

Relationships of the southern African genus *Bobartia* (Iridaceae–Iridoideae)

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The southern African *Bobartia* L. is currently considered a member of Iridoideae tribe Sisyrinchieae, largely because its unspecialized flowers accord with those of most members of the tribe. However, it is geographically isolated from the rest of the tribe, from which it also differs in certain morphological, leaf anatomical and karyological characters. Occasional presence of scattered fibres in the phloem, sticky stems, a pubescent peduncle, and large chromosomes with a basic number of $x = 10$ accord in particular with the African members of Irideae including *Dietes*, and the more specialized genus *Moraea*. Except for *Bobartia*, Sisyrinchieae are exclusively American and Australasian whereas Irideae, with which several characters of *Bobartia* accord, is largely Old World and diverse in Africa. Although most parsimonious phylogenetic hypotheses place *Bobartia* either in Sisyrinchieae or as the sister taxon to the clade Irideae, Mariceae and Tigridieae, the remaining tribes of Iridoideae, the possibility that it is more closely related to genera of Irideae, especially *Dietes*, remains a reasonable alternative hypothesis.

Die Suider-Afrikaanse genus *Bobartia* L. word tans as 'n lid van die Iridoideae-tribus Sisyrinchieae beskou, hoofsaaklik omdat die ongespesialiseerde blomme met dié van die meeste lede van die tribus ooreenstem. Dit is egter geografies geïsoleer van die res van die tribus, waarvan dit ook ten opsigte van sekere morfologiese, blaaranatomiese en kariologiese kenmerke verskil. Toevallige aanwesigheid van verspreide vesels in die floëem, klewerige stingels, 'n sagharige bloeisteel, en groot chromosome met basisgetal $x = 10$, stem in die besonder ooreen met die Afrika-lede van die Irideae waaronder *Dietes*, en die meer gespesialiseerde genus *Moraea*. Met uitsondering van *Bobartia* kom die Sisyrinchieae uitsluitlik in Amerika en Australasië voor terwyl die Irideae, waarmee verskeie kenmerke van *Bobartia* ooreenstem, hoofsaaklik in die Ou Wêreld aangetref word en uiteenlopend in Afrika is. Alhoewel die meeste filogenetiese hipoteses *Bobartia* in die Sisyrinchieae plaas, of dit beskou as die sustertakson van die klade Irideae, Mariceae en Tigridieae, die oorblywende tribusse van die Iridoideae, bly die moontlikheid dat dit nader verwant is aan genusse van die Irideae, veral *Dietes*, steeds 'n aanvaarbare alternatiewe hipotese.

Keywords: Cladistics, classification, phylogeny, phytogeography.

Introduction

The affinities of *Bobartia* Linnaeus, a genus of 15 species (Strid 1974) restricted to the Cape Province of South Africa, have long seemed clear (Bentham & Hooker 1883; Diels 1930; Hutchinson 1934; Lewis 1954; Goldblatt 1971). The simple floral morphology and rhizomatous rootstock of this member of Iridaceae subfam. Iridoideae, correspond closely with *Sisyrinchium*, *Libertia* and *Orthrosanthus*, the larger genera of the American–Australasian tribe Sisyrinchieae (Goldblatt *et al.* 1990), one of the four tribes of Iridoideae (Goldblatt 1990, 1991). The actinomorphic flowers are fugacious, lasting less than a day, and consist of six subequal, spreading tepals (united into a tube only in *B. macrospatha* Baker), and a style with three long tubular, terminally stigmatic branches. This is the basal floral morphology for Iridoideae; both a fugacious perianth and tubular style branches are synapomorphies for the subfamily. The position of the style branches, lying between the stamens, may be the only significant synapomorphy for Sisyrinchieae (Goldblatt 1990).

Placement of *Bobartia* in the predominantly American Sisyrinchieae (Goldblatt *et al.* 1990) (two genera, *Libertia* and *Orthrosanthus*, also occur in Australasia, and *Diplarrhena* is endemic in Australia–Tasmania) has until now been attributed to an ancient southern Gondwanan connection (Goldblatt 1971). However, a number of unusual

morphological and leaf anatomical attributes of *Bobartia*, correlated with a karyotype that is discordant in Sisyrinchieae, now make it seem reasonable to review its tribal position. *Bobartia* may be better placed in Irideae, a predominantly Old World tribe that has radiated extensively in sub-Saharan Africa.

Material and Methods

Material examined anatomically was obtained either from herbarium specimens at Kew (K), from previously prepared microscope slides in the Jodrell Laboratory collection (JL), or from fresh material collected in South Africa. Living material was fixed in FAA and stored in 70% ethanol. Dried material was boiled in water before sectioning. For light microscope observation, material was sectioned using a Reichert OME sliding microtome. Sections were stained with safranin and alcian blue, dehydrated through an alcohol series and mounted in Euparal.

Species examined are the following:

- Bobartia aphylla* (L.f.) Ker – Levyns *s.n.* (10.10.1968) (K).
- B. gracilis* Baker – 286-73-03440 B & C 91.999 (JL).
- B. gladiata* subsp. *major* (Lewis) Strid – Barker *s.n.* (13.11.1932) (K).
- B. gladiata* (L.f.) Ker subsp. *gladiata* – Dahlgren & Strid 2825 (K).

B. lilacina Lewis – Esterhuysen s.n. – Herb. Benth. 1538 (K).

B. paniculata Lewis – Goldblatt 7468 (fresh material) – Dahlgren & Strid 4863 (K).

For cladistic analyses, trees were generated using the MS-DOS program Hennig-86 (Farris 1988), using the ie option and a hypothetical outgroup.

Observations

Leaf anatomy

Leaf surface

Epidermal cells generally thick-walled, largest over vascular bundles, axially elongated and more or less rectangular in surface view, although in *B. paniculata* 'subsidiary' cells surrounding stomata often with oblique end walls, as in *Dietes* and *Diplarrhena* (Rudall 1983). Short papillae (one

per cell) often present, especially in intervascular regions surrounding stomata; or longer unicellular hairs present in surface furrows in some species (e.g. *B. gracilis*, Figure 1B). *Stomata* anomocytic, confined to intervascular regions, sometimes sunken.

Leaf blade

Outline: Leaf shape in cross-section either (a) elliptical, without pseudomidrib, with more or less prominent ridges over vascular bundles (in *B. paniculata*, Figures 1D, 2A; *B. gladiata*, Figures 2C, 2F); (b) circular or oval with deep (*B. gracilis*, Figures 1A, 1B, 2B) or shallow (*B. aphylla*, Figure 2D) depressions between vascular bundles; (c) relatively narrow, with epidermises more or less parallel ('flat' according to Strid 1974), though sometimes raised over main veins (*B. lilacina*, Figure 2G). Surface furrows and hairs were

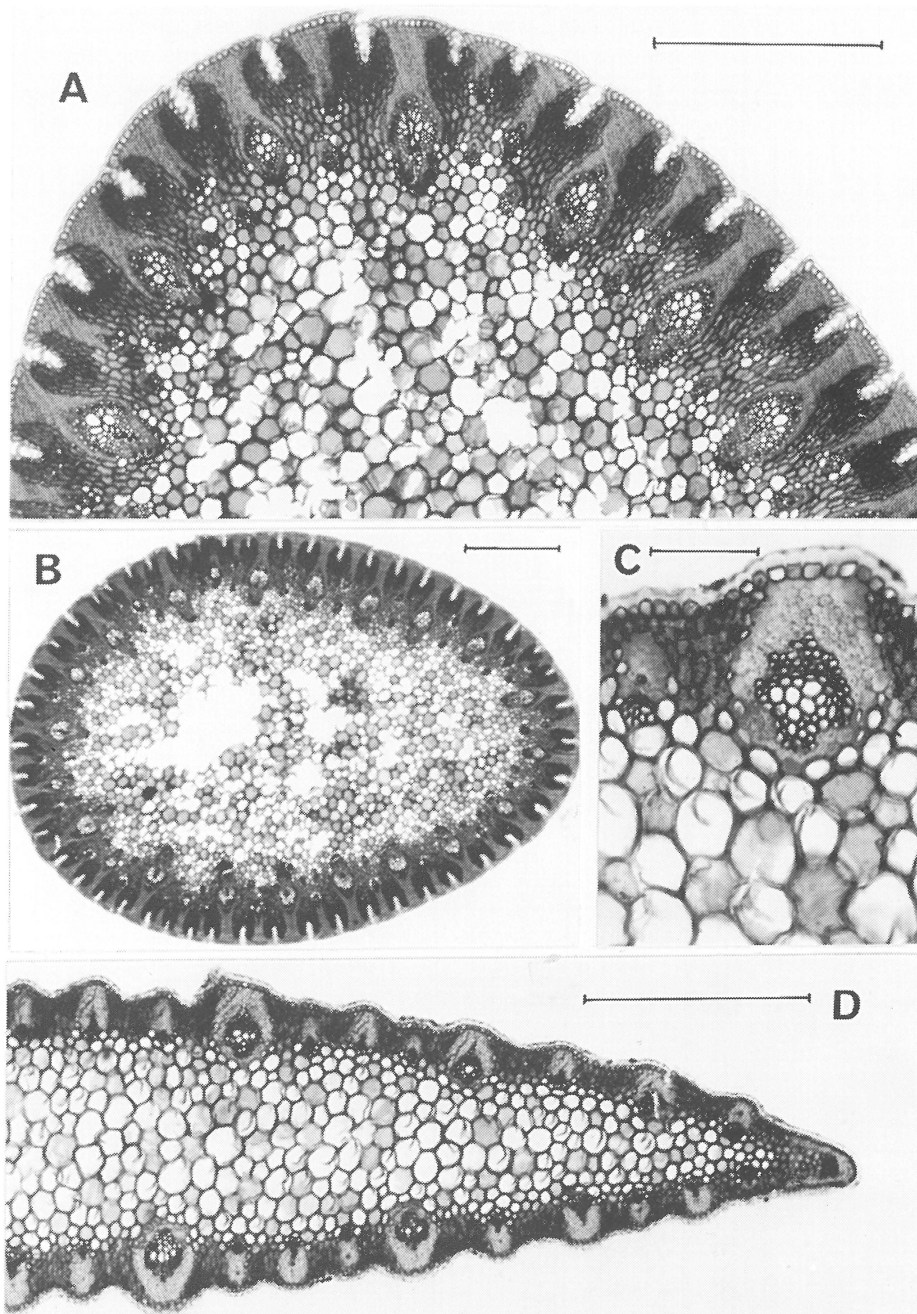


Figure 1 Photomicrographs of leaf blade cross-sections. A & B, *Bobartia gracilis*. C & D, *B. paniculata*. Scales bars: in A, B & D: 500 μm ; in C: 100 μm .

described by Strid (1974) in both stems and leaves of many species (*B. indica*, *B. longicyma*, *B. robusta*, *B. aphylla*, *B. gracilis*, *B. orientalis*, *B. macrocarpa*, *B. fasciculata*, *B. macrospatha*, *B. parva* and *B. rufa*) but they are absent in *B. gladiata*, *B. filiformis* and *B. paniculata*. However, the difference here in *B. aphylla* suggests that this aspect may be variable. *Epidermis*: cells with thickened outer periclinal walls and thick cuticle, except in intervascular stomatal furrows in *B. gracilis*. *Margins*: in leaves that are rounded in cross-section, no distinct margins present (Figures 1A, 1B, 2B, 2D). In other species, margins with a U-shaped region of subepidermal margin fibres, often relatively unligified and gelatinous (Figures 1D, 2A, 2C, 2F, 2G). *Mesophyll cells*: in most species outer 3 – 5 cell layers chlorenchymatous, palisade, oval in both cross-section and longitudinal section (also occasionally slightly axially elongated and lobed in longitudinal section); innermost cell layers relatively large, axially elongated, sometimes slightly thick-walled (except in *B. lilacina*, where central cells only slightly larger than outer layers, and often with dark contents). *Vascular bundles* in 2 rows in narrow and elliptical leaves (Figure 2A); in one row around circumference in terete leaves (*B. gracilis*, *B. aphylla*, Figure 2D), sometimes with additional small inner bundles (in *B. gracilis*, Figures 1A, 2B). Phloem region of larger bundles narrow and sometimes interspersed with fibres. *Bundle*

sheaths: sclerenchymatous sheath present at phloem pole, usually (except at smallest bundles) extending as an often elongated girder to epidermis (Figure 1C); sclerenchyma also present around xylem poles of larger vascular bundles. *Crystals*: small styloid crystals often present in outer bundle sheath cells; especially immediately within epidermis.

Sheathing leaf base

Vascular bundles in one row, with more sclerenchyma than in leaf blade, and often not extending to epidermis (Figure 2E).

Morphology

Notable characters of *Bobartia* are: (a) centric (terete) leaves; (b) scapose flowering stem with a terminal synflorescence of apically crowded rhipidia [monochasial cymes with collapsed axes (*cf.* Goldblatt 1990) enclosed in large opposed sheathing bracts or spathes]; and (c) pedicels pubescent apically. Only the last is consistent throughout the genus, but not necessarily apomorphic. The leaf and inflorescence characters are not universal in the genus, but are almost certainly synapomorphic and thus define species clusters.

The plesiomorphic leaf condition is the more or less plane to elliptic unifacial blade (in *Bobartia lilacina*, *B. paniculata* and *B. gladiata*) that corresponds with the basal leaf type for

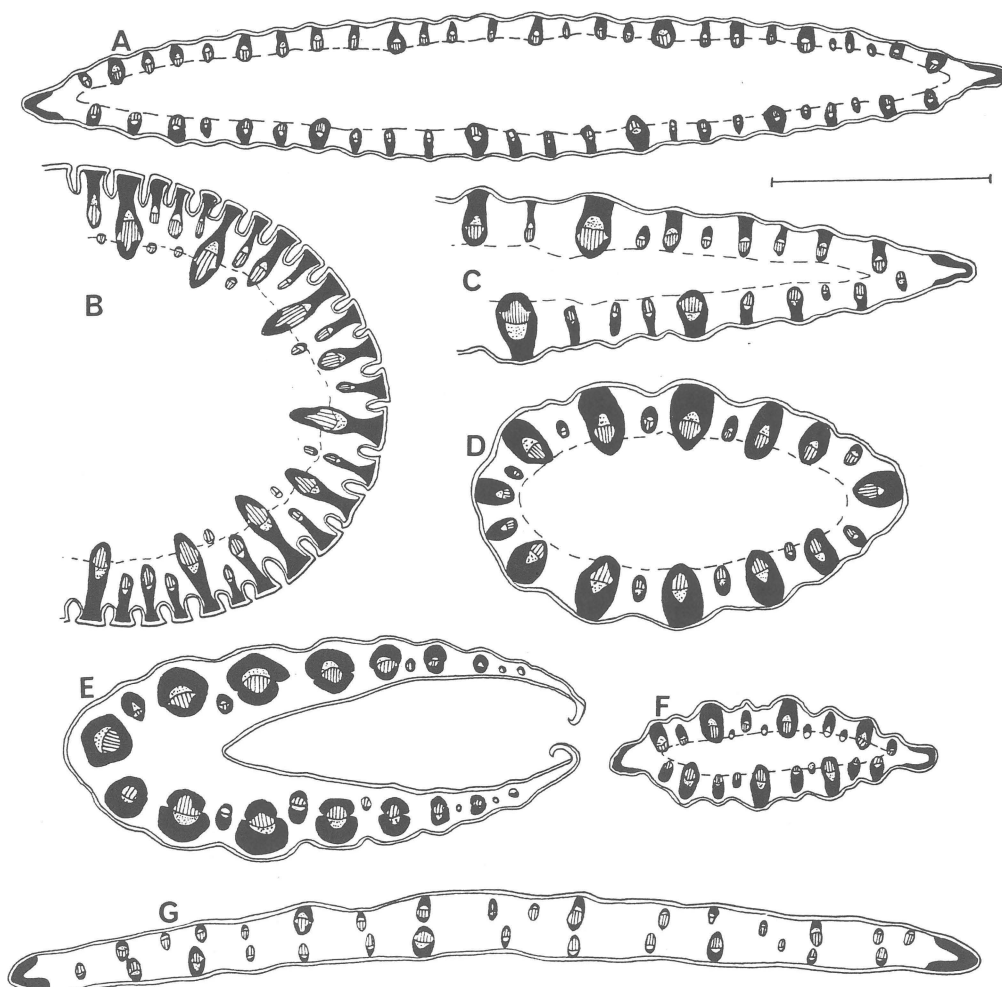


Figure 2 Transverse sections of leaves of *Bobartia* (all leaf blades except E, sheathing leaf base). A, *B. paniculata*. B, *B. gracilis*. C, *B. gladiata* subsp. *major*. D, *B. aphylla*. E & F, *B. gladiata* subsp. *gladiata*. G, *B. lilacina*. Scale bar: 1 mm.

Iridaceae (Goldblatt 1990).

The branched pseudopanicule of *Bobartia lilacina* and *B. paniculata* with pedunculate rhipidia was considered the primitive inflorescence type in the genus by Lewis (1954), and we concur. Two or more rhipidia crowded together on a single stalk are undoubtedly derived in Iridaceae. In *B. lilacina* the flowering stem is not scapose, and the inflorescence is a pseudopanicule (of rhipidia). In *B. paniculata* the rhipidia are somewhat crowded apically on a long peduncle, but all the rhipidia are stalked.

Pediceal pubescence is a character otherwise known in Iridaceae only in *Dietes*, a relatively unspecialized African genus of Irideae. With *Bobartia* treated as a member of Sisyrinchieae, the condition would be convergent but apomorphic for both genera. Pediceal pubescence is one of few synapomorphies for *Dietes* and its presence in *Bobartia* seems striking.

Flower colour in *Bobartia* is yellow except in *B. lilacina* which has blue-purple flowers. Other characters of *Bobartia* that may be of phylogenetic significance are the thick horizontal rhizome, found in most species, and presence of gummy exudate below the nodes in *B. lilacina* and *B. paniculata*. Sticky exudate on the stems occurs elsewhere in the family only in one species of *Ferraria* and several of *Moraea*, both African members of Irideae. Thick rhizomes are found in *Dietes* but are unknown in Sisyrinchieae. Polarization of the character is, however, uncertain, and is not included in the cladistic analysis.

Pollen grain structure of *Bobartia* (Strid 1974) is unremarkable, and the sulcate grains with tectate-reticulate exine seems no different from that in many other monocots, including all Iridaceae excepting Ixioideae (Goldblatt 1990). Seeds are not well known, but seem to accord with the basic type for Iridaceae.

Discussion

If correctly assigned to Sisyrinchieae, *Bobartia* is a taxonomically isolated genus with several autapomorphies, all of which are also present in some African genera of Irideae. Most of the characters that it shares with other genera of Sisyrinchieae are symplesiomorphic. Within *Bobartia*, *B. lilacina* and *B. paniculata* are the best species for comparison with other taxa because these unusual but, nevertheless, largely unspecialized members of *Bobartia* embody most if not all of the basal morphological states for the genus. *Bobartia lilacina*, considered by Lewis (1954) to be the most primitive species of the genus, is the only species of *Bobartia* that has blue-purple flowers, and in this also accords with the presumed basal perianth colour for Iridoideae (Goldblatt 1990). However, since perianth colour is fairly labile in Iridaceae, it may be equally valid to regard a yellow perianth (shared with *Dietes* and other Irideae) as plesiomorphic for the genus, and the blue perianth of *B. lilacina* apomorphic. The character is scored as a ? (equivocal) for the cladistic analysis.

Species of *Bobartia* with leaves elliptic in section, notably *B. paniculata*, closely resemble species of several Australian genera, such as *Isophysis* (Isophysidoideae), *Patersonia* (Nivenioideae) and *Orthrosanthus* (Iridoideae). These genera share characters such as leaf shape in cross-section (thick, elliptical), margin type (with subepidermal marginal

sclerenchyma) and sclerenchyma girders between the epidermis and larger vascular bundles (Rudall 1986). However, these similarities are probably symplesiomorphic, and are therefore non-informative about relationship.

Most anatomical characters suggest affinities with Iridoideae, but point to different tribes. There are some similarities with *Dietes* (Irideae), such as the 'subsidiary' cells around stomata in a few species — also present in *Diplarrhena*, usually regarded as a specialized genus of Sisyrinchieae — and xeromorphic features such as phloem often interspersed with fibres. However, *Bobartia* lacks some of the more striking characteristic features of *Dietes*, such as the leaf margin shape, and the presence of additional sclerenchyma bundles in the sheath (Rudall 1983). Terete leaves are rare or absent outside Iridoideae, but occur in three of the four tribes: Irideae (*Moraea* species, *Barnardiella*, *Roggeveldia*), Sisyrinchieae (*Olsynium*, *Solenomelus*) and Mariceae (*Trimezia*, *Pseudotrimezia*), in the two last with deep surface furrows and hairs in some species.

Chromosome morphology may be helpful in placing the genus. Base number is $x = 10$ (Goldblatt 1971; Strid 1974) and the chromosomes are of moderate size, but according to Goldblatt's (1971) criteria, large rather than small. Base number for Irideae is also probably $x = 10$. The karyotype of *Dietes* (Goldblatt 1971, 1981a) is comparable with that of *Bobartia*. Although a base number of $x = 10$ is probably basic for Iridoideae (Goldblatt 1990), it is significant that most Sisyrinchieae have small chromosomes, particularly *Libertia* ($x = 19$) and *Orthrosanthus* ($x = ?9$), genera which within Sisyrinchieae seem most closely to resemble *Bobartia*. Outgroup comparison suggests that small chromosomes are plesiomorphic for Iridaceae (Goldblatt 1971). In Sisyrinchieae, the large chromosomes of *Bobartia* would be autapomorphic for the genus, but a synapomorphy for the clade including Irideae, Mariceae and Tigridae.

Although the position of *Bobartia* in Iridoideae is supported by the presence of free 3-carboxy non-protein amino acids (Larsen *et al.* 1981, 1987 — compounds characteristic of Iridoideae alone of the four subfamilies of Iridaceae and otherwise rare in the monocots), the two species sampled (Larsen *et al.* 1987) do not have the gamma-glutamyl peptides that are typical of Irideae, especially *Dietes*, and which also occur in Mariceae and Tigridae. Absence of these compounds (or lack of detection) is known in other undoubted members of Irideae (*Barnardiella*, *Galaxia*), so absence alone is not always definitive, and in this case cannot be used as evidence for exclusion of *Bobartia* from any group.

Our cladistic analysis yielded three equally parsimonious trees (Figures 3A – 3C), but only two different positions for *Bobartia*, the traditional one in which the genus falls within the Sisyrinchieae clade (Figure 3A) and the other with *Bobartia* the sister group to the remaining Iridoideae. The third tree differs from the others in the placement of Mariceae, on the last branch of the tree, and sister group to *Iris*. This particular tree seems least attractive as it assumes a reversal for character 11 (compressed style branches), which we find unlikely.

The two possible positions of *Bobartia* seem equally plausible. In both tree 3A and 3B characters 13, 15 and 16

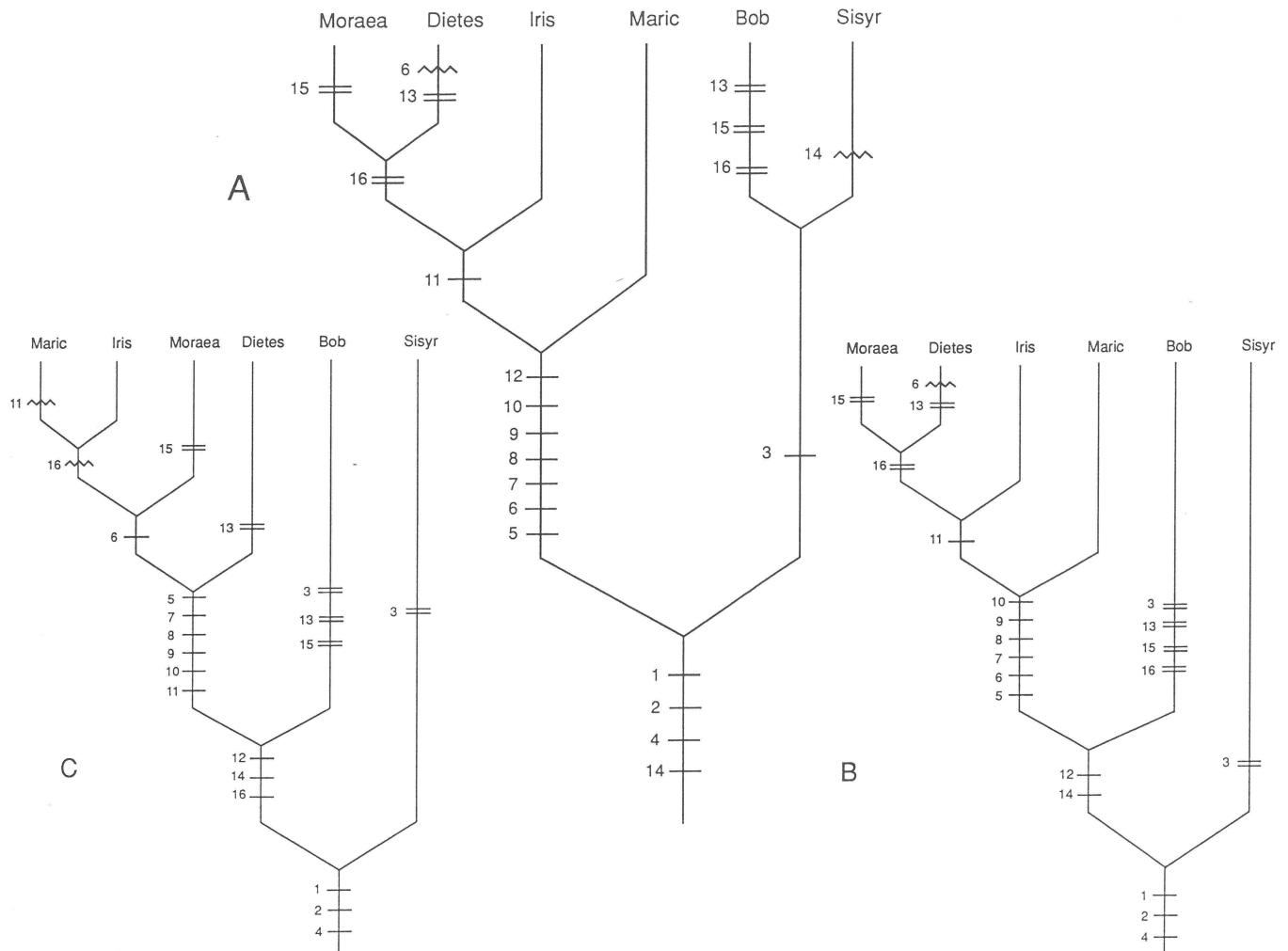


Figure 3 The three most parsimonious phylogenies based on the data matrix (Table 1) obtained using Hennig-86. Tree length: 21; consistency index (CI): 0.76 for tree A.

Table 1 Characters and data matrix used to generate the cladograms (Figures 3A – 3C) of possible relationships of *Bobartia*. Apomorphic states (1) are listed first, followed by the plesiomorphic condition (0). Polarization of characters is discussed in the text, or by Goldblatt (1990, 1991)

Taxon	Character number ^a															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SISYRINCRIEAE	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bobartia</i>	1	1	1	1	0	0	0	0	0	0	0	?	1	1	1	1
<i>Dietes</i>	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1
<i>Iris</i> clade	?	1	0	1	1	1	1	1	1	1	1	?	0	1	0	0
<i>Moraea</i>	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1
MARICEAE/TIGRIDIEAE	1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0

^a Character list:

1. Flowers fugacious – flowers long-lasting.
2. Style branches tubular – style branches flat or channelled.
3. Style branches alternate to anthers – style branches opposite anthers.
4. Free *meta*-carboxy amino acids present – not present.
5. γ -Glutamyl peptides present – not present.
6. Nectaries when present perigonal – nectaries septal.
7. Tepals clawed – tepals not clawed.
8. Style apex 2-lobed and crested – style branch apices simple.
9. Anther appressed to style arm – anther free of style branches.
10. Stigmas transverse and subapical – stigma lobes round and apical.
11. Style branches compressed and petaloid – style branches filiform.
12. Perianth yellow – perianth blue.
13. Pedicels pubescent – pedicels glabrous.
14. Chromosomes large – chromosomes small.
15. Stems sometimes sticky – stems never sticky.
16. Phloem sometimes with scattered fibres – phloem without scattered fibres.

are homoplasies shared variously with *Dietes* and *Moraea*, but in tree 3A character 3 (style branches alternate with the stamens) is the synapomorphy linking *Bobartia* and *Sisyrrinchieae* while it is a parallelism for *Bobartia* and the *Sisyrrinchieae* lineage in 3B. In tree 3A, character 14 (large chromosomes) may be either basal for Iridoideae and then reversed in *Sisyrrinchieae*, or equally parsimoniously, derived independently in *Bobartia* and Iridoideae minus *Sisyrrinchieae*, as figured.

In no tree is *Bobartia* the sister genus of *Dietes*, with which it shares unusual pubescent pedicels (character 13) and with *Dietes* and *Moraea* scattered phloem fibres (character 16) in some species. This is because of the complexity of the basic flower of Irideae with its clawed tepals, thickened and often petaloid and apically forked style branches, style appressed stamens and transverse non-terminal stigmas (Goldblatt 1990, 1991). We simply do not know whether to regard this flower as one apomorphy (a linked series of specializations) or as several (five in this analysis). The similarities *Bobartia* shares with *Sisyrrinchieae* may easily be the result of the kind of floral simplification that has repeatedly occurred in Iridoideae, both in Irideae (e.g. *Homeria*, Goldblatt 1981b, 1986; *Hexaglottis*, Goldblatt 1987; or *Roggeveldia*, Goldblatt 1979) and Tigridiae (e.g., *Gelasine*, *Calydorea*, Goldblatt & Henrich 1991; or *Eleutherine*, Goldblatt & Snow 1991). At present, *Bobartia* cannot be confidently assigned to either Irideae or *Sisyrrinchieae* nor treated as sister genus to Iridoideae minus *Sisyrrinchieae* (trees 3B & 3C) and thus meriting its own tribe. On balance, we believe the genus should remain a questionable member of *Sisyrrinchieae*, despite the fact that it accords poorly with *Sisyrrinchieae* geographically. *Bobartia* may, in fact, be the genus closest to the line that gave rise to Irideae, Mariceae and Tigridiae.

That its large chromosomes, pubescent pedicels, sticky internodes, and phloem with scattered fibres, all arose independently, and are thus convergent with African Irideae, remains in doubt. The problem cannot be answered with the available information. Possibly only DNA hybridization or restriction enzyme studies will provide a final answer.

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