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PATTERNS OF EVOLUTION IN CHARACTERS THAT DEFINE *IRIS* SUBGENERA AND SECTIONS

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ABSTRACT

Subgeneric groups have been circumscribed in *Iris* based on a small number of morphological characters. Recent DNA sequence data has indicated that several of the subgenera, sections, and series that have previously been delineated are paraphyletic or polyphyletic. The evolution of characters that have traditionally been used to distinguish subgeneric and sectional groups within *Iris* was investigated by mapping these characters on a phylogenetic tree based on *matK* sequence data. Results indicate that rhizomes are pleiomorphic for the genus and that three bulb types have arisen independently. My analysis shows that sepal beards, sepal crests, and seed arils show extensive homoplasy. Most of the homoplasy seen is associated with the circumscription of polyphyletic subgeneric groups such as the beardless subgenus *Limniris*. Some additional homoplasy is due to diversity within supported clades or the historical use of a single character in circumscribing more than one subgeneric group.

Key words: aril, character evolution, geophytic organ, Iridaceae, *Iris*, phylogeny, sepal ornamentation.

INTRODUCTION

The family Iridaceae is considered to be Gondwanan in origin with about 60 genera, most occurring in Africa and Central/South America (Raven and Axelrod 1981). The largest genus, *Iris* L., is a temperate group of perennial herbs with about 300 species and many infraspecific taxa. *Iris* species share several characters that are uncommon in other Iridaceae, including petaloid style branches, distinct perianth whorls where petals are often smaller than sepals, inflorescences that are flattened in one plane, and a geographic distribution in the Northern Hemisphere. The genus has diversified into mesic and xeric habitats across the temperate north, with the greatest number of species occurring in the Mediterranean area and Asia. *Iris* illustrates a diversity of morphologies among and along its lineages. Three features that illustrate the diverse morphologies found in *Iris* are their geophytic organs, leaf development, and sepal ornamentations. The first is related to the xerophytic environment inhabited by many *Iris* and the last to pollinator attraction. It is less obvious why some *Iris* species have dorsiventral leaves while most have unifacial leaves, a leaf form common in monocotyledons. In addition, *Iris* demonstrates a complexity of floral whorls where stamens are opposite to petals and styles have petaloid crests.

The genus is currently divided into six subgenera and 12 sections with *Iris* sect. *Limniris* Tausch further divided into 16 series. This classification (Mathew 1989) is based largely on work by Dykes (1913), Lawrence (1953), and Rodionenko (1987). The Species Group of the British Iris Society (1997) published an updated species account following Mathew's classification. Rodionenko (1987) emphasized seedling morphology and proposed a number of taxonomic changes that have generally not been accepted (Dahlgren et al. 1985). He recognized the subgenera *Hermodyloides* Spach, *Scorpiris* Spach, and *Xiphium* (Miller) Spach as distinct genera (*Iridodictyum* Rodion., *Juno* Tratt., and *Xiphium* (Miller) Rodion., respectively), and combined several sections within *Iris* subgen. *Iris* recognizing only two sections,

Iris and *Hexapogon* (Bunge) Baker. Taylor (1976) disputed the combining of all arilate species within subgen. *Iris* into a single sect. *Hexapogon*. Each of the studies cited above is based on observed morphological, cytological, and/or geographical similarities among species within the genus. Five phylogenetic studies have been undertaken using morphological (Wilson 1998), nrDNA (Wilson 2003), cpDNA (Tillie et al. 2001; Wilson 2004), and RAPDs and cpDNA data (Makarevitch et al. 2003). Only the Tillie et al. (2001) and Wilson (2004) papers are comprehensive, as others are regional or report on a subgroup within the genus.

The current classification of *Iris* is primarily based on four morphological characters. These characters are the type of geophytic organs present, and the presence or absence of arils on seeds, raised elaborations on sepal midveins (crests), and obvious linear arrays of sepal hairs (beards). Although these characters are considered defining features for the subgenera and sections described they are not always present in all species nor are they exclusively present within defined subgroups. An example of the first condition is *Iris kolpakowskiana* Regel that lacks an aril even though it is within subgen. *Hermodyloides*, an arilate group. Examples of the latter condition are subgen. *Iris* that is considered characterized by the presence of a beard and subgen. *Limniris* (Tausch) Spach sect. *Lophiris* (Tausch) Tausch that is characterized as possessing a crest. However, several species in subgen. *Scorpiris* and *Nepalensis* (Dykes) Lawr. have crests and some of the crests are bearded. Some species within subgen. *Limniris* sect. *Limniris* also have obvious sepal hairs. It is also evident that the homologies of some morphological characters have not been rigorously determined. An example is seen in the descriptions of geophytic organs. Terminology used in descriptions includes rhizomes, corms, stolons, bulbs, tubers, stolon-like rhizomes, bulb-like rhizomes, and tuber-like rhizomes.

The use of existing morphological characters to define groupings within *Iris* is further complicated by recent phylogenetic studies. Results from molecular data (Wilson 2004)

Table 1. List of species included in study with collector, collection number, herbarium of deposit, date of collection, locality where collected. UBCG indicates living collections at the University of California Botanical Garden, Berkeley, California, USA.

Species	Collection data
<i>I. aphylla</i> L.	Mosulishvili G99-09 (RSA), 11 Jun 1999, Mtskheta, Republic of Georgia
<i>I. barnumae</i> Foster & Baker	Usta T03-08 (RSA), 7 Apr 2003, Turkey
<i>I. brevicaulis</i> Raf.	Karst US01-14 (RSA), 22 Aug 2001, Gray Summit, Missouri, USA
<i>I. caucasica</i> Hoffm.	Mosulishvili G00-3 (RSA), 9 Apr 2000, Betama, Republic of Georgia
<i>I. colchica</i> Kem.-Nath.	Wilson G98-19 (RSA), 17 Jun 1998, Tbilisi Botanical Garden, Republic of Georgia
<i>I. collettii</i> Hook. f.	UCBG 02.0215 (UC), 19 Jun 2003, UC Botanical Garden, Berkeley, California, USA
<i>I. cristata</i> Sol.	Karst US01-16 (RSA), 22 Aug 2001, Gray Summit, Missouri, USA
<i>I. cuniculiformis</i> Noltie & K. Y. Guan	Ace 181 (KEW), Dec 1984, China
<i>I. danfordiae</i> (Baker) Boiss.	Usta T02-13 (RSA), 10 Jun 2002, Turkey
<i>I. elegantissima</i> Sosn.	Mosulishvili G00-04 (RSA), 21 Apr 2000, Tbilisi Botanical Garden, Republic of Georgia
<i>I. falcifolia</i> Bunge	Ashabad s.n. (KEW), Mar 1897, Turcomania [Iraq]
<i>I. forrestii</i> Dykes	UCBG 90.2497 (UC), 25 May 2002, UC Botanical Garden, Berkeley, California, USA
<i>I. fosteriana</i> Aitch. & Baker	Polunin 11838 (KEW), May 1973, Iran
<i>I. fulva</i> Ker Gawl.	Karst US01-14 (RSA), 22 Aug 2001, Gray Summit, Missouri, USA
<i>I. histrioides</i> (G. Wilson) Arn.	Guner 5500 (KEW), May 1977, Turkey
<i>I. humilis</i> Georgi	Alexeeva R01-19 (RSA), Jul 2001, Altay Mts., Russia
<i>I. iberica</i> Hoffm.	Mosulishvili G99-13 (RSA), 12 Jun 1999, Tbilisi Botanical Garden, Republic of Georgia
<i>I. imbricata</i> Lindl.	Wilson G98-17 (RSA), 17 Jun 1998, Tbilisi Botanical Garden, Republic of Georgia
<i>I. lazica</i> Albov	Usta T03-12 (RSA), 7 Apr 2003, Turkey
<i>I. loczyi</i> Kanitz	R. B. & L. Gibbons 61 (KEW), Apr 1971, Iran
<i>I. masia</i> Dykes	Guner 1518 (KEW), Apr 1984, Turkey
<i>I. missouriensis</i> Nutt.	Wilson US01-01 (RSA), 16 Jun 2001, Trout Mts., Oregon, USA
<i>I. musulmanica</i> Fomin	Mosulishvili G99-11 (RSA), 5 Jun 1999, Pantishara, Republic of Georgia
<i>I. orientalis</i> Mill.	Akhalkatsi D99-01 (no voucher), Botanic Garden of the University of Düsseldorf
<i>I. persica</i> L.	Usta T02-15 (RSA), 10 Jun 2002, Turkey
<i>I. potaninii</i> Maxim.	Alexeeva R01-22 (RSA), Jul 2001, Altay Mts., Russia
<i>I. pseudocaucaucasica</i> Grossh.	Ingham 182 (KEW), May 1976, Iran
<i>I. pseudacorus</i> L.	Mosulishvili G99-10 (RSA), 24 Apr 1999, Golaskuri, Republic of Georgia
<i>I. reticulata</i> M. Bieb.	Mosulishvili G00-02 (RSA), 15 Apr 2000, Mtatsminda, Republic of Georgia
<i>I. sanguinea</i> Donn ex Hornem.	Bogner 1628 (KEW), Jun 1983, Korea
<i>I. sari</i> Schott ex Baker	Usta T02-11 (RSA), 10 Jun 2002, Turkey
<i>I. schachtii</i> Markgr.	Usta T03-01 (RSA), 4 Jul 2003, Turkey
<i>I. setosa</i> Pall. ex Link	Pfauth US02-09 (RSA), 9 Jul 2002, Anchorage, Alaska, USA
<i>I. sibirica</i> L.	Mosulishvili G99-12 (RSA), 25 May 1999, Kazbegi, Republic of Georgia
<i>I. spuria</i> L.	Wilson G99-21 (RSA), 17 Jun 1998, Tbilisi Botanical Garden, Republic of Georgia
<i>I. stenophylla</i> Hausskn. & Siehe	Usta T03-03 (RSA), 4 Jul 2003, Turkey
<i>I. tenax</i> Douglas ex Lindl.	Wilson 92-ph-28 (RSA), 4 May 1998, Newport, Oregon, USA
<i>I. tenuis</i> S. Watson	Wilson US01-12 (RSA), 31 Jul 2001, Clackamas, Oregon, USA
<i>I. tigridia</i> Bunge ex Ledeb.	Alexeeva R01-18 (RSA), Jul 2001, Altay Mts., Russia
<i>I. tingitana</i> Boiss. & Reut.	UCBG 2001.0507 (UC), 6 Mar 2003, UC Botanical Garden, Berkeley, California, USA
<i>I. turcica</i> B. Mathew	Pesmew 2778 (KEW), May 1972, Turkey
<i>I. unguicularis</i> Poir.	Usta T03-07 (RSA), 7 Apr 2003, Turkey
<i>I. virginica</i> var. <i>shrevei</i> (Small) E. S. Anders.	Karst US01-15 (RSA), 22 Aug 2001, Gray Summit, Missouri, USA
<i>I. wattii</i> Baker	UCBG 92.155 (UC), 25 May 2002, UC Botanical Garden, Berkeley, California, USA
<i>Belamcanda chinensis</i> (L.) DC.	UCBG 65.0289 (UC), 25 May 2002, UC Botanical Garden, Berkeley, California, USA
<i>Gladiolus caucasicus</i> Herb.	Wilson G98-20 (RSA), 19 Jun 1998, Kazbegi, Republic of Georgia
<i>Moraea sisyrrinchium</i> Ker Gawl.	UCBG 96.0051 (UC), 6 Mar 2003, UC Botanical Garden, Berkeley, California, USA
<i>Patersonia sericea</i> R. Br.	Wilson AU01-07 (RSA), 20 Sep 1999, St. Albans, New South Wales, Australia

indicate that the current classification does not consistently describe monophyletic groups. This finding suggests that the morphological characters used to determine currently circumscribed *Iris* subgenera and sections may have arisen more than once. This paper reports on the evolution of each of these characters, documenting the number of times they are likely to have evolved. Of particular interest is whether they occur as synapomorphies on major branches resolved by cpDNA data (Wilson 2004). This study is part of a project

to determine an overall outline of phylogeny for the genus *Iris*.

MATERIALS AND METHODS

Species Included in Study

The 44 taxa included in this study are listed in Table 1 with the primary source used to determine character states. Species from each of the six subgenera within *Iris* are in-

cluded and represent nine of the 12 recognized sections. Species from subgen. *Iris* sect. *Regelia* Lynch, and *Hermodyloides* sects. *Brevituba* B. Mathew and *Monolepis* (Rodion.) B. Mathew were not available for this study. An attempt was made to sample widely within subgen. *Iris* sect. *Limniris* because 16 series have been circumscribed within the section. Species from nine series within sect. *Limniris* were included. The series to which a species is assigned was not identified in the resulting trees of character evolution because an analysis of the many characters used to circumscribe these series was beyond the scope of this study. Also included in the morphological analysis was *Belamcanda chinensis*, a monotypic genus from China that has been proposed as belonging within *Iris* (Tillie et al. 2001; Wilson 2004), a placement that is consistent with my findings. Most of the morphological data was collected from field studies of living plants in their native habitats, observations of plants growing in the author's living collection, plants growing in botanical gardens, or from herbarium specimens. Where complete material was not available I used published sources. I visited the Republic of Georgia and surrounding territories in June 1998 where I collected living or dried material and/or morphological data from 11 Caucasian taxa that were included in this study. From 2000–2003 I collected or obtained from colleagues, living or dried specimens from 39 *Iris* included in this study. Some of this material supplemented collections or data from my earlier trip to the Republic of Georgia. These collections were from wild populations with the exception of eight *Iris* from botanical gardens. Additional morphological data was collected from 12 *Iris* during trips in 2001 to the Herbarium at The Royal Botanic Gardens, Kew, UK, and in 2002 to the Wisconsin State Herbarium, Madison, USA.

Phylogenetic Tree Used

The data set used in this study of character evolution was the same one analyzed in Wilson (2004). Four outgroup taxa (Table 1) from Iridaceae were selected, based on research at the family level (Souza-Chies et al. 1997; Fay et al. 2000; Reeves et al. 2001; Goldblatt et al. 2002). Two outgroups, *Belamcanda chinensis* and *Moraea sisyrinchium* (*Gynandris sisyrinchium*), also in subfamily Iridoideae, were resolved as closely aligned to *Iris* (Reeves et al. 2001). Subfamily Ixiodeae was represented by *Gladiolus caucasicus* and subfamily Nivenioideae by *Paterosonia sericea*. *Paterosonia* R. Br. and *Gladiolus* L. were resolved as more distantly related to *Iris* (Reeves et al. 2001). Because *Belamcanda chinensis* was resolved within *Iris* by Wilson (2004) (Fig. 1), this taxon was included in the analysis of the evolution of arils, crests, beards, and geophytic organs. Other outgroup taxa were used to root the tree but were not coded for morphological character states.

The single maximum likelihood (ML) tree ($-\ln L = 9275.171$) resulting from an analysis of the entire *matK* gene and partial sequences of the flanking *trnK* introns (Wilson 2004) was used to determine character evolution within *Iris*. All nucleotide sites (1996 base pairs [bp]) in the sequence data set were aligned and included in the data set. Comparing *Iris* species, 477 (24%) of the nucleotide sites were variable and 253 (13%) were potentially parsimony informative.

The percent of variable and potentially parsimony-informative nucleotide characters differed by less than 2% between the gene and intron regions. Insertions and deletions (indels) were ignored during the analyses. Based on results from MODELTEST vers. 3.06 (Posada and Crandall 1998), the TRN + G model, a variation of general time reversal (GTR), was used in the phylogenetic analyses. The ML tree was found using PAUP* vers. 4.0b10 (Swofford 2002) and the "heuristic" option with random stepwise addition of taxa (10 additions) and tree-bisection-reconnection (TBR) (500 replications). Bootstrap (Felsenstein 1985) analysis (500 replications) was used to determine the robustness of trees obtained. Bootstrap percentages greater than 50% were reported.

Morphological Characters Included in Study

Characters included were the type of geophytic organ and the presence or absence of arils, beards, and crests (Table 2). Geophytic organs were present in all species and were recorded as rhizomes, bulbs (three types), or root tubers. Bulbs comprised of a single leaf scale, multiple leaf scales that were partially fused and formed a compact bulb, and multiple but separate leaf scales that formed loose bulbs were recognized. Arils were subdivided into arils that occurred either terminally on seeds or parallel to seed long axis (lateral), and crests were subdivided into simple crests that consisted of a raised area along the sepal midvein or dissected crests that were more elaborate and terminated in conspicuous teeth or fringes. The absence of an aril or crest, or the presence of one of the two types of aril or crest was recorded for each species. Sepal beards were recorded as present or absent.

Hypotheses of character evolution were determined by individually tracing character state distributions onto the *matK* sequence data phylogenetic tree (Fig. 1) described briefly above. Characters were mapped onto the tree using MacClade vers. 3.04 (Maddison and Maddison 1992) and the DELTRAN (delayed transformation) option. This option assigns state changes to ancestors occupying more terminal positions and favors parallel evolution over reversals.

RESULTS

Analyses of character evolution indicated that most of the characters supporting the current subgeneric classification of *Iris* have evolved multiple times (Table 2). The gain of each type of geophytic organ occurred only once on the tree, indicating that the evolution of these organs was not homoplastic in the species studied. On the other hand, gains and losses of arils, crests, and beards indicated multiple origins for each of these characters. Two clades (A and B) are indicated in Fig. 2 and 3 to facilitate the presentation of results. Neither of these clades are supported by bootstrap values.

Evolution of Geophytic Organs

My analysis suggested that the ancestral geophytic organ was a rhizome and that bulbs have evolved several times within the genus (Fig. 2, Table 2). When bulbs were subdivided into three types each evolved only once (Fig. 2, Table 2). For multi-scaled bulbs I have indicated one gain, in sub-

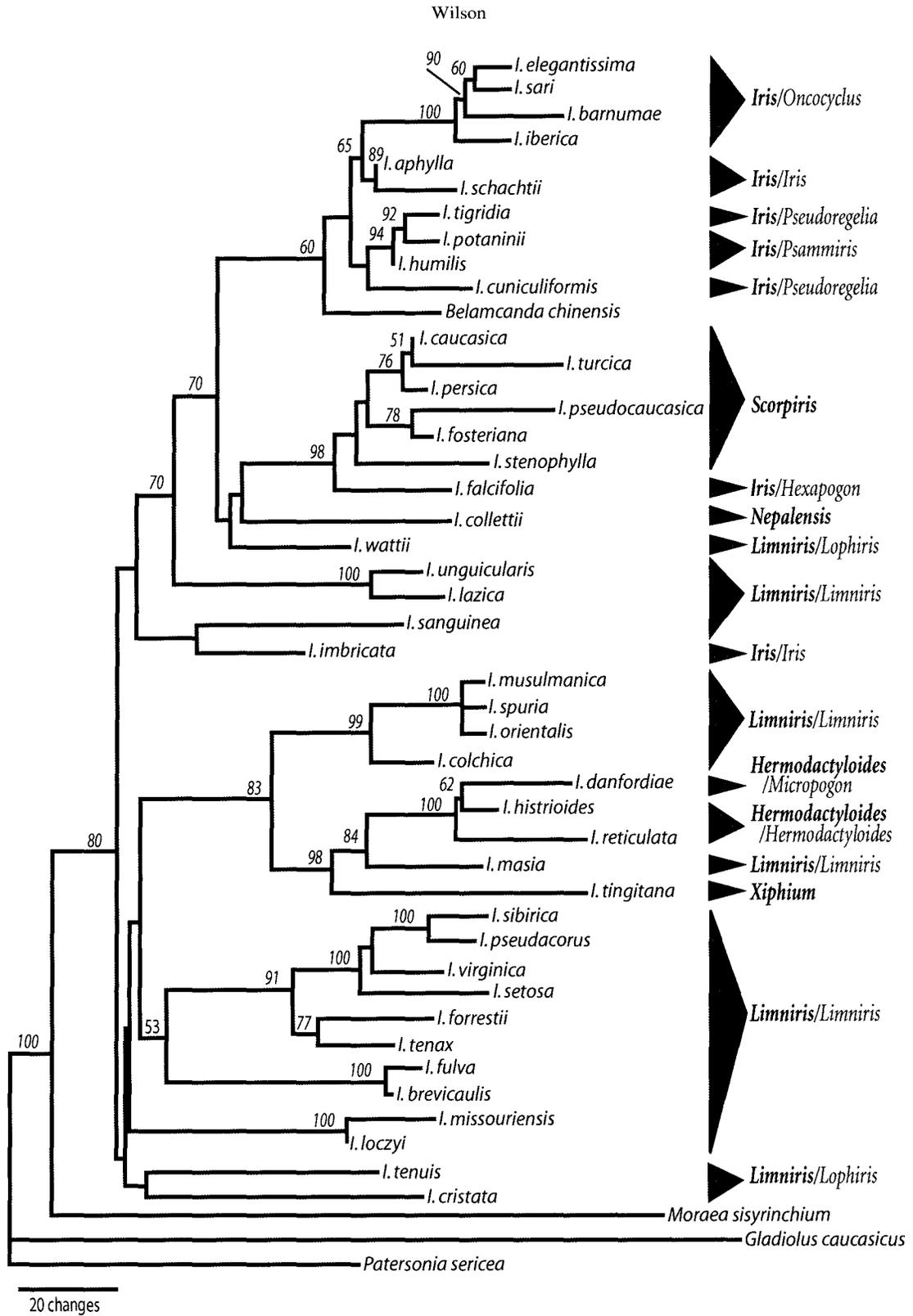


Fig. 1.—Maximum-likelihood tree that was resolved using *matK* data (Wilson 2004). Bootstrap values greater than 50% are shown above branches. The current placement of species within subgenera (bold) and sections is indicated to the right. This tree was used to determine the patterns of evolution for morphological characters in *Iris*.

Table 2. Characters included in study and number of proposed gains and losses based on an analysis of character evolution.

Character	# of proposed gains & losses	Character	# of proposed gains & losses
Geophytic Structure		Arils	
Rhizome	1	Terminal	4
Multi-scaled bulb	1	Lateral	2
Free-scaled bulb	1	Crests	
Single-scaled bulb	1	Simple	6
Root tubers	1	Dissected	2
		Beards	3

gen. *Scorpiris*, but because bootstrap values were at or below 50% for the clade comprised of species from subgen. *Scorpiris* (Fig. 1), it is possible that evolution in multi-scaled bulbs may have been homoplasious. *Iris masia* shared single-scaled bulbs with subgen. *Hermodactyloides* species, but older specimens also had short rhizomes present. Free-scaled bulbs were only present in subgen. *Xiphium*. Tuberous roots, as a sole organ of storage, evolved only in subgen. *Nepalensis*. However, storage roots were present in conjunction with bulbs or rhizomes in several other species.

Evolution of Arils

Arils evolved multiple times in *Iris* (Table 2). Subdividing this character into arils terminal or lateral (parallel to long axis of seed) did not resolve the homoplasy of this character (Fig. 2). Both of the aril types evolved independently in clades A and B. Terminal arils were gained four times, with three gains in the polyphyletic subgen. *Iris*. Terminal arils although common in species of subgen. *Iris* were lacking in the polyphyletic sect. *Iris* and one species of sect. *Psammiris* (Spach) J. J. Taylor (*I. potaninii*). They were also present in all of the subgen. *Hermodactyloides* species included in this study. Lateral arils were gained twice, once in each clade of the polyphyletic subgen. *Limniris* sect. *Lophiris*.

Evolution of Crests

Crests were also homoplastic on the tree, having evolved multiple times (Table 2, Fig. 3). Subdividing the character into simple and dissected crests did not resolve the homoplasy present in this character. Dissected crests were gained twice in the polyphyletic subgen. *Limniris* sect. *Lophiris*, once in clade A and once in clade B (Fig. 3). Simple crests were gained four times in clade B, once each in subgen. *Hermodactyloides* and *Xiphium*, in the clade comprised of *I. missouriensis* and *I. loczyi*, and in *I. tenuis* (Fig. 3). My results indicated that simple crests were gained twice in clade A, once each in subgen. *Scorpiris* and *Nepalensis* (Fig. 3). The ACCTRAN (accelerated transformation) option would have traced simple crests as evolved once in the ancestor to the clade comprised of subgen. *Scorpiris* and *Nepalensis* and *I. falcifolia* (subgen. *Iris* sect. *Hexapogon*) and then lost in *I. falcifolia*.

Evolution of Beards

The final character, presence or absence of a beard on sepals, was homoplastic in this analysis (Table 2, Fig. 3).

Beards were restricted to species resolved within clade A. I considered beards to have evolved three times in clade A, in the clade comprised of most of the species of subgen. *Iris* sect. *Oncocyclus* (Siemssen) Baker, *Iris*, *Pseudoregelia* Dykes, and *Psammiris*, in *I. falcifolia* (subgen. *Iris* sect. *Hexapogon*), and in *I. imbricata* (subgen. *Iris* sect. *Iris*) (Fig. 3). *Iris stenophylla* in subgen. *Scorpiris* had a sepal crest with hairs and *I. virginica* had a patch of hairs on its sepal. Neither of these species was coded as having a beard because the hairs were not dense and linearly aligned.

DISCUSSION

This study found that the type of geophytic organ is useful in defining monophyletic groups and that the ancestral organ type is likely to be the rhizome. Earlier workers have speculated whether rhizomes or bulbs arose first in *Iris* (Dykes 1913; Rodionenko 1987). Dykes indicated that in *Iris grant-duffii* Baker bulbs appeared early in development and were later replaced by rhizomes, implying that rhizomes may have developed from bulbs. Rodionenko (1987) concluded that bulbs arose from rhizomes. He used as an example the subgen. *Scorpiris* where he interpreted bulbs as a new organ form that evolved concordant with the loss of the sword-shaped leaves that are common in rhizomatous species. He cites the presence of sword-shaped bracts only in reproductive shoots of *Scorpiris* species as evidence of the direction of leaf shape change from sword-shaped to rounded or channeled. He goes on to state that bulbs are particularly adapted to the xeric Mediterranean climates where they are found. Although I am not convinced by his reasoning, my data support his conclusions.

Treatment of the bulbous species of *Iris* has not been consistent among researchers. The current classification (Mathew 1989) recognizes three bulbous groups: subgen. *Scorpiris*, *Hermodactyloides*, and *Xiphium*. This arrangement is similar to Dykes (1913) who recognized three sections of bulbous *Iris*. Lawrence (1953) recognized two bulbous groups, one with bulbs lacking fleshy roots (subgen. *Xiphium*) and one with bulbs and fleshy roots (subgen. *Scorpiris*). He placed species from subgen. *Hermodactyloides* within subgen. *Xiphium*. Rodionenko (1987) elevated the three bulbous groups of *Iris* to the genera *Juno*, *Iriodictyum*, and *Xiphium*, respectively. Rodionenko's research emphasized seedling morphology and development in evolutionary groupings and he determined that each bulbous group was characterized by a distinct type of bulb development and final morphology. In my studies, I have also looked at bulb morphology and subdivided the character into bulbs comprised of single scale leaf, of multiple scale leaves that are partially united resulting in compact bulbs, and those where the multiple scale leaves are not united. These bulb categories are in agreement with Rodionenko's studies even though my data does not support Rodionenko's classification where he ranks the three groups of species with distinct bulb types at the generic level. Molecular data (Wilson 2004) resolves each of these groups as embedded within *Iris*.

Of interest is the placement of *I. masia* (subgen. *Limniris* sect. *Limniris*) as sister to the subgen. *Hermodactyloides* clade. This is in agreement with the findings of Tillie et al. (2001), and has been suggested prior to molecular studies

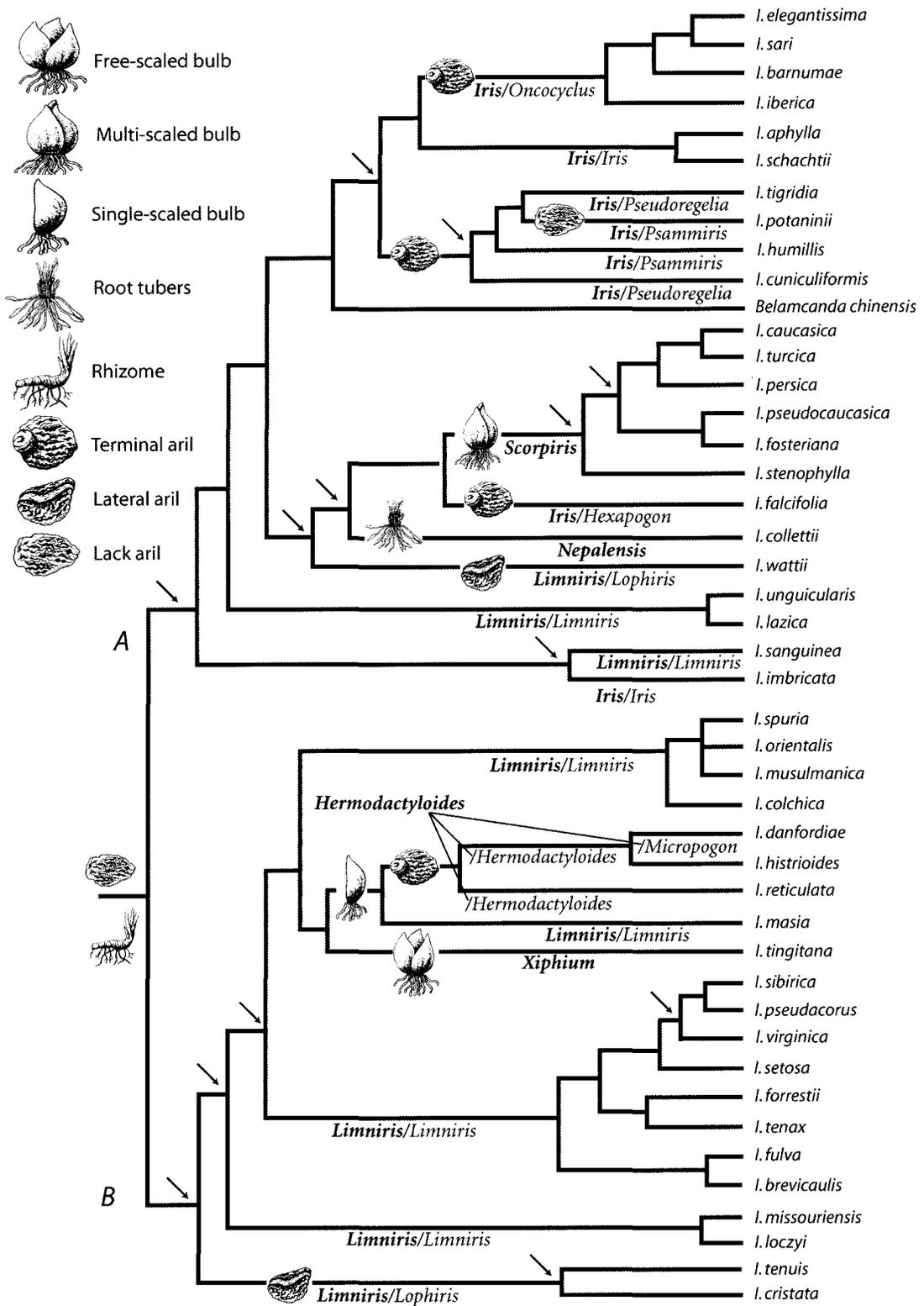


Fig. 2.—Distribution of geophytic organs and arils in *Iris*. The current placement of species in subgenera (bold) and sections is shown below branches. Clades A and B, although unsupported, are indicated to facilitate the presentation of results. Arrows indicate branches with bootstrap values below 50%.

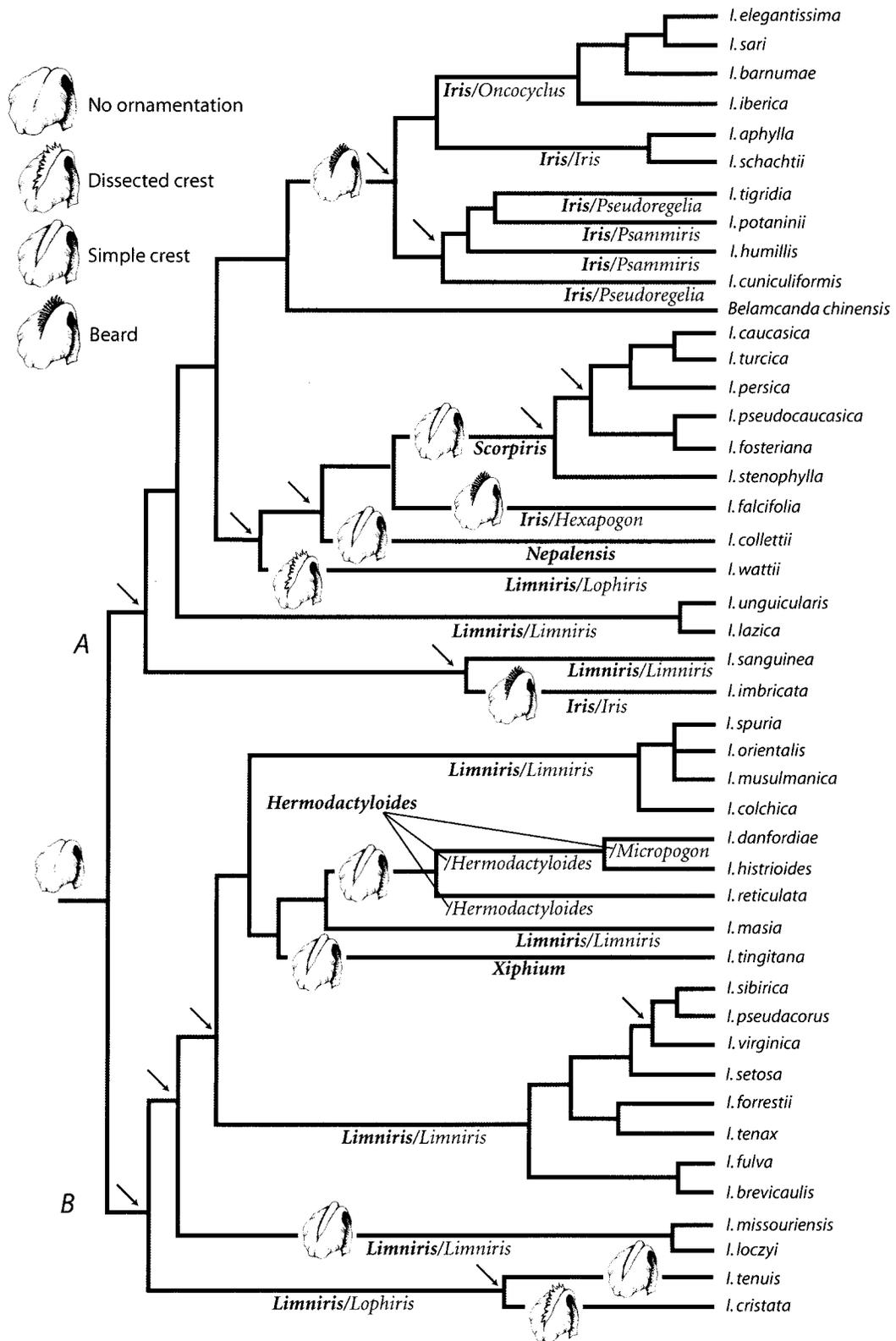


Fig. 3.—Distribution of sepal beards and crests in *Iris*. The current placement of species in subgenera (bold) and sections are shown below branches. Clades A and B, although unsupported, are indicated to facilitate the presentation of results. Arrows indicate branches with bootstrap values below 50%.

based on rhizome morphology. Dykes (1913) noted the appearance at the end of the growing season of small bulb-like structures similar to those of *I. reticulata* (subgen. *Hermodyloides*) although he considered the basic geophytic organ a rhizome. He was describing *I. grant-duffii* and considered *I. masia* a color form of the former species. Other researchers (Rodionenko 1987; Hall et al. 2001; Mathew 2001) have also noted the similarity of the geophytic organ between these species and species from subgen. *Hermodyloides*. Each of these descriptions indicates that at least a short rhizome was also present. Most of my specimens of *I. masia* have bulbs that appear to have a single storage leaf and lack obvious rhizomes. One specimen that was collected from a large and presumably older clump of *I. masia* had several bulbs and also a short horizontal rhizome. Rudall (1989) considered bulbs in *Iris* to typically arise from a truncated, upright rhizome or basal plate. It is probable that the bulbs I studied arose from a basal plate and lacked an upright rhizome. My findings are preliminary as some of the specimens I studied were dried herbarium material in flower, a time when food reserves are low. Molecular and morphological data support the placement of *I. masia* (and probably other subgen. *Limniris* sect. *Limniris* ser. *Syricae* (Diels) Lawr. species) as sister to subgen. *Hermodyloides* and indicate that the bulb with a single storage leaf evolved once in an ancestor to these species. Species in ser. *Syricae* appear to form a rhizome after the formation of bulbs. These rhizomes may be ephemeral or may be persistent in at least some older plants. Developmental studies in this series may provide information on the relationships between rhizomes and bulbs.

The presence or absence of beards, crests, and arils are homoplastic along the tree. This is largely because subgenera and sections within *Iris* are not monophyletic as currently circumscribed. The two largest subgenera, *Iris* and *Limniris*, are called the bearded and beardless *Iris*, respectively, reflecting the significance given to this character in *Iris* classifications. The placement of *I. falcifolia* (subgen. *Iris* sect. *Hexapogon*), a bearded species, as sister to subgen. *Scorpiris* species that are beardless demonstrates that the placement of species within subgen. *Iris* based on the presence or absence of a beard leads to polyphyletic groupings. In addition, although subgen. *Limniris* species are considered beardless some species have sepal hairs. The hairs are not typically linear as in the beards of subgen. *Iris* species, but instead occur as a patch such as in *I. virginica* or as a diffuse pubescence across the sepals as I have observed in several species in sect. *Limniris* ser. *Californicae* (Diels) G. H. M. Lawr.

Sepals in some *Iris* are ornamented with raised areas along the midvein (crests) rather than beards. These crests are often colored and may be highly dissected. Some crests are pubescent, such as was found in *I. stenophylla* (subgen. *Scorpiris*), but the presence of both a crest and beard is not typical within the genus. Some species, such as *I. brevicaulis*, have a slightly elevated median ridge of thickened tissue along the midvein but were not coded as having a simple crest because the raised area is not obvious. Dissected crests occur in *I. wattii* and *I. cristata* of subgen. *Limniris* sect. *Lophiris*. These species are placed within different clades indicating that dissected crests have evolved twice. *Iris* with

rhizomes and a prominent crest have historically been placed within sect. *Lophiris*. Several authors have considered sect. *Lophiris* an artificial grouping, suggesting that species placement is incorrect (Wu and Cutler 1985; Rodionenko 1987; Tillie et al. 2001; Wilson 2004). Simple crests have also evolved independently along branches, suggesting that the presence of the two types of crests may be helpful in recognizing species but do not reflect phylogenetic events.

Arils were subdivided into two types, terminal on seeds and lateral on seeds. Each of these two types is homoplastic on the tree. The significance attached to arils as a classificatory character has differed among researchers, although all workers have recognized that arils have multiple origins. Rodionenko (1987) combined the rhizomatous, bearded species with arils into subgen. *Iris* sect. *Hexapogon*. He also recognized an arilate non-bearded subgenus (subgen. *Crossiris* Spach) and an arilate bulbous genus (*Iridodictyum*). Taylor (1976) segregated Rodionenko's (1987) sect. *Hexapogon* into five sections (sects. *Hexapogon*, *Oncocyclus*, *Regelia*, *Psammiris*, and *Pseudoregelia*) concluding that species in sect. *Pseudoregelia* were not closely related to other arilate species in subgen. *Iris*. Matthew (1989) adopted Taylor's work on the subgen. *Iris* and also recognized Rodionenko's (1987) subgen. *Crossiris* at the sectional level (subgen. *Limniris* sect. *Lophiris*) and genus *Iridodictyum* at the subgeneric level (subgen. *Hermodyloides*). This study illustrates that aril evolution is further complicated because two arilate sections, *Pseudoregelia* and *Psammiris*, in subgen. *Iris* are not monophyletic, and in subgen. *Limniris* the arilate sect. *Lophiris* is polyphyletic. In addition, within sections described as arilate or non-arilate some diversity in this character occurs. *Iris potaninii* (sect. *Psammiris*) lacks an aril. *Iris ruthenica* Ker Gawl. from the non-arilate subgen. *Limniris* sect. *Limniris* is reported to have an aril. This species was not included in my study.

The nature of arils, the term used to describe the whitish outgrowths found on some *Iris* seeds, is not fully known. Arils are typically described as developing from the funiculus. A prominent whitish protuberance found on seeds of some plants is termed a caruncle and is considered to develop from the hilum. The prominent terminal protuberance found on some *Iris* seeds may be more correctly termed a caruncle. However, Rodionenko (1987) found that prominent terminal arils present in at least some species developed from the integuments. It is possible that in species with lateral arils the outgrowth is produced by the raphe, a ridge along the seed formed from the funiculus (Berg 1958). Beattie and Lyons (1975) considered the aril in *Iris* to have an elaiosome aiding in seed dispersal by ants. Rodionenko (1987) found that the aril in subgen. *Iris* was neither sticky nor attractive to ants. Planisek's (1983) study of reproduction in *I. lacustris* Nuttall (subgen. *Limniris* sect. *Lophiris*) revealed that the aril in this species does not contain lipids but does attract ants. These studies indicate that the aril in *Iris* may not be a typical oil-bearing body but at least in some species may be related to ant dispersal of seeds.

In conclusion, DNA sequence data is beginning to resolve relationships within the large genus *Iris* and has shown that several of the subgeneric, sectional, and series groups currently recognized are not monophyletic. Because of these findings the morphological characters that have historically

defined groupings are inadequate to describe monophyletic groups. An examination of bulb morphology helped to resolve homoplasy in the distribution of geophytic organs within groups, but it is unlikely sepal characters can be resolved with further analyses of homology. *Iris* sepals are highly ornamented with beards, crests, color spots, and linear pollinator guides. It is likely that these characters are quite labile and will not define monophyletic groups. It is also unlikely that arils will provide synapomorphies for groups resolved. Before dismissing this character, however, a systematic survey of the origin and chemical content of aril material should be completed. If the nature of arils provides phylogenetically relevant information, a further examination of aril morphology could provide additional information on the homology of arils in *Iris* seeds. I am currently exploring the nature and presence of persistent basal leaf fibers, pollen type, presence of pollen operculum, presence of exine protuberances, photosynthetic leaf form, petal reduction, and seed coat characters as potential synapomorphies for monophyletic groups.

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