The Commelinaceae of Northeast Tropical Africa (Eritrea, Ethiopia, Djibouti, Somalia and Kenya): Diversity and phytogeography

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Northeast Tropical Africa (NETA, comprising Eritrea, Ethiopia, Djibouti, Somalia and Kenya) is rich in Commelinaceae, with 95 species in 10 genera. Twenty-four species, all belonging to Aneilema, Commelina or Cyanotis, are endemic to the region, with country rates of endemism ranging from zero to 35%. Three of the six sections of Aneilema present in NETA have endemic species there, including section Somaliensia, which is wholly endemic to NETA. The forest genera of Commelinaceae in NETA comprise only 4% of the total species. NETA is richer in Commelinaceae than West Tropical Africa or Southern Africa. The most strongly represented flora element is the Somali-Masai flora element. NETA shares 12-13 species with the Arabian Peninsula and 14 species with India.

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Introduction

The Commelinaceae are the fourth largest family of monocots in tropical Africa (after the Poaceae, Orchidaceae and Cyperaceae). Approximately 270 species in 18 genera occur on mainland tropical Africa and Madagascar (Faden 1983; Faden & Evans 1999). Generic diversity is highest in West and Central Africa, but species diversity is greatest in eastern Africa. Species occur in almost all habitats from sea level to about 4200 m.

Our knowledge of African Commelinaceae is constrained by a relative scarcity of modern floristic treatments and monographs. Floristic accounts have been published for West Tropical Africa (Brenan 1968); Senegal (Vanden Bergen 1988); Togo (Brunel et al. 1984); Sudan (Andrews 1956); Ethiopia and Eritrea (Ensermu & Faden 1997); Somalia (Faden 1995); Upland Kenya (Faden 1974b, 1994); Rwanda (Malaise 1988); Southern Africa (Obermeyer & Faden 1985); and Madagascar (Perrier de la Bâthie 1938). Only Aneilema has been monographed (Faden 1991). Despite these shortcomings, I believe that it is still meaningful to examine diversity within areas that are relatively well known floristically and to look for phytogeographic patterns.

Table 1. The number of species in genera of Commelinaceae in the floras of Djibouti, Somalia, Ethiopia and Eritrea, and	
Kenya (Northeast Tropical Africa). * = naturalised.	

Genus	Djibouti	Somalia	Ethiopia/Eritrea	Kenya	Northeast Tropical Africa
Aneilema	1	7	18	28	34
Anthericopsis	_	1	1	1	1
Coleotrype	_	_	_	1	1
Commelina	4	13	19	30	36
Cyanotis	_	1	8	9	13
Floscopa	_	-	1	1	1
Murdannia	_	1	2	4	5
Pollia	-	-	2	1	2
Stanfieldiella	_		1	-	1
Tradescantia*	_	_	-	1	1
Total:	5	23	52	76	95

The Study Area

Northeast Tropical Africa has been defined to comprise Sudan, Eritrea, Ethiopia, Djibouti and Somalia, or these countries excluding Sudan (Friis 1992). For the purposes of this paper I define Northeast Tropical Africa (NETA) differently herein, including Kenya and excluding Sudan. I have circumscribed the area thus for two reasons. First, the newly defined area much more closely matches the Somali-Masai regional center of endemism of White (1983) than do the earlier demarcations. Second, although there is a published flora of Sudan (Andrews 1956), but none for the whole of Kenya, the Commelinaceae of Kenya are much better known. The 1980 collections of Friis & Vollesen from the Imatong Mountains in Sudan - specimens studied at the University of Copenhagen - added at least two genera and seven species of Commelinaceae to Andrews' flora, clearly demonstrating how incomplete our knowledge is of the flora of that country. In contrast, my many years of collecting Commelinaceae in Kenya, studies of the family for Upland Kenya Wild Flowers (Faden 1974b, 1994), and ongoing work on the Flora of Tropical East Africa Commelinaceae have provided me with a detailed knowledge of the Commelinaceae of Kenya.

The propriety of including Kenya in NETA may be questioned further because Kenya is also part of Tropical East Africa. However, there are precedents for including African countries, or parts of countries, in more than one flora, such as Botswana in Flora Zambesiaca and Flora of Southern Africa, the Red Sea Hills in floras of Egypt and Sudan, and the former British Cameroons in both Flora of West Tropical Africa and Flore du Cameroun. The flora of the greater, arid part of Kenya clearly has affinities to the north. Similarly, many species of middle to high elevations in Kenya also occur in Ethiopia. Thus for a phytogeographic study of northeastern Africa, it is quite appropriate to also include Kenya.

Other floristic regions of White (1983) that are represented in the newly defined NETA are the Sudanian regional center of endemism (in western Ethiopia), the Afromontane and Afroalpine regional center of endemism (Kenya

and Ethiopia), the Lake Victoria regional mosaic (western Kenya) and the Zanzibar-Inhambane regional mosaic (southern Somalia and coastal Kenya).

The Commelinaceae of Northeast Tropical Africa

The Commelinaceae recognized from NETA are listed in Appendix 1. Ninety-five species and at least eight additional infraspecific taxa belonging to 10 genera have been recorded. Among these, the genus Tradescantia is neotropical, with several species cultivated, one of which, T. zebrina, is locally naturalized in Kenya. Cyanotis axillaris and C. cristata are mainly tropical Asian weedy species. The former is widespread but rarely collected in tropical Africa, where it may be considered an established, although perhaps not indigenous, species. Cyanotis cristata is known in mainland Africa from a single Eritrean collection made in 1969, so it may well have reached continental Africa recently. The remaining nine genera and 92 species of Commelinaceae are unquestionably indigenous to NETA.

When the species in NETA are summarized by regional flora (Table 1), the flora of Kenya is clearly much richer is species (76 species, or 80% of the total in NETA) than the other floras: Ethiopia and Eritrea together: 52 species (55%); Somalia: 23 species (24%); Djibouti: 5 species (5%). When area is taken into account, there is one species of Commelinaceae per 25,955 km sq for NETA as a whole. The species per km sq for the individual floras are: Kenya (1/7671), Ethiopia and Eritrea together (1/23498), Somalia (1/27724) and Djibouti (1/4640). Thus Kenya, which is a little less than half the area of Ethiopia plus Eritrea, is approximately three times as rich in species as Ethiopia plus Eritrea. Djibouti appears rich in species, but that is an artifact of its small size: it contains a few widespread species.

The bulk of the Commelinaceae species in NETA (83 species or 87% of the total species) belong to only three genera, *Aneilema, Commelina* and *Cyanotis*. These genera comprise 100% of the species in Djibouti (Lebrun *et al.* 1989), 91% of the Commelinaceae of Somalia, 87% of the species of Ethiopia and Eritrea, and 88% of the Kenya species. Country size and habitat diversity within NETA countries appear to have had little bearing on the floristic dominance by these three genera.

Endemism

The taxa of Commelinaceae that are endemic to NETA are indicated in Appendix 1. Twentyfour species (25%) are endemic to NETA. Endemism per regional flora is variable, with none of the five species endemic to Djibouti, eight of 23 species (35%) endemic to Somalia, four of 52 species (8%) endemic to the Flora of Ethiopia and Eritrea area (with none in Eritrea), and six of 76 species (8%) endemic to Kenya. In addition to one-country endemics, Aneilema gillettii and A. sebitense are endemic to Ethiopia and Kenya, and Aneilema lamuense is known only from Kenya and Somalia. Curiously, no species are shared solely between Ethiopia and Somalia. Three species occur exclusively in Ethiopia, Somalia and Kenya: Aneilema somaliense, A. pusillum and Commelina stefaniniana.

The 24 species of Commelinaceae that are endemic to NETA all belong to Aneilema, Commelina or Cyanotis (Appendix 1). Both Aneilema and Commelina have high rates of endemism in NETA: 13 of 34 species (38%) of Aneilema endemic; 10 of 36 (28%) of Commelina endemic. Cyanotis, however, has just one endemic species, C. polyrrhiza, out of 13 species present (8%).

A measure of the distinctness of the flora of a country within a region comprising several countries, such as NETA, is the number of species that occur exclusively in the country, whether or not the species are endemic to the

Table 2. The number and percentage of Northeast Tropical African species, and the number of endemic Northeast Tropi-
cal African species in the sections of Aneilema.

Section	Total number of species	Number of Northeast Tropical African Species	% of total number of species	Species endemic to Northeast Tropical Africa
Amelina	8	6	75	2
Rendlei	4	3	75	-
Somaliensia	5	5	100	5
Lamprodithyros	14	13	93	6
Brevibarbata	17	2	12	-
Pedunculosa	9	5	56	-

country. For example, none of the species that occur in Djibouti are exclusive to that country within NETA. In Eritrea, one of the 11 species (9%) occurs only in that country, but it is not endemic. When Eritrea is combined with Ethiopia, only eight of the 52 species (15%) do not occur elsewhere in NETA, and half of those eight species comprise the four Ethiopian endemics. Because Somalia is wholly surrounded by other countries of NETA, it is hardly surprising that all eight of the species of Commelinaceae that are exclusive to it are also endemic, these eight constituting 35% of the total species present. Kenya is unusual in that it has a high rate of exclusivity (30 of 76 species (39%) not occurring elsewhere in NETA), but only six of those species are endemic to Kenya. Among the 24 exclusive, non-endemics, only three, Aneilema lanceolatum, Murdannia clarkeana, and the introduced Tradescantia zebrina, do not also occur in Tanzania. Seven of the species shared between Kenya and Tanzania are endemic to these two countries (Aneilema brenanianum, A. calceolus, A. clarkei, A. taylorii, Coleotrype brueckneriana, Commelina trilobosperma, Murdannia axillaris), as compared with six species that Kenya shares exclusively with Ethiopia and/or Somalia.

The significance of endemics in a region can be understood best when phylogenetic relationships of the species are known. In *Commelina* and *Cyanotis*, species relationships are

largely unknown, and even the division of these genera into sections is unsettled. Although the monograph of *Aneilema* (Faden 1991) lacks a phylogenetic analysis, it clearly defines the sections of the genus. Moreover, some relationships among the species are evident. Therefore, only *Aneilema* endemics in NETA will be considered further here.

All six sections of *Aneilema* that are present in continental Africa have species in NETA (Table 2). Three of the four sections that are best represented in NETA, in terms of percentage of total species, have endemics in this area, including section *Somaliensia* which is wholly endemic to NETA. The fourth well-represented section, section *Rendlei*, has no endemics in the flora because the NETA species (*A. brenanianum*, *A. rendlei*, *A. taylorii*) occur mainly in southern Kenya, and all extend into northern Tanzania where the section is most diverse (Faden 1991).

The NETA endemics of *Aneilema* section *Amelina* are mainly Kenyan. *Aneilema ephemerum* is a yellow-flowered annual that is endemic to northeastern Kenya and is probably most closely related to the widespread (in Africa as a whole) forest perennial *A. aequinoctiale*. *Aneilema gillettii*, is restricted to a small area on both sides of the Kenya-Ethiopia border. It is most likely related to the widespread *A. hockii*.

Four species groups of section Lamprodithyros

have endemics in NETA. The first group is represented by Aneilema sebitense which occurs at moderate elevations in western Kenya and southern Ethiopia. It is clearly the sister species of A. forskalii of Ethiopia and seasonally moist hills along the Red Sea and the Gulf of Aden. Aneilema trispermum, a Somalian endemic, represents the second species group. Its closest relative may be A. petersii, which occurs from southern Sudan, southern Ethiopia and Kenya southwards. The three species of the third species group occur near or just interior to the Indian Ocean coast. Aneilema benadirense is endemic to Somalia and A. tanaense to Kenya. Aneilema calceolus occurs in Kenya and Tanzania. The fourth species group has a similar range to the third group. Aneilema succulentum, a Kenyan endemic, occurs in dry habitats, just interior to the coastal strip, whereas A. clarkei of Kenya and Tanzania, and A. lamuense, of Kenya and Somalia, occur in moister habitats nearer the coast.

Section *Somaliensia* comprises five species of geophytic perennials, which sort into three groups. The section as a whole is endemic to NETA, with the greatest taxonomic diversity in Somalia (Faden 1991). The first group consists of *A. somaliense*, which is characterized by its bracteoles non-perfoliate, seeds often more than two per ventral locule, and flowers polygamomonoecious. *Aneilema somaliense* occurs mainly in Kenya and Ethiopia, being rare in Somalia, unlike the other two groups.

The second species group comprises A. obbiadense, A. longicapsa and A. grandibracteolatum. The group is characterized by very long, pointed capsules, perfoliate bracteoles, and consistently two seeds per ventral locule. Aneilema obbiadense is confined to the coastal plain of Somalia, whereas closely related A. longicapsa occurs further inland in Somalia, except around Hobyo (Obbia), where both species are present. Aneilema grandibracteolatum is known from a single collection from the Ogaden area in Ethiopia.

The third group consists of A. pusillum, which is divided into four subspecies that are not always easily distinguishable. However, the most distinctive of the subspecies, subsp. thulinii, could possibly merit species rank. The A. pusillum group is characterized by the diminutive size of the plants, inflorescences, and flowers, very succulent leaves, and a basic chromosome number of x = 14 (versus x = 16 in the other two groups). Three of the four subspecies are confined to Somalia; the fourth, subsp. variabile, which is the most problematic taxonomically, extends to Kenya and Ethiopia.

Ecology of Northeast Tropical African Commelinaceae

Faden (1983) classified the African genera of Commelinaceae ecologically as forest and nonforest genera, according to the predominant habit of most species in the genus. In NETA, only three forest genera, Coleotrype, Pollia, and Stanfieldiella, are native, and these contain only four species (4% of the total Commelinaceae) in the area. The forest genera occur only in Ethiopia (Stanfieldiella), Kenya (Coleotrype) or both countries (Pollia). The species of Stanfieldiella and Pollia are confined to southwestern Ethiopia and western Kenya in forests that are known to have West African floral elements (Friis 1992). Coleotrype brueckneriana occurs in moist forest along the Kenya coast, a region also known to have West African species and affinities (Faden 1974a).

There are only twice as many non-forest genera (*Aneilema*, *Anthericopsis*, *Commelina*, *Cyanotis*, *Floscopa* and *Murdannia*) as forest genera in NETA, but the non-forest genera contain more than 20 times as many species. The two largest non-forest genera, *Commelina* and *Aneilema*, both contain forest species, *e.g.*, *C. albiflora* and *A. aequinoctiale*, but these represent only small percentages of the total species of these genera.

Comparisons with other African floras

The Commelinaceae of NETA may be compared with those of West Tropical Africa (WTA) and Southern Africa (Table 3). West Tropical Africa has one-third more indigenous genera than NETA because of the presence of four forest genera (Amischotolype, Buforrestia, Palisota, and Polyspatha) that do not extend to NETA, versus only one non-forest genus, Anthericopsis, in NETA that does not extend to WTA. The proportion of forest genera (7 of 12, or 58%, versus 3 of 9, or 33%) is accordingly much higher in WTA. The forest genera in WTA contain 22 species, or 28% of the species in the flora, as compared to only four species (4%) in NETA. Despite the greater diversity of forest genera and species of Commelinaceae in WTA, the three largest genera in both floras are the same, Commelina, Aneilema and Cyanotis, all non-forest genera. However, whereas these three genera comprise 83% of the species in NETA, they constitute only 57% of the species in WTA. The greater species diversity of these three genera in NETA than in WTA, especially of Aneilema and Commelina, more than offsets the paucity of forest genera and species in NETA. Thus NETA has more species (95 versus 78). When area is taken into account, NETA is more than twice as rich in species of Commelinaceae as WTA (1 species per 25955 square km in NETA versus 1/60000 square km in WTA).

The amount and distribution of endemism differ between NETA and WTA. Species endemism is slightly higher in NETA (24 species or 25% of total species endemic) than in WTA (16 species (21%) endemic), but endemics occur in only three of the nine

Table 3. The number and percentage of endemic species in genera of of Commelinaceae in Northeast Tropical Africa, West Tropical Africa and Southern Africa. total = total number of species; endem. = number of endemic species; % = percentage of endemic species.

	North	east Tropical	Africa	V	West Tropical Africa		S	outhern Afric	ca
	total	endem.	%	total	endem.	%	total	endem.	%
Amischotolype				1					
Aneilema	34	13	38	10	4	40	11	1	9
Anthericopsis	1								
Buforrestia				2	1	50			
Coleotrype	1			1			1		
Commelina	36	10	28	23	3	13	17	3	18
Cyanotis	13	1	8	11	5	45	7	3	43
Floscopa	1			9	1	11	3		
Murdannia	5			3			1		
Palisota				9	2	22			
Pollia	2			2					
Polyspatha				3					
Stanfieldiella	1			4					
Tradescantia	1						1		
Total	95	24	25	78	16	21	41	7	17

indigenous genera in NETA, as compared with six of the 12 genera in WTA. Two of the forest genera, *Buforrestia* and *Palisota*, in WTA have endemics, whereas none of the forest genera in NETA has endemic species. The non-forest genus *Cyanotis* has much higher endemism in WTA than in NETA, but *Aneilema* and *Commelina* have far fewer endemic species in the former. *Aneilema*, however, has about the same percentage endemism in both floras (13 of 38 species (38%) endemic in NETA versus 4 of 10 (40%) in WTA).

The flora of Southern Africa, a region that is largely extra tropical, is poorer in genera (seven) and species (41) of Commelinaceae than both NETA and WTA (Table 3). All six of its native genera also occur in the other two floras. Its relative strengths are the presence of more species of *Floscopa* than NETA and more *Aneilema* species than WTA. It also has the same number of *Coleotrype* species (one) as the other two floras, although each flora has a different species. *Coleotrype* is the only forest genus in Southern Africa, its single species constituting just 2% of the Commelinaceae in the region.

Overall, species endemism in Southern African Commelinaceae (17%) is lower than in NETA or WTA. Like NETA, endemics occur only in *Aneilema, Commelina* and *Cyanotis*. In Southern Africa endemism is high in *Cyanotis* (43%, much higher than in NETA (11%), about the same as in WTA (45%)), moderate in *Commelina* (18% versus 28% in NETA and 13% in WTA), and low in *Aneilema* (9%, compared to 38% in NETA and 40% in WTA).

Phytogeographic Patterns of Northeast Tropical African Commelinaceae

The phytogeography of the Commelinaceae in NETA might be summarized by listing all the species that are present in each floristic zone of White (1983) that occurs in NETA. However,

the detailed distributions of most Commelinaceae species in NETA have not been compiled, so any such list would be very incomplete. Moreover, it is the total distribution of a species that determines its phytogeographic relationships, not just its distribution within NETA. NETA Commelinaceae species may occur primarily outside the region in floristic zones that are themselves not present in NETA. Thus the phytogeographic patterns of the Commelinaceae of NETA will be presented in terms of floristic elements, that is, the floristic zone, or combination of zones, that represents the broad distribution patterns of the species.

Widespread Species

Some Commelinaceae that occur in NETA are so widespread elsewhere in Africa, and sometimes also outside of Africa, that trying to characterize them phytogeographically, in terms of White's floristic zones (White 1983), would be meaningless. These include Commelina africana, C. benghalensis, C. bracteosa, C. diffusa, C. erecta, C. forskaolii, C. subulata, Floscopa glomerata and Murdannia simplex. All of these species, except C. bracteosa and Floscopa glomerata, are also recorded outside of Africa.

The Somali-Masai Element

White's Somali-Masai regional center of endemism covers the greatest area of any floristic zone in NETA. It also encompasses a diverse array of climatic conditions and habitats. Therefore, it is hardly surprising that the majority of Commelinaceae species in NETA occur in this region. The species that characterize the Somali-Masai floristic zone can be separated into three groups on the basis of their distributions.

The Somali Endemics – The flora of Somalia is poor in numbers of species of Commelinaceae but high in endemism (see above). The endemic species of Aneilema have been dis-

cussed above. The endemic species of *Commelina* in Somalia, like those of *Aneilema*, do not represent a single lineage. The one-seeded capsule locules and nearly linear lower petal in *C. somalensis* and *C. frutescens* suggest a possible relationship with *C. erecta* and *C. bracteosa*, but the Somalian endemics are too incompletely known to do more than speculate about their affinities.

The relationships of the two other endemic Somalian *Commelina* species are more certain. *Commelina arenicola* was first described as *C. africana* var. *circinata* by Chiovenda (1936) and accepted as such by Brenan (1964). However, its annual habit, buff-orange to apricot-pink flowers, and testa pattern all indicate a closer relationship with *Commelina subulata* and related species than with *C. africana* (Faden 1996). *Commelina arenicola* differs from other species of the *C. subulata* group by its bivalved (rather than trivalved) capsules and its occurrence at very low elevations near the coast.

Commelina sp. 8 of Flora of Somalia (Faden 1995) is very similar to and presumably closely related to *C. forskaolii*, differing chiefly by its putatively yellow flowers. This apparently new species is noteworthy because it would represent a local endemic within the very wide range of *C. forskaolii*.

Northern Somali-Masai Species – These species are confined to the Somali-Masai floristic zone within NETA but are not largely or entirely restricted to Somalia. They also do not extend south of the equator in Kenya. These species include Aneilema somaliense, A. grandibracteolatum, A. gillettii, A. ephemerum, A. sebitense and Commelina stefaniniana. The possible relationships of the Aneilema species have been discussed above. Commelina stefaniniana has so many unusual features, such as purple-spotted leaves, scented flowers and pubescent sepals, that its relationships are unclear.

Southern Somali-Masai Species - These species are restricted to the Somali-Masai floral zone within NETA and are entirely or chiefly in Kenya within the region, occurring at least partly south of the equator, or they extend south to Tanzania or west, at least to Uganda. Taxa that are mainly Kenyan but reach southern Ethiopia include Aneilema rendlei (also occurs in northern Tanzania), A. indehiscens subsp. keniense (also in Rwanda), A. recurvatum (also in Uganda and northwestern Tanzania), and Commelina reptans (extends to Rwanda, Burundi and northern Tanzania). Somali-Masai species in Kenya that do not reach Ethiopia include Aneilema brenanianum (extends to Tanzania), A succulentum, A. tanaense, Commelina lugardii (extends to eastern Congo (Kinshasa) and northern Tanzania), C. melanorrhiza (which has a sister species in Ethiopia: C. sp. 17), C. nairobiensis and Murdannia clarkeana (plants from Chad and Central African Republic may be conspecific).

The Sudanian Element

There are few Commelinaceae that are mainly restricted to the Sudanian floristic region in Africa as a whole. They constitute a group of five related species of *Aneilema* section *Brevibarbata* that is centered in West Tropical Africa (Faden 1991; Morton 1967). Only *A. lanceolatum* enters NETA where it is known from a single collection from the Lake Turkana region of Kenya in the Somali-Masai floristic zone.

The Zambesian Element

The Zambesian element in the NETA Commelinaceae species consists of those species that occur primarily to the south of NETA in the Zambesian regional center of endemism. These include *Aneilema hockii*, *A. johnstonii*, *Commelina petersii* and *C. kotschyi* that occur in NETA in the Somali-Masai floristic zone. Zambesian species requiring a higher rainfall, *e.g. Aneilema spekei* and *A. hirtum*, occur in the

Lake Victoria floristic zone in Kenya and Sudanian floristic zone in Ethiopia. A third group of Zambesian species, such as *Commelina imberbis*, *C. zambesica* and *Cyanotis foecunda*, are mainly Zambesian in their distributions but have apparently minor range extensions into West or Central Africa. A fourth group of Zambesian species reach Kenya but not Ethiopia. They may occur in the Somali-Masai floristic zone (*Aneilema nicholsonii*) or Lake Victoria floristic zone (*Cyanotis paludosa* and *Murdannia semiteres*). It is noteworthy that the latter two species are aquatic or semiaquatic.

The Sudanian/Zambesian Element

This flora element consists of species that are widespread in both the Sudanian and Zambesian floristic zones. They are best exemplified by *Cyanotis caespitosa*, *C. lanata* and *C. longifolia*. The aquatic, *Murdannia tenuissima*, also shows this general pattern, but it also occurs in the transitional zone to the Guineo-Congolian floristic zone. No *Aneilema* species shows this pattern, and the *Commelina* species that more or less exemplify it appear to be primarily Zambesian with much poorer representation in the Sudanian floristic zone, based on Brenan (1968), unless this is an artifact of undercollecting. They have been treated as Zambesian above.

The Afromontane Element

Although Commelinaceae have been recorded up to 4,200 m in Africa (see Ensermu and Faden 1997, for *Cyanotis barbata*), few species grow above 2000 m. The most characteristic species that occur in the Afromontane floristic zone in NETA are *Aneilema leiocaule* and *Cyanotis barbata* of Kenya and Ethiopia, *Aneilema minutiflorum* of Kenya and *Cyanotis polyrrhiza* of Ethiopia. The *Aneilema* species are forest plants, whereas the *Cyanotis* species grow in open, exposed situations. *Commelina africana* frequently occurs in open habitats in the

Afromontane floristic zone, especially in Ethiopia, but it is also well-represented in the Somali-Masai and Zanzibar-Inhambane floristic zones. *Aneilema aequinoctiale* occurs in forest and at forest edges, but it occurs mainly outside the Afromontane floristic zone of White (1983). *Commelina foliacea* can occur in the Afromontane floristic zone in montane forest, but it is more common at lower elevations in other floristic zones, at least in Kenya. The sole collection of *Commelina* sp. 2 of Ensermu and Faden (1997) is recorded from montane forest.

The Zanzibar-Inhambane Element

The Zanzibar-Inhambane regional mosaic extends mainly along the coast from southern Somalia to southern Mozambique. The Commelinaceae that characterize this floristic zone in NETA are relatively local endemics, e.g. Aneilema clarkei, A. calceolus, A. lamuense, A. taylorii and Murdannia axillaris (see Faden 1991 for distribution maps of the Aneilema species). The Aneilema species are related to species from the Somali-Masai floristic zone. Murdannia axillaris, the only African Murdannia with biseriate seeds, is more closely related to the Asian M. blumei (Hassk.) Brenan than to any other African species.

The Guineo-Congolian Element

The Guineo-Congolian regional center of endemism (White 1983) does not occur in NETA. Consequently there are few Guineo-Congolian species of Commelinaceae in the flora. Six Guineo-Congolian species or subspecies extend from West and Central Africa to NETA: Aneilema aequinoctiale subsp. aequinoctiale (Ethiopia), A. beniniense (Ethiopia and Kenya), Commelina capitata (Kenya), Pollia condensata (Ethiopia and Kenya), P. mannii (Ethiopia) and Stanfieldiella imperforata (Ethiopia).

The Guineo-Congolian species are all

restricted in their distributions in NETA and are disjunct from their nearest localities to the west or south. Those species that are recorded from Ethiopia occur in moist forest, mainly between 1000 and 1300 m elevation. Such forests are afromontane in structure and species composition, but they include number of Guineo-Congolian species, according to Friis (1992). Because of their low elevations, such forests lie in the Sudanian floristic zone of Illubabor and Kefa regions. In Kenya the Guineo-Congolian species are found mainly in the Kakamega Forest or nearby forests, between 1550-1680 m, in western Kenya in the Lake Victoria floristic zone. An endemic forest species in the Kakamega area, Commelina albiflora, might have Guineo-Congolian affinities, but its actual relationships are unclear.

Guineo-Congolian species or taxa related to them may also occur in coastal forests of Kenya and Tanzania in the Zanzibar-Inhambane floristic zone (Faden 1974a). Aneilema nyasense, known in NETA by a single collection from the Shimba Hills in coastal Kenya, occurs primarily in eastern Congolian forests, although it also is present in Tanzania, Malawi and Mozambique. Coleotrype brueckneriana Mildbr., known only from a single locality along the Kenya coast and two localities in eastern Tanzania, has a sister relationship with the Guineo-Congolian species C. laurentii K. Schum., which extends from West Africa to central Uganda. These are two white-flowered species of the only Coleotrype.

Relationships with the Arabian Peninsula and India

Fourteen species of Commelinaceae were recorded from Yemen by Wood (1997). I have not been able to find convincing records of other species from the Arabian Peninsula – e.g., Migahid (1989) includes C. boissieriana C. B.

Clarke from Saudi Arabia, but that apparently is a synonym of *C. imberbis* – so Wood's flora will serve as the basis for the following comparison. Two species, *Aneilema woodii* Faden and *Cyanotis nyctitropa* Deflers, were considered endemic to Yemen (Wood 1997). The remaining 12 species also occur in NETA (Table 4). Among these, five are clearly African species that extend only to the Arabian Peninsula: *Aneilema forskalii*, *Commelina africana*, *C. imberbis*, *C. latifolia* and *Cyanotis lanata*. The remaining seven also extend at least as far as India, if a broad interpretation of *Commelina erecta* is used (see below).

A further uncertainty concerns *Cyanotis nyctitropa*, which is exceedingly close, both morphologically and geographically, to *C. somaliense* of northern Somalia. They are at least very closely related, if not conspecific. Their relationships appear to be with African species such as *C. foecunda* Hassk. It may be noted here that the plant in horticulture under the epithet *C. somaliensis* is not conspecific with the Somalian plant.

The one certain endemic Commelinaceae in the Arabian Peninsula is *Aneilema woodii*, which presently is known from a single locality in Yemen. It naturally hybridizes with *Aneilema forskalii*, with the hybrids possibly competing with *A. woodii* for space and perhaps pushing it to the brink of extinction. Both *A. woodii* and *A. forskalii* belong to *Aneilema* section *Lamprodithyros* which is otherwise confined to Africa, so the African, especially Northeast Tropical African, relationships of *A. woodii* are certain.

A surprisingly large number of species (14, or 15% of total species in NETA) is shared between NETA and India (Table 4). This exceeds the number shared between NETA and the Arabian Peninsula. The seven species that occur in NETA and India, but are lacking from the Arabian Peninsula, are especially noteworthy. Two of these, *Cyanotis axillaris* and

Table 4. The Northeast Tropical African species of Commelinaceae with distributions in the Arabian Peninsula or India. * = conspecificity of the Asian and African plants is uncertain; ** = correct name is uncertain.

Species	Northeast Africa	Arabian Peninsula	India
Aneilema forskalii	+	+	
Commelina africana	+	+	
C. albescens	+	+	+
C. benghalensis	+	+	+
C. diffusa	+	+	+
C. erecta*	+	+	+
C. forskaolii	+	+	+
C. imberbis	+	+	
C. kotschyi*	+		+
C. latifolia	+	+	
C. petersii	+		+
C. subulata	+	+	+
Cyanotis arachnoidea*	+		+
C. axillaris	+		+
C. barbata/vaga**	+	+	+
C. cristata	+		+
C. lanata	+	+	
C. somaliensis/nyctitropa*	+	+	
Murdannia semiteres*	+		+
Murdannia simplex*	+		+

C. cristata, are clearly Asian species with weedy tendencies that may have reached Africa only recently. Indeed, as noted above, C. cristata, which has also collected from Socotra, is known in continental Africa from a single, recent collection. Cyanotis axillaris has been found in Africa in Kenya, Tanzania, Malawi, Sudan, Chad and Cameroon, but there are few collections.

The two species of *Commelina* that are disjunct between NETA and India, *C. kotschyi* and *C. petersii*, have much more restricted Asian than African ranges. *Commelina kotschyi* ranges in Africa from northern Ethiopia south to Swaziland. South Africa and Botswana. Rao

(1967) suggested that, in view of its scarcity in India, where it occurs only in the Western Ghats, *C. kotschyi* might have arrived there from Africa only recently.

Commelina petersii has only just been reported from the Indian subregion (Faden 2000). Until recently, the species was known in India and Sri Lanka as 'C. persicariaefolia Wight' (Clarke 1881; Hooker 1892, 1898), a later homonym for *C. persicariifolia* Delile. Rao (1967) correctly concluded that it was an African species, but misidentified it as *C. imberbis*, which is not found in India. In Africa Commelina petersii ranges from Eritrea to Botswana, Angola and Namibia. Its report from West Tropical Africa

by Brenan (1968) was based on erroneously determined collections, but I have seen a specimen from Sao Tomé in the Gulf of Guinea (Figueiredo & Arriegas 55, K), where perhaps it was introduced. In Asia, Rao (1967) recorded it from "very limited localities in Peninsular India." I found this species to be fairly common in Sri Lanka in 1976-1977. It is also reported from Burma (Clarke 1881; Hooker 1898).

The absence of *Commelina kotschyi* and *C. petersii* from the Arabian Peninsula is surprising. The occurrence of *C. kotschyi* in northern Ethiopia and *C. petersii* in Eritrea (Ensermu & Faden 1997) would anticipate their presence across the Red Sea. Wood (1997) treated a Schweinfurth record of *C. petersii* from Yemen as likely to have been *C. imberbis*, but neither he nor I have seen a Schweinfurth collection determined as *C. petersii* to confirm this.

The three other species that occur in NETA and India but ostensibly not in between, *Cyanotis arachnoidea*, *Murdannia semiteres* and *M. simplex*, all have taxonomic problems. There are varying degrees of uncertainty about the conspecificity of the Asian and African plants in each case. All are currently being investigated.

The remaining seven species present both in NETA and India also occur in Yemen. The only species that in controversial is Commelina erecta. This American and African species definitely occurs in Yemen. Morton (1967) concluded that C. erecta also occurred in India and Australia, with Indian C. kurzii being conspecific with C. erecta. Brenan (1968) and Rao et al. (1972) accepted Morton's distribution for C. erecta. My field observations of C. kurzii in Sri Lanka showed that it consistently has lilac to lavender flowers, whereas American and African C. erecta is blue-flowered. Commelina kurzii is a plant of shady locations, and has been reported as hexaploid and octaploid (see Rao et al. (1972) for a summary of published counts). Commelina erecta occurs mainly in more open habitats, at least in Africa, and has only been recorded as tetraploid (Faden unpublished; Rao *et al.* 1972). Thus, the conspecificity of African *C. erecta* and Indian *C. kurzii* is hardly established.

Discussion

A major problem in determining biogeographic patterns and relationships in a group is the certainty of the taxonomy. The taxonomy is reasonably well established for the overwhelming majority of Commelinaceae of NETA. Ten new species of *Aneilema* and five of *Commelina* (plus seven new subspecies within these genera) from this area have been described in recent years (Faden 1984, 1991, 1994, 1996). Yet others remain to be described, such as two species of *Commelina* from Ethiopia cited in Ensermu & Faden (1997).

The status of some taxa remains uncertain. For example, plants that have been called *Com*melina velutina in Kenya (Faden 1994) do not closely resemble typical plants of that species from Cameroon. The species that was called Commelina elgonensis in Upland Kenya Wild Flowers (Faden 1994) and C. schweinfurthii in Flora of Ethiopia and Eritrea (Ensermu & Faden 1997) is a member of a species group that has its center of morphological and taxonomic diversity south of our area. This species group has not been studied fully, so species limits and their nomenclatural consequences remain unclear. Similar problems exist in the Commelina eckloniana complex. The plants treated under this name in Ethiopia (Ensermu & Faden 1997) and in Upland Kenya (Faden 1994) may not belong to the same species.

Other taxonomic problems concern species that have been typified by non-African material, *e.g. Cyanotis arachnoidea* and *Murdannia semiteres*, which are both typified by specimens from India. The African plants treated under these epithets have yet to be shown convinc-

ingly to be conspecific with the Indian material.

Comparing the Commelinaceae of NETA with those of other floras has additional problems. The taxonomy of those authors has to be checked critically by examining specimens, when possible. Furthermore, distribution records from even the most recent floras soon become outdated as a result of active collecting, both within and outside the flora area.

The treatment of the Commelinaceae for the Flora of West Tropical Africa (Brenan 1968) may serve as an example. I have added two species to Brenan's total, an undescribed Polyspatha species, which was overlooked by Brenan, and Commelina gambiae C. B. Clarke, which was treated as a variety of C. nigritana Benth., but I now consider a distinct species. I have also deducted one species, Commelina petersii, because the cited specimens, when examined recently at Kew, proved to be C. imberbis. Brenan listed 20 species exclusively from the WTA area. That number has been reduced to 16 by collections from outside the WTA area.

More recent floristic treatments of Commelinaceae have had changes too. I now recognize Commelina scandens Welw. ex C. B. Clarke as distinct from C. diffusa, which adds one species to the Flora of Southern Africa (Obermeyer & Faden 1985). Commelina sp. aff. erecta, a robust plant from coastal Kenya with three dehiscent capsule locules, has been added to the Commelinaceae of Somalia (Faden 1995), based on the collection Alstrup & Michelsen 144 (C) examined in 1999. Cyanotis sp. 7 in Flora of Ethiopia and Eritrea (Ensermu and Faden 1997), which was reported only from Ethiopia, has recently been matched with a specimen in the Kew Herbarium from Ivory Coast (Aké Assi 6578). Whether it is a rare species with a widely disjunct distribution or an odd form of C. lanata that crops up occasionally remains to be determined, but it is not an Ethiopian endemic.

With 95 species, NETA is rich in Commelinaceae, especially when compared with West Tropical Africa and Southern Africa. However, Tropical East Africa (Kenya, Uganda and Tanzania) is richer still, with an estimated 133 species (Faden 1983), and Tanzania alone has approximately 100 species. The richness of all these floras is largely due to the diversity of species in the non-forest genera, especially *Aneilema* and *Commelina*.

The Somali-Masai floristic zone has been a source of origin of some groups of Commelinaceae and of the diversification of others. Aneilema section Somaliensia and perhaps section Lamprodithyros originated within NETA. A secondary radiation of Aneilema section Lamprodithyros species occurred in the Zanzibar-Inhambane floristic zone. The blue-flowered Commelina species belonging to Clarke's section Disseocarpus (Clarke 1881), e.g. C. kotschyi, C. latifolia and C. petersii, are well represented within NETA and may have diversified within the Somali-Masai floristic zone.

Endemism is relatively high in the Commelinaceae of NETA, but it is unevenly distributed. It is lacking in Djibouti and Eritrea, low in Ethiopia and Kenya, and high in Somalia. The endemics tend to be locally distributed, and only six of the 24 species endemic to NETA occur in more than one country. Many of the endemics are poorly collected and incompletely known.

The endemic Commelinaceae of Somalia are not only numerous but unusual morphologically. The roots of *Aneilema obbiadense* spread out just beneath the surface of the sand for up to 150 cm and are used locally for weaving containers. The spherical inflorescences are up to 30 cm in diameter-the largest in the genus-and function as tumbleweeds for seed dispersal (Faden 1995). The large papery spathes of *Commelina frutescens*, the only shrublike species of *Commelina*, may also serve for wind dispersal. The yellow flower color

reported for this species and for *C.* sp. 8 is unusual in *Commelina*.

The major phytogeographic relationships of the Commelinaceae of NETA appear to be to the south, particularly with Tanzania. Relationships with West Africa are few, and are represented by small Guineo-Congolian and Sudanian flora elements. The Commelinaceae of the Arabian Peninsula are all species that occur in NETA or are related to NETA species. Some curious disjunctions between species in NETA and India may indicate occasional long-distance dispersal. Some reported African-Indian distributions might be due to faulty taxonomy.

A commonality of Commelinaceae in African floras is the preponderance of non-forest species, even in floras that contain large areas of lowland rainforest. This may be related to the usually greater extent of non-forest than forest habitats in the total flora area. In contrast, a probably incomplete tally that I have made of the Commelinaceae species of Gabon, a country that is mainly rainforest, includes 20 species of forest genera and only 13 of non-forest genera. Perhaps most striking is the overall low species diversity when non-forest habitats are scarce.

The non-forest genera have diversified ecologically into a much greater range of habitats than have the forest genera. Thus there are significant numbers of forest species of *Commelina* and *Aneilema*, some of which are very local and others widespread. The forest genera species, in contrast, always seem to need moisture or shade or both to succeed, even when they occur in disturbed situations, including cultivation. There are no non-forest species of forest genera.

Several lines of evidence support that rainforest was once more widespread in eastern Africa than it is at present. The numerous shared species and sister species relationships between the coastal forests of East Africa and the Guineo-Congolian forests led me to conclude that these forests had been directly con-

nected in the past (Faden 1974a), probably during two different periods. Moreau (1966) came to the same conclusion based on bird distributions.

Palynological studies have provided much information about the climate of East Africa during the Pleiostocene. This evidence was reviewed by Hamilton (1974). A pollen core from Lake Victoria by Kendall (1969) showed that the period between 8000 and 3000 years B.P. showed the greatest forest expansion since 12500 B.P., but the extent of the forest is unknown.

Clear evidence of a wet forest in a presently non-forested region is supported by a middle Miocene flora from the Rift Valley of Kenya (Jacobs & Kabuye 1987). Macrofossils include a new species of *Pollia, P. tugenensis* Jacobs & Kabuye (Jacobs & Kabuye 1989). The 12.6 million year old fossils of a forest genus of Commelinaceae and other species unambiguously demonstrate the presence of wet forest. The temperature at the time of deposition appears to have been similar to present temperatures, but the rainfall must have been higher and less seasonal (Jacobs & Deino 1996).

The expansion and contraction of forests in Africa would have had profound effects upon the diversity of Commelinaceae. Expansion of the forest would have allowed the forest genera to expand their ranges and perhaps diversify. Whether most species of the non-forest genera would have just retreated, adapted to moister conditions, or become extinct is unclear.

The effects of the contraction of the forests are more predictable. Forest species would have retreated or become extinct. Those that found suitable habitat might have persisted, disjunct from the main populations. Those disjuncts would have speciated occasionally, *e.g. Coleotrype brueckneriana*. The expanding nonforest habitats would have provided much new territory into which the non-forest genera could radiate and diversify.

Commelina and Aneilema appear preadapted for success in seasonally dry environments. To withstand drought some species have developed annual or geophytic habits. The spathes in Commelina provide mechanical protection for the buds and developing fruits. Probably more significantly, the mucilaginous secretions produced within the spathes protect the buds and young fruits against desiccation, regardless of the external weather conditions. In Aneilema a similar role is played by the glands on the cup-shaped bracteoles that surround the youngest buds, by the glands on the sepals that in bud moisturize the inner floral whorls, and by the glandular hairs that cover the ovaries and young fruits in nearly all species.

Cyanotis also appears well adapted to dry conditions, but whether this was due to a preadaptation is unclear. A well developed adaxial hypodermis gives the leaves great water-storing capacity. Despite this, many of the species have developed a wide array of underground storage organs, such as rhizomes, root tubers, bulbs and corms, and a few are annuals. Cyanotis buds and fruits are protected by large, usually hairy, overlapping, shingle-like bracteoles.

The great richness of African Commelinaceae is mainly due to speciation of the nonforest genera. Only when we can thoroughly document present distributions, determine phylogenetic relationships, and compare these to shifting climates and vegetation patterns can we understand how and when this diversity arose.

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Appendix 1. The Commelinaceae of Northeast Tropical Africa.

FEE = Flora of Ethiopia and Eritrea (Ensermu & Faden 1997); FS = Flora of Somalia (Faden 1995); UKWF2 = Upland Kenya Wild Flowers (Faden 1994); + = species present in the country; * = endemic in the country or in countries in Northeast Tropical Africa.

Species	Djibouti	Somalia	Eritrea	Ethiopia	Kenya
Aneilema aequinoctiale (P.Beauv.) Loudon subsp.				+	
aequinoctiale					
A. aequinoctiale (P.Beauv.) Loudon subsp. nov.					+
A. benadirense Chiov.		*			
A. beniniense (P.Beauv.) Kunth				+	+
A. brenanianum Faden					+
A. calceolus Brenan					+
A. clarkei Rendle					+
A. ephemerum Faden					*
A. forskalii Kunth	+		+	+	
A. gillettii Brenan				*	*
A. grandibracteolatum Faden				*	
A. hirtum A.Rich.				+	+
A. hockii De Wild.				+	+
A. indehiscens Faden subsp. indehiscens					+
A. indehiscens Faden subsp. keniense Faden				+	+
A. johnstonii K.Schum.				+	+
A. lamuense Faden		*			*
A. lanceolatum Benth.					+
A. leiocaule K.Schum.				+	+
A. longicapsa Faden		*			
A. minutiflorum Faden					+
A. nicholsonii C.B.Clarke					+
A. nyasense C.B.Clarke					+
A. obbiadense Chiov.		*			
A. petersii (Hassk.) C.B.Clarke subsp. pallidiflorum Faden					+
A. petersii (Hassk.) C.B.Clarke subsp. petersii				+	+
A. pusillum Chiov. subsp. gypsophilum Faden		*			
A. pusillum Chiov. subsp. pusillum		*			
A. pusillum Chiov. subsp. thulinii Faden		*			
A. pusillum Chiov. subsp. variabile Faden		*		*	*
A. recurvatum Faden				+	+
A. rendlei C.B.Clarke				+	+
A. sebitense Faden				*	*
A. somaliense C.B.Clarke		*		*	*
A. spekei C.B.Clarke				+	+
A. succulentum Faden				,	*
A. tanaense Faden					*
A. taylorii C.B.Clarke					+
A. trispermum Faden		*			1
A. zebrinum Chiov.				+	+
Anthericopsis sepalosa (C.B.Clarke) Engl.		+		+	
Coleotrype brueckneriana Mildbr.		T			+

Species	Djibouti	Somalia	Eritrea	Ethiopia	Kenya
Commelina africana L.	+	+	+	+	+
C. albescens Hassk.	+	+	+	+	+
C. albiflora Faden					*
C. arenicola Faden		*			
C. benghalensis L.	+	+	+	+	+
C. bracteosa Hassk.					+
C. capitata Benth.					+
C. diffusa Burm.f.				+	+
C. echinosperma K.Schum.					+
C. eckloniana Kunth				+	+
C. elgonensis Bullock / C. schweinfurthii C.B.Clarke				+	+
C. erecta L.		+		+	+
C. foliacea Chiov. subsp. amplexicaulis Faden					+
C. foliacea Chiov. subsp. foliacea				+	+
C. forskaolii Vahl	+	+	+	+	+
C. frutescens Faden		*		1	1
C. inberbis Ehrenb. ex Hassk.			+	+	+
C. timoetois Effetib. ex Hassk. C. kotschyi Hassk.				+	+
				+	+
C. latifolia Hochst. ex A.Rich. C. lugardii Bullock			+	+	
C. tugurati Bunock C. melanorrhiza Faden					+
					*
C. nairobiensis Faden					
C. petersii Hassk.		+	+	+	+
C. reptans Brenan				+	+
C. sp. aff. erecta L.		+			+
C. sp. aff. imberbis Ehrenb. ex Hassk		*			+
C. sp. 8 of FS		*		d.	
C. sp. 2 of FEE				*	
C. sp. 17 of FEE				*	
C. sp. D of UKWF2 (=C. sp. 5 of FS)		+			+
C. somalensis Chiov.		*			
C. stefaniniana Chiov.		*		*	*
C. subulata Roth			+	+	+
C. triangulispatha Mildbr.					+
C. trilobosperma K.Schum.					+
C. velutina Mildbr.					+
C. zambesica C.B.Clarke				+	+
Cyanotis arachnoidea C.B.Clarke					+
C. axillaris (L.) Sweet					+
C. barbata D.Don			+	+	+
C. caespitosa Kotschy & Peyr.				+	+
C. cristata (L.) D.Don			+		
C. foecunda Hochst. ex Hassk.				+	+
C. lanata Benth.				+	+
C. longifolia Benth.				+	+
C. paludosa Brenan					+
C. polyrrhiza Hochst. ex Hassk.				*	
C. somaliensis C.B.Clarke		+			
C. sp. A of UKWF2					+
C. sp. 7 of FEE				+	

Species	Djibouti	Somalia	Eritrea	Ethiopia	Kenya
Floscopa glomerata (Willd. ex Schult. & Schult.f.) Hassk.				+	+
Murdannia axillaris Brenan					+
M. clarkeana Brenan					+
M. semiteres (Dalz.) Santapau					+
M. simplex (Vahl) Brenan		+		+	+
M. tenuissima (A.Chev.) Brenan				+	
Pollia condensata C.B.Clarke				+	+
P. mannii C.B.Clarke				+	
Stanfieldiella imperforata (C.B.Clarke) Brenan var.				+	
glabrisepala (De Wild.) Brenan					
S. imperforata (C.B.Clarke) Brenan var. imperforata				+	
Tradescantia zebrina Hort. ex Bosse					+