

A RE-EVALUATION OF THE BULBOUS IRISES

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ABSTRACT - This paper examines the results of recent morphological and molecular studies on the bulbous irises. The following taxa are discussed: (1) subgenus *Scorpiris* and its relationship to the bearded irises and subgenus *Nepalensis*; (2) subgenus *Xiphium* and the *Spuriae* - *Tenuifoliae* alliance; (3) the reticulata irises and their links with the *Syriacae*.

KEY WORDS - *Iridaceae*, *Iris*, systematics, bulbs

INTRODUCTION

The precise relationships of the three bulbous groups of irises, the junos (subgenus *Scorpiris*), the reticulatas (subgenus *Hermodactyloides*) and the xiphiums (subgenus *Xiphium*), have been the subject of much discussion. They have been treated by various authors as sections or subgenera within the genus *Iris* L. Lawrence (1953) treated the reticulatas and xiphiums as separate sections, but within one subgenus. On the other hand, Rodionenko (1961, 1987) considered the bulbous irises sufficiently distinct to be placed in their own three genera (*Juno* Tratt., *Iridodictyum* Rodion. and *Xiphium* Mill. respectively). It is generally held that within the genus *Iris*, unifacial leaves and a rhizomatous habit are ancestral and that the bulbous irises, the junos and xiphiums (with bifacial leaves) and the unifacial-leaved reticulatas have developed from these forms. Bulbs are specialised buds with a truncated underground rhizome (in this case a basal plate) (Rudall, 1989): just one of the many modifications to a seasonally-dry habitat. This paper discusses the systematics of the bulbous irises in the context of preliminary molecular studies in *Iris* (see Tillie *et al.*, this volume), mainly using the classification given in Mathew (1981).

THE JUNO IRISES (SUBGENUS *SCORPIRIS*)

The juno irises form a large and distinct monophyletic group, with bulbs, fleshy persistent roots, generally reduced standards and petaloid style crests. There are exceptions to this: *Iris leptorrhiza* Vved. (as its name implies) has an ordinary, thin

root system that is entirely deciduous; preliminary molecular work (Tillie *et al.*, this volume) indicates that it is probably part of the *I. rosenbachiana* complex (the physocaulons), which include *I. nicolai* Vved.

The affinities of subgenus *Scorpiris* have always been considered obscure. Indeed, junos are unique within *Iridaceae* in having entirely bifacial leaves, even as seedlings, although these may be comparable to the bifacial sheaths of the unifacial-leaved rhizomatous *Iris* species (Rudall & Mathew, 1993). There is little doubt that this bulbous group forms part of a much larger natural assemblage of dryland or (at most) mesic irises (Group 3 of Tillie *et al.*, this volume: Fig. 2b). This group includes subgenus *Iris* (although no samples of section *Hexapogon* were available for molecular study), subgenus *Nepalensis*, the two genera *Belamcanda* Adans. and *Pardanthopsis* (Hance) Lenz (considered by many authors to be ancestral to *Iris*), and the ‘bamboo’ irises of subgenus *Limniris* section *Lophiris*, which probably should include both *I. cristata* Solander and *I. lacustris* Nuttall, although these were not sampled for molecular work. This seemingly disparate assemblage is linked by two leitmotifs: (1) a distinct dormant period for most species (although some are from winter-dry, summer-rainfall regions) with xerophytic characters expressed as deciduous leaves and an extensive or tuberous root system; (2) a well-defined ridge, a crenate or dissected crest, or a beard of sorts, from the velvety microscopic beard of *I. verna* L. (section *Limniris*, series *Vernae*) to the highly evolved ‘bee’s bum’ of *Iris paradoxa* Steven (section *Oncocylus*). Leaf anatomy adds weight to the relationships between the seemingly anomalous rhizomatous groups (Wu & Cutler, 1985). *Iris milesii* M. Foster, for example, is linked to subgenus *Nepalensis* by its internal leaf structure and fan-shaped sterile foliage.

It is still premature to suggest exactly where the junos fit in, but molecular evidence indicates that they are closely allied to the winter-dormant subgenus *Nepalensis* (in Group 3 of Tillie *et al.*, this volume: Fig. 2b). Arils are found on the seeds of some junos, as well as in subgenus *Nepalensis*, the genus *Pardanthopsis* and most of subgenus *Iris* (although not in section *Iris*). A similar mesophyll arrangement occurs in leaves of subgenera *Nepalensis* and *Scorpiris*, which differs from that of the other two bulbous subgenera (Wu & Cutler, 1985; Rudall & Mathew, 1993). There may also be a similarity between the pollen structure of the *Nepalensis* and that of certain junos (the physocaulons). Rodionenko (1961, 1987) considered the physocaulon group of junos to be more ‘primitive’; there may be a possible link between the reduced rhizomes of subgenus *Nepalensis* and the swollen stem-base characteristic of section *Physocaulon* in the junos. Molecular evidence supports the inclusion of *I. cycloglossa* Wendelbo, with its unusual and characteristic floral morphology, amongst the junos, rather than as an isolated ‘primitive’ taxon, as some have suggested (Wendelbo & Mathew, 1975). *Iris cycloglossa* has relatively large standards held above the horizontal, lacks a clearly-defined ridge on its falls, and its branched inflorescence and pollen morphology are more similar to those of bearded irises; the last two features are also shared by *I. aitchisonii* (Baker) Boiss.

THE SPURIAE-TENUIFOLIAE ALLIANCE

This grouping (Group 2 of Tillie *et al.*, this volume: Fig. 2a) contains the other two bulbous iris groups, the reticulatas (subgenus *Hermodactyloides*) and the xiphiums

(subgenus *Xiphium*). *Iris speculatrix* Hance is probably sister to an assemblage that includes the *Spuriae*, the *Tenuifoliae*, *I. foetidissima* L. and the *Syriacae* (all section *Limniris*), together with the *reticulatas* and the *xiphiums*. Plants of this group, which are all from dry or dryish habitats, exhibit a high degree of xeromorphism. Leaves of the rhizomatous species are narrow and leathery, and their rootsocks tough or wiry. Flowers are somewhat thick-textured (less so in the *reticulatas*) and similar in their relatively narrow segments, and there is often a constriction on the fall between the haft and broader blade. There is no really pronounced ridge (even on the *reticulatas* when compared with the majority of *junos*) although papillae and (exceptionally) beard-like structures are present in some species.

Previously, Rodionenko (1997) separated the Russian central Asian species *I. kolpakowskiana* Regel and the recently rediscovered *I. winkleri* Regel from the *reticulatas* and placed them in their own genus *Alatavia* Rodion. *Iris kolpakowskiana* (and by implication *I. winkleri*), which were previously tentatively associated with subgenus *Hermodactyloides*, are, on both molecular and morphological evidence, clearly related to subgenus *Xiphium* (the Spanish irises), possibly as a geographically isolated sister group, although more work is needed. They all have similar bifacial, channelled leaves (though unifacial at some stage in their development) and shell-like or membranous tunics. The apparent homology between the near-reticulate fibrous tunic of *I. kolpakowskiana* and tunics of the true *reticulatas*, as well as their comparable bulb-scale morphology, are probably expressions of their adaptation to near-identical mountains habitats: these are plants that flower primarily near melting snow. (*I. kolpakowskiana* is more often a foothills plant, although *I. winkleri* is an alpine).

Dykes (1913) and many others have commented on the remarkable similarity between flowers of the rhizomatous series *Spuriae* and the bulbous subgenus *Xiphium*. It is probable that the two evolved from a common ancestor, *Xiphium*, to occupy a more Mediterranean-type climate in the Iberian peninsular and North Africa. Both are allied to the series *Tenuifoliae* and *I. foetidissima*.

Perhaps the most fascinating link between the bulbous and rhizomatous taxa of *Iris* occurs between the bulbous subgenus *Hermodactyloides* (the *reticulatas*) and the rhizomatous series *Syriacae* (see Tillie *et al.*, this volume). One of us (TH) has raised *I. masia* Stapf ex Foster (series *Syriacae*) from seed and observed its development from a small bulb with reticulate fibres and contractile roots, to an organ with large, bulb-like terminal buds (the swollen leaf-bases), near-vertical compact rhizomes and a neck of vicious spines just below each bud. Rodionenko (1961; 1987) noted a relationship between the *Syriacae* and subgenus *Hermodactyloides*, although he was unaware of *I. pamphylica* Hedge (subgenus *Hermodactyloides*) at that time, since it was described in 1961. Not only are the flowers of *I. masia* and *I. pamphylica* alike in shape and colour, but *I. pamphylica* also has rudimentary spines (easily seen in dormant buds), and rhizome-like tissue (extensions of the basal plate area) connects the daughter-bulbs of an established clump. The two species are also linked by their pollen morphology (Mathew, 1989).

If the *reticulatas* are closely allied to the *Syriacae*, then it is possible to imagine that ancestors of the *Tenuifoliae*, with their tufted habit and vertical rhizomes, gave rise to the *Syriacae*; their leaf anatomy (Wu & Cutler, 1985) would support such a hypothesis, although the molecular data are scant.

CONCLUSIONS

The juno irises (*Scorpiris*) have evolved from the same Asian ancestors as the crested/bearded irises, and independently to the reticulatas (*Hermodactyloides*) and the xiphiums (*Xiphium*), although junos occupy roughly the same geographic range as the latter two groups combined. On the other hand, the reticulatas and xiphiums are relatively closely related within the genus *Iris*. The xiphiums (with *I. kolpakowskiana* and *I. winkleri*) are tentatively linked with the *Spuriae-Tenuifoliae* alliance, whereas the reticulatas (including *Hermodactylus* Mill., which is usually treated as a separate genus) are strongly associated with the *Syriacae*.

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