

PHYLOGENY AND CLASSIFICATION OF THE *IRIDACEAE* AND THE RELATIONSHIPS OF *IRIS*

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ABSTRACT - *Iridaceae* are a well defined family of some 1800 species and between 60 and 70 genera. Molecular studies of chloroplast DNA has confirmed the position of the family in the order Asparagales, contrary to earlier work that placed the *Iridaceae* in Liliales. The family comprises two large assemblages of species, currently regarded as subfamilies *Ixioideae* and *Iridaceae*. The relationships of the remaining seven genera, included in subfamilies *Isophysidoideae* and *Nivenioideae*, have been rendered uncertain because of the lack of congruence between molecular and morphological studies using different outgroups and/or different data sets. *Ixioideae*, the largest subfamily, comprises more than half the total species in the family. Largely African, with fair representation in Eurasia, the generic phylogeny of *Ixioideae* is poorly understood. Most genera exhibit a considerable range of floral diversity based on floral zygomorphy and the elaboration or reduction of the perianth tube. Production of floral nectar and pollination by long-tongued insects including anthophorine bees, Lepidoptera, long-proboscid flies and birds is a recurring theme but reversals to actinomorphy, often accompanied by the suppression of nectar production, has occurred in species of several genera that are pollinated by hopliine beetles. Virtually worldwide in distribution, *Iridoideae* comprise five tribes, the Australian *Diplarrheneae*, the Australasian and American *Sisyrrhynchieae*, the exclusively American *Trimezieae* (= *Mariceae*) and *Tigridieae*, and the Old World *Irideae*. *Iris* and *Moraea* constitute the major genera of this last tribe, *Iris* a North Temperate genus and *Moraea* largely sub-Saharan African. Several small genera allied to *Iris* or *Moraea* are believed to have flowers modified for different pollination strategies and have been shown by molecular data to be nested with one or other of the larger genera. Vegetative diversity, especially in the leaf and rootstock, is an important variable in *Iris* whereas floral divergence and vegetative uniformity characterize *Moraea*. Genera of *Irideae* appear to be primarily adapted for pollination by bees foraging for nectar and pollen transfer is passive. Specialization has shifted the pollination strategy either to a generalist system using flies, bees and beetles, or a specialist system using bees foraging for pollen, or carrion flies attracted to foul odors, or hopliine beetles that use flowers as sites for assembly and mating.

KEY WORDS - classification, phylogeny, *Iridaceae*, adaptive radiation

INTRODUCTION

The family *Iridaceae* is a well defined assemblage of approximately 1800 species belonging to the *Liliidae* (the monocotyledons). Virtually worldwide in distribution, the family has a marked concentration in Africa south of the Sahara, including Madagascar. Over 1130 species occur there, of which almost 1000 are restricted to southern Africa. In contrast some 335 species occur in Eurasia including North Africa and the Canary Islands, about 290 species occur in the New World and just 36 species occur in Australasia.

The phylogenetic relationships of the *Iridaceae* only began to be explored seriously after the Swedish botanist, Rolf Dahlgren began to refine the classification of the monocotyledons in the 1980s. Dahlgren and his collaborators (e.g. Dahlgren and Rasmussen, 1983; Dahlgren *et al.*, 1985) first recognized two and then three orders to accommodate the families and genera comprising what are loosely called the petaloid monocots, *Asparagales*, *Liliales*, and *Melanthiales*. The status of the two first orders has since been confirmed by molecular studies (e.g., Chase *et al.*, 1995). The *Melanthiales* have, however, proven heterogeneous, including some families (*Melanthiaceae*) nested in the *Liliales*, but *Tofieldiaceae* (formerly *Tofieldieae*) fall in *Alismatales*, and the affinities of *Nartheciaceae* (*Narthecieae*) may lie with *Dioscoreales* (Chase *et al.*, 1995; Goldblatt, 1995; Angiosperm Phylogeny Group, 1998). The composition of *Asparagales* and *Liliales*, as circumscribed by Dahlgren *et al.* (1985), has broadly been confirmed by subsequent molecular study. However, the affinities of the *Iridaceae*, assigned to *Liliales* by Dahlgren *et al.* (1985), largely on the basis of mottled tepals and perigonal nectaries, are contradicted by molecular data. The family is nested among some basal families of *Asparagales*.

The position of the *Iridaceae* within *Asparagales* at first seems difficult to justify on the basis of morphology. Most *Asparagales* with dry fruits have seeds with a black seed coat (with a layer of phytomelan), extrorse anthers, and septal nectaries. The difficulty is without foundation although seeds of all *Iridaceae* do lack phytomelan. New information (Goldblatt, 1990, 1991; Goldblatt and Manning, unpubl.) has shown that septal nectaries are ancestral in the *Iridaceae* and anthers are consistently extrorse (Table 1). Both these features make an association of *Iridaceae* with *Liliales*, in which anthers are ancestrally introrse and nectaries perigonal, difficult to maintain. The only apparent inconsistency in assigning *Iridaceae* to *Asparagales* now appears to be the seeds and we must regard this as representing an evolutionary reversal, not incidentally restricted to the family, but also found in *Orchidaceae* and *Doryanthaceae* among others.

The relationships of the *Iridaceae* within the *Asparagales* appear to lie with three small families, the predominantly Southern Hemisphere *Tecophilaeaceae* (including *Cyanastraceae*), the Australian *Doryanthaceae*, and the Asian *Ixioliriaceae*. This association does not seem indicated by external morphology, and to date, the more precise identification of the families immediately allied to the *Iridaceae* has not proved useful in understanding the phylogeny and evolution within the *Iridaceae*. DNA sequence studies, however, consistently indicate this pattern (Chase *et al.*, 1995). I conclude that the *Iridaceae* and those families most closely allied to it differentiated a very long time ago (late Cretaceous or early Tertiary) and that their living descendants have diverged so much from their ancestral stock that their relationships have been obscured at the morphological level. *Iridaceae* thus appear phylogenetically isolated, easy to define, and are always easy to recognize.

The derived features of *Iridaceae* (Table 1) include two morphological characters, a unifacial isobilateral leaf and the presence of only three stamens (the outer whorl present in related families is lost). At the anatomical level, cellular inclusions of calcium oxalate take the form of styloid crystals whereas related families have raphide bundles (Goldblatt *et al.*, 1986). Except for the Tasmanian genus *Isophysis*, *Iridaceae* also have an inferior ovary. Most other Asparagalean families have a superior ovary, but families now regarded as allied to the *Iridaceae*, including *Doryanthaceae*, *Ixioliriaceae* and *Tecophilaeaceae* also have an inferior ovary. Both septal and perigonal nectaries occur in the family (Daumann, 1970; Goldblatt, 1990), and phylogenetic studies now suggest that septal nectaries are ancestral in the family. Perigonal nectaries are common only in the more specialized genera of subfamily *Iridaceae* and are known in one species of

TABLE 1 - FAMILY CHARACTERS AND CLASSIFICATION OF *IRIDACEAE* ADAPTED FROM GOLDBLATT (1990) WITH SOME CHANGES (SEE TABLE 2)

Order: Asparagales. *IRIDACEAE* ca. 64 genera: 1805 species

Subfamily	Tribes	Typical Genera
<i>Isophysidoideae</i> (1:1)		
<i>Nivenioideae</i> (6:86)	<i>Patersonieae</i>	<i>Patersonia</i>
	<i>Nivenieae</i>	<i>Aristea, Nivenia</i>
<i>Ixioideae</i> (27: ca. 948)	<i>Watsonieae</i>	<i>Watsonia, Lapeirousia</i>
	<i>Pillansieae</i>	<i>Pillansia, Thereianthus</i>
	<i>Croceae</i>	<i>Gladiolus, Crocus</i>
	<i>Ixieae</i>	<i>Gladiolus, Ixia, Tritonia</i>
<i>Iridoideae</i> (ca. 31:765)	<i>Diplarrheneae</i>	<i>Diplarrhena</i>
	<i>Sisyrrhinoideae</i>	<i>Libertia, Orthrosanthus, Sisyrrhinchium</i>
	<i>Trimezeiae</i>	<i>Neomarica, Trimezia</i>
	<i>Tigridieae</i>	<i>Cipura, Cypella, Tigridia</i>
	<i>Irideae</i>	<i>Dietes, Iris, Moraea</i>

Apomorphic (derived) family characters:

1. Unifacial leaf blades, oriented edgewise to the stem
2. Tissues with styloid crystals
3. Three stamens (or two)
4. Seeds with phlobaphene pigment

Ancestral (plesiomorphic) features also present in those asparagalean families most closely related to *Iridaceae* and so do not define the family:

5. A petaloid perianth
6. Anthers extrorse during development
7. Septal nectaries
8. Ovary inferior (reversed in *Isophysis*)
9. Loculicidal capsular fruits

Aristea (Goldblatt, 1990; Goldblatt and Manning, 1996). A large and morphologically diverse family, *Iridaceae* are heterogeneous for most other characters considered important in assessing and defining monocot families.

CLASSIFICATION WITHIN THE *IRIDACEAE*

There are two large generic assemblages within the *Iridaceae* (Table 1, 2), and they have been accorded tribal or subfamilial rank, as *Ixioideae* and *Iridaceae* (or *Ixieae* and *Irideae*) respectively, depending on the highest infrafamilial rank recognized (Diels, 1930; Goldblatt, 1990). Together these subfamilies comprise over 95% of the species and genera. *Ixioideae*, with ca. 950 species and 27 genera, are largely African with reduced representation in Europe and western Asia where *Crocus L.* is centered. *Iridaceae* with ca. 765 species and ca. 30 genera are more or less worldwide with centers in the North Temperate zone, in southern Africa and in temperate and Andean South America. The remaining seven genera present challenging questions about their relationships and classification.

Isophysis seems taxonomically isolated, and because of its superior ovary has been assumed to be close to the ancestral stock of the family (Goldblatt, 1990) when included in *Iridaceae* at all. A superior ovary is usually regarded as primitive and an inferior ovary derived. However, because an inferior ovary is characteristic of several families of *Asparagales*, including those closest to the *Iridaceae*, the presence of an inferior ovary does not appear to constitute proof of primitiveness in this case. *Isophysis* also has vessels in the roots with only scalariform perforation plates, normally considered unspecialized compared to vessels with simple perforation plates (found in all *Ixioideae* and *Irideae sensu* Goldblatt, 1990). For the present *Isophysis* should thus be interpreted as a relatively unspecialized member of the *Iridaceae*. Molecular studies largely support this (Chase *et al.*, 1995; Sousa-Chies *et al.*, 1997; Reeves *et al.*, this volume). In two of three chloroplast genes sequenced to date, *Isophysis* falls at the base of the *Iridaceae*. In a third, the genus is sister to *Iridaceae* which together are sister to the rest of the family. In a combined analysis of all three genes, *Isophysis* also assumes a basal position (Fig. 1). In preliminary analyses, using the *rbcLL* gene, *Isophysis* sometimes even fell outside the family, between *Doryanthaceae* and *Tecophilaeaceae* (M. W. Chase, pers. comm.). The relationships of *Isophysis* remain somewhat problematical, but subfamilial status for the genus (Tables 1, 2), as proposed by Goldblatt (1990), still seems the best solution for its classification.

The remaining six genera of the *Iridaceae* have been assigned to a fourth subfamily *Nivenioideae* (Goldblatt, 1990). The genera *Klattia*, *Nivenia* and *Witsenia*, together just 14 species, are woody shrubs restricted to the Cape Region of South Africa. They represent a close-knit alliance and are linked by several derived floral, vegetative and seed features (Manning and Goldblatt, 1991; Goldblatt, 1993). The African and Madagascan genus *Aristea* with ca. 52 species is the largest genus of *Nivenioideae*, and though superficially unspecialized, has several unusual derived features (papillose seeds, derived leaf margin anatomy) and, within the genus, the widest range of pollen grain morphology of any monocot genus so far studied (Goldblatt and Le Thomas, 1992; 1997). Resembling *Aristea* florally, the Madagascan saprophyte, *Geosiris*, is achlorophyllous and has leaves reduced to small scales (Goldblatt *et al.*, 1987).

TABLE 2 - GENERIC CLASSIFICATION OF THE *IRIDACEAE* AFTER GOLDBLATT (1990), WITH SUBFAMILIES AND TRIBES REARRANGED IN LIGHT OF NEW MOLECULAR DATA

New elements in the classification are the expansion of *Pillansieae* to include *Micranthus* and *Thereianthus* (transferred from *Watsonieae*) (see Reeves *et al.*, this volume), the restriction of *Ixieae* to include genera with the seed vascular excluded (see Goldblatt and Manning, 1995) and the referral of the remaining genera to a tribe, the earliest name for which is *Croceae*, essentially a residual group that requires further investigation. *Patersonia* is now regarded as a monotypic tribe of *Nivenioideae*, hence the remaining genera fall by default into *Nivenieae*. *Diplarrhena* is treated as a monotypic tribe of *Irideae*, *Diplarrheneae*, Rudall and Goldblatt, this volume. Some small genera of *Tigridieae* are now included in *Tigridia* (following Rodriguez, 1997, although formal taxonomic changes have not been made) although they have not formally been reduced to synonymy. Likewise, *Belamcanda*, *Hermodactylus* and *Pardanthopsis* are included in *Iris* following Tillie *et al.* (this volume). The dates after authors of infrafamilial taxa indicate year of original publication but are not referenced. Numbers in parentheses indicate the total genera and species for tribe or subfamily or total species for a genus. Only important generic synonyms are indicated. Total 64 genera: ca. 1800 species.

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1. Subfamily *Isophysidoideae* Takhtajan (1980) (1: 1)
 - Isophysis* T. Moore (1) – Tasmania
 2. Subfamily *Nivenioideae* Schulze ex Goldblatt (1990) (6: ca. 85)
 - Tribe *Patersonieae* Baker (1877) (1: 21)
 - Patersonia* R.Br. (ca. 21) – Australia, Borneo, Sumatra, New Guinea
 - Tribe *Nivenieae* Goldblatt (1999) (5: 64)
 - Aristea* Ait. (ca. 50) – Africa and Madagascar
 - Geosiris* Baill. (1) – Madagascar
 - Klattia* Baker (3) – Cape Region, South Africa
 - Nivenia* Vent. (10) – Cape Region, South Africa
 - Witsenia* Thunb. (1) – Cape Region, South Africa
 3. Subfamily *Ixioidae* Klatt 1866 (as subordo *Ixieae*) (27: ca. 948)
 - Tribe *Watsonieae* Klatt (1882) (2: 93)
 - Lapeirousia* Pourr. (42) – tropical and southern Africa
 - Watsonia* Mill. (51) – southern Africa
 - Tribe *Pillansieae* Goldblatt (1990) (3: 11)
 - Micranthus* (Pers.) Ecklon. (3) – southwestern Cape, South Africa
 - Pillansia* L. Bolus (1) – southwestern Cape, South Africa
 - Thereianthus* G. Lewis (7) – southwestern Cape, South Africa
 - Tribe *Croceae* von Berchtold & Presl (1820) (14: ca. 695)
 - Babiana* Ker (including *Antholyza* L.) (65) – southern Africa, Socotra
 - Crocus* L. (ca. 80) – Europe, Asia, North Africa
 - Freesia* Klatt (including *Anomatheca*) Ker (14) – eastern tropical and southern Africa
 - Geissorhiza* Ker-Gowler (85) – South Africa, mainly southwestern Cape
 - Gladiolus* L. (incl. *Homoglossum* Salisb., *Oenostachys* Bullock) (ca. 255) – Africa, Madagascar, Eurasia
 - Hesperantha* Ker (including *Schizostylis* Black. & Harv.) (ca. 70) – tropical and southern Africa
 - Melasphaerula* Ker (1) – southern Africa
 - Radinosophon* N.E. Br. (1/2) – south tropical and southern Africa

Romulea Maratti (ca. 85) – Africa, Mediterranean, Canary Is.
Savannosiphon Goldb. & Marais (1) – south tropical Africa
Syringodea Hook f.(8) – southern Africa
Tritoniopsis L. Bolus (including *Anapalina* N.E. Br.) (22) – southwestern and southern Cape, South Africa
Xenoscapa (2) – southern Africa
Zygotritonia Mildbr. (4) – tropical Africa

Tribe *Ixieae* Dumortier (1822) (8: 148)

Chasmanthe N.E. Br. (3) – southwestern Cape, South Africa
Crocoshia Panchon (8) – south tropical and southern Africa, Madagascar
Devia Goldb. & J. C. Manning (1) – W Karoo, South Africa
Dierama K. Koch (44) – tropical and southern Africa
Duthieastrum de Vos (1) – southern Africa
Ixia L. (ca. 51) – southern Africa
Sparaxis Ker.-Gawler (including *Synnotia* Sweet) (15) – southwestern Cape, South Africa
Tritonia Ker.-Gawler (28) – south tropical and southern Africa

4. Subfamily *Iridoideae* (30: ca. 765)

Tribe *Diplarrheneae* Goldblatt (1: 2)

Diplarrhena Labill. (2) – Australia

Tribe *Sisyrinchieae* Presl. (1846) (6: ca. 115)

Libertia Sprengel(ca. 12) – South America and Australasia
Olsynium Rafin. (including *Chamelum* Philippi, *Phaiophleps* Rafin.) (ca. 10) – South America and W North America
Orthrosanthus Sweet (10) – South and Central America, and Australia
Sisyrinchium L. (ca. 80) – South and North America
Solenomelus Miers. (2) – South America
Tapeinia Juss. (1) – South America

Tribe *Irideae* von Berchtold & Presl (1820) (5: ca. 473)

Iris L. (including *Belamcanda*, *Hermodactylus*, *Pardanthopsis*) (ca. 250) – Eurasia, North Africa, North America
Bobartia L. (12) – southern Africa, mainly Cape Region
Dietes Salisb. ex Klatt. (6) – eastern and southern Africa, Lord Howe Island
Ferraria Burm. ex Mill. (10) – southern Africa
Moraea Mill. (including *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandriris* Parl., *Hexaglottis* Vent., *Homeria* Vent., *Roggeveldia* Goldblatt (195) – mainly sub-Saharan Africa, also Eurasia

Tribe *Trimezieae* Goldblatt ined. (= *Mariceae* Hutchinson, 1934, nom. illeg.) (3: 35)

Trimezia Salisb. ex Herb. (ca. 15) – South and Central America
Neomarica Sprague (ca. 8) – South and Central America
Pseudotrimezia R.C. Foster (12) – eastern Brazil

Tribe *Tigridieae* Baker (1878) (15: ca. 140)

Calydorea Herb. (including *Cardiostigma* Bak., *Catila* Rav., *Itysa*) (ca. 10) – South America, Mexico, Florida
Cipura Aubl. (ca. 6) – South and Central America
Cypella Herb. (ca. 20) – South America, Mexico and Cuba
Eleutherine Herb. (2) – South and Central America, West Indies
Ennealophus N.E. Br. (including *Tucma* Rav.) (5) – South America
Gelasine Herb. (4) – South America
Herbertia Sweet (ca. 8) – southern South America

Kelissa Rav. (1) – Brazil
Mastigostyla I.M. Johnst. (ca. 16) – South America
Onira Rav.(1) – Brazil
Cardenanthus R.C. Foster (ca. 8) – South America
Nemastylis Nutt. (5) – Central and southern North America
Alophia Herb. (ca. 5) – tropical South America, Central America, Mexico, USA
Ainea Ravenna (2) – Mexico
Tigridia Juss. (including *Cobana* Rav., *Fosteria* Mol., *Rigidella* Lindl., *Sessilanthera* Mol. and *Cruden*)(ca. 45)–Mexico, Central America, Andes

Molecular data (Chase *et al.*, 1995; Reeves *et al.*, this volume) confirm its position in the *Iridaceae*, although this has not always been clear from morphology so that the genus has in the past been referred to *Burmanniaceae* or *Geosiridaceae*. Lastly, the Australasian *Patersonia* appears to have no close allies. It has been seen as allied to the shrubby South Africa genera (Manning and Goldblatt, 1991) because some species have secondary growth in the woody caudex and are more or less evergreen subshrubs, but they lack truly woody stems with secondary growth.

The genera of *Nivenioideae* are united by an unusual inflorescence, which is biseriate, consisting of two terminal monochasia enclosed by their outer subtending bracts (a binate rhipidium sensu Weimarck, 1939). This feature was regarded by Goldblatt (1990) as derived because of its complexity relative to the typical single monochasium enclosed in large opposed bracts (a rhipidium) of the *Iridaceae*. In addition, a blue flower and tepals united in a perianth tube appear to be fundamental, and derived features linking the six genera of *Nivenioideae*.

Molecular data show that the current classification that admits four subfamilies, adopted by Goldblatt (1990), may not adequately represent the phylogeny of the family. The chloroplast gene, *rps4* (Sousa-Chies *et al.*, 1997) showed that *Ixioideae* and the genera of *Nivenioideae* comprise a lineage but did not confirm the monophyly of *Nivenioideae*. Instead, *Patersonia* appeared ancestral to the remainder of the clade (Figure 1), and *Aristea* was sister to two clades, the core genera of *Nivenioideae* and *Ixioideae*. That topology was also obtained by Reeves *et al.* (this volume) for *rbcL* and a third gene, *trnL-F*. For the present it seems best to retain the four subfamily classification, but the possibility that *Patersonia* should be assigned a fifth (apparently monotypic) subfamily seems an attractive alternative. Within *Nivenioideae*, *Patersonia* is here placed in its own tribe to reflect its phylogenetic isolation (Table 2), a decision first made by J. G. Baker (1887), who included *Libertia* in the same tribe.

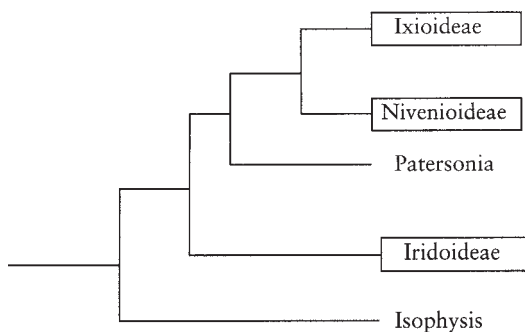


Figure 1 - Major clades of the Iridaceae, adapted from Goldblatt (1990) and Reeves *et al.* (this volume).

An important fundamental question, the phylogeny of the major clades of the *Iridaceae* now seems largely resolved, although the relationship of *Patersonia* remains puzzling. This is now a small question among many in the family. Particularly interesting is the profound difference in the patterns of evolutionary radiation of the two large subfamilies.

RADIATION AND CLASSIFICATION OF THE *IXIOIDEAE*

Ixioideae are well defined morphologically, having a derived, cormous rootstock, closed leaf sheaths, and sessile, long-lasting flowers always with the tepals basally united in a tube (Goldblatt, 1990). The leaf anatomy is also derived, and the leaf blades have a midvein (strictly a pseudomidrib) (Rudall and Goldblatt, 1991; Rudall, 1995). The pollen is also unique in the family in having an operculate aperture and perforate-scabrate exine (Goldblatt *et al.*, 1991). Although many species have radially symmetric flowers, zygomorphy is characteristic of most genera. The presence of a tube (which contains nectar produced in septal nectaries) and a zygomorphic flower appears to have allowed adaptive radiation within the subfamily to proceed rapidly, leading to an almost overwhelming floral diversity. In many genera, including *Geissorhiza*, *Gladiolus*, *Tritoniopsis*, *Watsonia*, flowers vary from a basic bee pollinated short-tubed, gullet form to elongate-tubed forms adapted for pollination a range of different specialist pollinators (Fig. 2) amongst which are sunbirds, long-proboscid flies, large butterflies, and night-flying moths (Vogel, 1954; Goldblatt *et al.*, 1995, Goldblatt and Manning, 1998; Manning and Goldblatt, 1996, 1997). In southwestern southern Africa this radiation has even included the apparent reversal to actinomorphy in several genera, a feature associated with pollination by hopliine beetles (*Ixia*, *Sparaxis*, *Tritonia*) or pollen collecting (rather than nectar-seeking) bees (*Ixia*, *Gladiolus*) (Goldblatt *et al.*, 1998).

The phylogeny of the *Ixioideae* is still poorly understood. The allocation of the 27 genera of the subfamily to three tribes (Goldblatt, 1990), including a monotypic *Pillansieae*, has not been supported by molecular studies. Even the *Watsonieae*, with six genera assigned to it by Goldblatt, is not supported. One of the better-supported clades obtained from molecular sequences is one including *Micranthus*, *Thereianthus* (both *Watsonieae sensu* Goldblatt, 1990) and *Pillansia* (Reeves *et al.*, this volume). Clearly the apparently unspecialized features of the latter (leaves without an pseudomidrib, actinomorphic flowers, a paniculate inflorescence) represent reversals to ancestral states. Together with *Pillansia*, *Micranthus* and *Thereianthus* may provisionally be regarded as comprising an expanded *Pillansieae* (Table 2). Another clade that is supported by morphology and molecular data is one including *Ixia*, *Crocasmia*, *Sparaxis* and *Tritonia* (amongst others) which have specialized seeds (excluded raphal vasculature) and derived columnar marginal epidermis (Goldblatt and Manning, 1995; Rudall and Goldblatt, 1991).

PHYLOGENY AND RADIATION WITHIN *IRIDOIDEAE*

Iridoideae comprise three major lineages, plus the taxonomically isolated genus *Diplarrhena* (Fig. 3). The four lineages, treated taxonomically as tribes, are united by a derived style which is deeply divided into three hollow arms (style branches) that are stigmatic apically or subapically in some specialized genera. The flowers are fugaceous (lasting less than a day) in most genera and longer lasting flowers, as in many *Iris* species, are most likely secondary in the subfamily. The flowers are radially symmetrical and,



Figure 2 - Comparative floral morphology of subfamily *Ixiodeae*, illustrating representative flowers for major pollination syndromes found in the subfamily. A. *Gladiolus huillensis*, with typical sunbird-pollinated flowers. B. *Geissorhiza aspera*, with generalist flowers, visited by a range of short-tongued insects. C. *Geissorhiza confusa*, with long-tubed flowers adapted for pollination by long-proboscid flies. D. *Lapeirousia anceps*, adapted for long-proboscid fly pollination, with *Moegistorhynchus longirostris*. E. *Sparaxis maculosa*, with flowers typical of hopliine beetle pollination. F. *Gladiolus emiliae*, with moth-pollinated flowers. G. *Gladiolus paludosa*, with zygomorphic flowers adapted for pollination by long-tongued anthophorine bees. H. *Romulea setifolia*, with flowers pollinated by honey bees and hopliine beetles.

with some notable exceptions (most *Iris* species) the tepals are free. The unity of *Iridoideae* has received unexpected support from phytochemistry. Members of the subfamily have unusual gamma-glutamyl peptides, not present in other subfamilies. Many species (but not all those examined) in the specialized tribes *Irideae* and *Tigridae* also have a second specialized compound, meta-carboxy amino acids (Larsen *et al.*, 1981; 1987). These compounds are not known elsewhere in the petaloid monocotyledons.

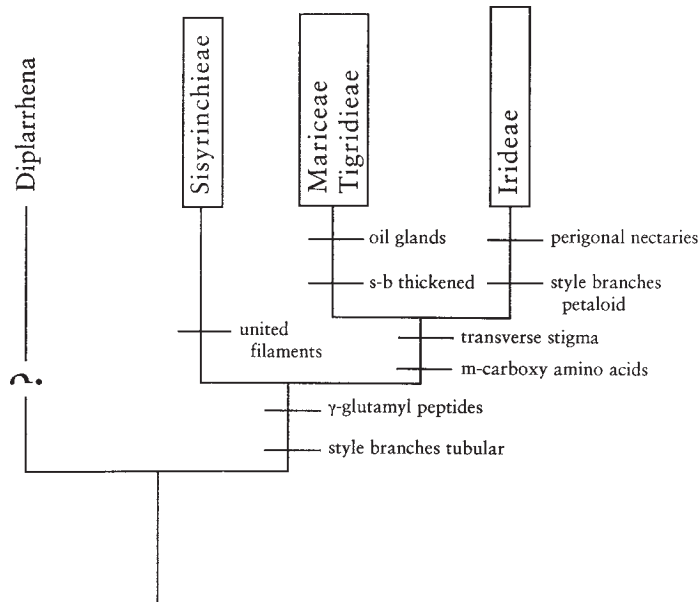


Figure 3 - Phylogeny of subfamily Iridoideae, adapted from GOLDBLATT (1990) and REEVES *et al.* (this volume). s-b= style branches.

Genera allied to the New World *Sisyrynchium* comprise one of the major lineages (Fig. 3) of the *Iridoideae* (Goldblatt *et al.*, 1990; Goldblatt, 1990). Almost all species of the six genera have small stellate or cupped flowers with filaments partly or fully united around the style and style branches extending between the anthers. *Libertia* and *Orthrosanthus* are shared between America and Australasia. Flowers lack conventional nectaries but many (perhaps most) species of *Sisyrynchium* produce oil, secreted from glandular hairs on the filament column. They are pollinated, at least in part, oil-collecting bees (Vogel, 1974), but the prominently displayed anthers at the apex of a staminal column suggest active pollen collection by different bees may be as important in their pollination. Misinterpretation of the relationships of *Aristea* and the southern African *Bobartia*, which have apparently unspecialized, *Sisyrynchium*-like flowers, lead to the inclusion of these genera in *Sisyrynchieae* by Bentham and Hooker (1883), for example. Significantly, they differ from *Sisyrynchieae* in having free filaments (at least basally united in all *Sisyrynchieae*) and *Aristea* has different style branches. Only as a result of molecular evidence has it been possible to convincingly show that *Bobartia* is, in fact, only distantly related to *Sisyrynchium* and, instead belongs in tribe *Irideae* close to *Dietes* (Goldblatt and Rudall, 1992; Reeves *et al.*, this volume).

Two more lineages, *Tigridae* and *Trimezieae* (= *Mariceae*), both New World and largely South American, show another aspect of the floral evolution of *Iridoideae* (Fig. 3). The ancestral condition in these tribes includes free, threadlike filaments and sturdy

style branches lying opposite the stamens and to which the anthers are attached. The tepals are free and clawed, typically with the outer tepal enlarged and with a conspicuous fold at the base of the inner tepal limb partly concealing a dense patch of oil-secreting glands. In genera allied to *Tigridia* (or nested within it) the filaments are united around the style, and the style branches are deeply, and sometimes completely, divided, thus six-armed. Floral radiation in *Tigridia* (*Tigridieae*) includes the evolution of bird pollination (the only example in the subfamily). Four species in that genus (sometimes segregated as *Rigidella*) have brilliant red flowers with the tepal claws forming a narrow tube containing nectar available only to hovering hummingbirds. *Tigridieae* are distinguished from *Trimezieae* by the rootstock a bulb, and a pleated leaf blade. *Trimezieae* appear to lack derived features separating it from *Tigridieae* and the two tribes should probably be united.

The Australian *Diplarrhena* lacks the floral specializations that characterize other *Iridoideae* and its affinities within the subfamily have long been uncertain. DNA sequences from both *rbcL* and *trnL-F* (Reeves *et al.*, this volume) place the genus at the base of the clade comprising the *Iridoideae* (which it closely resembles vegetatively). The flowers are unique in the family in having only two stamens and unique in *Iridaceae* in having zygomorphic flowers. The genus is best included in *Iridoideae* although it is evidently isolated within the subfamily. It cannot be accommodated within any of the existing tribes and has now been accorded a tribe of its own (Rudall and Goldblatt, this volume, Table 2).

The remaining tribe, *Irideae*, is largely African and Eurasian in distribution, and includes more than ca. 470 species (of ca. 765 in the subfamily). *Iris*, largest genus of the *Iridaceae* with ca. 250 species (Mathew, 1981), extends across the north temperate zone to North America, and is most diverse in Asia. The eastern Asian *Belamcanda* Adans. and *Pardanthopsis* (Hance) L.Lenz are nested in *Iris*, as is the Mediterranean *Hermodactylus* Miller (Tillie *et al.*, this volume) according to molecular data. All three

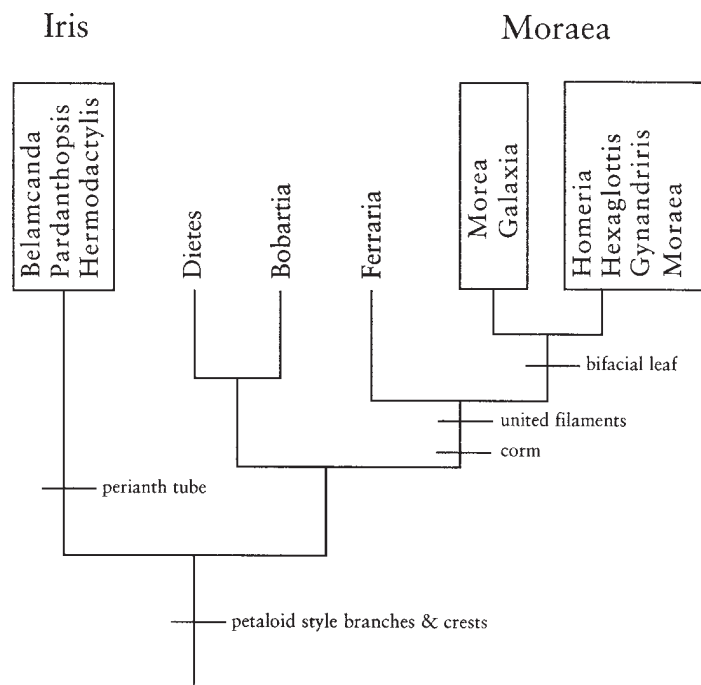


Figure 4 - Phylogeny of *Irideae* and the relationships of *Iris*

must be included in the larger genus. Likewise, *Scorpiris* (*Iris* subgenus *Juno*) and *Xiphium*, treated as separate genera by various authors, appear on the basis of molecular studies to be nested within *Iris* as traditionally defined. There no longer seems to be any doubt about their immediate relationships and recognition as separate genera appears phylogenetically untenable.

Other genera of *Irideae* include the African *Dietes* and *Bobartia* (Table 2) which have, like *Iris*, rhizomatous rootstocks, and *Ferraria* and *Moraea*, which have radiated across southern Africa. Several more African genera, some long-recognized, including *Galaxia*, *Gynandriris*, and *Homeria*, are nested in *Moraea*, and are now included within that genus (Goldblatt, 1998). The basic flower type in *Irideae* is complex and worth careful examination to understand (Figs. 3, 4). The style branches are flattened tangentially, usually petaloid, and apically divided into a pair of petaloid crests. Each stamen is appressed to its opposed style branch and the stigma is a transverse lobe lying below the style crests and usually just above the anther. The tepals are clawed and the claw of the outer tepal is more or less erect and reaches close to the apex of the style branch. The limb spreads at right angles to the claw and has a contrasting mark at its base. Each style branch, anther and outer tepal together form an independent reproductive unit (meranthium).

Each unit or meranthium of the *Iris* flower has been likened to an entire bilabiate flower of, for example, *Salvia* L. or *Stachys* L. The comparison is more than just superficial. The labiate flower and the floral unit of *Iris* function in a similar way. A pollinator visiting the flower in search of nectar alights on the lower lip (outer tepal limb) and pushes its head and mouth parts into the gullet (the space between the tepal claw and style branch). In doing so its upper thorax passively brushes against the anther, becoming dusted with pollen. Visiting another flower, its thorax will brush against the stigmatic lobe transferring any pollen onto the receptive tissue.

This flower is similar in many species of *Irideae* and is the basic (plesiomorphic) flower type in *Dietes* and *Moraea* (Fig. 5 A–D). In *Dietes*, the pollination biology of which is unknown, nectar is not produced and pollination may be by deception. In *Iris* the tepals are united in a tube, the walls of which bear nectaries and the tube forms a nectar reservoir. In *Moraea* the tepals are typically free, but the filaments are united, an important generic distinction. Pollination in *Iris* and *Moraea* is fundamentally the same in species with flattened style branches and crests. I suspect that the flowers of *Iris* are larger than in most *Moraea* species because the pollinators are often large bumble bees whereas in *Moraea* the pollinators are smaller bees, mostly anthophorine bees or *Apis mellifera* (*Apidae*) (Goldblatt *et al.*, 1990). In these flowers geitonogamous pollination must occasionally occur but bees often visit floral units of different flowers in succession, rather than all floral units of a flower first, thus avoiding either selfing or stigma clogging if their flowers are self-incompatible (usually the case in *Moraea*).

Floral adaptive radiation in *Moraea* is now moderately well understood. A common trend is for a loss distinction between the inner and outer tepals which then form an open cup. Associated reduction of the size of the style branches and crests and enlargement of the anthers render the flower morphologically and functionally very different (Fig. 5 E–H). It no longer consists of separate functional units. These flowers offer pollen as the primary reward to bees, or depending on marking and scent, may attract both bees and flies or beetles. The flies are rewarded by small quantities of nectar and beetles use the flat flowers for assembling or mating. This apparently simpler floral morphology has evolved repeatedly in *Moraea* (Goldblatt, 1980; 1986; 1998) and has

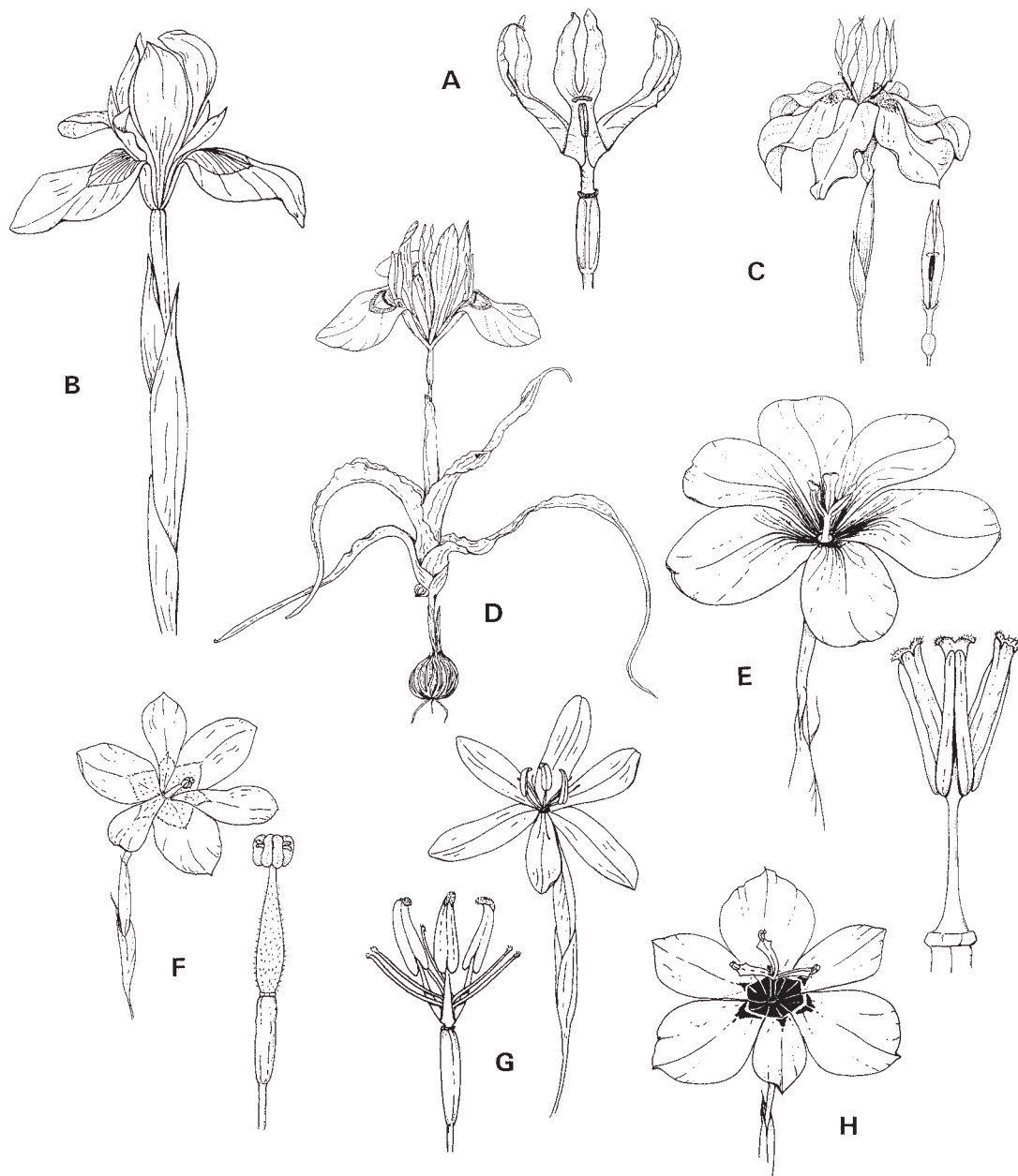


Figure 5 - Comparative floral morphology of *Irideae*, showing the major flower types in the tribe. A. The ancestral style branch and stamen organization, with flattened style branches bearing paired petal-like crests above the abaxial, transverse stigma lobe, and each stamen closely appressed to a style branch. B. *Moraea spathulata*, with a typical *Iris*-like flower composed of three functional units, adapted for pollination by nectar-foraging bees. C. *Moraea namaquamontana*, with *Iris*-like flowers but the inner tepals spreading. D. *Moraea ciliata*, with a flower composed of three functional units. E. *Moraea ochroleuca*, with open cupped tepals adapted for pollination by muscid and scathophagid flies as well as honey bees, the style and stamen apparatus much modified. F. *Moraea bifida*, with subequal spreading tepals and anthers mounted on a filament column, the pollen exposed and available to pollen-collecting bees. G. *Moraea lewisiae*, with filiform style branches and spreading tepals, with prominent anthers. H. *Moraea insolens*, with spreading, brilliantly colored tepals and a dark central blotch, adapted for pollination by hopliine beetles.

been used as the basis for recognizing separate genera, including *Hexaglottis* and *Homeria*, and the acaulescent *Galaxia* (now sections *Hexaglottis*, *Homeria* and *Galaxia* of *Moraea*). The very un-*Iris*-like flower of *Belamcanda* is most likely a comparable evolutionary trend within the *Iris* clade, although the pollination strategy associated with its unusual flower is unknown at present.

In the African lineage of *Irideae*, *Dietes* maintains an *Iris*-like floral form and rhizomatous rootstock. *Ferraria* and *Moraea* (including the genera nested within it) have a corm of surprisingly uniform structure in which the roots are produced from the base of the apical shoot (not from the lower part of the corm as in conventional corms) (Goldblatt, 1990). Floral divergence is, however, quite extraordinary. The star-like or cup-flowers with prominent stamens have evolved repeatedly, and occur in almost every section of the genus. *Ferraria* too has such a flower, associated in the genus with foul odors and dark coloring and fringed tepals. Until recently not properly understood, *Bobartia* also belongs here. The unspecialized flowers are stellate, the tepals lack a claw, and the simple style branches extend between the anthers. Except for the free filaments, the flower closely resembles that of a *Sisyrinchium* (explaining why until now it has been referred to *Sisyrinchieae*). Only molecular data has shown unquestionably that the *Bobartia* is sister to *Dietes* and hence its flower is secondarily simple (Reeves *et al.*, this volume).

The two lineages of *Irideae* make an interesting contrast. On the one hand, *Iris* and the nested segregates, *Scorpiris* (subgenus *Juno*), *Xiphium*, *Reticulata*, *Belamcanda*, *Hermodactylus* and so on show a striking range of vegetative morphology. The basic rhizome has become modified in several ways. Bulbs have evolved twice, tuberous roots also twice, and *Hermodactylus* has a tuberlike rootstock. In almost all species the flower is, however, so similar that there is no question of identity and the pollination biology may not differ significantly. In the *Moraea* lineage floral diversification is pronounced in contrast to the vegetative uniformity and adaptive radiation of pollination systems is striking.

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