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Phytogeography and interspecies relationships in *Monsonia* (Geraniaceae)

H. J. T. VENTER*

ABSTRACT

The geographical distribution of *Monsonia* and its 25 species is examined. It is shown that the genus inhabits various climatic regions (desert, semi-desert, savanna and temperate grassland) of Africa, south-west Asia and Madagascar. Attention is also paid to the interrelationships of the *Monsonia* species in comparison to their distribution patterns. Possible links between the species of southern Africa and those of northern Africa are also discussed.

RÉSUMÉ

LA PHYTOGÉOGRAPHIE ET LES RELATIONS INTERSPÉCIFIQUES DE MONSONIA *(GERANIACEAE)*

La répartition géographique de Monsonia *et des ses 25 espèces est examinée. Il est montré que le genre habite des régions climatiques variées (désert, semi-désert, savanne et formation herbeuse tempérée) de l'Afrique, du Sud-Ouest asiatique et de Madagascar. Une attention est aussi accordée aux relations entre les espèces de* Monsonia *en comparaison avec leur mode de distribution. Les liens possibles entre les espèces d'Afrique australe et celles d'Afrique du Nord sont aussi discutés.*

INTRODUCTION

Monsonia is one of five genera recognized in the Geraniaceae (Hutchinson, 1969). The character in common to the five genera and which is distinctive for the family, is the schizocarp fruit which, at maturity, divides into five mericarps.

The family is dispersed over both hemispheres in Africa, America, Europe, Asia and Australia.

Hutchinson (1969) claims that the main centre of distribution of the Geraniaceae is southern Africa where all the genera excepting *Erodium* L'Hérit. are abundant to very abundant. White (1971), however, warns that major climatic changes swept over Africa since the separation of the continents and that these changes were certain to have had important impact on the distribution of plant families.

Monsonia is a genus of 25 species (Venter, 1979). The species are rather uniform in morphology, especially with respect to their floral structure. The genus is distinguished from the other four genera in the family by having actinomorphic flowers with 15 stamens and by being herbaceous.

DISCUSSION

Monsonia is found in Africa, Madagascar and south-west Asia as far east as Pakistan and India. The main concentration of species occurs in southern Africa where 21 species are found, of which 18 are endemic to the region. Two species are endemic to east Africa. Another two are endemic to the Sahara and Sind deserts.

Ecologically *Monsonia* inhabits a variety of niches. A number of species are found in deserts (Namib, Sahara and Sind deserts), several occur in semi-desert areas, whereas another group inhabits subtropical or tropical bushlands or grasslands which may be dry or moderately moist. A small number, mainly weedlike annuals with wide ecological amplitudes, are encountered over large areas under a variety of climatic conditions. A few species are found in high altitude temperate grassland. One species occurs only in the winter rainfall south-west Cape of South Africa.

Two sections may be distinguished, viz. *Plumosae* Boiss. and *Barbatae* Boiss.. They are distinguished from each other not only by the structure of the mericarp, but also by the free or connate sepals and the presence or absence of sepal spurs (Fig. 1).

Section **Plumosae:**

Diagnostic features: Prostrate or decumbent suffrutescent herbs, some members with erect rhizomes. *Leaves* broadly ovate to orbicular, venation palmate. *Inflorescenses* 1–14-flowered. *Sepals* mostly connate and spurred at their bases. *Petals* obtriangular, obovate or elliptic. *Stamens* in a cylindrical column around the gynoecium. *Mericarps* obconical with the tail in most of the members plumose.

Plumosae comprises 11 species, viz. *M. desertico-la* Dinter ex Knuth, *M. drudeana* Schinz, *M. heliotropioides* (Cav.) Boiss., *M. ignorata* Merxm. & Schreiber, *M. longipes* Knuth, *M. luederitziana* Focke & Schinz, *M. nivea* (Decne.) Webb, *M. parvifolia* Schinz, *M. speciosa* L., *M. trilobata* Kers and *M. umbellata* Harv.

The members of *Plumosae* inhabit deserts and semi-deserts at altitudes between sea-level and approximately 1 700 m above sea-level (Figs 2 & 3). *M. speciosa* and *M. longipes* are the two exceptions, being found in the winter rainfall area of the south-western Cape in South Africa and the highlands of eastern Africa respectively.

Seven species are endemic to the Karoo-Namib Region. Two are endemic to the Mediterranean and

* Department of Botany, University of the Orange Free State, P.O. Box 339, Bloemfontein 9300, South Africa.

FIG. 1.—*Monsonia drudeana* of section *Plumosae:* 1, habit, × 0,75; 2, mericarp with plumose tail, × 2. *M. burkeana* of *Barbatae*: 3, habit, × 0, 75; 4, mericarp with crested tail.

Saharo-Sindian Regions of north Africa and south-west Asia.

M. deserticola, M. drudeana and *M. ignorata* inhabit the southern part of the Namib Desert in SWA/Namibia. Extremely arid conditions prevail here. The little precipitation is derived from fog and winter rain. The habitat varies from windswept sand dunes to sandy river washes. All three species are perennial and possess orthotropous subterrestrial rhizomes. *M. speciosa* is the only other species in *Monsonia* that has a rhizome and, although it does not inhabit desert, it also grows in a sandy habitat and has to withstand long, dry summers by remaining dormant subterrestrially.

In the vast semi-desert Karoo north, east and south of the Namib Desert proper four more species are found. They are all endemic to the area and comprise *M. leuderitziana, M. parvifolia, M. umbellata* and *M. trilobata.* The first three species are in all respects closely related. They are also related to *M. drudeana* through their identical pollen (Venter, 1980). In contrast to *M. luederitziana, M. parvifolia* and *M. umbellata* which are widely distributed over the area, *M. trilobata* is restricted to a very small area in South West Africa/Namibia on the eastern border of the Karoo-Namib Region. Although it belongs to the *Plumosae* of the Karoo-Namib, its relation to the other members is not clear.

The position of *M. ignorata* within the group is also unclear. Although it resembles *M. drudeana* vegetatively, its flower, pollen and fruit differ markedly. *M. deserticola* differs even more with distinct, spurless sepals.

M. heliotropioides and *M. nivea* inhabit the Mediterranean and Saharo-Sindian Regions of north Africa and south-west Asia as far east as Pakistan and the western border of India (Figs 2 & 3). They are very similar in appearance and are obviously closely related, especially on account of their distinctive type of pollen (Bortenschlager, 1967; Venter, 1980). They are distinguishable from the Karoo-Namib species because of their very small

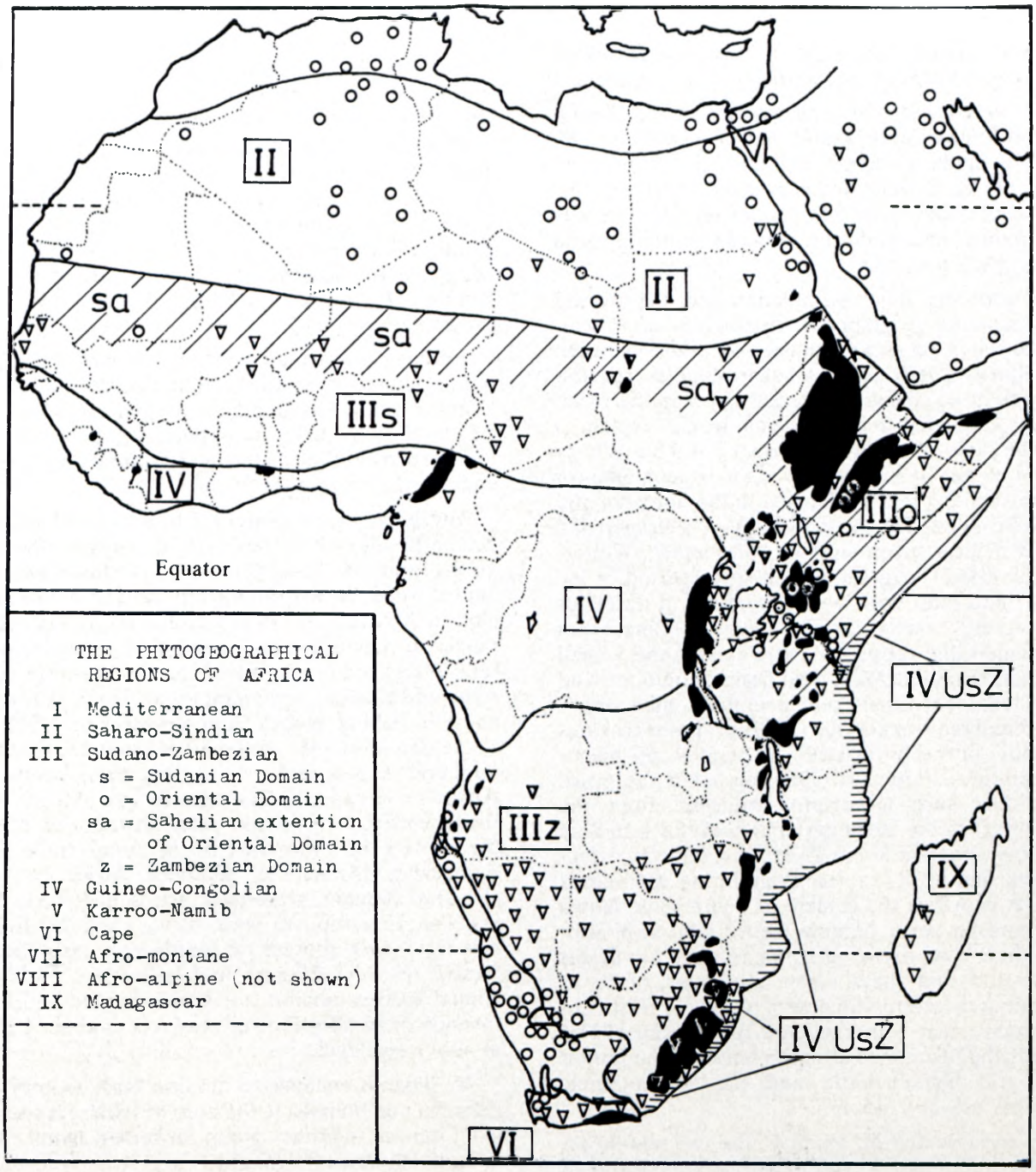

FIG. 2.—The geographical distribution of *Monsonia* and its sections, *Barbatae* (▽) and *Plumosae* (O) in Africa (map after White, 1971).

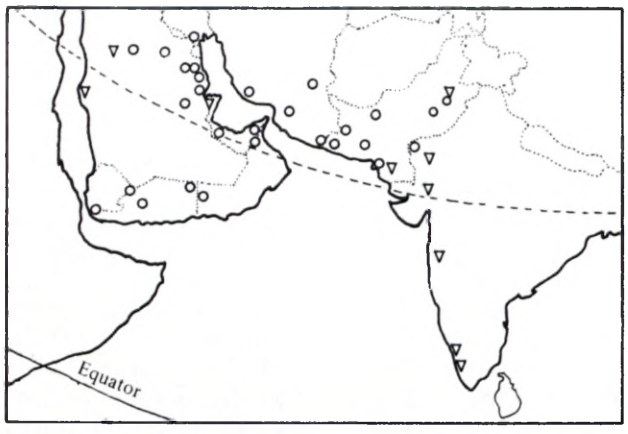

FIG. 3.—The geographical distribution of *Monsonia* and its sections, *Barbatae* (▽) and *Plumosae* (O) in south-west Asia.

flowers bearing only eight relatively large pollen grains per anther cell, and by their pollen sculpture.

M. deserticola, the 'odd' species in the Karoo-Namib Region resembles *M. heliotropioides* and *M. nivea* to quite a degree, especially in the size and form of the flower. If the distance separating *M. deserticola* from *M. heliotropioides* and *M. nivea* was not known, one would be tempted to group these three species together.

Considering this resemblance and the overall discontinuous geographical distribution of *Plumosae*, the question arises whether a link exists between the Karoo-Namib and the Saharo-Sindian species. At present no climatic link exists between these two widely separated regions which would explain a possible link. Was there a former link? De Winter (1966) writes: 'It is evident from the large number of species which occur unchanged in the northern and southern areas that the possibility of a former link between these areas must be considered'. Winterbottom (1967) suggests 'that at some period in the past, there must have been a corridor of desert or semi-desert country across central Tanganyika (Tanzania) and through Zambia linking the Somali Arid and the South West Arid Districts of today' and 'that these conditions obtained more than once'. Van Zinderen Bakker Snr (1969) proposes that this corridor probably existed in periods of higher temperature. Verdcourt (1969) discussed the possibility that such a corridor stretched from the south-west to the north-east and henceforth to Sind and Rasjasthan in South-West Asia. It is important to note that he states that even during the wettest periods in Africa the climate of South-West Africa and Somalia never became wetter than semi-arid, that these two areas acted as refuges for desert plants and that these areas, moreover, acted as evolutionary centres of desert plants. It is also of importance that Van Zinderen Bakker Snr (1975) regards the taxonomic affinities between the proper hyper-arid Namib biota and the Sahara-Sindic elements as very old.

M. speciosa and *M. longipes*, the two non-desert species of *Plumosae* correspond to a large degree in vegetative and floral morphology, but they are separated by some 5 000 km, *M. speciosa* being from the Cape in South Africa and *M. longipes* from Kenya, Ethiopia and Tanzania in eastern Africa. As was the case with the desert elements, the question is whether a link exits or existed between these two species. The arid corridor, already mentioned, may have been the link, but both species are more temperate in character, although *M. speciosa* reveals xeromorphic trends. An alternative, cool, humid link via the mountains along the eastern part of Africa may have existed in the past (Bader, 1965; Van Zinderen Bakker Snr, 1970; Coetzee, 1978), but at present this route is certainly disjunct because of hot arid barriers such as the Limpopo and Zambezi Valleys.

Section **Barbatae:**

Diagnostic features: Prostrate, decumbent or erect perennial or annual herbs. *Leaves* linear, ovate or elliptic; venation linear to subpalmate. *Inflorescenses* 1–3–(4)-flowered. *Sepals* free. *Petals* obtriangular. *Stamens* arranged in a cup-shaped column around the pistil. *Mericarps* obliquely obovoid with their tails crested at the base.

Barbatae comprises *M. angustifolia* E. Mey. ex A. Rich., *M. attenuata* Harv., *M. brevirostrata* Knuth, *M. burkeana* Planch. ex Harv., *M. emarginata* (L.f.) L'Hérit., *M. galpinii* Schltr. ex Knuth, *M. glauca* Knuth, *M. grandifolia* Knuth, *M. lanuginosa* Knuth, *M. natalensis* Knuth, *M. praemorsa* E. Mey. ex Knuth, *M. senegalensis* Guill. & Perr. and *M. transvaalensis* Knuth.

Barbatae is distributed over a large part of Africa, but its main concentration is found in the Zambezian Domain and Afromontane Region of southern Africa (Fig. 2). Only four species of *Barbatae* are found north of the equator and of these only one is endemic to the region.

The most widely dispersed species in *Monsonia* belong to *Barbatae*. These are *M. angustifolia*, *M. glauca* and *M. senegalensis*. *M. angustifolia*, an annual weed, occurs throughout most of Africa and also in Madagascar. It is adapted to a very wide range of environmental conditions that include semi-desert scrub veld, savanna, humid subtropical scrub and tropical to temperate grassland. Altitudinally its habitat ranges from sea-level to 2 500 m above sea-level. *M. glauca* is encountered in hot semi-arid karoo veld to savanna from southern Africa to Kenya and Tanzania in east Africa. *M. senegalensis* has by far the widest distribution of all the species of *Monsonia*. It is found from the Zambezian Domain in southern Africa to the Oriental Domain of eastern Africa and along its Sahelian Extension to west Africa (Fig. 2). It is, however, also present in south-west Asia from Arabia to West Pakistan and India (Fig. 3). This annual species inhabits hot semi-arid veld and dry savanna or scrub veld from sea-level to about 1 600 m above sea-level.

M. ignea is endemic to the arid bush country of Ethiopia and Somalia in the horn of Africa. It seems to form a natural group together with *M. senegalensis* and *M. glauca*.

All other members of *Barbatae* are restricted to southern Africa.

M. burkeana, M. praemorsa and *M. natalesis* are predominantly found in subtropical bushveld.

M. attenuata, M. lanuginosa and *M. transvaalensis* are quite similar in appearance and are found in grassland of mountain sides or highveld areas above approximately 1 300 m above sea-level. Although *M. brevirostrata* is encountered in the same habitat as the above three species, it is not related to these species, but rather to *M. angustifolia.*

M. emarginata, M. grandifolia and *M. galpinii* are related. They inhabit coastal scrub and lower altitude mountain grassland in the Cape Region and the Usambara-Zululand Domain (Fig. 2). *M. galpinii* has the smallest range of distribution of any species in *Monsonia.* It is found only in a very restricted area in coast dune scrub at East London in South Africa.

The vague interrelationships of such a high proportion of species in *Monsonia,* especially in *Barbatae* which is the more primitive section of the genus (Venter 1980), may perhaps be due to the present species being isolated remnants of a once richer assortment of species with wider and more confluent distribution over Africa. The climatic changes that have oscillated over Africa since the drift of the continents may have impoverished the genus, resulting in the rather unrelated assortment of today. Very few specimens exist which may be regarded as hybrids and this may also indicate that the present day species are not closely related genetically. The very small distribution areas and the scarcity of specimens in some of the species may also indicate that these members of *Monsonia* are becoming extinct, although one must always keep in mind that the opposite may be as true. *Monsonia,* however, exhibits some of the most primitive characteristics in the Geraniaceae (Moffett, 1978; Venter, 1980) from which the assumption may be made that it belongs to the oldest stock of the family and may therefore be less active in speciation today.

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