male bee species found in Iris species. Plus (+) sign denotes the presence of at least one individual of the bee species. Undescribed bee species (new to science) are designated by, e.g., "Eucera sp. nov. Sapir1". Last row summarizes the number of bee species found in a certain Iris species. Male bees were collected within Iris flowers after sunset in the peak of the flowering season of each species in the years 1999–2001. Bee species were identified by C. O'Toole from the Hope Entomological Collections in Oxford University Museum of Natural History.

<table>
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<tr>
<th>Bee species</th>
<th>I. atropurpurea</th>
<th>I. atropurpurea</th>
<th>I. bismarckiana</th>
<th>I. haynei</th>
<th>I. hermona</th>
<th>I. lortetii</th>
<th>I. mariae</th>
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<td>Andrena ocreata (Christ)</td>
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<td>Andrena sp. aff. curiosa (Morawitz)</td>
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<td>Andrena sp. Nov. Sapir1</td>
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<td>Chalicodoma sicula (Rossi)</td>
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<td>Eucera caulebs Dours</td>
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<td>Eucera grandis (Fonscolombe)</td>
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<td>Eucera plumigera Kohl</td>
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<td>Eucera sp. aff. plumigera Kohl</td>
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<td>Eucera duplicata Dusnet</td>
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<td>Eucera sp. nov. Sapir4</td>
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<td>Eucera sp. nov. Sapir5</td>
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<td>Eucera sp. nov. Sapir6</td>
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<td>Eucera sp. nov. Sapir8</td>
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<td>Eucera sp. nov. Sapir9</td>
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<tr>
<td>Eucera sp. nov. Sapir10</td>
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<td>Total number of bee species</td>
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variation within the groups. In the Oncocyclus data set of characters examined (see above), clear borders between putative taxa may be found only in the morphological trait of floral colors, and in that case, only four taxa are noticeable with clear separation between them (Sapir et al., 2002). Otherwise, no gaps could be found between the taxa, and all other morphological, ecological, ethological, and genetic characters are insufficient for species delimitation according to all species concepts mentioned above.

Although a systematic conclusion from the findings above may suggest merging most of the Oncocyclus species in the Southern Levant into one or a few taxa, a practical approach would demand the opposite. Conservation biology of plants is based mainly on the species level (Maddock and du Plessis, 1999; Myers et al., 2000; Gardenfors et al., 2001; IUCN, 2001), but in the Oncocyclus irises, preserving only few morpho-species would not satisfy the need to preserve the evolutionary diversity (Cohen and Avishai, 2001). As it is important to conserve the actual morphological and ecological diversity (Mallet, 1995), every variant, race, or subspecies may be important.

Evolutionary trends among Oncocyclus irises: I. Towards divergence

Natural selection may lead the populations in one of two directions: Towards radiation and divergence into many entities, or towards stabilizing the present situation without producing clear separation. This is without considering a third direction of demise and extinction (Levin, 2000).

Several speciation processes might enhance the probability of divergence in the Oncocyclus irises. Correlation of morphological traits of the plants with environmental conditions (Sapir et al., 2001b) may represent local adaptations of the populations. Morphological changes along gradients were shown in other plants (Montagnes and Vitt, 1991; Steppan, 1991; Small and Fawzy, 1992; Allen et al., 1996), and the effect of the aridity gradient was shown to cause species differentiation into morphological forms, as well as genetic
diversity (Endler, 1977; Fragman and Shmida, 1995; Nevo, 1998). The pattern of Ecogeographical Speciation Cline is common among plant species in regions of environmental clines, where in some cases the centroids are considered as separate vicariant species.

The patchy distribution of the populations of Oncocyclus irises in Israel and Jordan can prevent gene flow and cause reproductive isolation de-facto between local races, which may lead to genetic isolation in the long run. On the other hand, the existence of Ecogeographical Speciation Cline without fragmentation in other plant species, suggests that Ecogeographical Speciation Cline is not the result of fragmentation. Thus, the patchy distribution of the Oncocyclus irises will not necessarily lead towards divergence.

Floral colors, which seem to be robust categorical characters, can be important to pollination (Faegry and van der Pijl, 1979; Menzel and Shmida, 1993; Proctor et al., 1996; Keasar et al., 1997). Although there is no species specificity in plant-pollinator relationships among Oncocyclus irises (see above), recognition patterns for certain colors might create preferences of the individual bee pollinator. Individual preference of the pollinator for a certain color pattern may prevent hybridization in cases of co-occurrence of two floral color forms. We conclude that adaptive differentiation of the Oncocyclus populations into discrete species, according to any of the evolutionary species concepts, is not to be rejected.

Evolutionary trends among Oncocyclus irises: II. Towards unity

The high variation found in both morphological and genetic (RAPD) traits within the Oncocyclus populations (Arafah et al., 2002; Sapir et al., 2002) may indicate lack of stabilizing selection that could decrease variation. The variation observed might be due to the relatively arid habitat of the Oncocyclus populations, which increases the microhabitat variability and, as a consequence, increases phenotypic and genotypic variability (Nevo 1998). The distances between populations (or clusters of populations) may be too large for most pollinators, but rare events of bee flight over large distances could supply the low-but-stable possibility for gene-flow between populations (Levin, 1981), hence preventing complete isolation between them. On a large scale, there is a gradual flow along a sequence of populations, although no gene flow is possible between far distant populations.

The complete picture that arises is that no clear species can be recognized within the Oncocyclus irises. Much data has been gathered that indicate the potential for divergence in the future, but there is also some data in support of stabilizing the present situation. The Ecogeographical Speciation Cline pattern of the morphology and genetics of the Oncocyclus irises, alongside the fragmented allopatric distribution, may reflect divergence in an evolutionary process, its direction still open to question.

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REFERENCES


Sapir and Shmida / Species concept for Oncocyclus irises
Maddock, A., de Plessis, M.A. 1999. Can species data only be appropriately used to conserve biodiversity? Biodiversity Conserv. 8: 603–615.


