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PHYLOGENY AND
CLASSIFICATION OF
IRIDACEAE¹

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ABSTRACT

A cladistic analysis of Iridaceae, a family of some 1,630 species and ca. 77 genera, and the closely allied *Geosiris* and *Isophysis*, both monotypic and sometimes accorded family status, suggests a phylogeny in which there are four major lineages, recognized as subfamilies. Characters used in the analysis include vegetative and floral morphology, anatomy, embryology, pollen ultrastructure, chromosome cytology, and flavonoid and amino acid chemistry. Isophysidoideae, with a superior ovary, include only the Tasmanian *Isophysis*. Nivenioideae include the Afro-Madagascan *Aristea*, three woody Cape genera, the Australasian *Patersonia*, and *Geosiris*. The last-mentioned, a saprophyte, restricted to Madagascar, appears to be most closely related to *Aristea* and is not recognized at the tribal level. Iridoideae have four reasonably well differentiated tribes and a worldwide but predominantly southern distribution. The subfamily is specialized in floral and phytochemical features. Ixiodeae, which comprise slightly more than half the total species of Iridaceae, are predominantly southern African and have derived leaf anatomy, pollen exine, flavonoids, and inflorescences. Three tribes are recognized in Ixiodeae and four in Iridoideae in both of which some subtribal groupings are suggested. Described formally here are Nivenioideae and Pillansieae.

Iridaceae are a relatively large family of petaloid monocots (Liliiflorae sensu Dahlgren et al., 1985) comprising over 1,630 species in ca. 77 genera. Although distributed worldwide, the family has a marked concentration on the southern continents and the major center of radiation in Africa south of the Sahara. Iridaceae are easily recognized among the monocots by having isobilateral equitant leaves, flowers with three stamens, and, with the exception of the monotypic Tasmanian *Isophysis*, an inferior

ovary. *Isophysis* (Fig. 1A) has in the past been assigned variously to Isophysidaceae, Hypoxidaceae, or Liliaceae–Melanthioideae as well as to Iridaceae (Goldblatt et al., 1984). Such is the morphological distinctness of Iridaceae that there is virtually no controversy over their status and circumscription, except for the treatment of *Isophysis* and the monotypic saprophyte *Geosiris* from Madagascar, both of which have been regarded as separate families (Jonker, 1939).

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Iridaceae are usually assigned to the order Liliales (the definition of which varies considerably) but have also been treated in Iridales, either alone (Hutchinson, 1934, 1973), or with Geosiridaceae, Burmanniaceae, and Corsiaceae (Takhtajan, 1969). The unanimity of opinion concerning the status and circumscription of Iridaceae has largely obscured any critical appraisal of the relationships of this family. Colchicaceae (Liliaceae–Melanthioideae in part) have been suggested as immediately allied to Iridaceae (Takhtajan, 1969, 1980), and Takhtajan (1980, 1985) has allied Iridaceae with Tecophilaeaceae in suborder Iridineae, a relationship first espoused by Hutchinson (1934) but discounted by Goldblatt et al. (1984). Dahlgren & Rasmussen (1983) have allied Iridaceae with the Pacific family Campynemataceae and the two to Colchicaceae. New evidence (Goldblatt et al., 1984; Goldblatt, 1986b) now makes this also seem untenable.

Infrafamilial phylogeny and classification of Iridaceae, the emphasis of this paper, have varied with each major treatment of the flowering plants (or monocots alone), but most systems have consistently accepted the existence of one of the main subfamilial categories, subfamily Ixioideae (tribe Ixieae of Bentham & Hooker, 1883; Diels, 1930). There has been little agreement, however, over the circumscription and rank of the other half of the family, here treated as subfamilies Isophysidoideae, Nivenioideae, and Iridoideae. Bentham & Hooker (1883) admitted two more tribes (their major infrafamilial category), Moraeae (now Irideae) and Sisyrinchieae, the latter including genera here referred to subfamilies Iridoideae and Nivenioideae. The rather different treatment of Pax (1888) recognizes the two major subfamilies admitted here, Ixioideae and Iridoideae (the latter including Nivenioideae as a tribe) and a third, Crocoideae, for four acaulescent genera, *Romulea*, *Syringodea*, *Crocus*, and *Galaxia*, now confidently referred either to Iridoideae or Ixioideae (Goldblatt, 1971). The treatment of Iridaceae by Hutchinson (1934, 1973) is similar to that of Bentham & Hooker but admits 11 tribes, essentially recognizing each of Bentham & Hooker's three tribes and subtribes at the same rank. Hutchinson was, however, the first to include *Isophysis* in Iridaceae, as the only member of Isophysideae.

Recent treatments of Takhtajan (1980: 310) and Thorne (1983) include *Geosiris* in Iridaceae as a subfamily, Takhtajan also including *Isophysis* and Campynemataceae (see Dahlgren et al., 1985) in Iridaceae as subfamilies. The recent and thorough studies of the monocots by Dahlgren and co-

workers recognize Geosiridaceae as distinct from Iridaceae, the latter (Dahlgren et al., 1985) including five subfamilies, Isophysidoideae, the nomen nudum Aristeoideae (Nivenioideae here), Sisyrinchioideae, Iridoideae, and Ixioideae.

This paper represents the first objective phylogenetic classification of Iridaceae using modern cladistic methods. It is also the first to use data extensively from fields other than morphology, adapting information from chromosome cytology, flavonoid and amino acid chemistry, anatomy, and pollen morphology. The results confirm that *Isophysis* is probably best included in Iridaceae in a separate subfamily Isophysidoideae and suggest that *Geosiris* be included in Iridaceae–Nivenioideae.

METHODS OF ANALYSIS

Cladistics affords the most objective and critical method of assessing phylogeny, and the results of my cladistic analysis of Iridaceae are presented in the following pages in several cladograms. The cladograms (Figs. 3–5) were constructed manually following concepts of grouping by shared derived characters (synapomorphies) established by Hennig (1966) together with the principle of parsimony as adapted by several botanists (Bremer, 1976; Funk, 1982; Dahlgren & Bremer, 1985; Goldblatt, 1985). The manually generated cladograms were tested using the PAUP Program (Swofford, 1985), which produced the same results.

The polarities of the characters were determined either by outgroup comparison or following widely accepted general character trends in the monocots or flowering plants. The characters used for the cladistic analysis are discussed in detail below, and are outlined in Table 1.

Anatomical data are taken from studies by Cheadle (1963) and Rudall (1983, 1984, 1986) and pollen data from the extensive studies of Schulze, summarized in 1971 (Schulze, 1971). Flavonoid data have only recently become available and information is adapted from a wide survey by Williams et al. (1986). Other important phytochemical data are from studies by Larsen et al. (1981, 1987). Chromosome cytology is comparatively well known for Iridaceae, but the unusually variable karyological data are of limited use above subtribal levels owing to the difficulty in establishing basic numbers for higher ranks.

The characteristics of the families and orders of the Liliiflorae are taken largely from the several recent works of Dahlgren and his co-workers (Dahlgren & Clifford, 1982; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985; Dahlgren & Bremer, 1985).

CIRCUMSCRIPTION OF TRIBES

Given the present state of our knowledge, it is impractical to deal with individual genera of Iridaceae for this type of analysis. Instead, I have chosen apparently natural generic groups (sometimes corresponding to tribes or subtribes) as working taxonomic units. It is clear that three of the four tribes of Iridoideae—Irideae, Mariceae, and Tigrideae—are natural and monophyletic groups, while the nature of the fourth, Sisyrinchieae, is less certain. Although it may be an unnatural alliance, for the purposes of this study it is regarded as monophyletic, and the data so far accumulated support this. However, an important question still remains as to whether *Orthrosanthus* and *Libertia* (both Pacific and South American) and *Bobartia* (South African) are in fact related to the core genera of Sisyrinchieae (all New World).

Nivenioideae may also be found to be unnatural, but no convincing data have yet come to light that indicate an alternative treatment. In Ixioideae I had no preconceived ideas about tribal groupings when I undertook this study, but Watsonieae have emerged as a tribe distinct from Ixieae, which still comprise a large number of genera that may in the future be found to be better treated in more than one tribe. It also became clear from the preliminary analysis that the monotypic *Pillansia* is very isolated in Ixioideae and probably the sister group of the rest of the subfamily (Fig. 5). It is referred to a monotypic tribe, a decision that could not be avoided.

Geosiris has all the derived states of Nivenioideae as well as some of its own, and according to the data available, is the sister genus of *Aristea*. *Isophysis* merits its own subfamily, and in this analysis emerges as the sister taxon of the rest of the Iridaceae. I must, however, emphasize that the embryology of both *Isophysis* and all Nivenioideae except *Geosiris* (Goldblatt et al., 1987) is unknown, and has been assumed to correspond with *Geosiris* (presence of a parietal cell in the ovule; secretory tapetum; successive microsporogenesis; helobial endosperm development) and not the embryologically better known Iridoideae and Ixioideae, which appear to be specialized in having simultaneous microsporogenesis and nuclear endosperm formation (the polarity of these two characters is uncertain). *Geosiris* and *Isophysis* have not been examined for free amino acids.

CHARACTER ANALYSIS

The features of systematic and phylogenetic significance are presented below under headings of

Morphology, Embryology, Cytology, Anatomy, and Phytochemistry. Only the more important characteristics are discussed at length. The reasons for assigning character polarities are indicated unless they are self-evident. The data are summarized in Table 1 and are used in the construction of the cladograms (Figs. 3–5).

MORPHOLOGY

Rootstock. The basic type of rootstock in Iridaceae is almost certainly a creeping persistent rhizome; bulbs and corms are independently derived from a rhizome. All members of Tigrideae have a bulb covered by dry brownish tunics. Elsewhere in the family, bulbs occur in *Iris* subgenera *Scorpiris*, *Xiphion*, and *Reticulata*, and they may have evolved independently in each (Mathew, 1981, and pers. comm.).

Corms are basic in Ixioideae and also occur in the several African genera of Irideae subtribes Homeriinae and Ferrariinae (Lewis, 1954; Goldblatt, 1976). In Ixioideae (Fig. 8) the corms have a distinct stele, produce roots from the base, and are usually composed of several internodes (Lewis, 1954; de Vos, 1977; Goldblatt, 1982a). Development proceeds in two different ways. In Watsonieae and Pillansieae the corm is formed entirely from an axillary bud (*Watsonia*-type sensu de Vos, 1977) at the base of the terminal flowering stem, and the corm's shoot primordium is apical. In Ixieae, by contrast, the corm develops at least partly from the base of the flowering stem (*Ixia*-type of de Vos, 1977), and a bud in the axil of the upper node of the corm produces the following season's growth. In the *Watsonia*-type the new corm is attached to the base of the flowering stem and thus lateral to it, and in the *Ixia*-type the new corm is basal to the flowering stem, and situated below its insertion.

In both cases the flowering axis is terminal and the growth pattern is sympodial and analogous to the sympodial growth of a rhizome where the flowering stem is terminal and buds lateral to it continue the next growth flush. The *Ixia*-type of corm appears to be derived and is here regarded as the major synapomorphy uniting the genera assigned to Ixieae.

In Irideae the corms have a diffuse stele (de Vos, 1977), produce roots (Fig. 6) from the apical bud (Goldblatt, 1987), and, except in *Ferraria* (only genus of Ferrariinae), are of a single internode. The *Homeria*-type corm is a major synapomorphy for this large subtribe of Irideae.

Leaves. The basic leaf type is ensiform and isobilateral (Arber, 1921) with an open sheathing

TABLE 1. Characters used in the cladograms (Figs. 3–5). The derived (apomorphic) states are listed first followed by the presumed ancestral (plesiomorphic) condition. Characters believed to have evolved independently (parallelisms) are indicated by double lines in the cladograms. Although characters 31 and 45 did not ultimately contribute to the cladograms, they were included in the study and hence remain in the table.

Apomorphic states	Presumed ancestral conditions
MORPHOLOGICAL CHARACTERISTICS	
1. Rootstock a bulb	Rootstock a persistent creeping rhizome
2. Rootstock a corm of several internodes	Rootstock a persistent creeping rhizome
3. Corm partly apical in origin and basal to the flowering stem	Corm axillary in origin and lateral to the flowering stem
4. Leaves ensiform and equitant	Leaves bifacial
5. Leaves plicate	Leaves flat
6. Leaf sheaths closed	Leaf sheaths open
7. Inflorescence consisting of one or more rhipidia, each enclosed in large spathes	The unspecialized condition is uncertain and will remain so until a specific outgroup has been identified
8. Rhipidia single-flowered	Rhipidia several to few-flowered
8A. Rhipidia binate	Rhipidia single
9. Flower sessile	Flowers pedicellate
10. Inflorescence a spike	Inflorescence not a spike
11. Flowers fugacious	Flowers lasting at least two days
12. Flowers blue	Flowers shades of yellow to orange
13. Tepals clearly divided into a limb and broad claw	Tepals not clawed
14. Tepals united in a tube	Tepals free
15. Stamens three (outer whorl absent)	Stamens six in two whorls
16. Filaments weak, anthers adhering to the style branches	Filaments supporting free anthers
17. Pollen grain exine micropunctate (punctitegillate)	Exine reticulate
18. Stem unbranched	Stem branched
19. Ovary inferior	Ovary superior
20. Style deeply three-forked to below the base of the anthers and each division conduplicate and terminally stigmatic	Style lobed or divided above the anthers and each branch stigmatic along its entire length
21. Style arms extended between the stamens	Style arms parallel to and appressed to the stamens
22. Style branch apices produced into erect paired appendages (crests) above, stigmatic only below	Style branch apices symmetrical and uniformly stigmatic
23. Style branches thickened and somewhat compressed radially	Style branches slender and symmetric
24. Style branches flattened and petaloid (compressed tangentially)	Style branches slender and symmetric
25. Style branches deeply forked	Style branches undivided or apically forked
26. Nectaries perigonal	Nectaries septal
27. Perigonal nectaries restricted to the base of the outer tepals	Nectaries located on inner and outer tepals
28. Perigonal nectaries most strongly developed on the inner tepals	Nectaries located on inner and outer tepals
29. Nectaries secreting oil from special elaiophores	Nectaries secreting only sugars
30. Nectaries lacking	Nectaries present
ANATOMICAL CHARACTERS	
31. Styloid crystals in vascular bundle sheaths and other tissues	Raphides present and styloids absent
32. Vessel perforations simple	Vessel perforations scalariform
33. Primary thickening meristem (PTM) reduced and pericyclic vasculature scant	PTM and pericyclic vasculature more or less extensive
34. Distinct midrib in leaf vein	No single major leaf vein present
35. Leaf margins with subepidermal sclerenchyma	Marginal subepidermal sclerenchyma not developed
36. Mesophyll cells elongated across the horizontal axis	Mesophyll cells $\pm$ isodiametric or longitudinally elongated
37. Epidermal cells with sinuous walls	Epidermal cells with $\pm$ straight walls
38. Epidermal cells with two-few papillae	Epidermal cells with one or no papillae

[There is no character 39.]

TABLE 1. Continued.

Apomorphic states	Presumed ancestral conditions
PHYTOCHEMICAL CHARACTERS	
FLAVONOIDS	
40. Flavonols absent	Flavonols abundant
41. Flavones present	Flavonols present
42. Mangiferin (xanthone C-glycoside) often present	Mangiferin absent
43. Flavonol O-glycosides predominant (to exclusive)	Flavone C-glycosides predominant
44. Flavone C-glycosides absent	Flavone C-glycosides present
45. Flavone O-glycosides accumulated	Flavonol O-glycosides and/or flavone C-glycosides present
46. Flavonol sulfate present	Flavonol sulfate absent
47. Biflavones absent	Biflavones present
FREE AMINO ACIDS AND PEPTIDES	
48. Free meta-carboxyphenylalanine and carboxyphenylglycine present	These compounds absent
49. Gamma-glutamyl peptides produced	Absent
[There is no character 50.]	
EMBRYOLOGICAL AND KARYOTYPIC CHARACTERS	
51. Microsporogenesis simultaneous	Microsporogenesis successive
52. Endosperm formation nuclear	Endosperm formation helobial
53. $x = 7$	$x = 10$

base. Depending on the choice of outgroup for the family, the equitant leaf may or may not be derived. Among possible immediate ancestors of Iridaceae, several genera of Melanthiaceae (Melanthiales sensu Dahlgren et al., 1985) have similar leaves, notably Tofieldieae, but dorsiventral leaves are basic for the core families of Liliales (e.g., Dahlgren & Rasmussen, 1983). Important modifications of the basic equitant leaf are the pleated (foliated) leaves of Tigridieae, the synapomorphy that unites the tribe, together with the bulbous rootstock. Plicate leaves also occur in some Ixiodeae, notably *Babiana* and most *Crocasmia* species, and appear to have evolved repeatedly in this subfamily. Secondly bifacial and dorsiventral leaves have evolved in several genera, most significantly in the largely African Irideae-Homeriinae (Fig. 6). This leaf type and an apically rooting single-internode corm define the subtribe. Similar bifacial leaves may also be basic for *Iris* subgenera *Scorpiris*, *Xiphium*, and *Reticulata*, all of which also have bulbs. In Ixiodeae, *Crocus* and the closely related southern African *Syringodea* have dorsiventral leaves. Closed leaf sheaths are a feature of Ixiodeae and are scattered in Iridoideae but are probably not basic in the latter.

Inflorescence. The basic inflorescence is probably the distinctive so-called rhipidium, a specialized monochasial cyme. There can be no doubt that its distinctive structure comprises at least one (as treated here) and perhaps three separate synapomorphic states if the spathe-like sheathing bracts

and the collapsed axis are considered separately from the arrangement of the flowers. All Iridoideae have rhipidia either terminal on the main and lateral branches in a variously elaborated paniculate arrangement, or there may be only one or a few rhipidia clustered terminally. The rhipidia consist of two large bract-like sheathing green spathes enclosing a few or sometimes several pedicellate flowers, these essentially attached at a single point. Each flower has a basal bract which also encloses all the younger buds. The flowers are raised successively out of the spathes over a period of a week or more depending on their number. The two rhipidal spathes are probably best interpreted as the outer representing the subtending bract of the inflorescence and the inner the bract of the first flower.

Various fused rhipidia, usually paired (binate) (Weimarck, 1939), characterize all genera of Nivenioideae. In *Isophysis* (Fig. 1A) the flower is solitary but enclosed in what appear to be the opposed spathes typical of an iridaceous rhipidium. The single-flowered state is presumed to be a derived condition for the genus. In Ixiodeae the flowers are always sessile and are subtended by an outer bract and an inner bracteole, the latter a double structure like the flower bracts in the rhipidia elsewhere in the family. Each flower and its bracts are here regarded as the homologue of a rhipidium. In most genera of Ixiodeae, notably excluding *Ptilansia*, the flowers are arranged along a straight or slightly flexuose axis, thus constituting a spike



FIGURE 1.—A. *Isophysis tasmanica* (Hook.) T. Moore (Isophysidoideae) (from Cooke, 1986).—B. *Nivenia dispar* Ecklon ex Baker (Nivenioideae), showing woody stem, compound inflorescence, flower, fruiting branch and detail of ovary. Habits $\times \frac{1}{2}$, details life size or variously enlarged.

(Fig. 8). In *Pillansia* the flowers are arranged in a panicle, the presumably ancestral condition. *Pillansia* is unspecialized in several ways in relation to other Ixioideae (Fig. 7). A few Ixioideae have a reduced spike, sometimes a single flower, notably *Romulea*, *Syringodea*, and *Crocus*, where the flowers are solitary, or solitary on each branch of the flowering stem.

The flower. The iridaceous flower is variable in color, size, and form, and it is difficult to treat the considerable variation in formal primitive or advanced states for higher categories. The flower is trimerous with a major synapomorphy for the family the loss of the inner whorl of stamens. Except for *Isophysis*, the ovary is inferior (Fig. 1A), and it seems reasonable to regard this specialization as

fundamental to the success and radiation of the rest of Iridaceae. However, with the inclusion of *Isophysis*, the inferior ovary is not a family synapomorphy. The inferior ovary is assumed to have evolved only once and it is the sole synapomorphy uniting subfamilies Nivenioideae, Iridoideae, and Ixioideae. Except in Ixioideae and the specialized *Diplarrhena* (Iridoideae), the flowers are radially symmetric. The tepals are united in a developed tube (not merely basally contiguous at the apex of the ovary) in some genera or species of Nivenioideae (*Patersonia*, *Nivenia*, *Witsenia*) and Iridoideae (*Iris*, *Moraea* sect. *Tubiflora*, *Olsynium* (incl. *Chamelum*, *Phaiophleps*)), and are always united in Ixioideae.

In Ixioideae the flowers are often medianly zy-

gomorphic but the basic state for the subfamily is radial symmetry. Zygomorphy has evolved independently in several lines in Ixioideae. A perianth tube is characteristic of all Ixioideae, and the flowers are long-lived, nondeliquescent, and last at least two days, a contrast with most Iridoideae and Nivenioideae, which have fugacious and usually deliquescent flowers. Notably, *Isophysis* also has long-lasting flowers, and this state is probably the basic one for the family. According to the cladogram generated here, fugacious flowers evolved independently twice, in Nivenioideae and Iridoideae. An alternative, that it is a shared development in the line leading to Iridoideae, Nivenioideae, and Ixioideae, means that a reversal for the condition must have occurred in the ancestral Ixioideae. A cladogram with this conformation is less parsimonious by at least three steps.

Nectaries. Perigonal nectaries are considered a derived condition for the families of Liliales (Dahlgren & Rasmussen, 1983), and septal nectaries are generally accepted to be basic for the monocots. *Nivenia* and *Klattia* and probably *Witsenia*, all Nivenioideae, have septal nectaries but other members of the subfamily apparently lack nectaries altogether, as does *Isophysis* (Cooke, 1986). When nectaries are present in Iridoideae they are located on the tepals, either near the base or variously placed on the tepal surface. In Iridoideae perigonal nectaries are apparently lacking or uncommon in the least specialized Sisyrinchioidae (this requires careful checking in living material) but are present at the base of all the tepals at least in *Bobartia paniculata* G. Lewis. The nectaries are restricted to the base of the outer tepals in some specialized genera or species of Irideae (regarded as apomorphic for the tribe although absent in the relatively unspecialized *Dietes*), but some specialized species have nectaries on both inner and outer tepals (a secondary condition?). In contrast, nectaries are best developed on the inner tepals in Mariceae and Tigridieae, where they are often partly concealed by folds in the tepal lamina. In the latter two tribes the nectaries secrete oil (Vogel, 1974) from special club-shaped glands (elaiophores). Similar glands may also be present on the filaments in *Sisyrinchium*.

Septal nectaries are present in all of the many genera of Ixioideae (Daumann, 1970) so far examined and this presumably represents the basic state for the subfamily.

Stamens. An important synapomorphy for Mariceae and Tigridieae is the weak filaments that are shared by several genera of both tribes. These

slender filaments do not support the anthers, which are lightly attached to the upper part of the style branches. (Some specialized genera of Tigridieae have typical sturdy filaments.) The filaments are united, either partly or completely in several Irideae and Tigridieae, but the condition is not basic in either tribe and has probably evolved more than once in each.

Pollen grains are basically monosulcate with a tectate-reticulate exine in Iridaceae (Schulze, 1971), thus conforming to the probable ancestral condition in the monocots. Ixioideae, including the taxonomically isolated *Pillansia* (Goldblatt & Stein, 1988), differ significantly in having micropunctate and usually microspinulate exine (Schulze, 1971; de Vos, 1982; Goldblatt & Stein, 1988). Nonaperturate grains occur in the specialized *Syringodea* and *Crocus*. Bisulcate grains are found in many Tigridieae, and may be a synapomorphy for subtribe Tigridiinae (Goldblatt, 1982b) although they also occur in some Cipurinae (Rudall & Wheeler, 1988). Syncolpate grains occur frequently in Iridoideae but are basic only to certain genera or species groups. Acolpate or anomatreme grains are recorded in some sections and subgenera of *Iris* (Schulze, 1971); they are not characteristic of any generic groups.

Style. Basic style and stigma structure is presumed to be the condition found in *Isophysis* and Nivenioideae, in which the branches or lobes are relatively short and stigmatic along the entire upper surface. Many Iridoideae differ in having long style branches (Fig. 2A), often exceeding the style, the margins of which are convolute so that the style branch is tubular and thus stigmatic only terminally. This modified structure is further specialized in Irideae, Mariceae, and several (presumably basal) genera of Tigridieae, apparently in a similar way. The apices of the style branches are produced above as a pair of flat, erect, nonstigmatic appendages, while the stigmatic surface is confined to the lower part (Fig. 6A).

In Irideae the style branches are, in addition, flattened and petaloid, and the stigmatic surface is often a small lobe restricted to the median ventral surface. In Mariceae and many Tigridieae the style branch is substantially thickened, and the stigma lobe often has a second pair of erect appendages similar to but smaller than the appendages at the upper apices of the style branches. Accompanying this are the weak filaments that do not support the anthers, which are lightly attached to the upper part of the style branch below the stigmatic surface. An elaborate style branch organization is not found



FIGURE 2. Iridoideae, tribes Sisyrinchieae and Tigridieae.—A. *Libertia chilensis* (Mol.) Gunkel, habit and detail of stamens and gynoecium.—B. *Sisyrinchium arenarium* Pöppig, habit and detail of stamens and gynoecium.—C. *Alophia drummondii* (Graham) R. Foster, habit and details of flower, fruit, and stamens and gynoecium (A, B from Correa, 1969). Habits $\times \frac{1}{2}$, details life-size or variously enlarged.

in all genera of Irideae and Tigridieae. The branches may be secondarily reduced and simplified in some genera, sometimes, as in *Eleutherine* and *Calydorea* (Tigridieae) and *Roggeveldia* (Irideae), to long filiform arms, or completely divided into paired and usually slender lobes (*Nemastylis*, *Alophia*, *Tigridia*—Tigridieae; *Hexaglottis*—Irideae).

A possible synapomorphy for Sisyrinchieae is the orientation of the long filiform style branches between, rather than opposite, the stamens (Fig. 2A), the latter being basic for the family. Although this may be a weak character, it is treated here as the synapomorphy that unites this tribe. The only other specialized condition that the genera appar-

ently share is the absence of flavonols, another weak synapomorphy, and one also found in Mariceae and Tigridieae.

Fruit and seed. Loculicidal capsules, presumably derived from septicidal capsules, are almost universal in Iridaceae. Septicidal capsules occur in most Melanthiales and Colchicaceae of Liliales and are probably basic for the order. Iridaceae may therefore be specialized in their possession of loculicidal capsules. The seeds of Liliiflorae have been extensively studied by Huber (1969), who found several features in the seeds of Iridaceae that distinguish generic groups. No seed characters have been used in this study as it seems likely that the basic seed type in the family is unspecialized and

TABLE 2. Embryological data known for Iridaceae. Abbreviations: su = successive; si = simultaneous; he = helobial; nu = nuclear. Unless specific references are given, the data are from Schnarf (1931).

	Micro- sporo- genesis	Parietal cell	Parietal tissue	Endo- sperm formation	References
ISOPHYSIDOIDEAE					
Unknown					
NIVENIOIDEAE					
<i>Geosiris aphylla</i>	su	+	+	he	Goldblatt et al. (1987)
IRIDOIDEAE					
<i>Iris tenax</i>	—	+	+	nu	Smith & Clarkson (1956)
<i>I. stylosa</i>	—	+	+	—	
<i>I. pseudacorus</i>	—	—	—	nu	
<i>I. fulva</i>	—	+	—	—	Riley (1942)
<i>I. hexagona</i> subsp. <i>giganticaerulea</i>	—	+	—	—	Riley (1942)
<i>Sisyrinchium striatum</i>	si	+	x	nu	Lakshmanan & Phillip (1971)
<i>S. californicum</i>	si	+	x	nu	Lakshmanan & Phillip (1971)
<i>Gelasine azurea</i>	—	x	x	nu	Kenton & Rudall (1987)
<i>Eleutherine latifolia</i>	—	x	x	nu	Kenton & Rudall (1987)
IXIOIDEAE					
<i>Crocus sieberi</i>	—	—	—	nu	Rudall et al. (1984)
<i>Romulea columnae</i>	—	+	—	nu	
<i>R. bulbocodium</i>	—	+	—	nu	
<i>R. rosea</i> var. <i>reflexa</i>	—	+	x	nu	Steyn (1973a, b)
<i>Tritonia crocata</i>	—	—	—	nu	

In addition, simultaneous microsporogenesis has been reported in the following: *Sisyrinchium bushii* (Farr, 1922); *S. striatum*; *S. bermudiana*; *Crocasmia crocosmiflora*; *C. aurea* (as *Tritonia*); *Chasmanthe aethiopica* (as *Antholyza*); *Gladiolus cunonius* (as *Antholyza*); *Ixia paniculata*; *I. coccinea*; *I. maculata*; and *Freesia refracta* (Guignard, 1915a); and *Tigridia pavonia*; *Crocus sativus*; *C. vernus*; *Gladiolus* × *gandavensis* (Guignard, 1915b).

almost identical with that in several other families of Liliales, notably Colchicaceae and Campynemataceae. Huber did, however, record the presence of a lipid layer in the inner layer of the outer integument of the testa as a family characteristic (thus presumably a synapomorphy). Seed storage products include protein, oil, and hemicellulose, the latter present in the thick cell walls of the endosperm.

EMBRYOLOGY

Embryology of Iridaceae is poorly known (Table 2), so the generalizations made below for the family are tentative. Microsporogenesis, so far as is known, is reported to be simultaneous in the few genera of Iridoideae and Ixioidae examined: *Iris*, *Sisyrinchium*, *Tigridia*, *Crocus*, *Freesia*, *Romulea*, *Crocasmia*, *Ixia*, *Chasmanthe*, *Gladiolus*, incl. *Anomalesia* (Guignard, 1915a, b). Until recently no Nivenioideae nor *Isophysis* had been investigated embryologically, but Rübsamen (pers. comm.;

Goldblatt et al., 1987) has found successive microsporogenesis in *Geosiris*. This suggests that the latter condition may be basic for Iridaceae, as it is for other families of Liliales and Melanthiales (Dahlgren & Bremer, 1985).

Unlike most Liliales, but typical of Melanthiales, the archesporial cell produces a parietal cell in most members of the family (*Iris*, *Romulea*, *Crocus*, *Crocasmia*, *Sisyrinchium*) and, except in *Sisyrinchium* where it degenerates, one or two layers of parietal tissue are formed (Wunderlich, 1959). In the two species of Tigridieae (*Gelasine* and *Eleutherine*) examined, the archesporial cell functions as the megaspore mother cell and the ovules are thus tenuinucellate. The embryo sac is of the *Polygonum*-type, basic for the monocots. Endosperm formation is nuclear (Wunderlich, 1959) in the few genera of Iridoideae (*Iris*, *Sisyrinchium*) and Ixioidae (*Romulea*, *Tritonia*) so far examined but helobial in *Geosiris* (Rübsamen, pers. comm.), the only species of Nivenioideae known in this

respect. By extension, helobial endosperm formation may be basic in Iridaceae if the condition is ancestral to nuclear endosperm formation, as some authorities believe (Dahlgren & Bremer, 1985). Embryological data are urgently needed for more genera of Nivenioideae and for *Isophysis*. In Melanthaceae endosperm formation is also helobial.

CYTOLOGY

Chromosome number, size, and morphology are variable in Iridaceae, and the basic number for the family is uncertain, particularly as *Isophysis* is unknown cytologically (Goldblatt, 1971, 1979a, 1982b; Kenton & Heywood, 1984). The most likely basic number for Nivenioideae, Iridoideae, and Ixioideae is $x = 10$, judging from the distribution of base numbers in the less specialized genera. A derived basic number is known for Tigridiae, which are unusually uniform cytologically and have $x = 7$ (Goldblatt, 1982b). The closely related Mariceae probably have $x = 10$. The base number of $x = 7$ may reasonably be treated as an autapomorphy for Tigridiae even though base numbers for other tribes are not certain. Irideae also possibly have $x = 10$, but the situation in *Iris* and its immediate allies is so complex that this is very speculative and 10 is in any event possibly basic for the family. For each tribe of Ixioideae the most likely base number is also $x = 10$.

ANATOMY

Several aspects of the anatomy of Iridaceae have recently been examined by Rudall (1983, 1984, 1986), and as a result a number of anatomical features can be used with some confidence for phylogenetic analysis. The primary thickening meristem (PTM) is characteristically well developed in the rhizomes of *Isophysis*, *Aristea*, and *Patersonia* (Nivenioideae) and *Orthrosanthus* and *Libertia* (Sisyrinchieae); consequently these genera have rhizomes with substantial pericyclic vasculature and usually a prominent endodermis. Irideae and Mariceae have a reduced PTM and little pericyclic vasculature. The endodermis thickening is reduced in many Irideae and absent in Mariceae. Similar reduction is characteristic of the corms of Ixioideae. The latter, excepting *Pillansia*, have a distinctive leaf epidermis, regarded as derived here, in which the cells have sinuous walls and two or more papillae. The mesophyll in many Ixioideae, but not *Pillansia*, is also modified in being elongated along the horizontal axis of the leaf (Rudall, pers. comm.).

Secondary growth occurs in most Nivenioideae.

Klattia, *Witsenia*, and *Nivenia* are woody shrubs while *Patersonia* has woody underground stems (Rudall, 1986). The apparently less specialized *Aristea* and *Geosiris*, however, do not have secondary growth and the condition is unlikely to be a synapomorphy for the tribe as a whole. Secondary growth may have evolved only once in the subfamily, for *Patersonia* shares with the shrubby Cape genera several specializations in leaf anatomy and similar flavonoid characters not present in *Aristea* (Rudall & Burns, 1989).

Leaf margins also provide characteristics that seem significant. These include subepidermal sclerenchyma, a synapomorphy for Irideae and for *Isophysis*. Subepidermal marginal sclerenchyma is an important xeromorphic feature and the condition is developed independently in several genera. In many Ixioideae the subepidermal marginal sclerenchyma is associated with a vein, which will be useful later in defining natural generic groupings and phylogeny in the large and diverse Ixieae, not attempted in this paper. Mariceae have marginal epidermal cells heavily thickened and radially elongated but lack subepidermal sclerenchyma (Rudall, pers. comm.). A similar epidermis occurs in a few genera of Ixieae, in which it may have evolved more than once. The presence of a distinct leaf midrib is most likely a derived condition in Iridaceae and is present in all Watsonieae and Ixieae (Ixioideae) but not in Pillansieae. In Iridoideae, Mariceae also have leaf midribs, but the related Tigridiae have plicate leaves with more than one major vein, this probably directed related to the foliated nature of the leaf. Most genera of Irideae and Sisyrinchieae lack leaf midribs.

It has been known for several years that vessels are confined to the roots of Iridaceae except *Sisyrinchium* (Cheadle, 1963). The vessel perforations are scalariform (the plesiomorphic condition) in *Isophysis* and Nivenioideae (including *Geosiris*) (Goldblatt et al., 1987). Elsewhere in the family the vessel perforations are simple or predominantly simple (Cheadle, 1963). This is regarded as a synapomorphy for Iridoideae and Ixioideae and is apparently a major synapomorphy (Fig. 3) uniting the two subfamilies. Vessels are present in the stems and leaves of *Sisyrinchium*. Too few species and genera of Sisyrinchieae have been examined for vessels, and their presence in the stems and leaves may be extended to the closer allies of *Sisyrinchium*. However, *Libertia*, *Orthrosanthus*, and *Bobartia* of the tribe have vessels only in the roots.

Styloid calcium oxalate crystals are a family characteristic (Goldblatt et al., 1984) for Iridaceae. Long styloids are found in most tissues of all genera,

especially in the vascular bundles. Styloids are, however, lacking in *Sisyrinchium* (Goldblatt et al., 1990) and its close relatives (e.g., *Olsynium*, *Solenomelus*). In Liliales no other family has styloids, but this type of crystal occurs in several genera of Melanthiaceae (tribes Melanthieae and Nartheceae) where they are confined to the vascular sheaths (Ambrose, 1980). Several genera of these tribes have, in addition, raphide bundles in parenchyma tissue. The polarization of the styloid character for Iridaceae largely depends on what family is regarded as the immediate ancestor or sister group of Iridaceae. Styloids, reported previously as lacking in *Geosiris* (from the scalelike leaves) by Goldblatt et al. (1984), have now been found in the stems and rhizomes of the genus (Goldblatt et al., 1987), and this is taken as important evidence for the placement of *Geosiris* in Iridaceae.

PHYTOCHEMISTRY

Flavonoids. Iridaceae have an unusually wide range of flavonoid compounds compared with other petaloid monocot families (Williams et al., 1986). Basic to the Liliiflorae are most likely *O*-glycosides of the flavonols quercetin and kaempferol (Williams, 1975), and perhaps flavone *C*-glycosides, the latter of wide distribution in the monocots although rare in Liliiflorae apart from Iridaceae and Orchidaceae. Basic for Iridaceae are flavonol *O*-glycosides and flavone *C*-glycosides, as well as biflavones. The last-mentioned are unusual in the flowering plants but have now been recorded in a few Liliiflorae: *Isoophys* and *Patersonia* in the Iridaceae and an unconfirmed report in *Lophiola* (Melanthiaceae). The distribution of biflavones in the petaloid monocots is inadequately known at present, but it seems likely that their presence may be basic for Liliiflorae as a whole rather than a specialization in Iridaceae. If plesiomorphic, they have been lost in Iridoideae and Ixioideae. The possible biflavones provisionally identified in Iridoideae are probably *C*-methylated flavonoids (C. Williams, pers. comm.).

Important flavonoid features for phylogenetic consideration (data from Williams et al., 1986) include the absence of flavone *C*-glycosides in *Pillansieae* and *Watsonieae* (both Ixioideae) (provisionally regarded as apomorphic states for these tribes) and the accumulation of flavones (apparently an important synapomorphy) and flavone *O*-glycosides in Ixieae. *Pillansia* has a flavonol sulfate, unique in Iridaceae. *Nivenioideae* appear unusual in having a predominance of flavonol *O*-glycosides, including unusual myricetin derivatives and only traces of or no flavone *C*-glycosides.

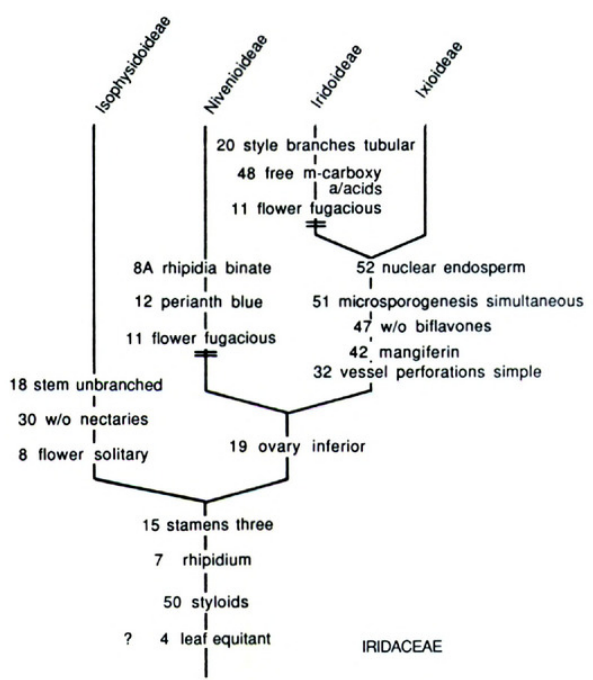


FIGURE 3. Cladogram of the major lineages of Iridaceae, here treated as subfamilies. Parallelisms are indicated by double lines. The characters are polarized assuming Iridaceae belong to Liliales. See Table 1 for explanation of characters used here.

Sisyrinchieae, *Mariceae*, and *Tigridieae* stand out in largely or entirely lacking flavonols. A significant synapomorphy for Iridoideae and Ixioideae appears to be the frequent, but not universal, accumulation of the xanthone *C*-glycoside mangiferin.

Free amino acids and peptides. The unusual free amino acids carboxyphenylalanine and carboxyphenylglycine have a distinctive distribution in Iridaceae (Larsen et al., 1981), occurring regularly in most species examined of Iridoideae, but these compounds are notably absent from *Sisyrinchium* (its immediate allies have not been surveyed), yet recorded in *Libertia*, *Bobartia*, and *Orthrosanthus*, also *Sisyrinchieae*. The presence of these distinctive amino acids, not reported elsewhere in the monocotyledons, is regarded as a major synapomorphy for Iridoideae, united otherwise by having a fugacious flower (a parallelism with *Nivenioideae*) and convolute style branches.

A second unusual group of compounds, γ -glutamyl peptides, have been found to be common in Iridaceae, and also present in about half the species of *Mariceae* examined. They have not been reported in *Tigridieae*, in which only three species have been surveyed. Gamma-glutamyl peptides are absent in all Ixioideae and *Nivenioideae* (known for

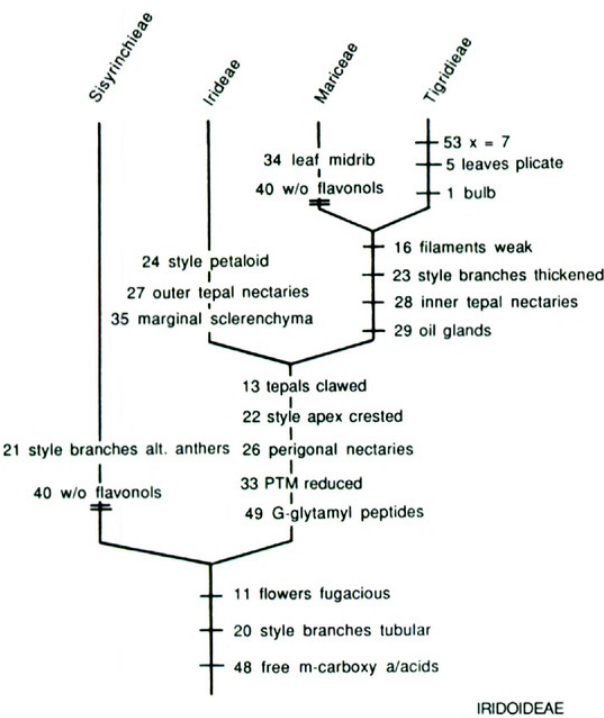


FIGURE 4. Cladogram of subfamily Iridoideae with the major lineages treated as tribes. Parallelisms are indicated by double lines. See Table 1 for explanation of characters used.

only two species of the latter) examined (Larsen et al., 1981, 1987). The presence of this class of compounds is treated as a synapomorphy for the line including Irideae, Mariceae, and Tigridieae. It seems likely that γ -glutamyl peptides will be found in Tigridieae when more species are surveyed, and their absence cannot at present be regarded as a reversal for the tribe. These peptides are not invariably present in Irideae, and are sometimes absent in some species in a genus in which they have been found, or even lacking in some genera. Further sampling is needed.

CLADISTIC ANALYSIS

The results of the cladistic analysis are presented in three diagrams (Figs. 3–5), the first for the major lineages of Iridaceae, and the second and third for the large subfamilies Iridoideae and Ixioideae. The manually generated cladograms were tested using the PAUP Program (Swofford, 1985), which produced the same results. There is good evidence that Iridaceae are monophyletic and defined by several synapomorphies, the number depending on the chosen outgroup, which for this study is the Melanthiales. There are four major lineages (Fig. 3), one for *Isophysis* alone, and the other three united by the possession of an inferior ovary. These four primary lineages are accorded subfamily rank.

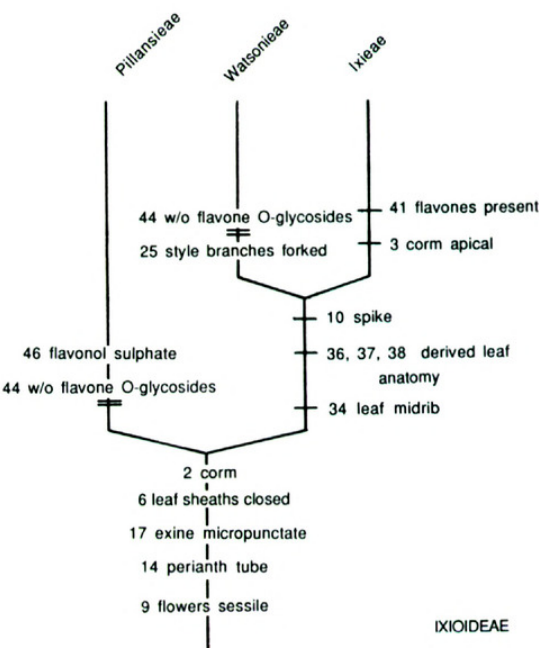


FIGURE 5. Cladogram of subfamily Ixioideae with lineages treated as tribes. Parallelisms are indicated by double lines. See Table 1 for explanation of characters.

Ixioideae are distinguished by five important apomorphic states. Iridoideae and Ixioideae share five synapomorphies. The xanthone, mangiferin, occurs in many genera of both subfamilies, and specialized vessels with simple perforations have been found in all genera so far examined. This clade also lacks biflavones and is specialized embryologically in having simultaneous microsporogenesis and nuclear endosperm formation, although too few genera have been studied embryologically. Biflavones are basic in Iridaceae but absent in Ixioideae and probably absent in Iridoideae since the unidentified DK/DK compounds suggested to be biflavonoids in a few Iridoideae (Williams et al., 1986) are most likely C-methylated flavonoids (Williams, pers. comm.). Nivenioideae are united by having compound rhipidia (usually binate). Their derived fugacious flowers with blue perianths appear to be basic for the subfamily.

The cladogram for Iridoideae (Fig. 4) also has four major lines, accorded tribal status, and corresponding closely to currently accepted tribal groups in the family. The status and composition of Sisyrinchieae, however, is still open to question. The core genera of the tribe, around *Sisyrinchium* and its close allies in South America, are clearly monophyletic, but it is not yet established with any confidence that the southern African *Bobartia*, or the Australasian–South American *Libertia* and *Orthosanthus* also belong here. Their present position

rests to some extent on inadequately investigated phytochemical data and on a subjective interpretation of the nature of style branch structure and orientation.

In Ixioideae there seem to be three distinct lines (Fig. 5) and each is accorded tribal rank. The monotypic Pillansieae are isolated from the line leading to Watsonieae and Ixieae and are clearly ancient and primitive relicts. Watsonieae and Ixieae are less well defined but nevertheless appear to comprise natural groups of equal rank. Ixieae comprise almost half the genera and species of the family and it would be most satisfactory if this tribe could be broken down into a few large groupings. However, at present this does not seem possible, although some 6–8 small generic groupings (see discussion below under Radiation and Composition of the Subfamilies—Ixioideae) are apparent.

RADIATION AND COMPOSITION OF THE SUBFAMILIES

ISOPHYSIDOIDEAE

Consisting only of the Tasmanian *Isophysis* (Fig. 1A), the subfamily is typical of Iridaceae in lacking the three stamens of the inner whorl, and in having styloid crystals (Goldblatt et al., 1984), extrorse anthers, and distichously arranged equitant leaves. It differs markedly, however, in having a superior ovary, which isolates *Isophysis* from the rest of the family. It is also somewhat discordant in its flavonoids: apart from traces of flavone C-glycosides, it has biflavones only (Williams et al., 1986), compounds also found in some Nivenioideae. The basic inflorescence of *Isophysis* is interpreted here as a rhipidium. It consists of a single terminal flower, but its arrangement in two large opposed spathe-like bracts that enclose the bud and pedicel is very like that of the rhipidium that is probably basic in Iridaceae. *Isophysis* apparently lacks nectaries (Cooke, 1986).

NIVENIOIDEAE

Including one Australasian and five Afro-Madagascan genera, the largest of which is the widespread *Aristea* (ca. 50 spp.), Nivenioideae comprise some 83 species. *Nivenia*, *Witsenia*, and *Klattia*, all shrubby (Fig. 1B) and with strongly developed secondary growth of the monocot type, are endemic to the southwestern Cape. *Geosiris*, an achlorophyllous saprophyte with scalelike leaves, is restricted to moist forests in eastern Madagascar. It has numerous ovules and fine seeds but in other

respects appears to conform with Nivenioideae (Goldblatt et al., 1987). Most notable are the styloid crystals in the stems and in the cormlike rhizomes, and the vessels with scalariform perforations (the basic condition in Iridaceae), and found in *Isophysis* and the genera of Nivenioideae. The non-African genus, *Patersonia*, is mainly Australian (Cooke, 1986) and occurs on New Guinea, Sumatra, and Borneo.

Nivenioideae are specialized in their fugacious and blue flowers (almost certainly derived in the family), either binate or variously fused rhipidia, and unusual flavonoid pattern with a predominance of flavonol O-glycosides rather than flavone C-glycosides, which are more common elsewhere in Iridaceae. *Aristea* exhibits little specialization except in capsule and seed morphology. The shrubby Cape genera all have flowers with a well-developed perianth tube, a derived condition. *Witsenia* is specialized for sunbird pollination and has yellow, green, and black flowers. *Nivenia* is unusual in its heterostyly, probably basic in the genus and found in five of the nine species.

Patersonia has a specialized floral morphology: the tepals are united in a long slender tube, the inner tepals are reduced to scales or are absent, and the stigma lobes are more or less fringed. The roots are woody and have secondary growth (Rudall, 1986). Woodiness in *Patersonia* and the shrubby Cape genera may have had a common origin, as these genera share a similar leaf anatomy and flavonoid profile (Rudall & Burns, 1989). However, the Cape genera share with *Aristea* the derived basic chromosome number, $x = 16$ (Goldblatt, 1971), while *Patersonia* may have $x = 11$ (Goldblatt, 1979a).

IRIDOIDEAE

Iridoideae share with Ixioideae vessels with specialized simple perforations and the arguably significant phytochemical character of having, in at least a few species of each, the xanthone mangiferin, an unusual compound in the monocots. All genera of both subfamilies also lack biflavones. Possibly these three features arose independently in each subfamily, and certainly they appear to share no significant morphological specializations while differing in a large number of features. Iridoideae are united by having fugacious flowers (a parallelism with Nivenioideae), perigonal nectaries, and an unusual style morphology in which the branches are long and divide below the level of the anthers while the margins are conduplicate so that each branch is stigmatic only apically. This style

TABLE 3. Classification of the Iridaceae, with the genera assigned to subfamily and tribe. Numbers in parentheses indicate the total genera and species for tribe or subfamily or total species for a genus. Important synonyms are indicated. Total 77 genera, 1,630 species.

-
1. Subfamily Isophysidoideae Takhtajan (1980) (1 : 1)
 - Isophysis* (1)—Tasmania
 2. Subfamily Nivenioideae Schulze (1971) ex Goldbl.¹ (6 : 83)
 - Aristea* (50)—Africa, Madagascar
 - Geosiris* (1)—Madagascar
 - Nivenia* (9)—Cape Region, South Africa
 - Klattia* (2)—Cape Region, South Africa
 - Witsenia* (1)—Cape Region, South Africa
 - Patersonia* (20)—Australia, Borneo, Sumatra, New Guinea
 3. Subfamily Iridoideae (42 : 690)
 - Tribe Sisyrinchieae Baker (1878) (8 : 124)
 - Bobartia* (12)—southern Africa
 - Libertia* (ca. 9)—Australasia, South America
 - Diplarrhena* (2)—southeastern Australia, Tasmania
 - Orthrosanthus* (9)—Australia, South and Central America
 - Sisyrinchium* (ca. 80)—North and South America
 - Olsynium* (incl. *Phaiophleps*, *Chamelum*, *Ona*) (11)—North and South America
 - Solenomelus* (2)—Chile, Argentina
 - Tapeinia* (1)—southern Chile and Argentina
 - Tribe Irideae (13 : 405)
 - Dietes* (6)—East and southern Africa, Lord Howe Island
 - Moraea* (120)—sub-Saharan Africa
 - Homeria* (incl. *Sessilistigma*) (32)—southern Africa
 - Rheome* (3)—western Cape, South Africa
 - Hexaglottis* (6)—western Cape, South Africa
 - Roggeveldia* (1)—Karoo, South Africa
 - Barnardiella* (1)—western Cape, South Africa
 - Gynandris* (9)—southern Africa, Mediterranean, Middle East
 - Galaxia* (14)—South Africa
 - Pardanthopsis* (1–2)—eastern Asia
 - Belamcanda* (1)—southeastern Asia
 - Iris* (ca. 210)—Europe, Asia, North Africa, North America
 - Hermodactylis* (1)—Mediterranean Middle East
 - Tribe Mariceae Hutchinson (1934) (3 : 40)
 - Trimezia* (ca. 20)—South and Central America
 - Pseudotrimezia* (6–8)—Brazil
 - Neomarica* (ca. 12)—South and Central America
 - Tribe Tigridieae Baker (1878) (18 : 125)
 - Cypella* (ca. 20)—South and Central America
 - Cipura* (ca. 6)—South and Central America, West Indies
 - Eleutherine* (2)—South and Central America, West Indies
 - Ennealophus* (5)—South America
 - Gelasine* (4)—South America
 - Calydorea* (incl. *Cardiostigma*, *Catila*, *Itysa*) (ca. 10)—temperate South America
 - Ainea* (2)—Mexico
 - Nemastylis* (5)—Central America, Mexico, southern U.S.A.
 - Herbertia* (ca. 6)—temperate South America, southern U.S.A.
 - Onira* (1)—temperate South America
 - Kelissa* (1)—temperate South America
 - Mastigostyla* (ca. 16)—South America
 - Cardenanthus* (ca. 8)—South America
 - Tigridia* (ca. 35)—South and Central America
 - Sessilanthera* (3)—Mexico and Central America
 - Alophia* (ca. 5)—tropical South and Central America, southern U.S.A.
 - Fosteria* (1)—Mexico
 - Cobana* (2)—Guatemala, Honduras
-

TABLE 3. Continued.

4. Subfamily Ixioidae Klatt (1866) (as subordo Ixieae) (28 : 860)
Tribe Pillansieae Goldblatt ² (1 : 1)
<i>Pillansia</i> (1)—southwestern Cape, South Africa
Tribe Watsonieae Klatt (1882) (5 : 99)
<i>Lapeirousia</i> (ca. 36)—tropical and southern Africa
<i>Savannosiphon</i> (1)—south tropical Africa
<i>Micranthus</i> (3)—southwestern Cape, South Africa
<i>Thereianthus</i> (7)—southwestern Cape, South Africa
<i>Watsonia</i> (52)—southern Africa
Tribe Ixieae Dumortier (1822) (22 : 760)
<i>Ixia</i> (45)—South Africa
<i>Dierama</i> (44)—tropical and southern Africa
<i>Sparaxis</i> (including <i>Synnotia</i>) (12)—southwestern Cape, South Africa
<i>Freesia</i> (11)—southern Africa
<i>Anomatheca</i> (6)—south tropical and southern Africa
<i>Crocsmia</i> (9)—south tropical and southern Africa
<i>Devia</i> (1)—southern Africa
<i>Chasmanthe</i> (3)—southwestern Cape, South Africa
<i>Tritonia</i> (28)—south tropical and southern Africa
<i>Duthieastrum</i> (1)—southern Africa
<i>Geissorhiza</i> (82)—South Africa
<i>Hesperantha</i> (ca. 62)—tropical and southern Africa
<i>Schizostylis</i> (1)—southern Africa
<i>Melaspheerula</i> (1)—southern Africa
<i>Gladiolus</i> (incl. <i>Homoglossum</i> , <i>Anomalesia</i> , <i>Oenostachys</i>) (ca. 195)—Africa, Madagascar, Eurasia
<i>Radinosisiphon</i> (1–2)—south tropical and southern Africa
<i>Babiana</i> (incl. <i>Antholyza</i>) (64)—southern Africa, Socotra
<i>Tritonopsis</i> (incl. <i>Anapalina</i>) (22)—South Africa
<i>Zygotritonia</i> (4)—tropical Africa
<i>Romulea</i> (ca. 90)—Africa, Mediterranean
<i>Syringodea</i> (8)—southern Africa
<i>Crocus</i> (ca. 80)—Europe, Asia, North Africa

¹ **Nivenioideae** Schulze ex Goldblatt, subfam. nov. Plantae foliis sine costis medianis, caulibus subterraneis vel aeriis et saepe lignosis, inflorescentiis binatis, floribus actinomorphae usitate caeruleis, tepalis plus minus liberis vel in tubum connatis.

² **Pillansieae** Goldblatt, trib. nov. Planta foliis sine costis medianis, inflorescentia paniculata, floribus sessilibus actinomorphae, tepalis in tubum connatis, stigmatibus plus minus integribus.

type seems basic to the subfamily but is variously modified in specialized lines. Another significant specialization in Iridoideae is the presence of the free amino acids meta-carboxyphenylalanine and glycine (Larsen et al., 1981, 1987).

Iridoideae comprise four important lines, which are treated here as tribes. The least specialized of these is the Sisyrinchieae (Fig. 2A, B). The tribe may be heterogeneous, and an absence of apomorphic features makes it difficult to deal with. Possibly it is united by having the long style branches extending between the stamens rather than opposite them (this feature may be basic for the subfamily). All the species so far examined for flavonoids are apparently derived in not accumulating flavonols (a reversal). *Libertia* and *Orthrosanthus* occur in Australasia and South America, the latter also in Central America, while *Diplar-*

rhenia is restricted to southeastern Australia and Tasmania. The large and diverse *Sisyrinchium* and its close allies, including *Olsynium* (incl. *Phaiophleps* and *Ona*), *Tapeinia*, and *Solenomelus*, all small genera, are solely New World and centered in South America. *Bobartia* appears unusual phytogeographically in being southern African (Strid, 1972).

The floral morphology of *Bobartia* is virtually identical with other Sisyrinchieae but it has two unusual features: pubescent pedicels and scattered fibers in the phloem (Rudall, 1983). The latter is a constant attribute of several African genera of Irideae, including *Diets* and *Moraea*, while pubescent pedicels are known elsewhere in Iridaceae only in *Diets*. If *Bobartia* is misplaced in Sisyrinchieae, it may have acquired its apparently simple floral morphology by a reversal to a more



FIGURE 6. Iridoideae tribe Irideae.—A. *Moraea atropunctata* Goldbl., habit and detail of the stamens and gynoecium.—B. Corm of *Moraea* with tunics removed showing apical origin of roots.—C. *Iris afghanica* Wendelbo, habit (from Hedge & Wendelbo, 1972—@ Crown copyright. Reproduced with the permission of the Controller of her Britannic Majesty's Stationery Office).—D. *Hexaglottis namaquana* Goldbl., habit, flower, and detail of the stamens and gynoecium.—E. *Galaxia luteo-alba* Goldbl., showing acaulescent habit. Habits $\times \frac{1}{2}$, details life-size or variously enlarged.

primitive condition, such as is likely to have occurred in *Eleutherine*—*Tigridieae* and *Roggevelandia*—*Irideae*, for example (Goldblatt, 1979b). Alternatively, the tribes as delimited here require reevaluation. The flavonoids and other phytochemical features of *Bobartia* are poorly sampled and further investigation may resolve the conflict.

The three other important assemblages in Iridoideae form a clade united by having flowers in which the tepals are differentiated into a limb and claw, and in which the upper apices of the style branches are produced into nonstigmatic paired appendages (crests). The unusual γ -glutamyl peptides are present in most members examined (but notably not yet reported in *Tigridieae*, of which only four species have been sampled). *Irideae*, centered in the Old World, have the style branches and crests flattened and petaloid (Fig. 6A), nectaries restricted to the base of the outer tepals (at least in the less specialized genera), and, in all genera, a characteristic subepidermal marginal sclerenchyma. The largest genus is *Iris*, mainly Eurasian but also in North America, and often treated as several genera (Rodionenko, 1961), including *Iridodictyum*, *Xiphium*, and *Scorpiris*, all of which have bulbs, and *Junopsis*, which has swollen roots and a vestigial rootstock. The phylogeny of *Iris* s.l. needs careful study before the several segregates are finally accepted. In sub-Saharan Africa there are *Dietes*, with one species on Lord Howe Island, and several genera with apically rooting corms, notably *Ferraria*, *Moraea*, *Homeria*, and *Galaxia*. All but *Ferraria* also have a secondarily bifacial dorsiventral leaf. *Moraea*, the largest genus with some 120 species, has radiated extensively in southern and east tropical Africa (Goldblatt, 1977, 1986a). The other genera, all apparently segregates of *Moraea* (Goldblatt, 1987 and in prep.), are centered in the winter rainfall area of the southwestern coast of southern Africa.

Three subtribes have been proposed for *Irideae* (Goldblatt, 1976): *Iridinae* (*Iris*, *Belamcanda*, *Hermodyctylis*, and *Pardanthopsis*); *Ferrariinae* (*Ferraria*); and *Homeriinae* (*Moraea*, *Homeria*, *Galaxia*, *Hexaglottis*, *Gynandris*, and other genera). The disposition of *Dietes* is somewhat uncertain although in the past I have aligned it with *Iridinae* (Goldblatt, 1981).

In the New World, *Mariceae* and *Tigridieae* share an apparently identical flower with thickened style branches (in contrast to the flattened branches of *Irideae*), nectaries best developed on the inner tepals, and unusual slender and weak filaments so that the anthers are supported by being attached to the style branches. The nectaries also produce oils (Vogel, 1974) secreted by clavate elaiophores.



FIGURE 7. *Ixioidae*. *Pillansia templemannii* L. Bolus. Inflorescence $\times \frac{1}{2}$, rootstock and leaf $\times \frac{1}{6}$.

Mariceae, comprising *Trimezia*, *Neomarica*, and possibly *Pseudotrimezia*, have leaves with distinct midribs and they apparently lack flavonols (a parallelism with *Sisyrinchieae*). *Tigridieae*, a larger tribe, are poorly understood taxonomically. They have three important synapomorphies: plicate leaves, a distinctive type of bulb, and the derived basic chromosome number of $x = 7$. *Tigridieae* have radiated extensively in temperate and Andean South America, and in Mexico. Major specializations are all floral and focus on the style and sta-



FIGURE 8. Ixioidae.—A. *Watsonia spectabilis* L. Bolus, habit.—B. Detail of corm of A with tunics removed showing basal origin of the roots.—C. *Hesperantha luticola* Goldbl., habit and flower.—D. *Geissorhiza mathewsii* L. Bolus, habit and detail of flower and leaf section.—E. *Lapeirousia lewisiae* B. Nord., habit and flower. Habits $\times \frac{1}{2}$, details life-size or variously enlarged.

mens. Several new and mostly monotypic genera have recently been described by Ravenna (1981, 1983, 1986), and it seems clear that the current systematics, based on the minor variations in the shape or disposition of the style branches and the degree of fusion of the filaments, is unsatisfactory and is leading to the chaotic proliferation of monotypes. Careful cladistic analysis may point the way to a more acceptable taxonomy, reflecting as far as possible, natural relationships.

Two subtribes have been proposed in Tigridieae (Goldblatt, 1982b), Cipurinae, with a base number of $x = 7$, monosulcate pollen grains, and generally simple, thickened style branches, and Tigridiinae, with x usually = 14, bisulcate pollen grains, style branches deeply divided into filiform arms, and stamens united.

IXIOIDEAE

Ixiodeae (Figs. 7, 8) are remarkably distinct from other Iridaceae in numerous features. The subfamily is centered in southern Africa, with the specialized genera *Romulea* and *Gladiolus* also in Eurasia, where the large genus *Crocus* has radiated. Synapomorphies for Ixiodeae (Fig. 5, Table 1) are presence of perianth tubes, basal rooting corms, inflorescences of sessile flowers arranged in a panicle or spike (Fig. 8), micropunctate pollen exines, and closed leaf sheaths. All Ixiodeae so far examined have septal nectaries (Daumann, 1970), which may be the basic condition in the family.

Ixiodeae comprise over 860 species, about half the family, and some 760 of these belong in Ixieae. The monotypic Cape *Pillansia* is taxonomically isolated in the subfamily, and is the only genus with a panicle (Fig. 7), presumably ancestral to the spike, which is basic to the other two tribes. These also have distinct leaf midribs and specialized leaf anatomy (Rudall, pers. comm., see earlier discussion of leaf anatomy). *Pillansia* also lacks flavone C-glycosides (a parallelism with Watsonieae). This genus is apparently unique in Iridaceae in having a flavonol sulfate. Despite the undesirability of monotypic groups, it seems necessary to treat *Pillansia* as the only member of a tribe Pillansieae.

Watsonieae comprise some 99 species in 5 genera, which share unusual deeply divided style branches as well as the absence of flavone C-glycosides (as does *Pillansia*). The tribe includes the southern African *Watsonia*; two endemic Cape genera, *Thereianthus* and *Micranthus*; *Lapeirousia*, spread through sub-Saharan Africa; and the monotypic south tropical African *Savannosiphon*. *Watsonia* is extremely variable in its floral morphology, and bird-pollinated flowers (e.g., Fig.

8A) have evolved independently in at least three lines in the genus (Goldblatt, 1989).

Ixieae have corms that develop partially from the apical bud (explained in detail earlier), an unusual array of flavones not found in the rest of the family, and flavone O-glycosides. Some eight subtribes have been recognized in Ixieae as here circumscribed (Lewis, 1954; Goldblatt, 1971), all relatively small monophyletic assemblages, each of which has a common basic chromosome number and unique character combination. These subtribes include Ixiinae (*Ixia*, *Dierama*, *Sparaxis*), $x = 10$, membranous and usually dry bracts, filiform style branches, and fibrous corm tunics; Tritoniinae (*Tritonia*, *Crocasmia*, *Chasmanthe*, *Duthieastrum*), $x = 11$, short subherbaceous bracts, orange flower colors, and fibrous corm tunics; Gladiolinae (*Gladiolus* including *Homoglossum*, *Anomalesia*, and *Oenostachys*; *Radinosophon*), $x = 15$, long herbaceous bracts, wiry corm tunics, spatulate style branches, and winged seeds; Hesperanthinae (*Geissorhiza*, *Hesperantha*, *Schizostylis*, and possibly *Melasphaerula*), $x = 13$, more or less herbaceous bracts, woody corm tunics, filiform style branches; Babianinae (only *Babiana*, $x = 7$, subfibrous tunics, plicate leaves, spatulate style branches, and herbaceous bracts; Romuleinae (*Crocus*, *Romulea*, *Syringodea*), possibly $x = 13$, woody corm tunics, flowers solitary on the branches of the flowering stems, often divided style branches. Additionally, *Freesia* and *Anomatheca*, both $x = 11$, and *Tritoniopsis*, apparently $x = 16$, are allied and have been placed in Freesiinae and Anapalinae respectively. Their affinities to other genera of Ixieae are uncertain, but similarities in leaf margin epidermis (Rudall & Goldblatt, in press) suggest links with Tritoniinae. The relationships of the tropical African *Zygotritonia* are likewise uncertain.

There are probably several old and taxonomically isolated lines in Ixieae. However, genera within each line are often not well defined and may be of comparatively recent origin. Zygomorphic flowers have evolved independently in most lines (Fig. 8A, E), sometimes, as in *Geissorhiza*, *Babiana*, and *Gladiolus*, more than once in each. Large bird-pollinated flowers with red to orange perianths, long dimorphic tubes, and exerted anthers and style branches have also evolved independently in at least three lines with *Gladiolus* (Goldblatt & de Vos, 1989), in *Babiana* (*B. ringens*), *Chasmanthe*, and *Tritoniopsis*, as well as in *Watsonia* (Watsonieae). Convergence in floral form has obscured the natural relationships of many Ixiodeae (Lewis, 1954), and vegetative morphology and chromosome cytology (Goldblatt, 1971) are now

accepted as more important for phylogenetic considerations above the species level than most floral features.

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