

A revised infrageneric classification and synopsis of the Afro-Eurasian genus *Moraea* (Iridaceae: Irideae)

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Keywords: Iridaceae, Iridoideae, *Moraea* Mill., new species, southern Africa, taxonomy

ABSTRACT

Molecular phylogenetic studies of *Moraea* Mill. and the inclusion of *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandris* Parl., *Hexaglottis* Vent., *Homeria* Vent. and *Roggeveldia* Goldblatt in the genus have rendered the existing infrageneric classification, dating from 1976, in need of substantial revision. In particular, subg. *Moraea* and subg. *Vieusseuxia* have been shown to be paraphyletic. We propose a new infrageneric classification, based, as far as current data permit, on phylogenetic principles. Monophyletic subgenera and sections are circumscribed based on molecular phylogenies alone or in combination with morphological considerations. We recognize 11 subgenera, 15 sections and three series, arranged as follows in phylogenetic sequence: **Plumarieae**; **Visciramosae** (with sect. **Multifoliae** and sect. **Visciramosae**); *Moraea* (with sect. *Moraea* and sect. **Polyphyllae**); **Galaxia** (with ser. **Unguiculatae**, ser. *Eurystigma* and ser. *Galaxia*); **Monocephalae**; **Acaules**; **Polyanthes** (with sect. **Serpentinae**, sect. *Deserticola*, sect. *Hexaglottis*, sect. *Gynandris*, sect. *Polyanthes* and sect. **Pseudopicatae**); **Grandiflorae**; **Vieusseuxia** (with sect. **Integres**, sect. **Vieusseuxia** and sect. **Villosae**); and **Homeria** (with sect. **Stipanthera**, sect. *Flexuosae*, sect. *Homeria* and sect. **Conantherae**). Most are moderately to well circumscribed at the morphological level either by floral or vegetative characters, except subg. *Moraea*, which includes a small number of unspecialized species apparently not linked by any apomorphic features. With over 27 new species described in the past 25 years and another 60 transferred to the genus, *Moraea* now includes 214 species. We provide a full taxonomic synopsis of the genus.

INTRODUCTION

Moraea Mill., the largest African genus of Iridaceae tribe Irideae, comprises ± 220 species (214 recognized species plus several more yet to be described). Following revisions of its southern and tropical African members (Goldblatt 1973, 1976a, 1977b), *Moraea* was believed to be well understood and was considered to be monophyletic, largely on the basis of phenetic considerations and outgroup comparison. A close correlation between morphology and chromosome cytology in the genus, then including some 110 species, led Goldblatt (1976b) to propose an infrageneric classification that used cytology as a major determinant in circumscribing subgenera and sections. Later research in *Moraea* and related genera led to the realization that *Moraea* as so circumscribed was paraphyletic when *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandris* Parl., *Hexaglottis* Vent., *Homeria* Vent. and *Roggeveldia* Goldblatt were recognized. A phylogenetic study of *Moraea* based on DNA sequence data subsequently confirmed this conclusion, thus fully supporting its expanded circumscription (Goldblatt *et al.* 2002). This study and a second, more extensive one (Schnitzler *et al.* 2011) also showed that Goldblatt's 1976 infrageneric classification of *Moraea* required considerable revision if a classification follow-

ing the principle of monophyly was to be implemented. In these molecular systematic studies some large species clusters comprised clades receiving moderate to strong support, but subg. *Moraea* included several disparate elements and required major restructuring to achieve a classification consistent with the phylogenetic principle of monophyly.

Some of the major changes include removal from subg. *Vieusseuxia* (D. Delaroché) Baker of sect. *Polyanthes* Goldblatt, which comprises a clade outside the subgenus and is sister to two lineages until now included in subg. *Moraea*. In addition, several individual species were shown by molecular, and sometimes cytological, data to be misplaced to subgenus or section. Re-evaluation of their morphology makes it clear that their position in the classification must be revised. This paper provides a new classification of *Moraea* based as far as possible on the principle of monophyly. *Moraea* now includes some 214 species, which we assign to 11 subgenera, 15 sections and three series. We also provide a full synopsis of the genus.

MATERIALS AND METHODS

Chromosome data for *Moraea* were obtained from studies by Goldblatt (1976a, 1976b) and later papers (most importantly Goldblatt 1981, 1986b, 1986c) and some chromosome counts not yet published (Goldblatt & Manning 2013). Morphological information is from Goldblatt (1976a, 1976b, 1981, 1986a) and several later papers.

The molecular studies of Goldblatt *et al.* (2002) and Schnitzler *et al.* (2011) are summarized here and provide the framework for the revised classification. Some 161 species were included in the latter study, and three additional taxa have been sequenced for the present

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MS. received: 2012-05-22.

TABLE 1.—Additional *Moraea* species sequenced in this study with voucher information and GenBank/EMBL accession number for each gene region. Accession numbers for taxa not listed here can be found in Goldblatt *et al.* (2002) and Schnitzler *et al.* (2011).

Species	Voucher	rbcL	rps16	trnL-F
<i>Moraea intermedia</i> Goldblatt & J.C.Manning	Goldblatt, Manning & Porter 13405 (NBG)	JQ846027	JQ846024	JQ846030
<i>Moraea nubigena</i> Goldblatt	Helme s.n. (NBG)	JQ846028	JQ846025	JQ846031
<i>Moraea pearsonii</i> Goldblatt & J.C.Manning	Manning 3128 (NBG)	JQ846029	JQ846026	JQ846032

study, over 75% of the genus (Table 1). PCR amplification and sequencing were performed as described in Goldblatt *et al.* (2002). Insertions/deletions (indels) were coded as present/absent following the ‘simple indel coding’ method of Simmons & Ochoterena (2000), implemented in SeqState (Müller 2005). The final matrix comprised 3 096 characters from three plastid markers (*rbcL*, *rps16*, and *trnL-F*) and 218 indels. Maximum parsimony analyses were performed using the heuristic search implemented in PAUP* (v. 4.0b10; Swofford 2002). Initial searches were carried out using 1 000 replicates of random taxon addition and the tree bisection and reconnection (TBR) algorithm with equal character weights, retaining a maximum of 10 trees per replicate. The resulting trees were used as starting trees in a second search using the same parameters with a limit of 10 000 trees, which were then used to reweight the characters according to the rescaled consistency index (RC). Successive searches were performed using the reweighted matrix until tree lengths reached stationarity. We performed 1 000 bootstrap replicates using equal character weights and the TBR swapping algorithm, again keeping only 10 trees at each step. Maximum likelihood analyses were performed in RAxML (v. 7.2.1; Stamatakis 2006) using the BINGAMMA function, with the alignment divided into partitions according to gene regions. This process implements the GTR+ Γ model for each gene with individual estimation and optimization of model parameters and a discrete morphological model as proposed by Lewis (2001) for the indels, which is comparable to the Jukes-Cantor model of nucleotide substitution. We performed 500 rapid bootstrap searches (Stamatakis *et al.* 2008), followed by a thorough ML search on the original alignment. Bayesian phylogenetic inference was performed using MrBayes (v.3.2.1; Huelsenbeck & Ronquist 2001). The best-fit models of nucleotide evolution were implemented according to the Akaike Information Criterion (AIC) scores for substitution models evaluated using MrModeltest (v.2.3; Nylander 2004). For binary traits, MrBayes implements an F81-like model. Three independent runs with four chains each were run for 30 000 000 generations, sampling the Markov chain every 1 000 generations. After removal of the first 3 000 000 generations as burn-in, all runs were combined to build the consensus tree. The alignment and consensus trees are available from Tree-Base (accession number S13606).

DISCUSSION

All approaches resulted in highly congruent tree topologies. The phylogenetic tree presented here reflects the

topology and branch length of the Maximum Likelihood analysis. Unless indicated otherwise, support values reported in the text (e.g. 1, 95, 92) represent Bayesian posterior probabilities (if higher than 0.5), and bootstrap support values from the Maximum Likelihood and Maximum Parsimony analyses (if higher than 50%), respectively. Most of the major species clusters correspond to existing, named infrageneric taxa but their relationships to one another are often quite different from past interpretations of their affinities. Not entirely surprisingly, several species of uncertain affinity based on morphological considerations remain unresolved in the molecular analyses, notably *M. cooperi*, *M. nubigena* and *M. papilionacea*. The relationships of other species of which the affinities were uncertain, e.g. *M. fergusoniae* and *M. radians*, are established in the trees generated. Conversely, a few species appear in the molecular trees in positions unacceptable on morphological grounds, especially *M. inclinata* and *M. rivulicola*. These exceptions are discussed in more detail below in our proposed classification.

1. Subg. *Plumariae*: *Moraea lugubris* is linked with low significant statistical support (pp = 0.55, 67 BP(MP)) to the *M. bubalina* clade (Figure 1) in an association without morphological support. This taxonomically isolated species was retrieved as sister to all other species of *Moraea* in an earlier analysis (Goldblatt *et al.* 2002). *M. lugubris* is unique in *Moraea* in having coarsely netted corm tunics not matched elsewhere in *Moraea*, plumose style crests and stigmas located at the distal tips of the bifurcate style branches rather than as discrete lobes abaxial to the style branches. We recognize the monotypic subg. *Plumariae* for *M. lugubris*. Both the position of the stigmatic surfaces and the plumose style branches recall the genus *Ferraria*, which is well established as sister genus to *Moraea* (Goldblatt *et al.* 2002, 2008).

2. Subg. *Visciramossae*: the eight species of subg. *Visciramossae* (six included in the current phylogenetic analysis) are united by at least three morphological synapomorphies, notably sticky stems, unique brown, \pm woody, longitudinally grooved corm tunics with a sticky secretion on the inner surfaces, and stigmatic lobes with a central forked tooth. The \pm free but closely contiguous filaments of some species of the alliance are also unique in *Moraea*, but might constitute an ancestral state (other *Moraea* species have filaments partially or completely united except in some species of the very derived *M. tripetala* complex and in *M. thomasiae*, both subg. *Viessuseuxia*). *Ferraria*, sister genus to *Moraea*, has partially united filaments in all species. Floral mor-

phology is unremarkable in subg. *Visciramosae* except in the species with free filaments and in those with the style branches reduced and lacking crests and the inner tepals as well as the outer with nectar guides (a derived condition that recurs in several other clades). *M. simplex* stands out here in having filiform style branches extending between the stamens, a condition shared by the unrelated *M. fistulosa* and *M. monticola* (assigned here to sect. *Pseudospicatae* of subg. *Polyanthes*, although neither was included in the molecular analysis).

The members of subg. *Visciramosae* comprise two separate, well supported (both $pp = 1$ and > 90 BP) clades (Figure 1). One, including the multi-leaved *Moraea bubalina* and *M. vespertina*, is weakly linked with *M. lugubris* and the other, including the remaining species, which are characterized by presence of two foliage leaves, is placed as sister to the rest of the genus with only moderate support. The clear morphological synapomorphies that the two clades share (sticky stems, sigmoid branching, unique corm type, stigmatic appendages) provide adequate justification for ignoring the weak molecular data in treating both lineages within a single subg. *Visciramosa*. We recognize the two lineages as separate sections, *Multifoliae* and *Visciramosae*.

3. Subg. *Umbellatae*: *M. longiflora* (sect. *Tubiflora* Goldblatt), plus several species from sect. *Moraea* (*M. intermedia*, *M. margaretae*, *M. nana* and *M. umbellata*) were retrieved as a well-supported clade (1, 99, 96; Figure 1) sister to *M. maximiliani*. The second member of sect. *Tubiflora*, *M. cooperi*, was retrieved in an isolated but only weakly supported / unsupported (4–14 BP) position (Figure 1). We find it most unlikely that the molecular topology reflects the true relationships of *M. cooperi* as the morphological evidence linking it to the *M. intermedia* clade (i.e. subg. *Umbellatae*) is strong. Unique brown corm tunics, woody with plane surface (without the sticky secretion on the brown, longitudinally grooved corm tunics of subg. *Visciramosa*), darkly veined, pale yellow tepals, blunt outer inflorescence spathes usually not sheathing distally, and flowers with a perianth tube are all evidently derived character states that are shared with *M. longiflora* of the subgenus. Those features in *M. cooperi* may be homoplasious, but it seems to us unlikely that the entire set could have evolved independently. Thus we prefer to place *M. cooperi* in subg. *Umbellatae* rather than recognize it as a separate genus with the same morphological circumscription as subg. *Umbellatae*. We include eight species in what we designate subg. *Umbellatae* (one species, *M. linderi*, was not included in the molecular analysis). We note that *M. maximiliani* was retrieved as sister to the remaining members of the subg. *Umbellatae* clade and its position is weakly supported; nevertheless, it has the morphological synapomorphies of the subgenus hence its inclusion therein. We see no need for its recognition as a separate, monospecific subgenus or section in light of the morphology.

Floral diversification in the subgenus parallels that in subg. *Visciramosae*, ranging from an unspecialized *Moraea*-type flower with well developed style branches and crests and larger outer tepals bearing nectar guides, to reduced style branches lacking crests (*M. maximiliani*, *M. umbellata*) and, in *M. nana*, to style branches

represented by paired, filiform arms extending on either side of the opposed stamen. The flower type in *M. nana* is convergent with that in the *Hexaglottis* group (subg. *Polyanthes* sect. *Hexaglottis*), in *M. hexaglottis* (not sequenced) and in *M. pearsonii* (now subg. *Polyanthes* sect. *Pseudospicatae*).

4. Subg. *Moraea*: here much reduced in size, includes *M. vejeta*, type of the genus, plus *M. gawleri* and its close relative, *M. vlokii*, which together form a well-supported clade (1, 100, 99). The phylogenetic position of this clade (sister to the first polytomy in the tree) was, however, not supported in the bootstrap analyses and thus remains uncertain. To this small alliance we provisionally add *M. namaquamontana* and *M. indecora*, a rare Namaqualand endemic, and not yet sequenced.

Moraea garipensis and *M. ramosissima* constitute another small clade (1, 100, 100) included by Goldblatt (1976b, 1986a) in subg. *Moraea*. A separate subgenus for the two species seems unwarranted as the molecular topology here is not well supported and we therefore provisionally retain them as a section of subg. *Moraea* pending additional molecular studies. At the morphological level, the species of subg. *Moraea* share pale-coloured corm tunics, mostly of fine fibres, except for *M. garipensis* and *M. ramosissima*. Further molecular analysis may show an alternative placement for these two species, the brown corm tunics of which recall those of subg. *Umbellatae*.

The rare Western Cape mountain endemic *Moraea nubigena* appears as isolated in the molecular phylogeny (Figure 1) as it does morphologically. The acaulescent habit, solitary leaf and unbranched stem are all distinctive but may be adaptations to its montane habit. Goldblatt (1986a) linked the species to *M. lugubris*, but that now seems unlikely. *M. nubigena* has a chromosome number of $n = 10$ and a fugaceous flower, both plesiomorphic in *Moraea*, and finely fibrous corm tunics, evidently an apomorphy for subg. *Moraea* but the blue perianth is otherwise unknown in the subgenus. We provisionally include it in subg. *Moraea*, with which the corm tunics are consistent, but it is not referred to any section. We note that it is the only blue-flowered and single-leaved member of the group. An argument can be made for the alternative, a separate subgenus for *M. nubigena*, but we see no value in a monospecific subgenus for the species.

5. Subg. *Monocephalae*: the lineage including *Moraea angusta* and two immediately related species is moderately well-supported (1, 89, 65) as one of a polytomy (Figure 1). The alliance (including *M. valisavium*, not sequenced) is united by unbranched stems, a single foliage leaf inserted well above ground level, a terete leaf blade, obtuse to truncate inflorescence spathes, sticky nodes, a prismatic ovary, and flattened, discoid seeds. The alliance was treated as the rank-less group *Monocephalae* by Baker (1896, then including *M. spathulata* of subg. *Grandiflora*), and as subg. *Monocephalae* by Goldblatt (1976b). Although *M. namaquamontana* is retrieved as sister to the *M. angusta* clade in all molecular analyses, this association is without statistical or morphological support and there is little reason to doubt that *M. namaquamontana* is allied to

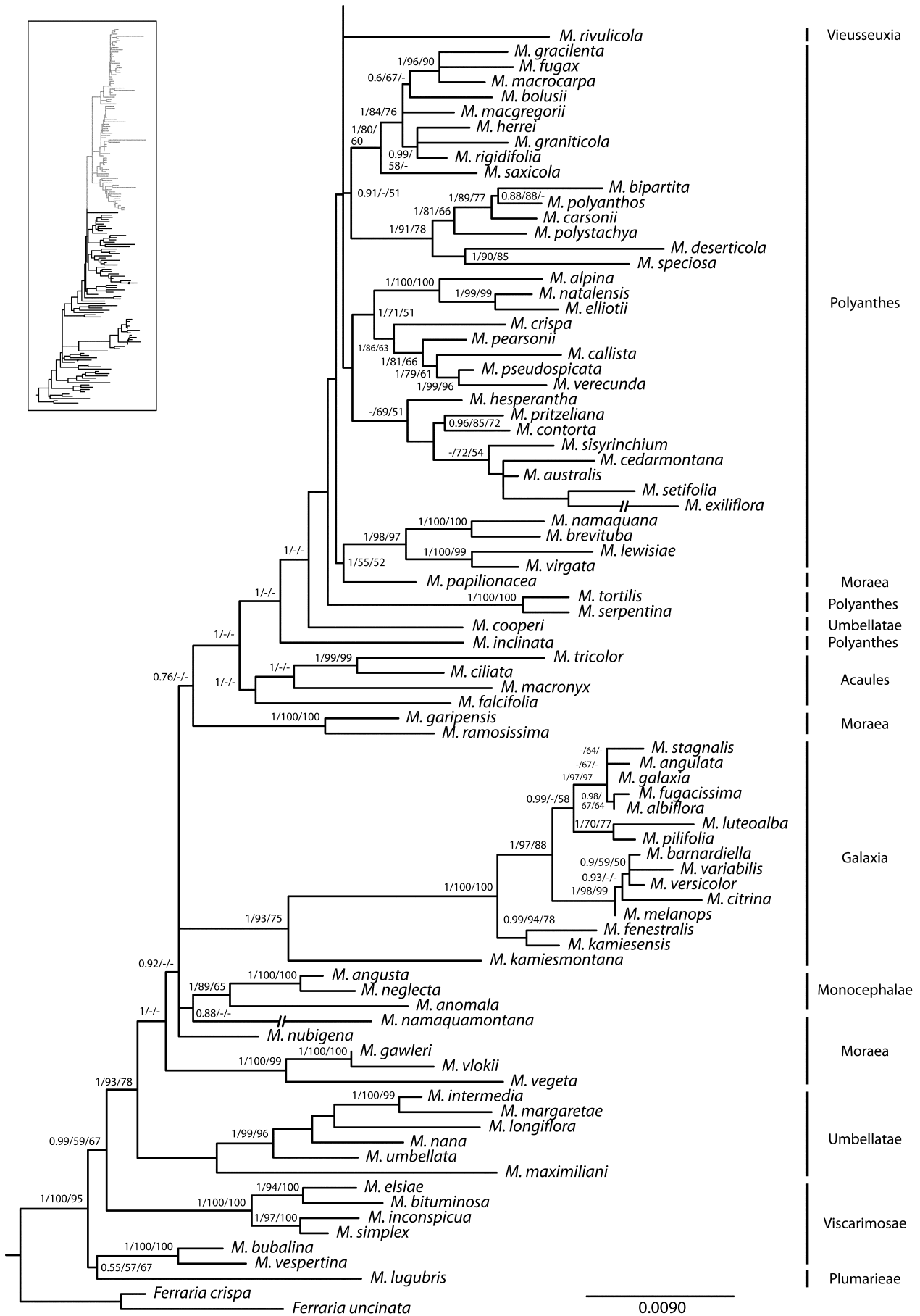
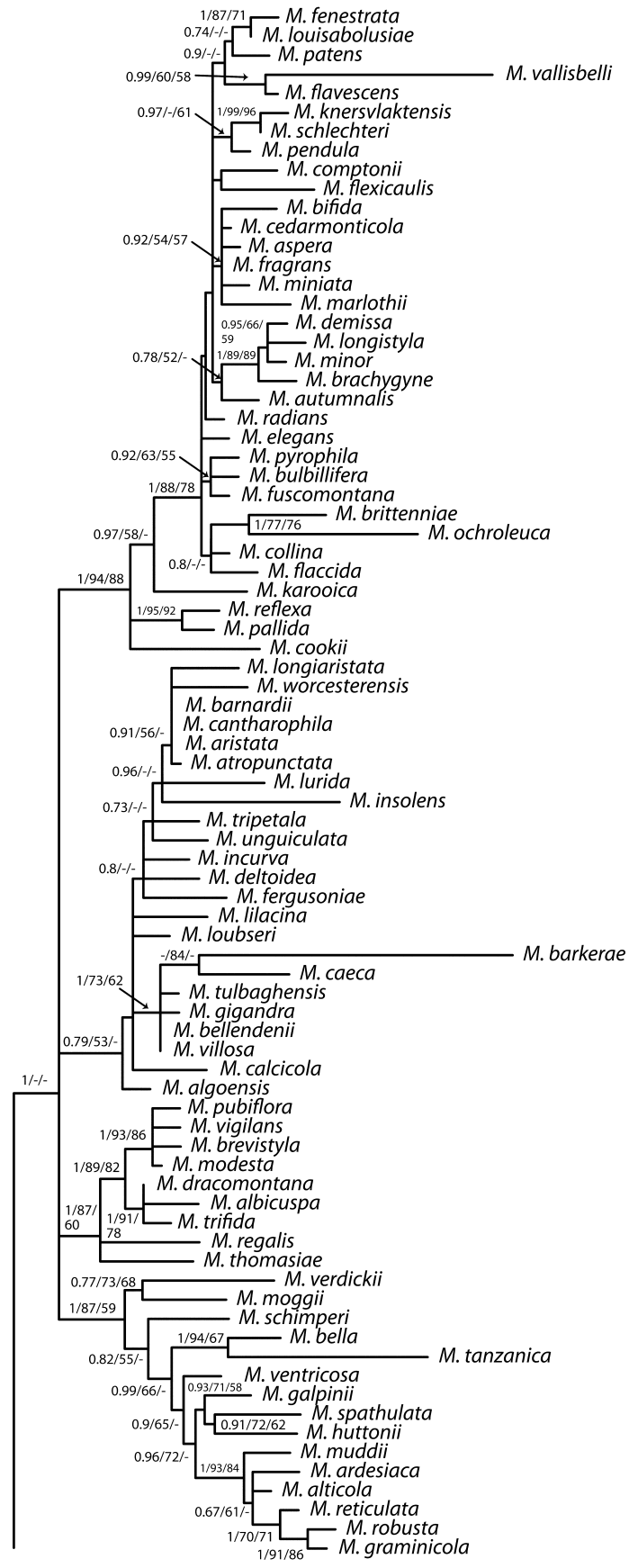
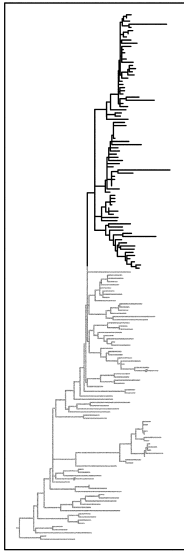


FIGURE 1.—Maximum Likelihood phylogeny of *Moraea*. Support values at nodes are Bayesian posterior probabilities, and bootstrap values from the Maximum Likelihood and Maximum Parsimony analyses respectively if pp > 0.5, or BS > 50%. The subgeneric classification is indicated by black bars on the right.



Homeria

Vieusseuxia

Grandiflorae

0.0090

M. gawleri (subg. *Moraea*), with which it shares a virtually identical flower, a distinctive, asymmetric corm, and globose capsules. The *M. angusta* alliance is phylogenetically isolated and well defined by several morphological synapomorphies, and we continue to accord it subgeneric rank.

6. Subg. *Galaxia*: all species previously treated as the genus *Galaxia* (Goldblatt 1984a) comprise a well-supported (1, 93, 75) clade. The alliance has several synapomorphies, not least an acaulescent habit, flowers always with a perianth tube, style branches short and lacking crests, and an asymmetric corm, and we recognize it as subg. *Galaxia*. Relationships within subg. *Galaxia* are more complex than reflected in Goldblatt's (1979b) recognition of two sections. Although sect. *Eurystigma* (species with entire style branches) is retrieved as monophyletic, sect. *Galaxia* (species with fringed style branches) is shown to comprise two lineages, the *M. galaxia* clade and *M. kamiesensis* plus *M. fenestralis*. A strictly phylogenetic classification would thus require the recognition of three or four sections, but we do not feel that this is justified in such a small group and suggest that the level of series is adequate. The position of the isolated *M. kamiesmontana* in the tree (Figure 1) as sister to the remaining members of the clade has morphological support; it is the only member of the subgenus that has clawed tepals, the plesiomorphic condition in *Moraea*. We thus admit three series, *Eurystigma*, *Galaxia* and *Unguiculatae*, this last monospecific.

7. Subg. *Acaules*: the species of the taxonomically isolated *Moraea ciliata* group were retrieved with strong support in the Bayesian analysis (pp = 1) as sister to the remaining species of *Moraea* and we accord the group subgeneric status. Within the group *M. ciliata*, *M. macronyx* and *M. tricolor* are obviously closely related, with the morphologically somewhat different *M. falcifolia* as sister. One more species belongs here, *M. longipes*, until recently included in *M. ciliata* (Goldblatt & Manning 2009). Synapomorphies for subg. *Acaules* include leaves clustered at the terminal node, stem usually below ground level at flowering time (not *M. longipes*), sessile flowers raised above the leaves and inflorescence spathes on an elongating, tubular stalk; possibly the sterile base of the ovary (called a contractile pedicel in older literature) that retracts after flowering. The alliance was treated as sect. *Acaules* by Goldblatt (1976b), following Baker (1896).

8. Subg. *Polyanthes*: the *Moraea serpentina*-*M. tortilis* species pair (1, 100, 100) is weakly placed as sister to the remaining species in the genus, but without statistical support. On morphological grounds, we include the six main clades (Figure 1) of this large group, including *M. serpentina*-*M. tortilis*, as sections of subg. *Polyanthes*. The alliance is united morphologically by distinctive blackish, wiry corm tunic fibres, but the multi-leaved habit (reduced in some species to a single leaf) and fugaceous flower are plesiomorphic. We note that, in addition, many species of the subgenus have an apomorphic, included ovary, but the condition is reversed in two sections. The subgenus is mixed for chromosome number: a base number of $x = 20$ is ancestral and basic for two sections, *Serpentinae* and *Deserticola* (but reduction to $x = 6$ (or 5) has occurred within

sect. *Deserticola*) and $x = 6$ is almost exclusive in sect. *Hexaglottis*, sect. *Gynandriris*, sect. *Polyanthes* and sect. *Pseudospicatae* (one species of sect. *Polyanthes*, *M. inclinata* has $n = 6$ and 11).

In the molecular analyses, *Moraea rivulicola* is retrieved in an unresolved polytomy in subg. *Polyanthes*, but without any statistical support. This species has all the morphological hallmarks of subg. *Vieusseuxia* as we noted in an earlier molecular analysis (Goldblatt *et al.* 2002) and sequences of a second and third sample of the species alters this topology hardly at all, ruling out experimental error. Another species that appears misplaced here on morphological grounds is *M. exiliflora*, which almost certainly belongs in sect. *Polyanthes* according to morphology. We have no explanation for the apparently anomalous position of these two species in our trees, but to suggest that their morphology is somehow convergent with those clades to which morphology suggest they belong, is unacceptable. The remaining species of the clade, which comprise sect. *Gynandriris* (Goldblatt 1998), and originally the genus *Gynandriris* (Goldblatt 1980b), have apomorphic, translucent inflorescence spathes and a sessile ovary with a tubular, sterile beak, which leaves no doubt that it is a monophyletic alliance. The clade receives moderate support in the molecular analyses (69 and 51 BP, respectively; pp = 0.6, but excluding *M. exiliflora*). Two species of sect. *Gynandriris*, *M. sisyrinchium* and *M. mediterranea* (= *G. monophylla* Boiss. & Heldr. ex Klatt and not sequenced), occur in the Mediterranean Basin and Middle East and constitute the only species of *Moraea* that occur north of the Sahara.

Sect. *Hexaglottis* [the genus *Hexaglottis sensu* Lewis (1959) and Goldblatt (1987)] has the derived, *Hexaglottis*-type flower with subequal, spreading tepals with short claws and style branches reduced to filiform arms extended on either side of the opposed stamen. The inclusion of *M. papilionacea* in the clade (Figure 1) receives only weak support in the bootstrap analyses (55 and 42 BP, respectively) and has no morphological basis, but the affinities of this species are uncertain and we prefer to retain it as unplaced in subg. *Moraea*, to which it was assigned by Goldblatt (1976b, 1986a).

Sect. *Pseudospicatae* (1, 71, 51), sect. *Deserticola* (1, 80, 60) and sect. *Polyanthes* (1, 91, 78) are retrieved as monophyletic in the molecular analysis and are also morphologically coherent. The members of sect. *Polyanthes sensu* Goldblatt (1976b, 1986a) fall in two lineages; the first (here sect. *Polyanthes*) mostly with multiple leaves and the second (sect. *Pseudospicatae*) with a single leaf. Both clades include species with typical *Moraea*-type flowers as well as others with reduced style branches and style crests. We include *M. inclinata* in sect. *Pseudospicatae* without hesitation, despite its anomalous position in the tree, sister to *M. cooperi* plus the rest of the genus. It has a single leaf, blue flower, exerted ovary and capsule, and basic chromosome number of $x = 6$, all of which accord with this decision. It is allied to, and sometimes has been included in, *M. natalensis* of sect. *Pseudospicatae*. Although sect. *Deserticola* (unranked *Subracemosae* Baker) likewise has species with the typical *Moraea* flower and others with reduced style branches and crests (the *M. rigidi-*

folia-*M. herrei* clade, BP 54), all members consistently have the ovary included in the spathes. The ovary is sessile in *M. herrei* and has a sterile beak, also present in a less developed state in *M. rigidifolia* and the *M. fugax* group (1, 96, 90). Sect. *Deserticola* closely resembles sect. *Serpentinae* in several morphological features and we would not be surprised if additional molecular data show them to be a clade. The available molecular data, however, preclude their union.

Subg. *Polyanthes* is sister to a polytomy formed by four large clades that include the remaining species in the genus. Two of these coincide exactly with subg. *Grandiflora sensu* Goldblatt (1976b) and subg. *Homeria sensu* Goldblatt (1981); and we continue to treat them as subgenera rather than sections because of their large size.

9. Subg. *Grandiflorae*: this subgenus (1, 87, 59) includes some 28 species of eastern, southern and tropical Africa. Most are tall, have unbranched stems and large, evidently unspecialized flowers that are long-lived in almost all species. All have a solitary leaf, distinctive, flattened, discoid seeds and a karyotype of large, subacrocentric chromosomes with a base number of $x = 6$. With only half its species sequenced for the molecular study, subg. *Grandiflora* is still inadequately sampled and no clear morphological patterns are evident in the tree topology.

10. Subg. *Vieusseuxia*: we treat the remaining two clades as constituting subg. *Vieusseuxia*, which has until now included sect. *Vieusseuxia* of Goldblatt (1976b) plus the monospecific sect. *Integres*. All species share a basic chromosome number of $x = 6$, but often a somewhat variable karyotype, although always of relatively large chromosomes. Members of the subgenus have derived, long-lived flowers (a fugaceous flower is plesiomorphic in *Moraea*), a single foliage leaf, also derived (multiple leaves only in *M. fergusoniae* must be interpreted as a striking reversal), and inner tepals that are typically much reduced, often 3-lobed or even absent.

There is no morphological support for the two separate clades (1, 87, 60 and 0.79, 53, respectively; Figure 1), and there are few obvious subclades in subg. *Vieusseuxia* that correlate with morphological patterns. A separate analysis of the alliance including additional molecular markers is probably needed to better resolve the phylogeny.

Moraea fergusoniae (included in subg. *Moraea* by Goldblatt 1976b) is inconsistent in subg. *Vieusseuxia* in its several leaves, but is shown to be nested in the subgenus, where its basic chromosome number, $x = 6$, and trilobed inner tepals accord perfectly. We include it here without hesitation. The Cape species, *M. thomasiae*, separated by Goldblatt (1986a) as sect. *Integres* on account of its entire inner tepals, yellow flowers (rare in the subgenus) and \pm free stamens, is morphologically isolated in subg. *Vieusseuxia* and we continue to refer it to a separate section. In the tree (Figure 1) it is allied with a second winter-rainfall species, *M. regalis* (possibly misplaced here and without morphological support), plus all the eastern southern African (and summer rainfall area) species of subg. *Vieusseuxia*, which constitute a well

supported (1, 87, 60) lineage. It is biogeographically significant that these eastern species constitute a clade, thus representing a minor radiation of the genus in the region.

We segregate the remaining species of subg. *Vieusseuxia* (BP 98) in two sections based primarily on morphology. These are the small sect. *Villosae*, which includes the species clustered around *M. villosa* and which share outer tepal limbs as wide or wider than long and usually both leaves and stems pilose (not *M. caeca*). The remaining species fall by default in sect. *Vieusseuxia*: molecular analysis provides modest support for this alliance (1, 73, 62; excluding *M. calcicola*). The isolated position of *M. algoensis* (sister to sect. *Vieusseuxia* plus sect. *Villosae*) and the position of *M. barkerae* in the *M. villosa* clade receive no morphological support and both are provisionally referred to sect. *Vieusseuxia*.

11. Subg. *Homeria*: this exclusively southern African alliance is well supported (1, 94, 88) in the molecular analysis and is united morphologically by its hard, black corm tunic fibres and by specialized flowers in which the style branches and crests are reduced, the crests sometimes lacking, and the inner tepals are scarcely smaller than the outer (the *Homeria*-type flower *sensu* Goldblatt (1986c)). Both fugaceous and long-lived flowers are present in the subgenus. Basic chromosome number is $x = 6$, but a few species have $n = 5$ or 4 (and $2n = 9$). Leaf number is reduced in some species from several to consistently one leaf, evidently the derived condition. The inclusion of *M. radians* in the subg. *Homeria* clade (originally a separate genus *Sessilistigma*) is consistent with Goldblatt's (1991) reduction of the genus in *Homeria*. *M. flexicaulis*, originally assigned to a monotypic section of *Moraea* (Goldblatt 1982) is likewise retrieved within the subg. *Homeria* clade, which is consistent with its chromosome number and karyotype. We have no hesitation in including it in subg. *Homeria*. Its rather unusual morphology (the stem is strongly flexuose and the flowers have well developed style branches and crests) is somewhat anomalous for the subgenus, but recall the species pair *M. knersvlaktensis* and *M. schlechteri* (originally treated as *Homeria* sect. *Namaquanae* by Goldblatt (1981)) and we provisionally unite the three species in an enlarged sect. *Flexuosae* (the earliest name in *Moraea* for the section). There is no molecular support for the inclusion of *M. louisabolusiae* with these species as proposed by Goldblatt (1981, as *H. bolusiae*) based on morphology. We place *M. louisabolusiae* in sect. *Homeria* close to *M. patens*; a treatment consistent with both morphology and the molecular tree topology. Within the subgenus, the group of species around *M. cookii* also merits taxonomic recognition and we treat the alliance as sect. *Stipantherae* Goldblatt (1981). It then comprised five species with the single leaf clasping the stem for some distance, fugaceous flowers and, in four species, the filaments free distally. Of the five species *M. britteniae* and *M. marlothii* fall outside the clade and their continued inclusion in sect. *Stipantherae* must be viewed as provisional.

There is no molecular support for species groups based on flower shape, namely those with very short tepal claws clasping the base of the filament column (e.g. sect. *Conantherae* including *Moraea bifida*, *M. miniata*, *M. pendula* and several more) versus those

with longer claws forming a wide, deep bowl (e.g. sect. *Homeria*, including *M. collina*, *M. minor*, *M. ochroleuca*, *M. pyrophila* and others). In fact, apart from three members of sect. *Stipantherae* and two of sect. *Flexuosae*, there are no significant species alliances retrieved in the molecular trees that merit taxonomic recognition and we fall back on the existing classification based on morphology in which two more sections were recognized (Goldblatt 1981): sects. *Conantherae* and *Homeria* as well as sect. *Flexuosae* and sect. *Stipantherae*. Separate molecular study of subg. *Homeria* using additional DNA sequences may help resolve relationships and provide a test for the current classification.

CLASSIFICATION AND SYNOPSIS OF *MORAEA*

Moraea Mill., Figures of Plants vol. 2: 159, t. 238 (1758) (as *Morea*), name and spelling conserved. Type also conserved: *M. vegeta* L.

1. Subg. **Plumariae** Goldblatt & J.C.Manning, subg. nov. Type species: *M. lugubris* (Salisb.) Goldblatt.

Plants with branched stems. *Foliage leaves* several, channelled. *Flowers* fugaceous, blue; tepals subequal but outer larger and with nectar guides, limbs laxly spreading; filaments united in lower half; style branches diverging at tips and stigmatic apically, crests plumose. *Capsules* ± globose. *Basic chromosome number* $x = 10$.

1. *M. lugubris* (Salisb.) Goldblatt

2. Subg. **Visciramosae** Goldblatt in Annals of the Missouri Botanical Garden 63: 7 (1976b). Type species: *M. bituminosa* (L.f.) Ker Gawl.

Plants with branched stems, nodes sticky; corm tunics ± woody, sticky on adaxial surface. *Foliage leaves* several or 2, channelled. *Flowers* fugaceous, variously coloured; tepals subequal or outer larger and with nectar guides, limbs reflexed; filaments united in lower half or free but contiguous; style branches broad with abaxial stigmatic lobe bearing a forked appendage in centre and well developed paired crests or style branches reduced, lacking crests, then flattened or filiform. *Capsules* ± globose. *Basic chromosome number* $x = 10$.

2a. Sect. **Multifoliae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. vespertina* Goldblatt & J.C.Manning.

Foliage leaves several. *Flowers* white, pale blue or predominantly buff-brown; style branches and crests moderately or well developed.

2. *M. vespertina* Goldblatt & J.C.Manning

3. *M. bubalina* Goldblatt

2b. Sect. **Visciramosae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. bituminosa* (L.f.) Ker Gawl.

Foliage leaves 2. *Flowers* yellow, blue or brown, occasionally white; style branches and crests moderately well developed or reduced and without crests (in *M. simplex* filiform and extending between the stamens).

4. *M. bituminosa* (L.f.) Ker Gawl.

5. *M. inconspicua* Goldblatt

6. *M. viscaria* (L.f.) Ker Gawl.

7. *M. saldanhae* Goldblatt & J.C.Manning

8. *M. elsiae* Goldblatt

9. *M. simplex* Goldblatt & J.C.Manning

3. Subg. **Umbellatae** Goldblatt & J.C.Manning, subg. nov. Type: *M. margaretae* Goldblatt.

Rheome Goldblatt: 92 (1980a). Type species: *R. maximiliani* (Schltr.) Goldblatt (= *Moraea maximiliani* (Schltr.) Goldblatt).

Plants with branched stems, branches and leaves usually clustered at first aerial node; corm tunics dark brown, initially unbroken, later splitting irregularly. *Foliage leaves* several or solitary. *Inflorescence spathes* blunt or truncate, with outer spathe often diverging apically. *Flowers* fugaceous, pale yellow to ± beige (rarely pale pink) with dark venation, sometimes with perianth tube; stamens united in lower half; style branches well developed or reduced and lacking crests (in *M. nana* with paired filiform arms extended horizontally). *Capsules* ± club-shaped. *Basic chromosome number* $x = 10$.

10. *M. linderi* Goldblatt

11. *M. margaretae* Goldblatt

12. *M. intermedia* Goldblatt & J.C.Manning

13. *M. cooperi* Baker

14. *M. longiflora* Ker Gawl.

15. *M. umbellata* Thunb.

16. *M. maximiliani* (Schltr.) Goldblatt

17. *M. nana* (L.Bolus) Goldblatt

4. Subg. **Moraea**

Moraea rankless *Corymbosae* Baker: 10 (1896), nom. illegit. superfl. Type species: *M. juncea* L. = *M. vegeta* L., type of the genus.

Plants with stems usually branched, sometimes repeatedly; corm tunics finely to coarsely fibrous or ± woody. *Foliage leaves* several to 2(1). *Flowers* mostly yellow to buff-brown, occasionally pink to red, or partly white (blue in *M. nubigena*); filaments united in lower half; style branches and crests well developed (reduced in *M. vlokii*). *Capsules* ± globose, exerted. *Basic chromosome number* $x = 10$.

4a. Sect. **Moraea**

Corms often asymmetric; tunics of pale, coarse or fine fibres. *Foliage leaves* several to 2(1). *Flowers* yellow, sometimes pink to red or brown; filaments partially united; style branches and crests usually well developed (not *M. vlokii*).

18. *M. vegeta* L.

19. *M. indecora* Goldblatt

20. *M. gawleri* Spreng.

21. *M. vlokii* Goldblatt

22. *M. namaquamontana* Goldblatt

4b. Sect. **Polyphyllae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. ramosissima* (L.f.) Ker Gawl.

Plants usually multi-branched. *Corm* tunics brown,

fragmenting irregularly. *Foliage leaves* several to many, broad and prominently channelled. *Flowers* yellow; filaments united in lower half or only at base; style branches and crests well developed.

23. *M. ramosissima* (L.f.) Druce
24. *M. garipeensis* Goldblatt

Uncertain position and provisionally placed here:

25. *M. papilionacea* (L.f.) Ker Gawl.
26. *M. nubigena* Goldblatt

5. Subg. **Galaxia** (Thunb.) Goldblatt & J.C.Manning, stat. nov. *Galaxia* Thunb.: 50 (1782). *Moraea* sect. *Galaxia* (Thunb.) Goldblatt: 376 (1998). Type species: *G. graminea* Thunb., lecto. designated by Phillips (1951) = *Moraea fugacissima* (L.f.) Goldblatt.

Plants acaulescent at anthesis; corm tunics pale, usually finely fibrous. *Leaves* several, often plane and ± prostrate, narrowly channelled or terete, hardly distinct from spathes. *Flowers* fugaceous, sessile, with solid perianth tube, yellow, white, or shades of pink to purple; tepals mostly without narrow claws (not *M. kamiesmontana*); style branches much reduced with crests obscure, stigma lobes entire or irregularly fringed. *Capsules* ± globose. *Basic chromosome number* $x = 9$.

5a. Series **Unguiculatae** Goldblatt & J.C.Manning, ser. nov. Type species: *M. kamiesmontana* (Goldblatt) Goldblatt.

Flowers pink with white cup; tepals prominently clawed; filaments partly united; style branches with stigma lobes entire.

27. *M. kamiesmontana* (Goldblatt) Goldblatt

5b. Series **Eurystigma** (Goldblatt) Goldblatt in Novon 8: 377 (1998). *Galaxia* subg. *Eurystigma* Goldblatt: 398 (1979a,b). *Galaxia* ser. *Eurystigma* (Goldblatt) Goldblatt: 376 (1998). Type species: *G. versicolor* Salisb. ex Klatt (= *Moraea versicolor* (Salisb. ex Klatt) Goldblatt).

Flowers pink to purple or white (yellow in *M. citrina*); filaments largely united; style branches with stigma lobes entire.

28. *M. citrina* (G.J.Lewis) Goldblatt
29. *M. barnardiella* Goldblatt
30. *M. melanops* Goldblatt & J.C. Manning
31. *M. versicolor* (Salisb. ex Klatt) Goldblatt
32. *M. variabilis* (G.J.Lewis) Goldblatt
33. *M. minima* Goldblatt
34. *M. fenestralis* (Goldblatt & E.G.H.Oliver) Goldblatt

5c. Series **Galaxia** (Thunb.) Goldblatt in Novon 8: 376 (1998). *Galaxia* Thunb.: 50 (1782). Type species: as for subgenus.

Flower yellow or white, filaments largely united or spreading from base (*M. luteoalba*); style branches with fringed stigma lobes.

35. *M. kamisensis* Goldblatt

36. *M. luteoalba* (Goldblatt) Goldblatt
37. *M. galaxia* (L.f.) Goldblatt & J.C.Manning
38. *M. pilifolia* Goldblatt
39. *M. vuvuzela* J.C.Manning & Goldblatt
40. *M. albiflora* (G.J.Lewis) Goldblatt
41. *M. fugacissima* (L.f.) Goldblatt
42. *M. stagnalis* (Goldblatt) Goldblatt
43. *M. angulata* Goldblatt

6. Subg. **Monocephalae** (Baker) Goldblatt in Annals of the Missouri Botanical Garden 63: 7 (1976b). Rankless *Monocephalae* Baker: 10 (1896). Type species: *M. angusta* (Thunb.) Ker Gawl., lecto. designated by Goldblatt: 7 (1976b).

Plants unbranched, usually with sticky nodes. *Foliage leaf* solitary, distally terete. *Flowers* fugaceous, yellow to buff-brown; stamens united only near base; style branches well developed; ovary sharply 3-angular. *Capsules* ovoid-oblong. *Seeds* flattened and discoid. *Basic chromosome number* $x = 10$.

44. *M. angusta* (Thunb.) Ker Gawl.
45. *M. anomala* G.J.Lewis
46. *M. neglecta* G.J.Lewis
47. *M. vallisavium* Goldblatt

7. Subg. **Acaules** (Baker) Goldblatt & J.C.Manning, stat. nov. Rankless *Acaules* Baker: 8 (1896) [as 'sect. *Acaules* Baker' (Goldblatt 1976b)]. Type species: *M. ciliata* (L.f.) Ker Gawl.

Plants usually acaulescent (not *M. longipes*), usually unbranched, often with single rhipidium; corm tunics usually pale and coarsely fibrous. *Foliage leaves* several to few, hardly distinct from spathes, channelled. *Flowers* fugaceous, retracted after anthesis to base of rhipidium, various colours; stamens united in lower half; style branches well developed. *Capsules* concealed in spathes. *Basic chromosome number* $x = 10$.

48. *M. falcifolia* Klatt
49. *M. ciliata* (L.f.) Ker Gawl.
50. *M. longipes* Goldblatt & J.C.Manning
51. *M. tricolor* Andrews
52. *M. macronyx* G.J.Lewis

8. Subg. **Polyanthes** (Goldblatt) Goldblatt & J.C.Manning, comb. nov. *Moraea* sect. *Polyanthes* Goldblatt (1976b). Type species: *M. polystachya* (L.f.) Ker Gawl.

Corm tunics mostly of hard, black fibres. *Foliage leaves* several to solitary. *Flowers* fugaceous, mostly blue to mauve, also yellow or white; stamens united in lower half; ovary often included, style branches well developed with prominent crest or much reduced, sometimes as paired or single filiform arms. *Capsules* oblong-ellipsoid, sometimes beaked, exerted or included. *Basic chromosome number* $x = 10$ but four sections have $x = 6$.

8a. Sect. **Serpentinae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. serpentina* Baker.

Foliage leaves 2 or 3, twisted or coiled. *Flowers* blue, yellow or mostly white; style branches and crests well developed. *Ovary* and *capsules* included.

53. *M. serpentina* Baker
54. *M. tortilis* Goldblatt

8b. Sect. **Deserticola** Goldblatt in *Annals of the Missouri Botanical Garden* 63: 7 (1976b). Type species: *M. bolusii* Baker.

Rankless *Subracemosae* Baker: 9 (1896) [as 'sect. *Subracemosae* Baker' in Goldblatt: 7 (1976b)]. Type species: *M. edulis* (L.f.) Ker Gawl. (= *M. fugax* (D.Delaroche) Ker Gawl.), lecto., designated by Goldblatt: 7 (1976b).

Barnardiella Goldblatt: 312 (1977a). Type species: *B. spiralis* (N.E.Br.) Goldblatt (= *Moraea herrei* (L.Bolus) Goldblatt).

Plants unbranched or branched, branches sometimes sessile. *Foliage leaves* solitary (sometimes 2 in *M. fugax* group). *Flowers* usually blue to mauve or violet (sometimes yellow or white); tepal claws short or ± as long as limbs; stamens united in lower half; style branches well developed with erect crests or reduced, without crests (as paired or filiform arms extended horizontally in *M. hexaglottis*). *Ovary* and *capsules* included, sometimes beaked.

55. *M. saxicola* Goldblatt
56. *M. macgregorii* Goldblatt
57. *M. namibensis* Goldblatt
58. *M. bolusii* Baker
59. *M. granitica* Goldblatt
60. *M. herrei* (L.Bolus) Goldblatt
61. *M. rigidifolia* Goldblatt
62. *M. hexaglottis* Goldblatt
63. *M. fugax* (D.Delaroche) Ker Gawl.
64. *M. gracilentia* Goldblatt
65. *M. filicaulis* Baker
66. *M. macrocarpa* Goldblatt

8c. Sect. **Hexaglottis** (Vent.) Goldblatt in *Novon* 8: 376 (1998). *Hexaglottis* Vent.: 6 (1808). Type species: *H. longifolia* (Jacq.) G.J.Lewis, lecto. designated by Lewis: 219 (1959) = *M. longifolia* (Jacq.) Pers.

Plantia Herbert: 89 (1844). Type species: *P. flava* Herb. (probably = *Moraea virgata* Jacq.).

Plants usually branched, secondary branches usually sessile. *Flowers* yellow, with tepals subequal with claws short; tepals united in tube in 2 species; style branches reduced to paired filiform arms extended either side of opposed stamen, ovary exserted or included and ± sessile in species with perianth tube. *Ovary* and *capsules* exserted or included.

67. *M. namaquana* (Goldblatt) Goldblatt
68. *M. lewisiae* (Goldblatt) Goldblatt
69. *M. longifolia* (Jacq.) Pers.
70. *M. riparia* (Goldblatt) Goldblatt
71. *M. brevituba* (Goldblatt) Goldblatt
72. *M. virgata* Jacq.

8d. Sect. **Gynandriris** (Parl.) Goldblatt in *Novon* 8: 376 (1998). *Gynandriris* Parl.: 49 (1854). *Iris* subg. *Gynandriris* (Parl.) Baker: 2 (1892). *Iris* sect. *Gynandriris* (Parl.) Dykes: 229 (1913). *Moraea* sect. *Gynandr-*

iris (Parl.) Goldblatt: 376 (1998). Type species: *M. sisyrinchium* (L.) Ker Gawl.

Helixyra Salisb. ex N.E.Br.: 348 (1929) [*Helixyra* Salisb., *Trans. Hort. Soc.* 1: 305 (1812), nom. nud.], nom. illeg. superf. pro *Gynandriris*. Type species: not indicated by author).

Moraea subg. *Helixyra* Salisb. ex Baker [as a combination but *Helixyra* Salisb. nom. inval.]: 48 (1892). Type species: *M. simulans* Baker, lecto., here designated.

Plants unbranched or few-branched; spathes translucent with dark veins. *Flowers* fugaceous, blue to purple or white; stamens united in lower half; style branches well developed with erect crests; ovary ± sessile and with sterile tubular beak. *Capsules* with transparent walls, remaining enclosed in spathes.

73. *M. australis* Goldblatt
74. *M. setifolia* (L.f.) Druce
75. *M. cedarmontana* (Goldblatt) Goldblatt
76. *M. simulans* Baker
77. *M. sisyrinchium* (L.) Ker Gawl.
78. *M. mediterranea* Goldblatt
79. *M. pritzeliana* Diels
80. *M. contorta* Goldblatt
81. *M. hesperantha* (Goldblatt) Goldblatt

8e. Sect. **Polyanthes** Goldblatt in *Annals of the Missouri Botanical Garden* 63: 8 (1976b). Type species: as for subgenus.

Plants few- to several-branched. *Foliage leaves* several to 2. *Flowers* shades of blue to violet or purple (rarely yellow); style branches well developed with prominent crests or reduced and crests vestigial. *Ovary* and *capsules* usually exserted.

82. *M. bipartita* L.Bolus
83. *M. polystachya* (L.f.) Ker Gawl.
84. *M. venenata* Dinter
85. *M. speciosa* (L.Bolus) Goldblatt
86. *M. polyanthos* Thunb.
87. *M. deserticola* Goldblatt
88. *M. tanquana* Goldblatt & J.C.Manning
89. *M. carsonii* Baker

8f. Sect. **Pseudospicatae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. pseudospicata* Goldblatt.

Roggeveldia Goldblatt: 840 (1979c publ. 1980). Type species: *R. fistulosa* Goldblatt (= *Moraea fistulosa* (Goldblatt) Goldblatt).

Plants unbranched or branched, secondary branches sometimes sessile. *Foliage leaves* solitary (2 in *M. calista*, which may be misplaced here). *Flowers* usually blue to mauve or violet; tepal claws short or ± as long as limbs; stamens united in lower half; style branches well developed with erect crests or reduced, without crests, sometimes as paired or single filiform arms extended horizontally. *Ovary* and *capsules* exserted or included.

90. *M. elliotii* Baker
91. *M. exiliflora* Goldblatt
92. *M. alpina* Goldblatt

- 93. *M. stricta* Baker
- 94. *M. thomsonii* Baker
- 95. *M. natalensis* Baker
- 96. *M. inclinata* Goldblatt
- 97. *M. iringensis* Goldblatt
- 98. *M. afro-orientale* Goldblatt
- 99. *M. callista* Goldblatt
- 100. *M. crispa* Thunb.
- 101. *M. verecunda* Goldblatt
- 102. *M. pseudospicata* Goldblatt
- 103. *M. pearsonii* Goldblatt & J.C.Manning
- 104. *M. monticola* Goldblatt
- 105. *M. marginata* J.C.Manning & Goldblatt
- 106. *M. fistulosa* (Goldblatt) Goldblatt

9. Subg. **Grandiflorae** Goldblatt in Annals of the Missouri Botanical Garden 63: 8 (1976b). Type species: *M. spathulata* (L.f.) Klatt.

Hymenostigma Hochst. in Flora 27: 24 (1844). Type species: *H. schimperii* Hochst. (= *Moraea schimperii* (Hochst.) Pic.-Serm.).

Iridopsis Welw. ex Baker in Transactions of the Linnean Society of London, Botany 1: 270 (1878), pro syn.

Plants unbranched. *Flowers* yellow (white) or blue to violet; stamens united in lower half; ovary usually 3-angled; style branches well developed with prominent crests. *Capsules* large, exserted. *Seeds* flattened, discoid. *Basic chromosome number* $x = 6$.

- 107. *M. spathulata* (L.f.) Klatt
- 108. *M. moggii* N.E.Br.
- 109. *M. huttonii* (Baker) Oberm.
- 110. *M. alticola* Goldblatt
- 111. *M. reticulata* Goldblatt
- 112. *M. robusta* (Goldblatt) Goldblatt
- 113. *M. galpinii* Baker) N.E.Br.
- 114. *M. muddii* N.E.Br.
- 115. *M. ardesiaca* Goldblatt
- 116. *M. carnea* Goldblatt
- 117. *M. graminicola* Oberm.
- 118. *M. hiemalis* Goldblatt
- 119. *M. unibracteata* Goldblatt
- 120. *M. bella* Harms
- 121. *M. macrantha* Baker
- 122. *M. textilis* Baker
- 123. *M. ventricosa* Baker
- 124. *M. schimperii* (Hochst.) Pic. Serm.
- 125. *M. verdickii* De Wild.
- 126. *M. tanzanica* Goldblatt
- 127. *M. brevifolia* Goldblatt
- 128. *M. inyangani* Goldblatt
- 129. *M. angolensis* Goldblatt
- 130. *M. upembana* Goldblatt
- 131. *M. clavata* Goldblatt
- 132. *M. bovonei* R.C.Foster
- 133. *M. balundana* Chiov.
- 134. *M. unifoliata* Goldblatt

10. Subg. **Viusseuxia** (*D.Delaroche*) Baker, Handbook of the Irideae: 48 (1892). *Viusseuxia* D.Delaroche: 31 (1766). Type species: *V. spiralis* D.Delaroche, lectotype designated by Goldblatt: 8 (1976b) = *M. bellendenii* (Sweet) N.E.Br.

Phaianthes Raf.: 30 (1836). Type species: *P. lurida* (Ker Gawl.) Raf. (= *Moraea lurida* Ker Gawl.).

Plants simple or few-branched; corm tunics of brown firm to soft fibres. *Foliage leaf* solitary (several in *Moraea fergusoniae*), sometimes villous abaxially. *Flowers* long-lived, variously coloured, usually with inner tepals 3-lobed with prominent central cusp or reduced to simple, hair-like cusps or absent (entire in a few species); stamens united in lower half or entirely, or united at base, rarely free or virtually so; style branches usually well developed with erect crests (reduced and crests vestigial in *M. worcesterensis*). *Capsules* ovoid-ellipsoid, usually exserted. *Basic chromosome number* $x = 6$.

10a. Sect. **Integres** Goldblatt & J.C.Manning, sect. nov. [Sect. *Thomasiae* Goldblatt in Annals of Kirstenbosch Botanic Garden 14: 138 (1986), invalid name]. Type species: *M. thomasiae* Goldblatt.

Plants often unbranched. *Foliage leaf* solitary. *Flowers* yellow, inner tepals spatulate, entire; filaments free or barely united at base.

135. *M. thomasiae* Goldblatt

10b. Sect. **Viusseuxia** (*D.Delaroche*) Goldblatt & J.C.Manning, comb. nov. *Viusseuxia* D.Delaroche: 31 (1766). Type species: as for subgenus.

Plants branched or not. *Foliage leaf* usually solitary (not *M. fergusoniae*). *Flowers* mostly blue to violet, pink, purple, white, rarely yellow; inner tepals often tricuspidate, hair-like, sometimes absent; filaments usually united in lower half, occasionally free or barely united at base.

- 136. *M. incurva* G.J.Lewis
- 137. *M. barkerae* Goldblatt
- 138. *M. lurida* Ker Gawl.
- 139. *M. cantharophila* Goldblatt & J.C.Manning
- 140. *M. insolens* Goldblatt
- 141. *M. worcesterensis* Goldblatt
- 142. *M. fergusoniae* L.Bolus
- 143. *M. unguiculata* Ker Gawl.
- 144. *M. rivulicola* Goldblatt & J.C.Manning
- 145. *M. algoensis* Goldblatt
- 146. *M. longiaristata* Goldblatt
- 147. *M. barnardii* L.Bolus
- 148. *M. debilis* Goldblatt
- 149. *M. lilacina* Goldblatt & J.C.Manning
- 150. *M. regalis* Goldblatt
- 151. *M. tricuspida* Goldblatt
- 152. *M. deltoidea* Goldblatt & J.C.Manning
- 153. *M. bellendenii* Ker Gawl.
- 154. *M. trifida* R.C.Foster
- 155. *M. marionae* Baker
- 156. *M. dracomontana* Goldblatt
- 157. *M. modesta* Killick
- 158. *M. pubiflora* N.E.Br.
- 159. *M. brevistyla* (Goldblatt) Goldblatt
- 160. *M. vigilans* Goldblatt & J.C.Manning
- 161. *M. albicuspa* Goldblatt
- 162. *M. decipiens* Goldblatt & J.C.Manning
- 163. *M. helmei* Goldblatt & J.C.Manning

164. *M. mutila* (C.H.Bergius ex Eckl.) Goldblatt & J.C.Manning
 165. *M. cuspidata* Goldblatt & J.C.Manning
 166. *M. tripetala* (L.f.) Ker Gawl.
 167. *M. ogamana* Goldblatt & J.C.Manning
 168. *M. hainebachiana* Goldblatt & J.C.Manning
 169. *M. amabilis* Diels
 170. *M. grandis* Goldblatt & J.C.Manning

10c. Sect. **Villosae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. villosa* (Ker Gawl.) Ker Gawl.

Foliage leaf and stem usually pilose or velvety abaxially (not *M. caeca*). *Flowers* variously coloured, large with outer tepal limbs exceeding claws, limbs rotund, as wide as or wider than long; inner tepals tricuspidate with central cusp long and trailing.

171. *M. aristata* (D.Delaroche) Asch. & Graeb.
 172. *M. caeca* Goldblatt
 173. *M. amissa* Goldblatt
 174. *M. atropunctata* Goldblatt
 175. *M. tulbaghensis* L.Bolus
 176. *M. villosa* (Ker Gawl.) Ker Gawl.
 177. *M. calcicola* Goldblatt
 178. *M. loubseri* Goldblatt
 179. *M. gigandra* L.Bolus

11. Subg. **Homeria** (Vent.) Goldblatt & J.C.Manning, comb. et stat. nov. *Homeria* Vent.: 2 (1808). Type species: *H. collina* (Thunb.) Salisb. (= *M. collina* Thunb.).

Sessilistigma Goldblatt: 156 (1984b). Type species: *S. radians* Goldblatt (= *Moraea radians* (Goldblatt) Goldblatt).

Plants simple or few-branched; corm tunics of wiry, black fibres. *Foliage leaves* few to solitary. *Flowers* fugaceous or long-lived, yellow, beige or pink to orange, sometimes with dark markings; outer and inner tepals subequal, both whorls usually with nectar guides, claws as long as limbs or much shorter; stamens with filaments united entirely or free near apices (free in *M. radians*); style branches reduced with crests vestigial or absent. *Capsules* ovoid-ellipsoid to cylindrical, included or exserted. *Basic chromosome number* $x = 6$.

11a. Sect. **Stipanthera** (Goldblatt) Goldblatt & J.C.Manning, comb. nov. *Homeria* sect. *Stipanthera* Goldblatt [*'Stipanthera'*] in Annals of the Missouri Botanical Garden 68: 426 (1981). Type species: *M. pallida* Baker.

Leaf solitary, clasping stem below. *Flowers* yellow (rarely pink); tepals with claws much shorter than limbs, clasping or forming a cup including base of filament column; stamens with filaments free near apices or fully united.

180. *M. cookii* L.Bolus
 181. *M. pallida* Baker
 182. *M. marlothii* L.Bolus
 183. *M. reflexa* Goldblatt
 184. *M. britteniae* (L.Bolus) Goldblatt

11b. Sect. **Flexuosae** Goldblatt in Annals of the Missouri Botanical Garden 69: 356 (1983, as 1982). Type

species: *M. flexuosa* Goldblatt (= *M. flexicaulis* Goldblatt).

Homeria sect. *Namaquanae* Goldblatt [*'Namaquana'*]: 425 (1981). Type species: *H. schlechteri* L. Bolus.

Leaves several, decreasing in size above. *Flowers* fugaceous, yellow; tepals with claws much shorter than limbs, clasping or forming a cup including base of filament column; stamens with filaments free near apices or ± fully united.

185. *M. schlechteri* (L.Bolus) Goldblatt
 186. *M. knersvlaktensis* Goldblatt
 187. *M. flexicaulis* Goldblatt

11b. Sect. **Homeria** (Vent.) Goldblatt in Novon 8: 374 (1998). Type species: *H. collina* (Thunb.) Salisb. (= *M. collina* Thunb.).

Stem straight or flexed. *Foliage leaves* several to one. *Flowers* fugaceous or lasting two days; tepal claws short and erect or long and forming a cup enclosing stamens; filaments usually united entirely (free in *M. radians*).

188. *M. cedarmonticola* Goldblatt
 189. *M. autumnalis* (Goldblatt) Goldblatt
 190. *M. ochroleuca* (Salisb.) Drapiez
 191. *M. flaccida* Sweet
 192. *M. collina* Thunb.
 193. *M. pyrophila* Goldblatt
 194. *M. minor* Eckl.
 195. *M. longistyla* (Goldblatt) Goldblatt
 196. *M. comptonii* (L.Bolus) Goldblatt
 197. *M. elegans* Jacq.
 198. *M. radians* (Goldblatt) Goldblatt
 199. *M. bulbifera* (G.J.Lewis) Goldblatt
 200. *M. serratostyla* (Goldblatt) Goldblatt
 201. *M. patens* (Goldblatt) Goldblatt
 202. *M. louisabolusiae* Goldblatt
 203. *M. vallisbelli* (Goldblatt) Goldblatt
 204. *M. flavescens* (Goldblatt) Goldblatt
 205. *M. demissa* Goldblatt

11c. Sect. **Conantherae** (Goldblatt) Goldblatt & J.C.Manning, comb. nov. *Homeria* sect. *Conantherae* Goldblatt [*'Conanthera'*]: 427 (1981). Type species: *Homeria miniata* (Andrews) Sweet (= *M. miniata* Andrews).

Stem straight or flexed. *Foliage leaves* several to one. *Flowers* fugaceous, members of both whorls well developed and bearing nectar guides; tepal claws short, erect, forming a cup enclosing base of filaments; filaments united entirely; anthers parallel with stigmatic surfaces emerging between anthers.

206. *M. aspera* Goldblatt
 207. *M. miniata* Andrews
 208. *M. pendula* (Goldblatt) Goldblatt
 209. *M. karooica* Goldblatt
 210. *M. fenestrata* Goldblatt
 211. *M. bifida* (L.Bolus) Goldblatt
 212. *M. fragrans* Goldblatt
 213. *M. fuscomontana* (Goldblatt) Goldblatt
 214. *M. brachygyne* (Schltr.) Goldblatt

ACKNOWLEDGEMENTS

We owe profuse thanks to Roy Gereau, Missouri Botanical Garden, for reviewing the manuscript and proffering corrections to the complex infrageneric nomenclature. Anthony Magee kindly assisted with the figures. JS was supported by the funding programme 'LOEWE-Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz' from the Ministry of Higher Education, Research, and the Arts, Hesse, Germany.

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