

Phytogeography of African Commelinaceae

R. B. FADEN*

ABSTRACT

Africa (including Madagascar) has nearly twice as many species of Commelinaceae as any other continent (approximately 270 species, or about 40% of the total in the family). Of the 17 genera which are native, seven (*Anthericopsis*, *Coleotrype*, *Palisota*, *Polyspatha*, *Pseudoparis*, *Stanfieldiella* and *Triceratella*) are endemic, the highest percentage generic endemism of any continent. Within Africa generic diversity is slightly higher in western than in eastern tropical floras. Species richness, however, is greatest in eastern Africa, mainly due to a high diversity of species of *Commelina* and *Aneilema*.

Africa shares more genera with Asia (nine) than with any other continent. Only one African genus, *Buforessia*, is neither endemic nor shared with Asia. Its western African/northeastern South American distribution is unique in the family. Besides *Buforessia*, only five other genera of Commelinaceae (out of a total of 50 in the family), occur in both the Old and New Worlds. These genera, *Aneilema*, *Commelina*, *Floscopa*, *Murdannia* and *Pollia* are all very widespread in the Old World, occurring in Australia and Asia in addition to Africa (both continental and Madagascar).

Madagascar is relatively poor in species (31), but these include the endemic Madagascan genus *Pseudoparis*, the sole African species of *Rhopalephora*, and the largest number of species of the Afro-Malagasy endemic genus *Coleotrype*.

The high rate of generic endemism of Commelinaceae in Africa probably indicates that Africa was one of the ancient centres of diversity for the family. The high species diversity is more likely due to relatively recent radiations by genera pre-adapted to survival in non-forest habitats. The occurrence of only a small number of genera on both sides of the Atlantic suggests that the Commelinaceae have been evolving independently in the eastern and western hemispheres for a long period.

RÉSUMÉ

PHYTOGÉOGRAPHIE DES COMMÉLINACÉES AFRICAINES

L'Afrique (y compris Madagascar) a presque deux fois plus d'espèces de Commelinaceae que n'importe quel autre continent (approximativement 270 espèces ou environ 40% du total de la famille). Des 17 genres qui sont indigènes, sept (*Anthericopsis*, *Coleotrype*, *Palisota*, *Polyspatha*, *Pseudoparis*, *Stanfieldiella* et *Triceratella*) sont endémiques; c'est le pourcentage d'endémisme générique le plus élevé de tous les continents. En Afrique la diversité générique est légèrement plus élevée dans les flores tropicales de l'Ouest que dans celles de l'Est. La richesse en espèces est cependant plus grande en Afrique orientale par suite d'une diversité élevée des espèces de *Commelina* et d'*Aneilema*.

L'Afrique a plus de genres en commun avec l'Asie (neuf) qu'avec n'importe quel autre continent. Seul un genre africain, *Buforessia*, n'est ni endémique ni commun avec l'Asie. Sa distribution en Afrique occidentale et au Nord-Est de l'Amérique du Sud est unique dans la famille. A part *Buforessia*, cinq autres genres seulement de Commelinaceae (sur un total de 50 dans la famille) se rencontrent à la fois dans l'Ancien et le Nouveau Monde. Ces genres, *Aneilema*, *Commelina*, *Floscopa*, *Murdannia* et *Pollia*, sont tous très largement répandus dans l'Ancien Monde, se trouvant en Asie et en Australie en plus de l'Afrique (continentale et Madagascar). Madagascar est relativement pauvre en espèces (31) mais celles-ci comprennent le genre endémique malgache, *Pseudoparis*, la seule espèce africaine de *Rhopalephora* et le plus grand nombre d'espèces de genre endémique Afro-Malgache, *Coleotrype*.

Le niveau élevé d'endémisme générique de Commelinaceae en Afrique, indique probablement que l'Afrique fut un des anciens centres de diversité pour la famille. La diversité élevée d'espèces est très vraisemblablement due à des radiations relativement récentes par des genres pré-adaptés à la survivance en habitats non forestiers. L'occurrence de seulement un petit nombre de genres sur les deux côtés de l'Atlantique suggère que les Commelinaceae ont évolué indépendamment dans les hémisphères Est et Ouest pour une longue période.

INTRODUCTION

The Commelinaceae are the fifth largest family of monocotyledons in tropical Africa (after the Poaceae, Orchidaceae, Cyperaceae and Liliaceae). The family is virtually absent from temperate and Saharan Africa, but it is widely distributed in all tropical parts of the continent (Table 1). Africa (including Madagascar) has, with approximately 270 species (40% of the family), in 17 genera, nearly twice as many species of Commelinaceae as any other continent. Accompanying this species richness there is a high degree of generic and specific

endemism. In the following account, the distribution of each African genus is summarized briefly. In the discussion distribution patterns in Africa for the family as a whole and the phytogeographic relationships of the African Commelinaceae are considered.

GENERIC CONCEPTS

Generic concepts within the Commelinaceae are presently in a state of flux, particularly for the New World genera. The generic concepts for the Old World genera used here differ from those of Brenan (1966) in that *Dictyospermum*, *Tricarpelema* and *Rhopalephora* are treated as distinct from *Aneilema* (see Faden, 1975; 1977); *Ballya* is included in

* Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560. U.S.A.

TABLE 1.—Distribution of Commelinaceae in Africa by floral region

Genus	W.T.A. *	Cameroun	Gabon	Afrique Centrale	Angola	S.W.A.	Southern Africa	Zambesiaca	T.E.A.	Ethiopia & Somalia	Madagascar	Total African species
<i>Amischotolype</i>	1**	1	1	1	—	—	—	—	—	—	—	1
<i>Aneilema</i>	10	6	3	12	6	2	10	22	37	18	1	56
<i>Anthericopsis</i>	—	—	—	1	—	—	—	1	1	1	—	1
<i>Buforrestia</i>	2	1	—	—	—	—	—	—	—	—	—	2
<i>Coleotrype</i>	1	—	—	1	—	—	1	1	2	—	6	9
<i>Commelina</i>	24	+	+	+	+	10	+	+	c. 60	+	c. 13	c. 125
<i>Cyanotis</i>	11	+	+	+	+	3	+	+	11	+	2	c. 20
<i>Floscopa</i>	10	+	+	+	+	1	1	+	7	1	1	c. 16
<i>Murdannia</i>	3	2	1	4	2	1	1	3	5	1	3	11
<i>Palisota</i>	9	+	+	+	1	—	—	1	4	—	—	c. 15
<i>Pollia</i>	2	2	+	+	1	—	—	—	3	2	1	4
<i>Polyspatha</i>	2	2	+	+	1	—	—	—	2	—	—	2
<i>Pseudoparis</i>	—	—	—	—	—	—	—	—	—	—	2	2
<i>Rhopalephora</i>	—	—	—	—	—	—	—	—	—	—	1	1
<i>Stanfieldiella</i>	4	3	1	1	1	—	—	—	1	1	—	4
<i>Tricarpelema</i>	—	1	—	—	—	—	—	—	—	—	—	1
<i>Triceratella</i>	—	—	—	—	—	—	—	1	—	—	—	1
Total species	79	—	—	—	—	17	—	—	c. 133	—	c. 30	c. 271
Total genera	12	12	10	12	9	5	6	9	11	8	9	17
Endemic African genera	4	3	3	5	3	0	1	4	5	2	2	7

*Geographic regions as defined in the following floras: Flora of West Tropical Africa, ed. 2; Flore du Cameroun; Flore du Gabon; Flore d'Afrique Centrale (= Flore du Congo Belge et du Ruanda-Urundi; = Flore du Congo, du Rwanda et du Burundi); Conspectus Florae Angolensis; Prodrum einer Flora von Südwest-afrika; Flora of Southern Africa; Flora Zambesiaca; Flora of Tropical East Africa; Adumbratio Florae Aethiopiae; Flore de Madagascar et des Comores.

** Numbers of species present are listed where known (based on published records, herbarium specimens, etc.). Otherwise presence (+) or absence (—) of the genus is indicated.

Aneilema (Faden, 1975); *Aclisia* is included in *Pollia* (Faden, 1975; Faden & Suda, 1980); and *Porandra* (Hong, 1974) is recognized as doubtfully distinct from *Amischotolype*. For the New World genera the differences from Brenan (1966) are as follows: *Setcreasea* and *Separothea* are included in *Tradescantia*, following Hunt (1975); *Cuthbertia* is considered distinct from *Phyodina*; and the new genera *Elasis*, *Gibasoides* and *Matudanthus* (Hunt, 1978) are accepted. A soon to be described genus related to *Geogenanthus*, ranging from Panama to Peru, is included in the total of 51 genera recognized for this treatment.

DISTRIBUTION OF GENERA

Amischotolype

Amischotolype (syn. *Forrestia* A. Rich.) is represented in Africa by a single western African species, *A. tenuis* (C. B. Clarke) Rolla Rao (Nigeria to Zaire). The 10–15 other species in the genus range from north-eastern India to New Guinea.

Aneilema

Fifty-six of the 62 species of *Aneilema* occur in Africa (Faden, 1975, and unpublished). Two of the African species, *A. umbrosum* (Vahl) Kunth and *A. forskalii* Kunth extend to tropical America and the Arabian Peninsula, respectively. Of the remaining six species, one (underscribed) is endemic to the Yemen Arab Republic and the other five to Australia and the surrounding islands including New Guinea.

Within Africa the principal centre of taxonomic and morphological diversity of *Aneilema* is in eastern and north-eastern Africa; from southern Ethiopia and central Somali Republic south to central Tanzania. Secondary concentrations of taxa occur in the miombo region of south-western Tanzania and adjacent Zambia and Zaire; from southern Mozambique and south-western Zimbabwe to northern and eastern Transvaal and the north-eastern Cape Province of South Africa; and in the savannah region of West Africa; Sierra Leone and Senegal to Nigeria (Faden, 1975). The single Madagascan species, the endemic *A. aparine* Perrier, is the sole African species of section *Aneilema* which otherwise includes all of the Australian region taxa.

Anthericopsis

The sole species of this endemic African genus, *A. sepalosa* (C. B. Clarke) Engl., ranges from Ethiopia to Malawi and Zaire.

Buforrestia

The two African species of *Buforrestia* are endemic and allopatric: *B. mannii* C. B. Clarke from Nigeria to Cameroun and *B. obovata* Brenan from Guinea to Ghana (Brenan, 1968). The third species, *B. candolleana* C. B. Clarke, is South American and stretches from Surinam to north-eastern Brazil.

Coleotrype

Coleotrype, a genus of 9 species, plus many infraspecific taxa described from Madagascar, is the

only endemic African genus of *Commelinaceae* which occurs both on Madagascar (six species) and on the mainland (three species). Perrier (1936; 1938) informally separated the Madagascan taxa from the continental species. He compared only *C. natalensis* C. B. Clarke on the basis of corolla and androecial morphology, a distinction which appears to be sound. The three mainland species are allopatric: *Coleotrype natalensis* (South Africa to Mozambique and Zimbabwe); *C. bruecknerana* Mildbr. (eastern Kenya and Tanzania); and *C. laurentii* K. Schum. (West Africa to Uganda).

Commelina

The nearly cosmopolitan genus *Commelina* is the largest in the family, with about 170 species. It is best developed in Africa where approximately 125 species, many still undescribed, occur. All but about 11 of the African species are endemic to the continent and/or Madagascar. Within Africa, *Commelina* has its greatest number of species in the *Flora of Tropical East Africa* and *Flora Zambesiaca* areas. It is especially diverse in the miombo areas of southern Tanzania, northern Zambia and south-eastern Zaire.

Cyanotis

About 20 of the approximately 45 species of *Cyanotis* occur in Africa. The remainder are mainly Asiatic. India is the centre of taxonomic diversity, but one species, *C. axillaris* (L.) Sweet, extends to northern Australia. The genus as used here includes *Amisophacelus* Rao Rolla & Kammathy (see Faden & Suda, 1980). The African species are more or less evenly distributed except for the forested areas where they are rare or lacking. The species in West Africa include a high proportion of local endemics (Brenan, 1968), whereas the species in Tropical East Africa are mostly widespread (Faden, unpublished). Five of the African species also occur outside of Africa.

Floscopa

Floscopa, with about 20 species, is a mainly African genus. A single species, according to all recent treatments, *F. scandens* Lour., ranges from India and Sri Lanka to Australia. A group of about four species occurs in South America with one of them, *F. robusta* (Seub.) C. B. Clarke, extending north to Nicaragua. All of the African species have generally been considered endemic, but the South American *F. glabrata* (Kunth) Hassk. may prove conspecific with the African *F. confusa* Brenan. Within Africa *Floscopa* is most diverse in West Africa, and only the most widespread African species, *F. glomerata* (J. A. & J. H. Schult.) Hassk., reaches Ethiopia, Kenya, South Africa and Madagascar.

Murdannia

Murdannia, a pantropical but principally Asiatic genus of about 50 species, has 11 taxa in Africa of which seven (or perhaps six) are endemic. The only questionable endemic is *M. axillaris* Brenan of the East African coast which is uncomfortably close to certain collections of the Asiatic *M. blumei* (Hassk.) Brenan.

Except for *M. simplex* (Vahl) Brenan and *M. tenuissima* (A. Chev.) Brenan, most African species are rather local. There is no concentration of species in any part of the continent. In Africa, *M. gigantea* (Vahl) Brückn. is restricted to Madagascar.

Palisota

With about 15 species (variously estimated up to 25 species: Morton, 1967; Willis, 1973) *Palisota* is the largest endemic African genus of *Commelinaceae*. Its centre of diversity is western Africa, especially Cameroun, but species occur as far east as the mountains of eastern Tanzania. The genus is present on the islands of the Gulf of Guinea but it is absent from Madagascar and the Indian Ocean islands.

Pollia

The four African species of *Pollia*, a mainly paleotropical genus of about 17 species, are all endemic: *P. gracilis* C. B. Clarke (Madagascar, Comoro Islands); *P. bracteosa* K. Schum. (Uluguru Mountains, Tanzania); *P. mannii* C. B. Clarke (widespread in West Africa east to Ethiopia, Uganda and Tanzania); *P. condensata* C. B. Clarke (widespread in West Africa east to eastern Tanzania). *Pollia sambiranensis* Perrier of Madagascar is a species of *Aneilema*. The genus was recently discovered in the New World (Faden, 1978).

Polyspatha

The two species of this endemic African genus, *Polyspatha paniculata* Benth. and *P. hirsuta* Mildbr., are widespread in western Africa (Sierra Leone to Angola), extending east to Uganda (Brenan, 1968).

Pseudoparis

Pseudoparis, with two described species, *P. monandra* Perrier and *P. cauliflora* Perrier, is the only genus of *Commelinaceae* which is confined to Madagascar.

Rhopalephora

The single African species of this genus is the endemic Madagascan *R. rugosa* (Perrier) Faden. The three other species range from India and Sri Lanka to the Fiji Islands (Faden, 1977).

Stanfieldiella

The six taxa (four species plus two varieties) of the African endemic genus *Stanfieldiella* are nearly restricted to West Africa (Brenan, 1960, 1968). Only *S. imperforata* (C. B. Clarke) Brenan extends further east (to eastern Tanzania) or south (to Angola) of Cameroun.

Tricarpelema

This genus was collected in Africa for the first time in 1964. The species, which will be described elsewhere, was gathered at N'Kolbisson, Cameroun (*De Wilde et al.* 3728, BR, K, WAG) and, to this author's knowledge, it has not been recollected. The remaining six species of the genus (as used in the sense of *Dictyospermum* subgen. *Tricarpelema* of Faden, 1975) are Asiatic, ranging from northeastern India to the Philippines and Borneo.

Triceratella

This morphologically eccentric, monotypic, African endemic genus is known from a single collection made in Zimbabwe in 1958 (Brenan, 1961).

DISCUSSION

The distributions of the African genera of Commelinaceae have been outlined above and are summarized in Table 1. Several generalizations may be made. The largest genera, except *Palisota*, are the most widely distributed. The five genera which occur in all eleven African floral regions, *Aneilema*, *Commelina*, *Cyanotis*, *Floscopa* and *Murdannia* are also widespread outside of Africa, occurring in Asia, Australia and, except *Cyanotis*, South and North America. These five genera include 228 African species or about 84% of the total species in the continent and Madagascar.

Significantly, all five of these genera comprise species principally of non-forest habitats. Among the remaining 12 genera only the monotypic African endemics *Anthericopsis* and *Triceratella* could be characterized as non-forest genera. Five of the 10 forest genera are endemic. Three of these endemic genera, *Palisota*, *Polyspatha* and *Stanfieldiella*, have their centres of diversity in western Africa; a fourth, *Pseudoparis*, is confined to Madagascar; and the fifth, *Coleotrype*, is most diverse in Madagascar, but is also scattered on the continent. Of the five non-endemic forest genera, the African species of *Amischotolype*, *Buforrestia* and *Tricarpelema* are restricted to western Africa; *Rhopalephora* occurs only in Madagascar; and only *Pollia* could be described as widespread: it is the sole forest genus in the family to occur in Asia, Australia and the New World, in addition to Africa.

The preponderance of forest genera in western Africa and Madagascar is a distribution pattern that is prevalent in many groups of flowering plants as well as in pteridophytes. This pattern is undoubtedly relictual, being the result of the increasing aridity in Africa during the Neogene and again since the late Pleistocene (Axelrod & Raven, 1978; Richardson & Richardson, 1972). This desiccation was in part associated with the onset of the formation of the Rift Valley system, and hence it was most severe in eastern Africa. Lowland forest taxa tended to become isolated in western Africa and Madagascar where climatic deterioration was less intense. Some taxa also survived in isolated coastal and subcoastal forests of eastern Africa, sometimes with subsequent morphological differentiation (Faden, 1973).

The occurrence of western African forest taxa or clear relatives thereof in these East African forests provides strong evidence that these genera and, by inference, others were once more widespread in the continent. In the Commelinaceae three species span the gap of 650–850 km of unsuitable habitat: *Palisota schweinfurthii* C. B. Clarke, *Pollia condensata* C. B. Clarke, and *Stanfieldiella imperforata* (C. B. Clarke) Brenan. Three genera are represented by vicariant forest species in the two areas: *Coleotrype* by *C. laurentii* K. Schum. in western Africa (east to

Uganda) and *C. bruecknerana* Mildbr. in eastern Kenya and Tanzania; *Palisota* by *P. ambigua* (P. Beauv.) C. B. Clarke in western Africa and *P. orientalis* K. Schum. in eastern Tanzania; and *Aneilema* by *A. beniniense* (P. Beauv.) Kunth in western Africa and *A. dispernum* Brenan in eastern Tanzania and Malawi. I do not regard the West African plants treated as *A. dispernum* (Brenan, 1968) as conspecific with the East African plants.

The increasing aridity in Africa during the Neogene led to a great increase in drier habitats, ranging from woodland to semidesert. This would have provided non-forest genera ample opportunities to diversify and speciate. The major radiations of *Commelina* and *Aneilema*, which are apparently still ongoing, probably began during this period. Therefore whereas the reduction of lowland rainforests in the Miocene may have decreased diversity among the forest genera of Commelinaceae, possibly leading to the extinction of some, its overall effect would probably have been to have greatly increased the total number of species in the family.

Phytogeographically the African Commelinaceae are most closely related to those of Asia (including Malesia). Nine of the ten nonendemic African genera — all but *Buforrestia* — also occur in Asia (vs. six in Australia and five each in North and South America). Three of those nine genera, *Amischotolype*, *Rhopalephora* and *Tricarpelema*, are restricted to these continents. Of the 23 African species (8% of the total), which are not endemic to the continent or Madagascar, 22 also occur in Asia (all but *Aneilema umbrosum*). No doubt the floristic similarity between Africa and Asia can be accounted for in part by the present direct land connection between the two continents. In a future paper the effects of the altering positions of the continents during the Tertiary will be considered.

REFERENCES

- AXELROD, D. I. & RAVEN, P. H., 1978. Late Cretaceous and Tertiary vegetation history of Africa. In M. J. A. Werger, *Biogeography and ecology of southern Africa* 77–130. The Hague: Junk.
- BRENAN, J. P. M., 1960. Notes on African Commelinaceae. II. The genus *Buforrestia* C. B. Cl. and a new related genus, *Stanfieldiella* Brenan. *Kew Bull.* 14: 280–286.
- BRENAN, J. P. M., 1961. *Triceratella*, a new genus of Commelinaceae from Southern Rhodesia. *Kirkia* 1: 14–19.
- BRENAN, J. P. M., 1966. The classification of Commelinaceae. *J. Linn. Soc. Bot.* 59: 349–370.
- BRENAN, J. P. M., 1968. Commelinaceae. In F. N. Hepper, *Flora of West Tropical Africa*, edn 2, 3, 1: 22–50. London: Crown Agents.
- FADEN, R. B., 1973. East African coastal—West African rain forest disjunctions. In E. M. Lind & M. E. S. Morrison, *East African Vegetation* 202–203. London: Longman.
- FADEN, R. B., 1975. *A biosystematic study of the genus Aneilema (Commelinaceae)*. Ph.D. dissertation, Washington University, St. Louis.
- FADEN, R. B., 1977. The genus *Rhopalephora* Hassk. (Commelinaceae). *Phytologia* 37: 479–481.
- FADEN, R. B., 1978. *Pollia* Thunb. (Commelinaceae): the first generic record from the New World. *Ann. Mo. bot. Gdn* 65: 676–680.

- FADEN, R. B. & SUDA, Y., 1980. Cytotaxonomy of Commelinaceae: chromosome numbers of some African and Asiatic species. *Bot. J. Linn. Soc.* 81: 301-325.
- HONG, D., 1974. Revisio Commelinacearum Sinicarum. *Acta phytotax. sin.* 12: 459-488.
- HUNT, D. R., 1975. The reunion of *Setcreasea* and *Separotheca* with *Tradescantia*. American Commelinaceae. I. *Kew Bull.* 30: 443-458.
- HUNT, D. R., 1978. Three new genera in Commelinaceae. American Commelinaceae. VI. *Kew Bull.* 33: 331-334.
- MORTON, J. K., 1967. The Commelinaceae of West Africa: a biosystematic survey. *J. Linn. Soc., Bot.* 60: 167-221.
- PERRIER DE LA BATHIE, H., 1936. Commélinacées de Madagascar. *Phanérogamie* 5: 173-216.
- PERRIER DE LA BATHIE, H., 1938. Commélinacées. In H. Humbert, *Flore de Madagascar et des Comores*. Tananarive: Imprimerie Officielle.
- RICHARDSON, J. L. & RICHARDSON, A. E., 1972. History of an African Rift lake and its climatic implications. *Ecol. Monogr.* 42: 499-534.
- WILLIS, J. C., 1973. *A dictionary of the flowering plants and ferns*. Cambridge: Cambridge University Press.