

Distribution patterns of Cyperaceae in East and Northeast Tropical Africa with special emphasis on local endemism

KÅRE ARNSTEIN LYE

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A total of 500 species of Cyperaceae have been recorded from East and Northeast Tropical Africa. Of these 450 are known from Tropical East Africa (Kenya, Uganda and Tanzania) and 268 from Tropical Northeast Africa (Eritrea, Ethiopia and Somalia). While about one half of the species has an African (mostly panafrican and East-South African) distribution, there are about 50 species with a pantropical distribution, 53 species with an Afro-Asian distribution, 13 species with an Afro-American distribution, while 13 species have European affinities. Distribution patterns within Africa are also discussed, and species listed in an appendix. There are 112 species endemic to the region, of which 65 are endemic to East Africa and 41 to Northeast Africa. Of these, 53 species are here classified as narrow endemics and are mostly endangered species. The percentage of species endemic to the two regions is approximately the same, with 14.4% for East Africa and 15.3% for Northeast Africa. However, endemism varies greatly from nation to nation with only 0.9% and 1.3% endemic species in Uganda and in Eritrea, 8.7% in Tanzania and 30.3% in Somalia. Endemism in Somalia is outstanding and is in tropical Africa only surpassed by that of Madagascar (37.7%). Endemism in our region is also compared to that of other African countries.

Kåre Arnstein Lye, Dept. of Biology and Nature Conservation, Agricultural University of Norway, P.O. Box 5014, N-1432 Aas, Norway. E-mail: kare.lye@ibn.nlh.no

Introduction

This paper deals with the countries of *Flora of Tropical East Africa* (Uganda, Kenya and Tanzania), *Flora of Ethiopia and Eritrea* (Eritrea and Ethiopia) and *Flora of Somalia* (South and North Somalia) with notes on neighbouring countries.

About 500 sedges are known from this area. Like grasses, sedges have their greatest diversity in the region of seasonal rainfall between forest and desert, but unlike grasses they only

dominate the vegetation in certain permanent swamps.

The generic concept adopted here is the same as that used for *Flora of Ethiopia and Eritrea* (Lye 1997d) and *Flora of Somalia* (Lye 1995). It differs much from that adopted for *The Families and Genera of Vascular Plants* (Goetghebeur 1998). The differences of opinion mainly concern the genus *Cyperus* where Goetghebeur (1989, 1998) recognises the segregate genera *Courtoisina*, *Ascopholis*, *Alinula*, *Pycreus*, *Queens-*

landiella and *Kyllinga*. However, recent molecular work (Muasya *et al.* 1998) has convincingly shown that such segregates are phylogenetically unacceptable. On the other hand it is possible that many other genera now widely accepted as separate from *Cyperus* should also be merged with that genus, viz. *Remirea*, *Oxycaryum* (Lye 1971), *Sphaerocyperus* (Lye 1972a), *Kyllingiella*, *Ascolepis* and *Lipocarpha*.

General distribution patterns

The total number of Cyperaceae from tropical Africa is about 800, while the number for tropical East and Northeast Africa is 497 (or about 500 when some undescribed taxa are included). Tropical East Africa has 450 species while 268 species are known from tropical Northeast Africa

Knowledge of African distribution patterns is best documented through the 1334 distribution maps published in *Distributiones Plantarum Africanarum* (until 1994). Other important general plant geographical publications are presented by White (1965, 1971, 1977, 1979, 1983, 1993), Friis (1983, 1993, 1994), and for afroalpines by Hedberg (1957, 1994), but none of the plants mapped in any of these publications are members of Cyperaceae. Wickens (1976) includes distribution maps of three sedges (but apparently based on Kew material only); these are *Cyperus rigidifolius* Steud., *Cyperus (Kyllinga) chlorotropis* and *Cyperus (Pycurus) mundtii*. Raynal (1967, 1971) mapped the distribution of two species of *Scleria* (*S. glabra* and *S. poaeoides*) and all African species of *Rhynchospora* (nine occur in our region), and Vorster (1983) has mapped *Cyperus (Mariscus) deciduus*. Otherwise the distribution of species of Cyperaceae in our area is mostly known only from general enumerations of countries or regions.

The highest number of Cyperaceae in Africa is recorded from southern Tanzania

and adjacent Zambia and Congo (Kinshasa). From this area the number decreases both southwards, westwards and northwards. The total number of species in the whole of West Africa is 304 (Hooper & Napper 1972) while Tanzania alone has 389 species. Nigeria with 221 species (Lowe & Stanfield 1974) is the West African country with the highest number of species, followed by Ghana and Senegal with 181 and 176 species respectively (Hooper & Napper 1972). The whole of North Africa has about 80 species (Maire 1957), see Figs. 1-2.

Nations receiving low rainfall in central and southern Africa also have relatively few Cyperaceae, *e.g.*, 79 species in Niger (Raynal 1976b), 131 species in Tchad (Raynal 1972) and 138 species in Namibia (Clarke & Mannheimer 1999). The two countries in Eastern Africa with a low rainfall, viz. Eritrea and Somalia have 77 and 89 species of Cyperaceae respectively (Lye 1995 & 1997d). The small South African country Swaziland has 75 species (Compton 1976).

The distribution patterns of wetland and dryland sedges are on the whole very different. While numerous wetland sedges have a pantropical distribution and a few species in our region even a temperate-subtropical distribution, many dryland sedges have restricted distributions and are often endemic to fairly small geographical regions. However, species with very restricted distributions are not necessarily endemic to a single nation, *e.g.* Ruwenzori endemics occur in Uganda and Congo (Kinshasa), Virunga endemics occur in Uganda and Rwanda, and Elgon endemics in Uganda and Kenya.

Of the 500 sedges known from our area, about one half (250 species) has an African (mostly panafrikan or East-South African) distribution. Of these 12 species have their main distribution in West Africa, 8 species are more common in North Africa to Arabia, and 12

species are most common in southern Africa. About 50 species have a pantropical and 54 species an Afro-Asian distribution, while 13 species have an Afro-American distribution. Only 13 species are found in Europe, but several of these occur in Asia also. In addition there are 112 species endemic to the region.

Distribution within countries

Sudan

Knowledge of Cyperaceae in the Sudan is rather scanty. According to Andrews (1956) there are 142 species; two of these are narrow endemics, viz. *Coleochloa schweinfurthiana* and *Coleochloa glabra*, which are each endemic to a single South Sudanian mountain, Jebel Bangeze (Yambio district) and Jebel Oda (Nelmes 1953). When better investigated, the number of sedges is likely to be in the order of 160-180. This is still a low number compared to its large size; it is the biggest country in Africa (bigger than Congo Kinshasa, which has about 400 species).

Eritrea

Being a dry country with little and often erratic rainfall, Eritrea's flora includes few Cyperaceae. The total number of species recorded is 77 (Lye 1997d), of which only one (1.3%) is endemic, viz. *Cyperus schweinfurthii*. Another rare sedge, *C. holostigma*, is shared with Ethiopia only.

Ethiopia

With 206 species of sedges (Lye 1997d) Ethiopia has a much higher number than the Sudan and Eritrea, and compared to West and North African countries it certainly has a much richer sedge flora. However, Uganda, Kenya and Tanzania have an even higher number of sedges. Ten species are endemic to Ethiopia (4.9%); three of these are narrow endemics known only from one 1 degree grid. The most

interesting ones are *Cyperus clandestinus*, which is sometimes placed in a monotypic genus *Chamaexiphium* or in *Ficinia*, and *Ficinia borealis* (Lye 1996f), which has its nearest relatives in South Africa.

Somalia

As this country is mostly very dry with a very prolonged dry season and often erratic rain, sedges are uncommon and mostly occur in small populations. Despite this, Somalia is the country in mainland tropical Africa with the highest percentage of endemic species (27 species out of 89), i.e. 30.3% (Lye 1995). Endemicity in Somalia is outstanding and it is in tropical Africa only surpassed by that of Madagascar (37.7%). Of the 27 endemics, 15 are known from only one 1 degree grid. The highest concentration of such species is found in the Mogadiscio grid with three species, and the Erigavo and Las Anod grids with two species. The latter two grids are not well collected. However, the Mogadiscio grid is possibly the best collected in Somalia, so the presence of the three endemics here may be explained by the distribution of collectors.

Uganda

Although this country has a very large sedge flora with 234 species (in fact it has one of the highest numbers per area), it has only two endemic species (0.9%), *Isolepis ruwenzoriensis* (Lye & Haines 1974) and *Kyllingiella ugandensis* (Haines & Lye 1978). *Isolepis ruwenzoriensis*, which is endemic to the Ugandan side of Mt. Ruwenzori, may not be a real national endemic species as it is likely to be found on the Congo side of the Ruwenzori also. However, *Isolepis ruwenzoriensis* is probably very rare as it has been recorded only once, and has been unsuccessfully searched for recently. Another species, *Carpha eminii*, has a similar distribution, but is also recorded on the Congo side of Mt. Ruwenzori (Robyns 1955).

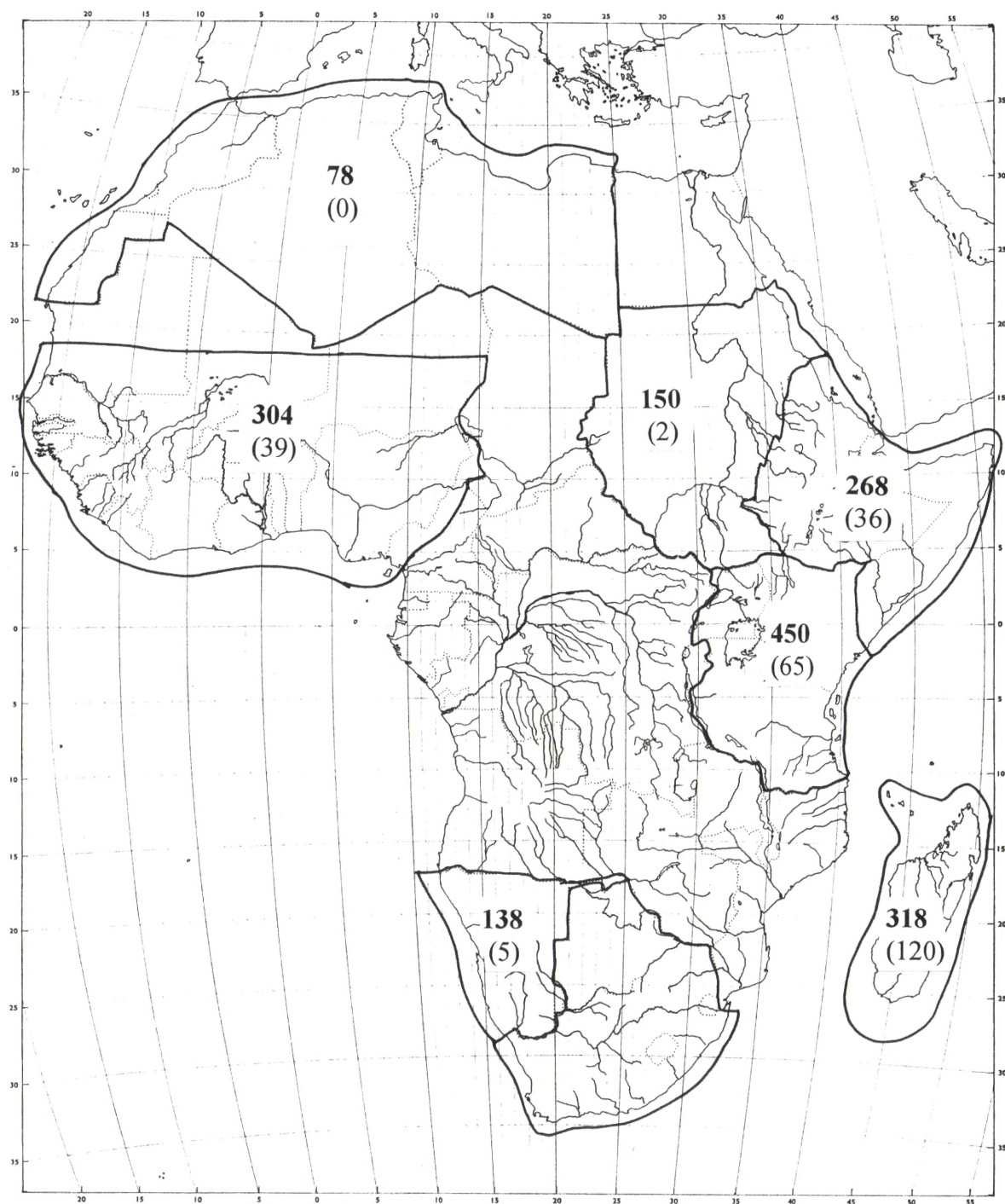


Fig. 1. Map of Africa showing number of species of Cyperaceae for major regions. Numbers in brackets indicate number of endemic species.

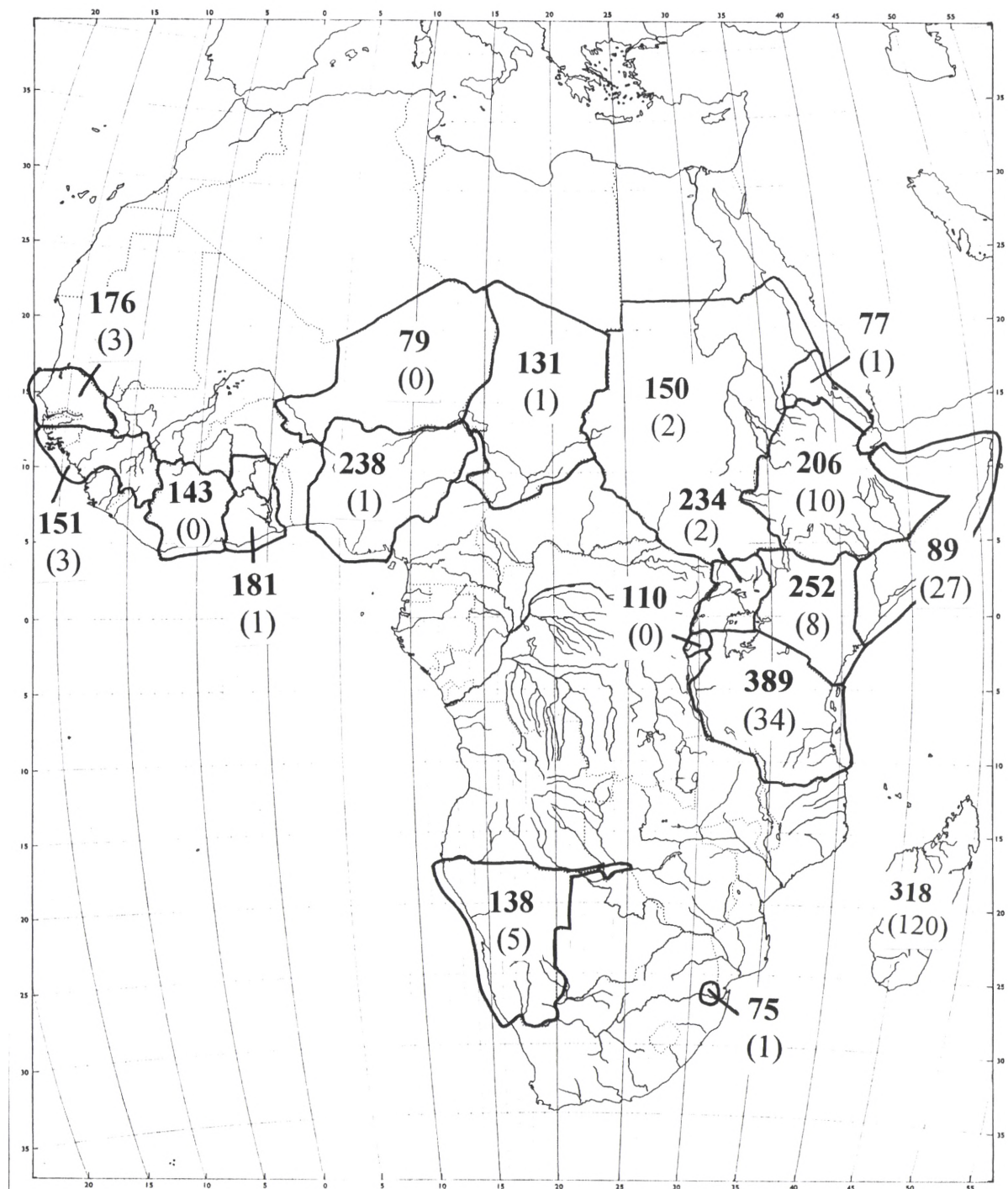


Fig. 2. Map of Africa showing number of species of Cyperaceae in individual African nations. Numbers in brackets indicate number of endemic species.

Kyllingiella ugandensis is probably a very rare and endangered species known from a single locality on the southern side of the Imatong Mountains.

Kenya

In our region Kenya is only surpassed by Tanzania in richness of species. It has 252 species of Cyperaceae (Haines & Lye 1983), of which 8 are endemic, all known from only one 1-degree grid (3.2%). The highest concentration of such species is found in the Kwale grid with three endemic species, viz. *Cyperus kwaleensis*, *C. boreobellus* and *C. microumbellatus*. It is possible that the high number of narrow endemics in the Kwale grid is due to extensive collecting. However, it is interesting that Linder (1998) investigated 794 species found this grid (but enlarged to cover a 2.5 x 2.5-degree square) the second richest in narrow endemic species in tropical Africa (only surpassed by the Dar es Salaam grid). *Isolepis keniaensis* is known only from Mt. Kenya, and has no known close relatives.

Tanzania

This country has an extremely rich sedge flora and with 389 species (Haines & Lye 1983) is in tropical mainland Africa possibly surpassed by Zambia and Congo (Kinshasa) only. No fewer than 34 species are endemic (8.7%), and of these 23 are narrow endemics known from just one 1 degree grid. The highest concentration of such species are found in the Dar es Salaam grid with four species, and the Songea, Mbeya and Sumbawanga grids all with two species. Although the Dar es Salaam grid square is one of the best investigated in Tanzania, it is interesting that Linder (1998) found that the same grid square (but enlarged to cover 2.5 x 2.5 degrees) is the richest in narrow endemic species in tropical Africa, viz. 22 narrow endemics out of 794 investigated species.

Rwanda

The flora of Rwanda includes 110 species of Cyperaceae (Maquet 1988). There are no endemic species. It shares *Bulbostylis ugandensis* (Lye 1974b) with Uganda and *Cyperus angustisima* with SW Uganda and adjacent parts of Congo. Other species are more widespread.

Burundi

The Cyperaceae flora of Burundi is not well studied. It contains at least one narrow endemic, *Bulbostylis nemoides* (Goetghebeur 1984).

Congo (Kinshasa)

The Cyperaceae flora of Congo (Kinshasa) is rich and varied as is expected from such a vast country with many different climatic regimes. It contains one endemic genus, *Nelmesia* (van der Veken 1955) and many endemic species. Many rare species are shared with Zambia and adjacent parts of Tanzania. It probably has about 400 species of Cyperaceae. For example the genus *Fimbristylis* has 18 species in Congo (Goetghebeur & Coudijzer 1984) as against 14 species in Tanzania (Haines & Lye 1983).

Zambia

The sedge flora of Zambia is very rich and has many endemics as well as undescribed species. It could possibly have more numerous species of Cyperaceae than Tanzania. For example the genus *Scleria* has 57 species in Zambia (Robinson 1966) as against 44 species in Tanzania (Haines & Lye 1983). *Scleria calcicola* E. A. Rob., *S. zambesica* E. A. Rob., *S. polyrrhiza* E. A. Rob., *S. fulvopilosa* E. A. Rob., *S. procumbens* E. A. Rob., *S. lucentinigricans* E. A. Rob., *S. xerophila* E. A. Rob. and *S. arcuata* E. A. Rob. are all endemic.

Zimbabwe

The sedge flora of Zimbabwe is rich and has a greater affinity with the South African flora than have the East African countries. However,

Table 1. Genera and subgenera of Cyperaceae in eastern and northeastern tropical Africa, their total number of species (tot.), number of endemic species in each country (end.) and percentage of endemic species.

Genus or subgenus	Eritrea		Ethiopia		Somalia		Kenya		Uganda		Tanzania	
	tot.	end.	tot.	end.	tot.	end.	tot.	end.	tot.	end.	tot.	end.
<i>Fuirena</i>	1	0	5	0	3	3	10	0	5	0	14	2
<i>Schoenoplectus</i> subg. <i>Actaeogeton</i>	1	0	4	0	4	0	6	0	7	0	9	0
<i>S.</i> subg. <i>Bolboschoenus</i>	0	0	1	0	1	0	1	0	0	0	1	0
<i>S.</i> subg. <i>Schoenoplectus</i>	2	0	4	0	3	0	3	0	4	0	5	0
<i>Eleocharis</i>	2	0	5	0	3	0	6	0	9	0	14	0
<i>Websteria</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Fimbristylis</i>	4	0	8	0	4	0	9	0	8	0	14	0
<i>Abildgaardia</i>	1	0	1	0	0	0	2	0	1	0	2	0
<i>Bulbostylis</i>	7	0	16	1	5	1	25	2	17	0	32	10
<i>Nemum</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Isolepis</i>	2	0	8	2	0	0	6	1	5	1	8	1
<i>Ficinia</i>	0	0	1	1	0	0	1	0	0	0	2	0
<i>Oxycaryum</i>	0	0	1	0	0	0	0	0	1	0	1	0
<i>Kyllingiella</i>	2	0	2	0	0	0	2	0	2	1	2	0
<i>Cyperus</i> subg. <i>Alinula</i>	0	0	1	0	0	0	1	0	1	0	1	0
<i>C.</i> subg. <i>Anosporum</i>	0	0	1	0	1	0	2	0	2	0	2	0
<i>C.</i> subg. <i>Chamaexiphium</i>	0	0	1	1	0	0	0	0	0	0	0	0
<i>C.</i> subg. <i>Courtoisina</i>	1	0	1	0	0	0	1	0	1	0	2	0
<i>C.</i> subg. <i>Cyperus</i>	30	1	56	3	59	19	78	3	57	0	89	9
<i>C.</i> subg. <i>Fimbricyperus</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>C.</i> subg. <i>Kyllinga</i>	10	0	19	0	12	0	23	1	20	0	33	6
<i>C.</i> subg. <i>Marisculus</i>	0	0	1	0	0	0	1	0	0	0	1	0
<i>C.</i> subg. <i>Pycnostachys</i>	3	0	10	0	7	2	16	1	19	0	23	3
<i>C.</i> subg. <i>Pycreus</i>	8	0	16	1	4	1	16	0	19	0	28	0
<i>C.</i> subg. <i>Queenslandiella</i>	0	0	0	0	1	0	1	0	0	0	2	1
<i>C.</i> subg. <i>Sorostachys</i>	0	0	1	0	2	1	1	0	1	0	1	0
<i>Sphaerocyperus</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Remirea</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Lipocarpha</i>	0	0	5	0	0	0	5	0	4	0	8	0
<i>Ascolepis</i>	0	0	3	1	0	0	2	0	3	0	8	0
<i>Schoenus</i>	1	0	0	0	1	0	0	0	0	0	0	0
<i>Rhynchospora</i>	0	0	2	0	0	0	1	0	5	0	9	0
<i>Tetaria</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Carpha</i>	0	0	0	0	0	0	0	0	2	0	1	0
<i>Cladium</i>	0	0	0	0	0	0	1	0	1	0	1	0
<i>Machaerina</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Hypolytrum</i>	0	0	0	0	0	0	0	0	1	0	2	0
<i>Scleria</i>	0	0	14	0	0	0	13	0	20	0	44	0
<i>Diplacrum</i>	0	0	0	0	0	0	0	0	1	0	1	0
<i>Coleochloa</i>	1	0	1	0	0	0	1	0	1	0	4	1
<i>Schoenoxiphium</i>	0	0	2	0	0	0	3	0	3	0	3	0
<i>Carex</i> subg. <i>Carex</i>	2	0	6	0	2	0	6	0	7	0	7	1
<i>C.</i> subg. <i>Indocarex</i>	0	0	6	0	0	0	4	0	3	0	7	0
<i>C.</i> subg. <i>Primocarex</i>	0	0	2	0	0	0	3	0	1	0	1	0
<i>C.</i> subg. <i>Vignea</i>	1	0	2	0	0	0	2	0	2	0	1	0
Number of Cyperaceae species	77	1	206	10	89	27	252	8	234	2	389	34
Percentage of endemic species		1.3		4.9		30.3		3.2		0.9		8.7

it lacks many of the species found in Zambia and southern Tanzania. The Chimanimani Mountains, so rich in endemics (41 species according to Wild 1964), do not have any endemic species of Cyperaceae.

Malawi

The sedge flora of Malawi is rich and, like that of Zimbabwe, has a closer affinity with the South African flora than have the East African countries. The South African genus *Tetrandia* has its other non-South African species here, viz. *T. mlanjensis*.

Species endemic to East and North East Africa

112 species of Cyperaceae are endemic to tropical East and Northeast Africa. Of these, 65 species are endemic to East Africa (14.4%) while 41 are endemic to Northeast Africa (15.3%). For individual nations the numbers are given in Table 1. The total numbers of endemic species for the regions are higher than the added numbers of endemic species for countries. This is due to some species being endemic to two or more countries or to both regions considered together.

In a work on grasses Clayton & Cope (1980) identified a centre of endemism in Ethiopia, but this is not so for Cyperaceae, where Somalia and Tanzania are the two nations richest in endemic species.

Narrow endemics

Here we shall define 'narrow endemics' as species confined to a one-degree square or grid (latitude and longitude). There are 53

such species in eastern and northeastern tropical Africa, and they are enumerated in Table 2. There are 23 such species in Tanzania, 15 in Somalia, eight in Kenya, four in Uganda (with neighbours), three in Ethiopia, and none in Eritrea. Such species are generally very vulnerable and most species are endangered and need some sort of protection to avoid extinction. It is true that not all species known from a single one-degree grid are vulnerable, but in Cyperaceae the great majority is.

Most of the narrow endemics have been described fairly recently by Goetghebeur (1984), Haines & Lye (1978), Hooper (1985), Lye (1972b, 1974a, 1974b, 1982a, 1982b, 1982c, 1982d, 1982e, 1983a, 1983b, 1983c, 1985, 1987, 1992, 1994, 1996a, 1996b, 1996c, 1996d, 1996e, 1996f, 1996g, 1997a, 1997b, 1997c), Lye & Haines (1974) and Simpson (1990, 1994). Only a handful of narrow endemic species were described much earlier (Schumann 1895, Clarke 1901, Chermeson 1935, Kükenthal 1936, Nelmes 1939).

As shown in Fig. 3, the highest concentration of narrow endemic species is found in three coastal grids, i.e. (1) the Dar es Salaam-Zanzibar grid in Tanzania with four endemics, *Bulbostylis taylorii*, *Cyperus micromariscus*, *C. gigantobulbes* and *C. stramineo-ferrugineus*, (2) the Kwale grid south of Mombasa in Kenya with three endemics, viz. *Cyperus kwaleensis*, *C. boreobellus*, and *C. microumbellatus*, and (3) the Mogadiscio square in Somalia with three species, viz. *Cyperus baobab*, *C. somalidunensis* and *C. scabriceaulis*. The two first grids are part of Clarke's (1998) 'new regional centre of endemism in Africa'.

The six grids encompassing the Erigavo Mountains, the Las Anod area (both Somalia), the Mt. Ruwenzori (Uganda/Congo), and the

Fig. 3. Map of eastern and northeastern tropical Africa showing presence of narrow endemic species of Cyperaceae for each one-degree square. Large dot = 3 or 4 narrow endemic species per square. Medium dot = 2 narrow endemic species per square. Small dot = 1 narrow endemic species per square. →

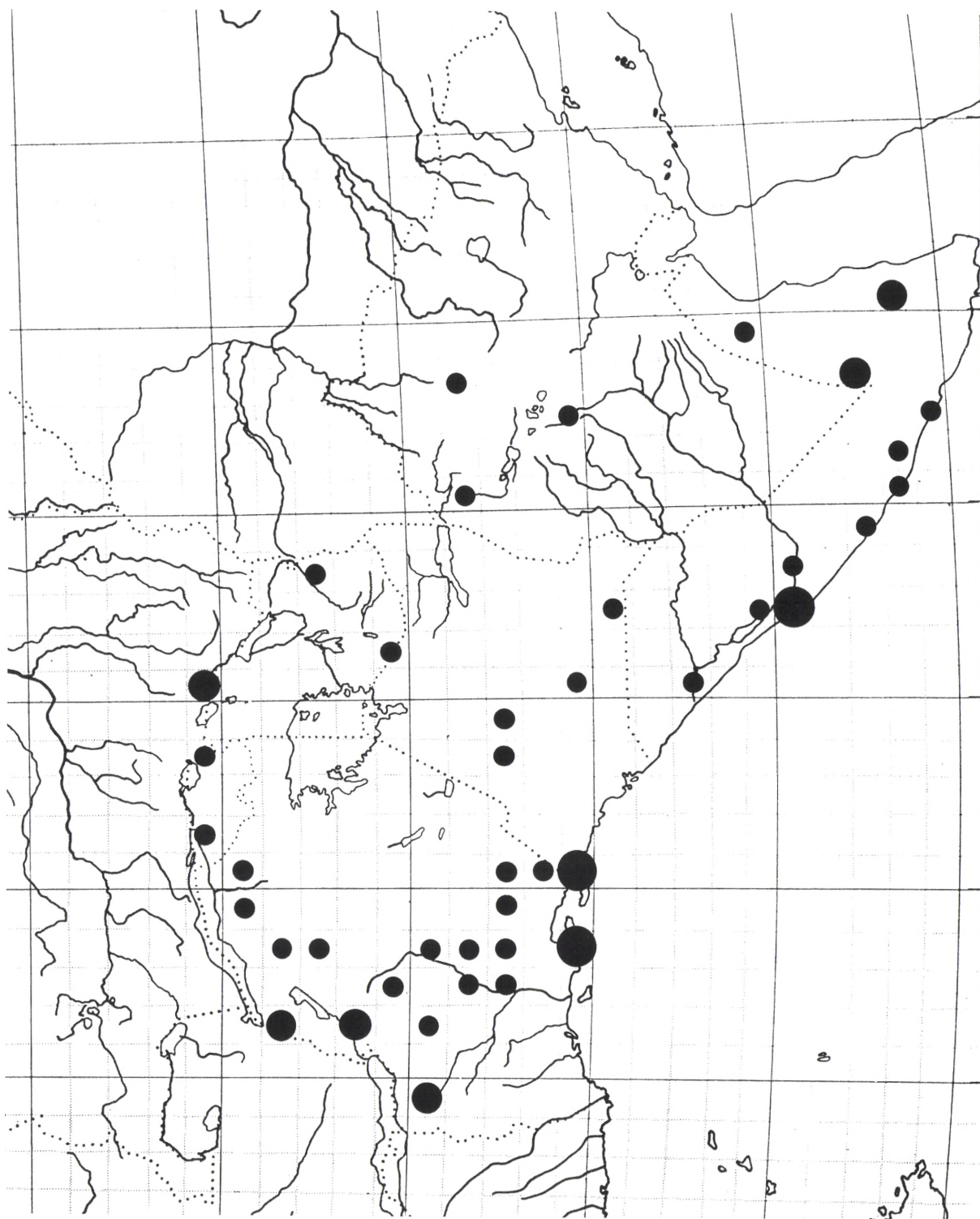


Table 2. The narrow endemic species of Cyperaceae in eastern and northeastern tropical Africa, country and latitude and longitude of their distribution areas.

Species	Country	Lat. Long.	Species	Country	Lat. Long.
<i>Bulbostylis angustespicata</i>	Tanzania	8°S 33°E	<i>Cyperus gypsophilus</i>	Somalia	8°N 47°E
<i>B. elegantissima</i>	Tanzania	7°S 34°E	<i>C. kwaleensis</i>	Kenya	4°S 39°E
<i>B. leiolepis</i>	Tanzania	4°S 30°E	<i>C. kyllingaeformis</i>	Kenya	1°N 34°E
<i>B. longespicata</i>	Ethiopia	5°N 36°E	<i>C. longi-involucratus</i>	Tanzania	7°S 36°E
<i>B. microcarpa</i>	Tanzania	4°S 37°E	<i>C. microbracteatus</i>	Tanzania	10°S 35°E
<i>B. microrotundata</i>	Tanzania	5°S 30°E	<i>C. microbulbosus</i>	Tanzania	5°S 37°E
<i>B. nemoides</i>	Burundi	3°S 29°E	<i>C. micromariscus</i>	Tanzania	6°S 39°E
<i>B. squarrosa</i>	Kenya	2°N 40°E	<i>C. micromedusaeus</i>	Somalia	7°N 49°E
<i>B. tanzaniae</i>	Tanzania	6°S 31°E	<i>C. micropelophilus</i>	Somalia	2°N 44°E
<i>B. taylorii</i>	Tanzania	6°S 39°E	<i>C. microumbellatus</i>	Kenya	4°S 39°E
<i>Carex papillosissima</i>	Tanzania	7°S 36°E	<i>C. mudugensis</i>	Somalia	5°N 48°E
<i>Carpha angustissima</i>	Uganda Rwanda Congo	1°S 29°E	<i>C. nyererei</i>	Tanzania	6°S 32°E
			<i>C. ossicaulis</i>	Somalia	4°N 47°E
			<i>C. pluricephalus</i>	Somalia	3°N 45°E
<i>C. eminii</i>	Uganda Congo	0°N 29°E	<i>C. poecilus</i>	Somalia	4°N 44°E
			<i>C. purpureoviridis</i>	Tanzania	6°S 37°E
<i>Cyperus afropumilus</i>	Tanzania	8°S 33°E	<i>C. recurvispicatus</i>	Somalia	6°N 48°E
<i>C. alba-purpureus</i>	Tanzania	8°S 31°E	<i>C. scabricaulis</i>	Somalia	2°N 45°E
<i>C. baobab</i>	Somalia	2°N 45°E	<i>C. somalidunensis</i>	Somalia	2°N 45°E
<i>C. bifolius</i>	Ethiopia	8°N 36°E	<i>C. stramineo-ferrugineus</i>	Tanzania	6°S 39°E
<i>C. boreobellus</i>	Kenya	4°S 39°E	<i>Ficinia borealis</i>	Ethiopia	7°N 39°E
<i>C. brunneoalbus</i>	Kenya	2°N 40°E	<i>Fuirena boreocoerulescens</i>	Somalia	10°N 48°E
<i>C. castaneobellus</i>	Tanzania	10°S 35°E	<i>F. somaliensis</i>	Somalia	0°N 42°E
<i>C. cremeomariscus</i>	Tanzania	8°S 31°E	<i>F. striatella</i>	Somalia	10°N 48°E
<i>C. densibulbosus</i>	Somalia	8°N 47°E	<i>Isolepis keniaensis</i>	Kenya	0°S 37°E
<i>C. flavoculmis</i>	Kenya	1°S 37°E	<i>I. ruwenzoriensis</i>	Uganda	0°N 29°E
<i>C. gigantobulbes</i>	Tanzania	6°S 39°E	<i>I. trollii</i>	Tanzania	7°S 37°E
<i>C. graciliculmis</i>	Tanzania	6°S 36°E	<i>Kyllingiella ugandensis</i>	Uganda	3°N 32°E

Sumbawanga, Mbeya, and Songea areas (Tanzania) all have two narrow endemics found in the same square.

Isolated mountains or hills (in addition to Mt. Ruwenzori) with narrow endemics are Mt.

Kenya (*Isolepis keniaensis*), Shimba Hills (*Cyperus microumbellatus*), Ukaguru Mountains (*Cyperus graciliculmis*), Nguru Mountains (*Cyperus purpureoviridis*) and the perhaps less isolated Mafinga (Sao Hill) area (*Carex papillosissima*).

Discussion

General history

It is unlikely that past geological history concerning continental drift and the old West Gondwanaland connections with South America (Raven & Axelrod 1972) has had a pronounced effect on present day distribution of tropical East and Northeast African sedges except for the occurrence of certain genera. Only 13 of our species are found in America (several are recent introductions by man) while more than 50 species are found in Asia. Therefore the eastern African sedge flora is much more closely related to that of India than to that of America. However, the African genus *Coleochloa* has its related genera in America and not in Asia, and could depend on past connections with America 45-60 million years ago.

The closer relationship between the sedge flora of Madagascar and eastern Africa as well as between India and eastern Africa could, however, at least in part depend on the past geographical position of Madagascar and India as part of or close to the African mainland.

Climate

It is the climate at present and during the more recent past, when continents occupied their present positions, which have set up modern patterns of vegetation and floras.

As most of present day tropical Africa was clothed with evergreen rainforest of tropical to warm temperate character 20 million years ago (Raven 1983), the evolution of most of our sedges must have occurred subsequently. The forest genus *Hypolytrum* could, however, be a remnant from that past continuous and unbroken forest.

Later thousands of metres of uplift have expanded habitats for plants characteristic of cooler areas and greatly enhanced the opportunities for north-south migration. The spreading aridity associated with the cool currents

resulting from massive glaciation has reduced the forest flora and allowed savannas and savanna species to spread and develop at the expense of the rainforest and rainforest species. The forest genus *Mapania* probably became extinct in eastern Africa during this period.

The climatic fluctuations during later periods and particularly during much of the Quaternary Period (last 1.8 million years) must have affected the distribution of some genera and species of Cyperaceae.

It is, however, likely that it is first and foremost the climate and the climatic changes during the last 20 000 years which formed the diversity in Cyperaceae in our region. Warmer and more humid periods interchanged with colder and drier periods. During the last ice age maximum 18 000 years B.P. Morrison (1968) working in SW Uganda found the mean annual temperature to be 6° C lower than at present. Due to this lowering of temperature during this period numerous temperate and subalpine species of sedges probably had a much-extended distribution.

The opening up of the vegetation of Africa during this dry and cold period probably provided a migration route between the arid northeastern parts of our area and Namibia for plants adapted to dry conditions. Lowland rainforest in our area probably persisted on parts of the Tanzanian Arc mountains and possibly in the Kwale area in Kenya only. This could explain the presence of local endemic species on these mountains and hills.

The presence of many lowland coastal endemics in drier habitats is more difficult to explain. It is, however, likely that at least in Somalia there were dry regions with open vegetation throughout the interglacial as well as the post-glacial periods. Such areas could serve as refugia during periods when dense forest covered most other parts of tropical Africa.

On the whole distribution patterns among

endemic Cyperaceae are not easily explained from the African plant geographical regions described by White and others. A better correlation is found using the land-cover maps produced by Tucker *et al.* (1985).

Edaphic conditions

Although the bedrock in tropical countries is apparently less important for the distribution of plants than it is in temperate countries, hard rocks are important in forming habitats with shallow soils unsuitable for the colonization of trees and larger shrubs. Such habitats are often important habitats for many annual sedges or sedges with special adaptation for dry conditions, *e.g.* *Cyperus dubius*. and the genus *Coleochloe*. The importance of inselbergs in allowing the survival of open-country species at times of forest expansion has been highlighted by Barthlott & Poremski (1996, 1998).

Also sediments poor in nutrients, such as the almost pure silica-sand on the NW side of Lake Victoria are important habitats for sedges as they are too nutrient-poor for colonisation by shrubs and trees at least when regularly grazed, *e.g.* *Bulbostylis ugandensis*, *B. cardiocarpoides* Cherm., *Cyperus tenuiculmis* Böckel. and *C. tenax* Böckel. However, nutrient-poor soils are sometimes covered by extensive forests such as in SE Tanzania (Vollesen 1981).

In Somalia very local soils such as gypsum soils provide habitats for very rare and endangered species, such as *Cyperus gypsophilus*. Soils with high metal contents sometimes have very specialized endemics also, but such soils are mostly found in the Zambia-Katanga region (Malaisse 1983), *e.g.* *Bulbostylis metalliphila* (Lye 1985).

Also seasonal water logging or flooding is an important edaphic factor keeping trees and larger shrubs away (White 1977; Lock 1998) thus providing optimal conditions for many rare sedges, particularly in southern Tanzania and northern Zambia. Permanently wet hab-

itats often contain extensive patches of sedges, but very rarely vulnerable or endangered species.

Dispersal mechanisms

Many sedges growing in permanently wet habitats have diaspores adapted to long-distance dispersal by birds (Ridley 1930), *e.g.* the genera *Fuirena*, *Schoenoplectus* (Raynal 1976a), *Eleocharis* and *Rhynchospora*. Such genera have a number of species with wide pantropical distributions, *e.g.* *Fuirena umbellata*, *Schoenoplectus maritimus*, *Eleocharis geniculata* and *Rhynchospora corymbosa*.

Many sea-shore species, particularly those growing immediately above the strand-line, have diaspores which float in sea-water and thus sometimes have very extensive pantropical distributions, *e.g.* *Fimbristylis cymosa*, *F. ferruginea* and *Remirea maritima*. Others have a widespread Afro-Asian distribution, *e.g.* *Fimbristylis polytrichoides* and *Abildgaardia triflora*.

Species growing in seasonally wet or in dry habitats and with diaspores without special development for long-distance dispersal sometimes have wide pantropical distributions also. Such distributions are difficult to understand particularly for dryland species unless they are considered as resulting from an old Gondwanaland continent or their diaspores being wind-blown during strong and unusual weather conditions, *e.g.* *Abildgaardia ovata*, *Bulbostylis hispidula*, *B. barbata* and *Cyperus laevigatus*.

During the last hundred years especially many species of sedges growing as weeds in cultivations and especially in rice fields, have been dispersed as weeds from continent to continent as contamination in crop seeds.

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Appendix 1. Major distribution patterns

Species in Uganda with West African affinities: *Cyperus fertilis* Böckel.; *C. mertonii* Lye; *C. renschii* Böckel. var. *scabrada* Lye; *C. socialis* C.B. Cl.; *C. submicrolepis* Kükenth.; *Fimbristylis gabonica* Cherm.; *Nemum spadiceum* (Lam.) Ham.; *Scleria globonux* C.B. Cl.

Species in Tanzania with West African affinities: *Cyperus clavinux* C.B. Cl.; *C. demangei* (Rayn.) Lye; *Hypolytrum testui* Cherm.

Species with South African affinities: *Bulbostylis striatella* C.B. Cl.; *Cyperus glomerata* (Thunb.) Nees; *Cyperus fulgens* C.B. Cl.; *C. marginatus* Thunb.; *C. merxmülleri* (Podl.) Lye; *C. vestitus* Krauss; *Ficinia gracilis* Schrad.; *F. stolonifera* Böckel.; *Isolepis natans* (Thunb.) A. Dietr.; *Schoenoxiphium caricoides* C.B. Cl.; *S. lehmannii* (Nees) Steud.; *S. sparteum* (Wahlenb.) Kük.

Species with North African to Arabian affinities: *Carex negrii* Chiov.; *Cyperus conglomeratus* Rottb.; *C. cruentus* Rottb.; *C. dives* Del.; *C. involucratus* Rottb.; *C. jeminicus* Rottb.; *C. macrorrhizus* Nees; *C. procerus* Rottb.

Species with European affinities: *Carex acutiformis* Ehrb.; *C. distans* L.; *C. divisa* Huds.; *C. longus* L.; *C. mundtii* (Nees) Kunth.; *C. rotundus* L.; *Fuirena pubescens* (Poir.) Kunth; *Isolepis cernua* (Vahl) Rö. & Schult.; *I. fluitans* (L.) R. Br.; *I. setacea* (L.) R. Br.; *Schoenoplectus lacustris* (L.) Palla; *S. maritimus* (L.) Lye; *S. mucronatus* (L.) Kerner; *Schoenus nigricans* L.

Afro-Asian species: *Abildgaardia triflora* (L.) Lye; *Bulbostylis densa* (Wall.) Han.-Mazz. s.lat.; *Cyperus alopecuroides* Rottb.; *C. aromaticus* (Ridl.) Mattf. & Kük.; *C. brevifolius* (Rottb.) Hasskn.; *C. bulbosus* Vahl; *C. corymbosus* Rottb.; *C. cyperoides* (L.) O. Ktze.; *C. denudatus* L. f.; *C. difformis* L.; *C. dubius* Rottb.; *C. exaltatus* Retz.; *C. hyalinus* Vahl; *C. imbricatus* Retz.; *C. iria* L.; *C. kyllingia* Endl.; *C. maderaspatanus* Willd.; *C. meeboldii* Kük.; *C. melanospermus* (Nees) Valc. Sur.; *C. metzii* (Steud.) Mattf. & Kük.; *C. mollipes* (C.B. Cl.) K. Schum.; *C. nitidus* Lam.; *C. niveus* Retz.; *C. nutans* Vahl var. *eleusinoides* (Kunth) Haines; *C. pseudokyllingoides* Kük.; *C. pulchellus* R. Br.; *C. pumilus* L.; *C. pygmaeus* Rottb.; *C. rubicundus* Vahl; *C. sanguinolentus* Vahl.; *C. triceps* Endl.; *C. zollingeri* Steud.; *Eleocharis dulcis* (Burm.f.) Heschel; *Fimbristylis bisumbellata* (Forssk.) Bub.; *F. dipsacea* (Rottb.) C.B. Cl.; *F. miliacea* (L.) Vahl; *F. polytrichoides* (Retz.) Vahl; *F. schoenoides* (Retz.) Vahl; *Fuirena ciliaris* (L.) Roxb.; *F. pubescens* (Poir.) Kunth; *Isolepis fluitans* (L.) R. Br.; *Lipocarpa chinensis* (Osb.) Kern; *L. hemisphaerica* (Roth) Goetgh.; *L. kernii* (Raymond) Goetgh.; *Rhynchospora brownii* Roem. & Schult. ssp. *brownii*; *R. rubra* (Lour.) Makino s. lat.; *Schoenoplectus*

articulatus (L.) Palla; *S. lateriflorus* (Gmel.) Lye; *S. mucronatus* (L.) Kerner; *S. subulatus* (Vahl) Lye; *Scleria mikawana* Makino; *S. pergracilis* (Nees) Kunth; *S. poaeformis* Retz.; *S. tessellata* Willd.

Afro-American species: *Cyperus lanceolatus* Poir.; *C. niger* Ruiz & Pavon; *C. sphacelatus* Rottb.; *Lipocarpa micrantha* (Vahl) G. Tuck.; *Rhynchospora brevirostris* Griseb.; *R. candida* (Nees) Böckel.; *R. holoschoenoides* (L.C. Rich.) Hert.; *Scleria bambariensis* Cherm.; *S. bulbifera* A. Rich.; *S. distans* Poir.; *S. lagoënsis* Böckel.; *S. melanomphala* Kunth; *S. pterota* Presl.

Pantropical species: *Abildgaardia ovata* (Burm. f.) Kral; *Bulbostylis barbata* (Rottb.) C.B. Cl.; *B. hispidula* (Vahl) R. Haines; *Cladium jamaicense* Crantz.; *Cyperus amabilis* L.; *C. articulatus* L.; *C. brevifolius* (Rottb.) Hassk.; *C. compressus* L.; *C. cuspidatus* H.B.K.; *C. densicaespitosus* Mattf. & Kük.; *C. difformis* L.; *C. distans* L. f.; *C. esculentus* L.; *C. flavescens* L.; *C. haspan* L.; *C. imbricatus* Retz.; *C. laevigatus* L.; *C. macrostachyos* Lam.; *C. mundtii* (Nees) Kunth; *C. polystachyos* Rottb.; *C. rotundus* L.; *C. sesquiflorus* (Torr.) Mattf. & Kük.; *C. sphacelatus* Rottb.; *C. squarrosus* L.; *C. tenuispica* Steud.; *C. uniolooides* R. Br.; *Eleocharis acutangula* (Roxb.) Schult.; *E. atropurpurea* (Retz.) Kunth; *E. geniculata* (L.) Rö. & Schult.; *E. mutata* (L.) Roem. & Schult.; *E. nigrescens* (Nees) Steud.; *E. retroflexa* (Poir.) Urban; *Fimbristylis complanata* (Retz.) Link; *F. cymosa* R. Br.; *F. dichotoma* (L.) Vahl; *F. ferruginea* (L.) Vahl; *F. littoralis* Gaud.; *F. squarrosa* Vahl; *Fuirena umbellata* Rottb.; *Isolepis setacea* (L.) R. Br.; *Oxycaryum cubensis* (Poep. & Kunth) Lye; *Remirea maritima* Aubl.; *Rhynchospora corymbosa* (L.) Britt.; *Schoenoplectus erectus* (Poir.) Rayn.; *S. maritimus* (L.) Lye; *Schoenus nigricans* L.; *Scleria lithosperma* (L.) Sw.; *Websteria confervoides* (Poir.) Hooper

Species with highly disjunct distributions: *Carex peregrina* Link; *Cyperus subparadoxus* Kük.; *Eleocharis decorigulumis* Bérhaut; *Isolepis cernua* (Vahl) Rö. & Schult.

Appendix 2. Endemic species in the various nations and geographical areas

Sudan: *Coleochloa glabra* Nelmes; *C. schweinfurthiana* (Böckel.) Nelmes.

Sudan and Somalia: *Cyperus nubicus* C.B. Cl.

Eritrea: *Cyperus schweinfurthii* (Chiov.) Kük.

Eritrea and Sudan: *Cyperus microbolbos* C.B. Cl.

Eritrea and Ethiopia: *Cyperus holostigma* Schweinf.

Ethiopia: *Ascolepis eriocaloides* (Steud.) Steud.; *Bulbostylis longespicata* (Lye) Lye; *Carex cognata* Kunth. var. *abyssinica* (Chiov.) Lye; *Cyperus atronervatus* Böckel. ssp. *angustifolius* Lye; *C. atronervatus* Böckel. ssp. *atronervatus*; *C. bifolius*

Lye; *C. boreohemisphericus* Lye; *C. clandestinus* Steud.; *C. maculatus* Böckel. ssp. *ogadensis* Lye; *C. pratensis* Böckel.; *Ficinia borealis* Lye; *Isolepis nervosa* A. Rich.; *I. omissa* Raynal.

Ethiopia and Sudan: *Carex thomasi* Nelmes.

Ethiopia and Somalia: *Carex brunnea* Thunb. subsp. *occidentalis* Lye; *Cyperus brunneofibrosus* Lye; *C. cunduduensis* Chiov.

Ethiopia, Somalia and Yemen: *Carex negrii* Chiov.

Ethiopia and Kenya: *Bulbostylis cruciformis* (Lye) R. Haines; *Cyperus costatus* Mattf. & Kükenth. ssp. *sidamoensis* (Mtoto.) Lye; *Fimbristylis keniaensis* Kük.

Ethiopia and Uganda: *Scleria hispidior* (C.B. Cl.) Nelmes.

Ethiopia and Burundi: *Lipocarpha constricta* Goetgh.

Ethiopia and Tanzania: *Bulbostylis sphaerocarpha* (Böckel.) C.B. Cl.; *Isolepis kilimanjarica* R. Haines & Lye.

Somalia (N = north; S = south): *Bulbostylis hispidula* (Vahl) R. Haines subsp. *macroglumis* Lye (S); *B. somaliensis* Lye subsp. *confusa* Lye (S); *B. somaliensis* Lye subsp. *somaliensis* (S); *Cyperus altomicroglumis* Lye (S); *C. baobab* Lye (S); *C. benadiensis* Chiov. (S); *C. chaetophyllus* (Chiov.) Kük. (S); *C. commixtus* Kük. (N); *C. densibulbosus* Lye (N); *C. erectus* (Schumach.) Mattf. & Kük. subsp. *jubensis* (Chiov.) Lye (S); *C. gypsophilus* Lye (N); *C. medusaeus* Chiov. (S); *C. microglumis* D. A. Simps. (S); *C. micromedusaeus* Lye (N); *C. micropephilus* Lye (S); *C. mogadoxensis* Chiov. (S); *C. mudugensis* D.A. Simps. (S); *C. obbiadensis* Chiov. (S); *C. oblongus* (C.B. Cl.) Kük. subsp. *jubensis* (Mtoto.) Lye (S); *C. ossicaulis* Lye (S); *C. pluricephalus* Lye (S); *C. poecilus* C.B. Cl. (N); *C. pseudosomaliensis* Kük. (N); *C. recurvispicatus* Lye (S); *C. rotundus* L. subsp. *divaricatus* Lye (N); *C. scabricaulis* Lye (S); *C. scleropodus* Chiov. (N); *C. somalidunensis* Lye (S); *C. somaliensis* C.B. Cl. (N); *Fuirena boreocoerulescens* Lye (N); *F. somaliensis* Lye (S); *F. striatella* Lye (N).

Somalia and Kenya (N = north Somalia; S = south Somalia): *Bulbostylis craspedota* Chiov. (S); *B. pallescens* Lye (S); *Cyperus afrodunensis* Lye (S); *C. chordorrhizus* Chiov. (S); *C. eximius* (C.B. Cl.) Mattf. & Kük. (S); *C. frerei* C.B. Cl. (S); *C. phillipsiae* (C.B. Cl.) Kük. (N + S).

Somalia and India (S = south Somalia): *Cyperus dwarkensis* Sahni & Naithani (S).

Kenya: *Bulbostylis afroorientalis* (Lye) R. Haines; *B. hispidula* (Vahl) R. Haines ssp. *intermedia* (Lye) R. Haines; *B. squarrosa* (Lye) Lye; *Cyperus boreobellus* Lye; *C. brunneoalbus* (Lye) Lye; *C. flavescens* L. ssp. *tanäensis* (Kükenth.) Lye; *C. flavoculmis* Lye; *C. kwaleensis* Lye; *C. kyllingaeformis* Lye; *C. microumbellatus* Lye; *C. sanguinolentus* Vahl ssp. *nairobiensis* (Lye) Lye; *C. soyauxii* Böckel. ssp. *pallescens* Lye; *Isolepis keniaensis* Lye.

Kenya and Uganda: *Carex elgonensis* Nelmes; *C. runssoroensis* K. Schum.; *Cyperus afroalpinus* Lye; *C. crassivaginatus* Lye; *Isolepis graminoides* R. Haines & Lye.

Kenya and Tanzania: *Bulbostylis argenteobrunnea* C.B. Cl.; *Carex phragmitoides* Kükenth.; *C. vallis-rosetto* K. Schum.; *Cyperus globifer* (C.B. Cl.) Lye; *C. kilimandscharicus* Kükenth.; *C. oblongo-incrassatus* Kükenth.; *C. pseudo-hildebrandtii* Kükenth.; *C. rohlfsii* Böckel.; *C. songeensis* (Lye) Lye; *C. undulatus* Kükenth.

Uganda: *Carex bequaertii* De Wild. var. *maxima* Lye; *Cyperus fischerianus* A. Rich. var. *ugandensis* Lye; *C. flavescens* L. ssp. *microglumis* (Lye) Lye; *C. melanospermus* (Nees) Valck. Sur var. *hexalatus* Lye; *Fimbristylis miliacea* (L.) Vahl ssp. *macroglumis* Lye; *Fuirena pubescens* (Poir.) Kunth var. *abbreviata* Lye; *Isolepis ruwenzoriensis* R. Haines & Lye; *Kyllingiella ugandensis* R. Haines & Lye; *Scleria distans* Poir. var. *chondrocarpa* (Nelmes) Lye.

Uganda and Congo (Kinshasa): *Carpha eminii* (K. Schum.) C. B. Cl.

Uganda and Tanzania: *Cyperus afromontanus* Lye.

Burundi: *Bulbostylis nemoides* Goetgh.

Burundi and Tanzania: *Ascolepis hemisphaerica* Goetgh.

Tanzania: *Ascolepis protea* Welw. ssp. *chrysocephala* Lye; *Bulbostylis angustepicata* (Lye) Lye; *B. elegantissima* (Lye) R. Haines; *B. hispidula* (Vahl) R. Haines ssp. *halophila* (Lye) R. Haines; *B. johnstonii* C.B. Cl.; *B. leioplepis* (Kük.) R. Haines; *B. macrostachya* (Lye) R. Haines; *B. microcarpa* (Lye) R. Haines; *B. microrotundata* (Lye) Lye; *B. rotundata* (Kük.) R. Haines; *B. tanzaniae* (Lye) R. Haines; *B. taylorii* (K. Schum.) C.B. Cl.; *Carex papillosissima* Nelmes; *Coleochloa microcephala* Nelmes; *Cyperus afrosumilus* (Lye) Lye; *C. afrovaricus* Lye; *C. alba-purpureus* (Lye) Lye; *C. castaneobellus* Lye; *C. cremeomarisculus* Lye; *C. endlichii* Kükenth.; *C. gigantobulbes* Lye; *C. graciliculmis* Lye; *C. longi-involucratus* Lye; *C. microbracteatus* (Lye) Lye; *C. microbulbosus* (Lye) Lye; *C. micromarisculus* Lye; *C. nyererei* Lye; *C. obsoletenervosus* A. Peter; *C. purpureoviridis* Lye; *C. stramineo-ferrugineus* Kük.; *C. tanganyicanus* (Kük.) Lye; *C. tanzaniae* (Lye) Lye; *C. ugogensis* Peter & Kük.; *Fimbristylis miliacea* (L.) Vahl ssp. *pallescens* Lye; *Fuirena claviseta* A. Peter; *F. sagittata* Lye; *Isolepis trollii* (Kükenth.) Lye.

Tanzania and Zambia: *Ascolepis protea* Welw. ssp. *rhizomatosa* Lye; *A. pusilla* Ridley var. *echinata* S. Hooper; *Cyperus albo-gracilis* (Lye) Lye; *C. chinsalensis* Podlech; *C. longistolon* Peter & Kükenth.; *C. peteri* Kükenth.; *?Fuirena abnormalis* C.B. Cl.; *Schoenoplectus rhodesicus* (Podlech) Lye; *Scleria adpresso-hirta* E.A. Robinson; *S. delicatula* Nelmes.

Tanzania and Zimbabwe: *Ascolepis erythrocephala* S. Hooper; *Scleria pachyrrhyncha* Nelmes.

Tanzania and Malawi: *Carex cyrtosaccus* C.B. Cl.; *Coleochloa virgata* (K. Schum.) Nelmes.

Tanzania and Congo (Kinshasa): *Tetraria usambarensis* K. Schum.

Tanzania and Madagascar: *Cyperus subparadoxus* Kük.; *Machaerina flexuosa* (Böckel.) Kern.