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West Africa's sedges: tribes, history, habitat and biogeography

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Abstract

West Africa's sedge history is considered in relation to tribal placement and habitat. Account is taken of recent refinement to the family's subfamily (2 subfamilies) and tribal taxonomy (14 tribes), and the shortcomings revealed in the standard floras. Neither tribe Scirpeae or genus *Scirpus* as now recognized occur in West Africa. The updated taxonomy is applied in an examination of when the tribes originated in geological history and their prominence in the main West African habitat types (savanna, forest, inselberg, coast, mountain). Overall, the best-represented tribe is Cypereae but not in the forest or inselberg habitats. The proportion of Africa-endemics is highest in the mountain and forest habitats, and all 19 of the region's Hypolytreae are Africa-endemics. Species known from most West African countries are very well represented except in the mountain habitat and tribes Cariceae and Hypolytreae. C_4 species predominate in all habitats except forest but are almost exclusively limited to the young tribes Abildgaardieae and Cypereae. Overall, perennial species dominate West Africa's sedge flora, although to a lesser extent in the inselberg and savanna habitats. In all tribal groups perennial species outnumber annual species. Nigeria, with the region's richest sedge flora is compared with the region overall, revealing differences with the savanna, forest and coast habitats, due to Nigeria's lack of endemics and species of restricted distribution. Suggestions are made for a new phylogenetic research initiative concerned primarily with West Africa's sedges, and that comparison with equivalent treatments of other species-rich West African plant families would be interesting.

Introduction

The sedge family (Cyperaceae) has long divided the opinions of plant enthusiasts in general - and even the opinions of specialists in the group! Because sedges present little visual appeal, and species identification relies so often on relatively obscure features, most plant enthusiasts assume they are of no interest and disregard them. Sedge specialist opinions represent decades of disagreement about classification and about the allocation of species to genera.

This article will, perhaps, go some way to show readers that a new era has dawned! On-going sedge investigations of many kinds are increasingly showing that the group is far from lacking in interest; two recent accounts in this journal hopefully have contributed. One has outlined the drama accompanying the development of familiarity with the group in Nigeria (Hall, 2021). The second, an initial consideration of the phytogeography of the West African sedge flora (Hall, submitted), reveals how rich it is in species, and that a remarkably high number of those sedges exemplify links with other continents, a consequence of relationships with migratory birds and their routes of travel. Larridon *et al.* (2021) give an informative and up-to-date summary of numerous further points of particular interest for sedges considered globally.

This account uses information from an African sedge database mainly extracted from literature in the public domain spanning the greater part of the last two centuries. The information has been updated where appropriate to achieve consistency with today's taxonomy and species circumscriptions. The account complements the previous phytogeographic study (Hall, submitted) by bringing information on geological history and habitat into the picture. However, the newly-developed classification of the family put forward by Larridon *et al.* (2021) is fundamental to an understanding of the historical aspect and is therefore outlined first. Through a number of studies the accepted classification of the Cyperaceae has been extensively changed and clarified in recent years, particularly in the delimitation of genera and tribes. Phylogenetic studies have been the main force behind this significant advance, and have resolved various long-standing uncertainties about species-relationships within the family. This has been a complex exercise requiring numerous researchers representing a wide variety of skills in data management and interpretation, in addition to more orthodox biology and taxonomy. Papers cited here have impressively extensive author-listings as a result! Of particular significance as an element of the new insight has been successful application of the molecular clock approach to the phylogenies determined, linking events with geological time.

Inevitably, the new taxonomy brings many name changes for species but there is compensation for this inconvenience through the light shed on the family's evolutionary history. Sedge taxonomy as now understood supports the concept of two Cyperaceae subfamilies (Muasya *et al.*, 2009) and 22 tribes (Larridon *et al.*, 2021). Subfamily

Mapanioideae, is small and represented in West Africa by only one of its two tribes, but the second subfamily (Cyperoideae) has 20 tribes, thirteen present in the region. The tribes vary widely in diversity, both in West Africa and globally. Larridon *et al.* (2021) provide estimates of the numbers of genera and species in each tribe, worldwide. In most tribes there are no more than two genera, but the genera may be enormously rich in species, as with *Carex*, the only genus in tribe Cariceae, with over 2000 spp.! At the other extreme, *Cladium*, the only genus in tribe Cladieae, has but three species. In West Africa, most of the tribes are represented by only a single genus while seven tribes, and about half of the 20 genera, are represented by no more than five species. In contrast, the most species-rich genus, *Cyperus*, is represented in West Africa by over 140 species.

The family's diversification, with the subfamilies diverging from the ancestral stock and separating into today's tribes over geological time, is revealed by recent studies. Phytogeographic differences among tribal lineages are indicated - in age and in the pathways by which tribes reached Africa (Escudero & Hipp, 2013; Spalink *et al.*, 2016).

Before consideration of sedge tribes and views of the process of tribal evolution in the family, shortcomings in the treatment of the sedges in the standard West African flora (Hooper & Napper, 1972) are addressed. Following this, a summary of the appearance through geological time of the tribal lineages relevant to West Africa is given. A further aspect of West African sedge phytogeography, allocation of species to broad habitat categories, with observations on their sedge floras, follows.

Sedge tribes and the Flora of West Tropical Africa

The treatment of the Cyperaceae in the Flora of West Tropical Africa (Hooper & Napper, 1972) is outdated in terms of nomenclature and classification. An update of nomenclature is given in Hall (2021), while the opportunity to update the classification is taken here. Standard floras generally organize coverage of a plant family in one of two ways. One way is alphabetically by genus (as for Nigeria by Lowe & Stanfield, 1974). The second way is according to a generic sequence from primitive to advanced, reflecting opinions held at the time of publication, with tribal placement determining the grouping and sequence of genera. In Hooper & Napper (1972) tribes are not explicitly mentioned but the underlying framework is clearly that detailed by Hooper (1973). Since the 1970s, tribal classification of the Cyperaceae has completely changed. Any up-to-date appreciation of the phytogeography of the family demands a current interpretation of the tribes. For West Africa there have been changes in the sequence from primitive to advanced, and in which tribes genera are placed. The sequence changes have arisen with the realisation that the long-standing, though frequently questioned, assumption that sedges with bisexual flowers were more primitive than those with flowers reduced to the unisexual condition was not reliable. Reconciliation of the diverging views on sedge evolution began in the 1980s and 1990s, as more extensive morphological and anatomical datasets were analysed using sophisticated multivariate and cladistic techniques. The main advances, however, belong to this century: they result from comprehensive family-wide molecular phylogenetic studies (*e.g.* Muasya *et al.*, 2009; Escudero & Hipp, 2013; Spalink *et al.*, 2016; Larridon *et al.*, 2021). Details remain to be clarified but generally the classification of the sedges is less controversial than it has ever been and little disagreement among specialists of the family continues. It should be emphasized that, while far-reaching, the updates required do not render the Hooper & Napper (1972) treatment of West Africa's sedges unfit for purpose. The flora was issued as an identification guide and its coverage, keys and distribution indications remain broadly sound, although currently accepted species names should replace those used in 1972.

Table 1 reveals the marked contrast between the classification of Hooper & Napper (1972) and that currently accepted (Larridon *et al.*, 2021). The number of tribes has risen from 8 to 14, and there are differences in tribal names (reflecting recognition of new groupings and revised tribal circumscriptions), and in the tribal sequence. Tribe Scirpeae no longer applies to West Africa, although there are members elsewhere on the continent. Hooper & Napper referred no fewer than 12 of their genera to tribe Scirpeae; these genera (which include two segregate genera of *Cyperus*) are now divided among seven other tribes! Twenty-four species referred to *Scirpus* itself (the type genus of the tribe) are now distributed to eight different genera (including three segregate genera of *Cyperus*), in five of today's tribes.

Past to present in West Africa

The Cyperaceae originated in the Late Cretaceous Period in South America (Spalink *et al.*, 2016). Descendants diversified and spread worldwide along various geographic pathways. For the sedge tribes of today, recent phylogenetic studies have identified lineages linking to ancestral predecessors, each tribe having its own lineage. Age estimates (Escudero & Hipp, 2013; Spalink *et al.*, 2016) have been made, using molecular clock approaches, and are expressed for a tribe as its tribal "crown age". The crown age is when the first taxon appeared which possessed that tribe's distinctive features – for the family Cyperaceae as a whole it is estimated at 85 million years. Sedges that would be referable to the oldest tribes recognized today are thought to have existed in the Eocene Epoch, over 40 million years ago. In West Africa the oldest lineages in subfamily Cyperoideae have culminated in five of today's sedge tribes: Trilepideae, Cladieae, Sclerieae, Bisboeckelereae, Rhynchosporeae. All five originated in South America, as (rather later) did the Hypolytreae in subfamily Mapaniodeae (Spalink *et al.*, 2016), and then migrated to other parts of the Southern Hemisphere. In most cases direct ancestral migration across the narrower Atlantic Ocean of the Cretaceous and Palaeocene Epochs is a possibility.

Table 1: Tribal placements of West African sedge genera currently (rows), and when the standard flora was published in 1972 (columns).

	Cypereae	**Scirpeae**	**Rhynchosporeae**	**Schoeneae**	**Hypolytreae**	**Sclerieae**	**Cryptangieae**	**Cariceae**
Hypolytreae					*Mapania* 9 *Hypolytrm* 7			
Trilepideae							*Coleochloa* 1 *Afrotrilepis* 2 *Microdracoides* 1	
Cladieae				*Cladium* 1				
Sclerieae						*Scleria* 36		
Bisboeckelereae						*Diplacrum* 2		
Rhynchosporeae			*Rhynchospora* 13					
Cariceae								*Carex* 6
Eleocharideae		*Eleocharis* 15 *Websteria* 1						
Abildgaardieae		*Bulbostylis* 17 *Fimbristylis* 26 *Scirpus* 2						
Bolboschoeneae		*Scirpus* 2						
Fuireneae		*Fuirena* 5						
Schoenoplecteae		*Scirpus* 1						
Pseudoschoeneae		*Scirpus* 11						
Cypereae	*Cyperus* s.s. 75 (*Mariscus* 16) (*Remirea* 1) (*Torulinium* 1) (*Pycreus* 29) (*Kyllinga* 18)	(*Ascolepis* 6) (*Lipocarpha* 6) *Scirpus* 8						

Numbers after generic names are tallies of species listed by Hooper & Napper (1972). Parentheses indicate segregate genera now considered part of *Cyperus*. Rows indicate tribes in a downward sequence from ancestral ("basal") to younger as in Larridon *et al.* (2021). Columns, from left to right, indicate tribes in the Hooper & Napper (1972) sequence from more primitive to more advanced.

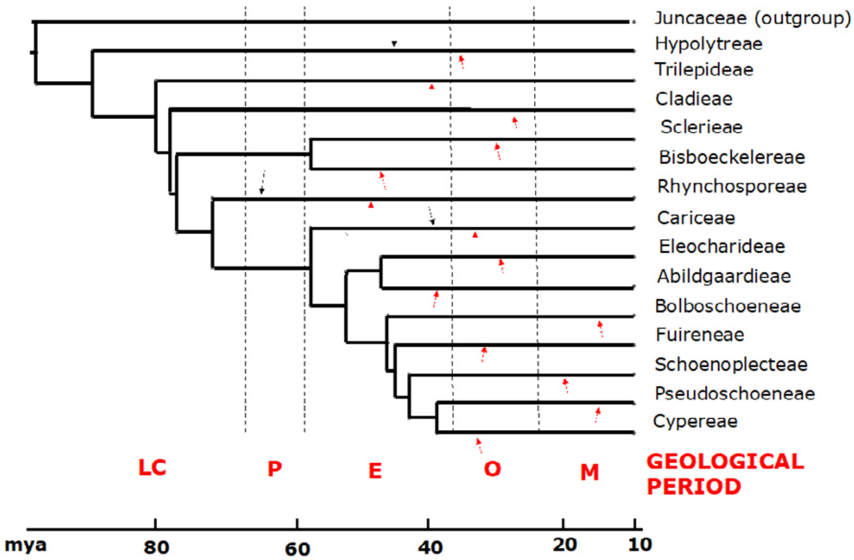

Fig. 1: Cladogram for the West African region showing sedge tribe phylogeny against a geological time scale, drawing on information in Escudero & Hipp (2013), Spalink et al. (2016) and Larridon et al. (2021). Red arrows indicate crown ages; tribal lineages are estimated to start at the left end of the tribal lines except with Hypolytreae, Rhynchosporeae and Cariceae where they are marked by black arrows (necessitated where tribes absent from West Africa have been excluded). Abbreviations: mya – million years ago; LC – Lower Cretaceous; P – Palaeocene; E – Eocene; O– Oligocene; M – Miocene. The dashed lines across the cladogram mark boundaries for the geological periods.

Other tribes reached Africa by more complex routes, but they share an ancestor that migrated into North America early in the Palaeocene Epoch. Later in the Palaeocene, two pathways arose. A branch diverging from one pathway 38 million years ago (Late Eocene Epoch) led to the Cariceae tribe, which arose a few million years later in eastern Eurasia. Southward and southeastward spread from Eurasia presumably brought the Cariceae into Africa along a route offering relatively temperate conditions. Along the second pathway, diversification commencing 52 million years ago (Early Eocene) gave rise to West Africa's remaining seven tribes (Eleocharideae, Abildgaardieae, Bolboschoeneae, Fuireneae, Schoenoplecteae, Pseudoschoeneae, Cypereae) and the greater proportion (>70%) of today's West African sedge species. In the later Miocene (15-7 million years ago) there was a significant diversification event within tropical Africa, on the Cypereae lineage (Spalink *et al.*, 2016): proliferation of species in *Cyperus*, the principal genus of the tribe, resulted. Fig. 1 shows the lineages of the tribes present in West Africa today against a scale of geological time; crown age positions are marked on the most recent segment of each tribe's path. Extending backwards in time, the unbroken path connecting the crown to where it meets another path is taken here as completing the tribe's lineage: the meeting points, marked on Fig. 1, are taken here to indicate the lineage age.

West African events onwards from the Eocene are relevant, too. Unaffected by the rifts and land uplift producing mountainous eastern Africa, West Africa has remained mainly an extensive low elevation area. Little of West Africa's landscape is above 500 m elevation, with 1000 m reached only in a few isolated places – notably at the eastern boundary. Landscape stability has been characteristic of the region since well before the Miocene (26 million years ago), and before the arrival in Africa of nearly all the region's current sedge tribes. Climatic conditions in West Africa from the Miocene onwards, however, have been far from stable (Sowunwi, 1986). One event of interest 15-13 million years ago was the first appearance of the ecologically important C_4 mode of photosynthesis in sedges – in tribe Abildgaardieae. This corresponded with a key period for the sedges of tropical Africa generally. Grassland and open woodland were expanding significantly, generating habitats where the enhanced water use efficiency of grasses using the C_4 photosynthetic pathway was beneficial. Some sedges benefited this way, but in many more C_4 characteristics are thought to have arisen in wetland situations where enhanced water use efficiency matters little. It has been suggested that in temperate wetlands C_4 photosynthesis might enhance nitrogen use efficiency, although Stock *et al.* (2004) caution against extending this idea to tropical wetlands. From the Mid-Miocene through the more recent Pliocene and Pleistocene Epochs (7-2 million years ago), plant and animal taxa associated with grassland and savanna diversified. Couvreur *et al.* (2021) suggest most of today's species and genera originated in the last 11 million years. This is when there was proliferation of a second sedge tribe rich in C_4 species, the Cypereae.

Habitat categories

It is convenient to recognize five broad habitats in West Africa and to assign each sedge species to the one where it is most typically found (Appendix). The most extensive is the savanna habitat (152 spp., including the widespread sedge weeds). The next largest is the forest climate zone habitat group (51 spp.); included in this are the sedges restricted to lowland areas where the climate would allow forest to develop even if forest cover has been lost. For convenience, the shorter term "forest habitat" is used in what follows. The remaining habitats are coast (20 spp.), inselberg (44 spp.) and mountain (36 spp.). Savanna, forest and coast habitats extend west to east through the region (although today the forest habitat is interrupted between Nigeria and Ghana), but past extents and limits have varied with climatic events. Inselberg and mountain habitats are discontinuous and more scattered through the region.

The savanna habitat extends southward from the southern margin of the Sahara, with mean annual rainfall progressively increasing from inland towards the coast. The familiar

West African savanna vegetation zones lie more or less parallel with the coast. As wet and dry climatic phases alternated through the last five million years, the savanna ecosystems underwent north-south zonal shifts but maintained the west-east continuity still evident. The savannas lie north of the forest habitat. For the forest habitat, during the wettest phases of the last five million years there was unbroken continuity from the Nigeria/Cameroun border westward to southern Senegal. In contrast, when arid conditions were most intense Guinea savanna reached the coast, except where refuges of closed forest persisted. A refuge was located at the Liberia/Ivory Coast border (at the seaward base of one of the few areas of land rising well above 500 m). There was a second, 2000 km to the east, where forest just reached Nigeria from adjoining Cameroun (at the southern extremity of hill country extending to the north). Even if the suggestion sometimes made of a third refuge in western Ghana is taken into account, West African forest refuges are separated from each other by at least 700 km. Such an interval is an effective barrier to dispersal for many of the species at each end. The coast habitat, like the savannas, presumably escaped fragmentation. When the shoreline shifted landward or seaward in response to climate-related sea level fluctuations, the coast habitat persisted immediately inland of the shore.

Locally, the geologically ancient inselbergs are present in West Africa within both savanna and forest areas (Nwajide, 1989). The inselberg habitat is harsher than that of the much more extensive surrounding landscapes. The environment is extreme, with frequent and rapid switches between moist and dry conditions through the more humid part of the year, and lengthy periods of very severe water deficit in the dry season. It seems likely that on inselbergs the impact of regional climate fluctuations has been reflected in relatively minor amelioration or intensification of the harsh conditions. Mountains have been present in West Africa since the Miocene or earlier, mainly at the eastern flank of the region but also where Guinea, Ivory Coast and Liberia meet. The influence of past climate change on West Africa's mountain habitats remains unknown but given the steady global decline (by 2-3°C – Couvreur *et al.*, 2021) in mean temperature which affected West Africa during the later Miocene, montane vegetation zones may have descended several hundred metres. On the mountains wet/dry climate phase alternations may have led to forest areas within mountain blocks fragmenting (dry phase) and coalescing (wet phase), but it is improbable that fragmentation generated gaps wide enough to be major dispersal barriers. Also, at higher elevation, lower temperatures may have reduced the severity of dry climate phase extremes.

Habitat sedge floras

The representation of each tribe in each habitat in terms of numbers of species is shown in Table 2. The tribes vary very widely in the numbers of species included. Cypereae are by far the best-represented tribe overall, with *Cyperus* accounting for all except one of its 144 species. There are also fairly high numbers of species in Sclerieae (all in *Scleria*) and Abildgaardieae (many *Bulbostylis* and *Fimbristylis*). At habitat level, the prominence of Cypereae varies; it is not the best-represented tribe of the forest or inselberg habitats.

Tribes (constituent genera indicated)	**Habitat categories**					
	Savanna	**Forest***	**Coast**	**Inselberg**	**Mountain**	**All habitats**
Hypolytreae (*Hypolytrum, Mapania*)	0	18	0	0	1	**19**
Trilepideae (*Afrotrilepis, Coleochloa, Microdracoides*)	0	0	0	3	1	**4**
Cladieae (*Cladium*)	0	0	1	0	0	**1**
Sclerieae (*Scleria*)	12	7	1	14	2	**36**
Bisboeckelereae (*Diplacrum*)	1	1	0	0	0	**2**
Rhynchosporeae (*Rhynchospora*)	6	2	3	1	1	**13**
Cariceae (*Carex*)	1	0	0	0	4	**5**
Eleocharideae (*Eleocharis*)	11	3	2	1	0	**17**
Abildgaardieae (*Abildgaardia, Bulbostylis, Fimbristylis*)	21	3	2	12	5	**43**
Bolboschoeneae (*Bolboschoenus*)	1	0	1	0	0	**2**
Fuireneae (*Fuirena*)	5	0	0	0	0	**5**
Schoenoplecteae (*Schoenoplectus*)	1	0	0	0	0	**1**
Pseudoschoeneae (*Schoenoplectiella*)	8	0	0	1	2	**11**
Cypereae (*Cyperus, Isolepis*)	85	17	10	12	20	**144**
All tribes	**152**	**51**	**20**	**44**	**36**	**303**

Table 2: Numbers of West African sedge species referred to habitat category, by sedge tribe

Adding tribal detail to this picture is complicated by the low diversity of most sedge tribes, especially when sorted by their typical habitats. To address this, in addition to Hypolytreae, Cariceae and Cyperaceae (all treated separately) three tribal groups are used. The first of these contains the five tribes closest to the subfamily Cyperoideae ancestral stock - sometimes known as "early-diverging" tribes (Trilepideae, Cladieae, Sclerieae, Bisboeckelereae, Rhynchosporeae). Eleocharideae and Abildgaardieae, which are most closely related to each other, form the second group. The third group covers species that, in the past, were all regarded as Fuireneae but are now divided among four related tribes (Bolboschoeneae, a narrower Fuireneae, Schoenoplecteae, Pseudoschoeneae).

To highlight tribal and habitat characteristics, the relative proportions of each tribal group flora showing the characteristics are indicated in Figs 2-5. Numbers of species involved for each tribal group and each habitat are given in Table 2; it should be noted that the smallest three tribal groups include fewer species than any habitat. Figs 2 and 3 relate to distributional characteristics. Fig. 2 reveals that the proportions of species endemic to Africa are highest in the mountain and forest habitats. At tribal group level, in the three groups with higher species numbers, Africa-endemic and pluricontinental species contribute similar proportions. In the other groups, proportions differ widely, Hypolytreae containing only Africa-endemic species. Fig. 3 considers distribution as numbers of countries within the region. In most habitats, and in the largest tribal groups, widespread species (in 8-15 countries) contribute the highest proportion. The obvious exception is the mountain habitat because major mountains are absent from most West African countries. Fig. 4 shows the incidence of West Africa's C_4 sedges in terms of tribal group and habitat. In all habitats there is a mix of C_3 and C_4 species, with a particularly high C_3 proportion in the forest habitat. Two of the tribal groups have consistent presence of C_4 species across habitats, and there is also an anomalous presence, *Rhynchospora rubra* from the coast habitat, in a third group ("early-diverging"). The balance between annual and perennial lifespans is presented in Fig. 5 (Fig. 5 also indicates that for a few species both the annual and perennial conditions are known). Overall, there are far fewer annual species than perennials, and out of the six tribal groups with typical mountain species only Cypereae includes any annuals. Annual species are strongly represented among species typifying the inselberg habitat and in the Eleocharideae + Abildgaardieae tribal group.

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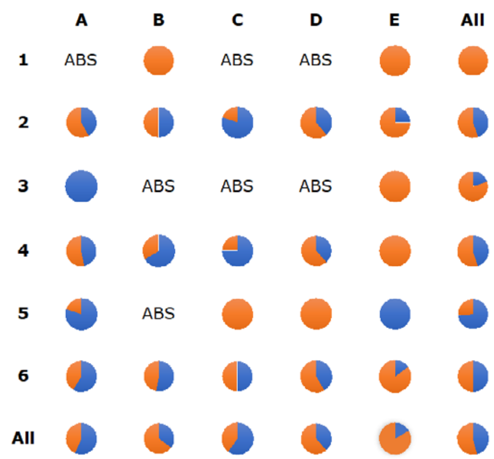

Fig. 2: West Africa's sedges: relative proportions of pluricontinental and Africa-endemic species by sedge tribal group (rows) within habitats (columns). Colour codes: blue, pluricontinental distribution; orange, Africa-endemic distribution. Tribal codes: 1, subfamily Mapanioideae; 2-6, subfamily Cyperoideae. 1, Hypolytreae; 2, Early-diverging tribes (Trilepideae, Cladieae, Bisboeckelereae, Sclerieae, Rhynchosporeae); 3, Cariceae; 4, Eleocharideae and Abildgaardieae; 5, Bolboschoeneae, Fuireneae, Schoenoplecteae and Pseudoschoeneae; 6, Cypereae. Habitat codes: A, Savanna; B, Forest climate; C, Coast; D, Inselberg; E, Mountains. ABS (absent) indicates that no West African species of the tribal group concerned is characteristic of the habitat.

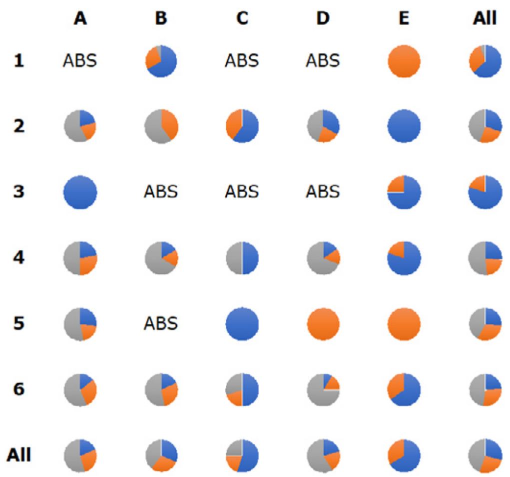

Fig. 3: West Africa's sedges: proportions of species by sedge tribal group (rows) and habitat (columns) reported from different numbers of the 15 West African countries. Colour codes: blue, 1-3 countries; orange, 4-7 countries; grey, 8-15 countries. Tribal codes: 1, subfamily Mapanioideae; 2-6, subfamily Cyperoideae. 1, Hypolytreae; 2, Early-diverging tribes (Trilepideae, Cladieae, Bisboeckelereae, Sclerieae, Rhynchosporeae); 3, Cariceae; 4, Eleocharideae and Abildgaardieae; 5, Bolboschoeneae, Fuireneae, Schoenoplecteae and Pseudoschoeneae; 6, Cypereae. Habitat codes: A, Savanna; B, Forest climate; C, Coast; D, Inselberg; E, Mountains. ABS (absent) indicates that no West African species of the tribal group concerned is characteristic of the habitat.

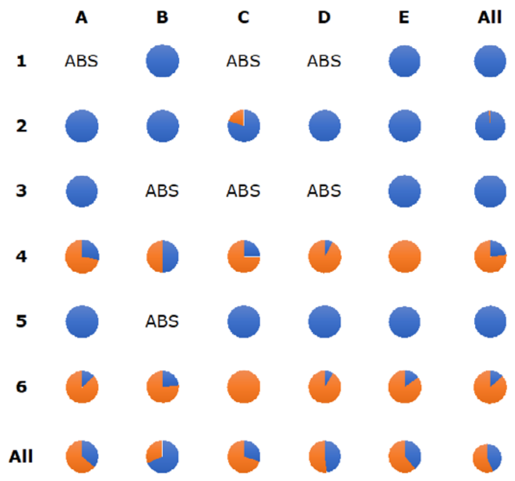

Fig. 4. West Africa's sedges: relative proportions of C3 and C4 photosynthetic pathways among species, by sedge tribal group (rows) within habitats (columns). Colour codes: blue, C3 photosynthetic pathway; orange, C4 photosynthetic pathway. Tribal codes: 1, subfamily Mapanioideae; 2-6, subfamily Cyperoideae. 1, Hypolytreae; 2, Early-diverging tribes (Trilepideae, Cladieae, Bisboeckelereae, Sclerieae, Rhynchosporeae); 3, Cariceae; 4, Eleocharideae and Abildgaardieae; 5, Bolboschoeneae, Fuireneae, Schoenoplecteae and Pseudoschoeneae; 6, Cypereae. Habitat codes: A, Savanna; B, Forest climate; C, Coast; D, Inselberg; E, Mountains. ABS (absent) indicates that no West African species of the tribal group concerned is characteristic of the habitat.

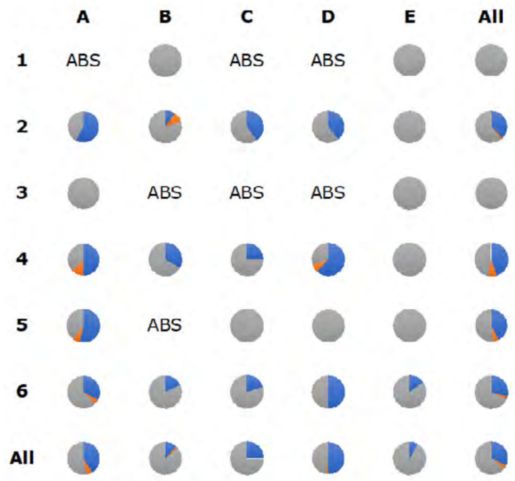

Fig. 5: West Africa's sedges: relative proportions of annual and perennial species, by sedge tribal group (rows) within habitats (columns). Colour codes: blue, annual species; orange, species with both annual and perennial life spans; grey, perennial species. Tribal codes: 1, subfamily Mapanioideae; 2-6, subfamily Cyperoideae. 1, Hypolytreae; 2, Early-diverging tribes (Trilepideae, Cladieae, Bisboeckelereae, Sclerieae, Rhynchosporeae); 3, Cariceae; 4, Eleocharideae and Abildgaardieae; 5, Bolboschoeneae, Fuireneae, Schoenoplecteae and Pseudoschoeneae; 6, Cypereae. Habitat codes: A, Savanna; B, Forest climate; C, Coast; D, Inselberg; E, Mountains. ABS (absent) indicates that no West African species of the tribal group concerned is characteristic of the habitat.

Discussion

The availability of the 85 million years timeline for the sedges has allowed the landscape and vegetation history of West Africa to be linked to the status of the region's main habitats, and their sedge floras. Additional interest in this context is introduced by differences in tribal representation within and between habitats, which can be considered alongside the more usual distributional and life-span characteristics. Dominance in the savanna habitat of species with wide ranges is consistent with the maintenance of continuity through the savanna in time and space. Also, over their 26 million years' history, Africa's savannas have enabled great diversification of Abildgaardieae and Cypereae, young tribal lineages, so that species of old lineage tribes seem under-represented today. Abildgaardieae and Cypereae account for 70% of the savanna sedge flora, and this savanna element represents 55% of the West African species utilizing the C_4 photosynthetic pathway.

In contrast with the savanna group, the forest group includes few pluricontinental species, and under half the species are reported from most of West African's 15 countries: almost one-third of the forest group are known from just 1-3 West African countries. This situation arises largely from significant localized speciation in the forest refuges, a reflection of West Africa's turbulent forest history. It is well-illustrated by *Hypolytrum* and *Mapania*, with nine local forest zone endemics where Liberia, Ivory Coast and Guinea meet. Overall, for West Africa, this habitat is where the proportion of species from subfamily Mapanioideae and the old tribal lineages of subfamily Cyperoideae is highest. Compared with the savanna flora the proportion of perennial species (*ca* 90%) in the forest habitat is much higher, consistent with little or no dry season disruption of growth. The forest habitat also has a higher proportion (69%) of species utilizing the C_3 photosynthetic pathway than any other habitat – the prominance of non-C_4 Hypolytreae and old lineage tribes, and species of shaded conditions (typically non-C_4), explains this.

The coast species group is distinctive in the relatively low representation (25%) of species present in ≥8 countries in the region. The high representation (55%) of species reported from ≤3 of them arises because of species limited to the region's western parts. It should be noted, however, that some of these are of disputed taxonomic status (*e.g. Cyperus subtilis*, *C. tibialis*, *Scleria chevalieri*). The best-represented tribe is the C_4-rich Cypereae. For other tribes, the small group size limits appreciation of relative importance but the Abildgaardieae and Sclerieae seem poorly represented.

The proportion (59%) of inselberg species present in ≥8 countries in the region is relatively high, and only 20% are reported from ≤3 countries. Cypereae account for only a minority of species and are even less prominent than in the forest habitat – in all other habitats more than half belong to this tribe. The old lineage tribes of Sclerieae and Trilepideae are relatively prominent, which is consistent with the inselberg habitat being of some antiquity. Possibly, ancestral members of these tribes reached West Africa's inselbergs directly from South America as long ago as the Eocene. The relatively low number of perennial species is clearly a result of habitat conditions favourable to annual/ephemeral species.

The mountain habitat group of species shares with the savanna habitat group a relative deficiency of species of old lineage tribes, and shares with the forest climate zone habitat group a strong representation of perennial species. No member of the group is reported from ≥8 countries in the region – a reflection of the absence of mountain terrain from most West African countries. Floristically, the group is noteworthy for richness in the Cariceae and the paucity of members of tribes Eleocharideae and Sclerieae.

Nigeria, with 231 species present, has by far the richest of the fifteen national floras – more than 75% of the region's sedge flora and over 40 more species than the next richest, Senegal (188 species) and Guinea (185 species). No fewer than 15 of the species listed for Nigeria, generally from the mountainous east, are unknown further west. These distinctive characteristics make it of interest to consider how closely Nigeria matches the region as a whole in terms of habitat sedge floras.

Nigeria's savanna sedge flora broadly conforms to the regional picture. In the regional savanna flora, however, 20% of the species are reported from three or fewer countries:

the corresponding estimate for Nigeria is 3%. Marginal intrusions from species ranging mainly north of West Africa and some poorly known endemic species explain the higher regional value. In terms of forest habitat, Nigeria's lack of any extensive endemic-rich forest zone refuge area leads to differences. The country has no endemics and very few species of localized distribution. Nigeria's forest zone sedges in general are shared with most West African countries having a forest zone. Where tribes are concerned, Hypolytreae is poorly represented – 11% of the species (the corresponding value for the region is 35%). The low endemism also explains why the forest zone proportion of pluricontinental species is higher for Nigeria than for forest habitat of West Africa overall. As a group, almost all Nigeria's coastal sedges have pluricontinental distributions and are regionally widespread; in contrast the coastal sedge flora for the region as a whole is enriched with several species, some regarded as endemic, confined to a few of its western countries (but note comments on these, above). The Nigerian sets of inselberg and mountain sedges broadly show characteristics generally applicable to the region. In the case of the mountain flora, apparent similarity reflects Nigeria's dominance of the regional montane flora; 86% of the regional mountain flora is in Nigeria but only 31% is recorded from the countries next-richest in species, Guinea and Sierra Leone. Included for Nigeria, of course, are several species absent further west. Indeed, compared with the rest of West Africa, Nigeria's strong floristic affinity with countries to the east, a noteworthy feature of its sedge flora, is due primarily to mountain species.

The account offered here would not have been possible without this century's new insights into the Cyperaceae. After disagreement persisting for decades, there is now broad acceptance of the subfamily and tribal foundation of the family's classification, recently publicised by Larridon *et al.* (2021). It is emphasized, however, that much of the past understanding of the family has proved sound, notably the integrity of the large groups now composing tribes Cariceae, Eleocharideae, Rhynchosporeae and Sclerieae. The key changes come from the re-sorting of species and genera to new positions in tribes Scirpeae and Cypereae, and extensive internal rearrangement of tribe Schoeneae (not one of West Africa's sedge tribes). These tribes now have the monophyletic structure essential for rewarding phylogenetic work at lower taxonomic levels. Also, the disjointed family history based on a fragmentary fossil record has been replaced by a timeline along which diversification events can be placed at approximate locations – broadly defined "ancestral areas" (Spalink *et al.*, 2016).

Future research will seek even better understanding of the sedges, and how their present status arose. Their subfamily and tribal structures have been resolved but doubts remain about groupings at species level within the large genera. When the first broad phylogenetic treatment was attempted (Muasya *et al.*, 2000), only a single gene sequence (*rbcL*) was used, combined with morphological data. Subsequent work centred on progressively more refined phylogenetic approaches. Lately, a switch from methods gathering genome information from very limited numbers of gene loci to methods where hundreds of loci contribute has proved rewarding. One of these methods, so-called "targeted sequencing", has preserved the settled subfamily and tribal structures while exposing meaningful groupings not previously detected at subgeneric level. Larridon *et al.* (2020), using this method, have dramatically increased awareness of species groupings in the particularly challenging genus *Cyperus* (globally over 950 spp., including 143 in West Africa), especially where the species (globally around 750, including 125 in West Africa) understood to use the C_4 photosynthetic pathway are concerned. Further interest calling for new research attaches to genus *Cyperus*: tropical Africa has been identified as its "cradle" (Spalink *et al.*, 2016) but this does not necessarily indicate that it is where all the species originated. The presence of non-African species of *Cyperus* on other continents suggests later secondary species radiation away from Africa.

Although not the tropical African region richest in sedge species, West Africa is the largest, with a well-understood flora, very rich in elements typical of tropical Africa generally. The region is thus eminently suited for an initiative taking advantage of the new methodologies to elaborate phylogenetic species groupings and ancestry. To complement recognition of more robust infrageneric species groupings, exploring "ancestral areas" of pluricontinental species from younger tribal lineages (Cypereae and Abildgaardieae) might be revealing.

Since the year 2000 about half of West Africa's 303 sedge species have been included in phylogenetic studies, and this has involved non-West African material of wide-ranging species in over 80 cases. In West Africa's *Cyperus*, its most diverse and interesting genus, species are mostly C_4, shared equally between pluricontinental and Africa-endemic species. However, the Africa-endemic group is poorly represented (33%) in phylogenetic work compared with the pluricontinental group (67%). For a new study, including molecular clock aspects and with a West Africa focus, a balanced and more comprehensive coverage is desirable. Material from multiple, well-separated, parts of the range (one part being West Africa) would need to be represented in the case of pluricontinental elements. As well as clarifying how closely gene pools of a species from different continents match, it might enable pluricontinental elements genuinely originating in Africa to be distinguished from ones that arose on other continents and were dispersed to Africa later. While this may appear a somewhat ambitious task, the recently published work of Larridon *et al.* (2020, 2021) suggests it would be quite feasible. Conveniently, relevant data already exist which could be accessed by arranging to tap the extensive archive of sedge information stored in publicly available DNA sequencing databases, notably GenBank and SRA (Sequence Read Archive). There would be a need to extend the cover to species so far un-investigated, achieved through field programmes or using herbarium material: an attractive strength of the so-called "target sequencing" (Larridon *et al.*, 2020) is effectiveness with DNA extracted from herbarium specimens. Ideally, the research would be undertaken in West Africa but it could also be achieved through co-operation with a partner outside the region. Worldwide, there are now many institutions able to routinely and cheaply carry out DNA analyses, among them a growing number with interest and experience in working with sedges.

Finally, the question arises of whether West Africa's sedges are unusual in the historical and biogeographical patterns outlined here. To answer this, the challenge of a similar consideration of some of the region's other species-rich families (Fabaceae, Poaceae, Rubiaceae, Orchidaceae, Euphorbiaceae, Asteraceae) will have to be met!

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Appendix. West Africa's Cyperaceae – sorted by habitat group. An asterisk following the authority denotes a species not recorded for Nigeria.

SAVANNA GROUP. ***Bolboschoenus*** *glaucus* (Lam.) S.G.Sm.*; ***Bulbostylis*** *barbata* (Rottb.) C.B.Clarke, *bodardii* S.S.Hooper*, *bulbostyloides* (S.S.Hooper) Larridon & Roalson*, *cioniana* (Pi.Savi) Lye, *contexta* (Nees) Bodard, *filamentosa* (Vahl) C.B.Clarke, *fimbristyloides* C.B.Clarke*, *hispidula* (Vahl) R.W.Haines, *lanifera* (Boeckeler) Kük., *viridecarinata* (De Wild.) Goetgh.; ***Carex*** *enokii* A.M.Molina, Acedo & Llamas*; ***Cyperus* (*Ascolepis*)** *ascocapensis* Bauters, *ascopusillus* Goetgh., *brasiliensis* (Kunth) Bauters, *dipsacoides* (Schumach.) Bauters; ***Cyperus* (*Cyperus*)** *alopecuroides* Rottb., *amabilis* Vahl, *articulatus* L., *bulbosus* Vahl, *clavinux* C.B.Clarke, *congensis* C.B.Clarke*, *conglomeratus* Rottb.*, *denudatus* L.f., *difformis* L., *digitatus* Roxb., *dilatatus* Schumach., *esculentus* L., *exaltatus* Retz., *haspan* L., *imbricatus* Retz., *incompressus* C.B.Clarke*, *involucratus* Rottb., *iria* L., *jeminicus* Rottb., *laevigatus* L., *lateriticus* J.Raynal*, *latifolius* Poir.*, *leucocephalus* Retz., *longus* L., *maculatus* Boeckeler, *margaritaceus* Vahl, *mauretaniensis* Väre & Kukkonen*, *meeboldii* Kük.*, *michelianus* (L.) Delile, *nutans* Vahl*, *papyrus* L., *pectinatus* Vahl, *permacer* C.B.Clarke, *podocarpus* Boeckeler, *procerus* Rottb., *pustulatus* Vahl, *reduncus* Hochst. *ex* Boeckeler, *remotispicatus* S.S.Hooper, *rotundus* L., *sahelii* Väre & Kukkonen*, *sphacelatus* Rottb., *tenuiculmis* Boeckeler, *tenuispica* Steud., *tonkinensis* C.B.Clarke, *zollingeri* Steud.*; ***Cyperus* (*Kyllinga*)** *afroechinatus* Lye*, *afro-occidentalis* (Lye) Huygh, *alatus* (Nees) F.Muell., *aromaticus* (Ridl.) Mattf. & Kük., *beninensis* (Samain, Reynders & Goetgh.) Huygh*, *carinalaevis* (Lye & Mesterházy) Huygh*, *leptorhachis* Mattf. & Kük., *metzii* (Hochst. *ex* Steud.) Mattf. & Kük., *welwitschii* (Ridl.) Lye; ***Cyperus* (*Kyllingiella*)** *kyllingiella* Larridon; ***Cyperus* (*Lipocarpha*)** *abietinus* (Goetgh.) Bauters*, *albescens* (Steud.) Larridon & Govaerts, *isolepis* (Nees) Bauters, *lipoater* Goetgh., *prieurianus* (Steud.) T.Koyama, *subsquarrosus* (Muhl.) Bauters*; ***Cyperus* (*Mariscus*)** *baoulensis* Kük.*, *cyperoides* (L.) Kuntze, *distans* L.f., *hamulosus* M.Bieb., *squarrosus* L.; ***Cyperus* (*Oxycaryum*)** *blepharoleptos* Steud.; ***Cyperus* (*Pycreus*)** *acuticarinatus* Kük., *demangei* (J.Raynal) Lye*, *flavescens* L., *macrostachyos* Lam., *mortonii* (S.S.Hooper) Lye, *mundii* (Nees) Kunth, *nitidus* Lam., *polystachyos* Rottb., *pseudodiaphanus* (S.S.Hooper) Lye, *pumilus* L., *testui* (Cherm.) Reynders, *unioloides* R.Br., *waillyi* (Cherm.) Lye*; ***Cyperus* (*Rikliella*)** *kernii* (Raymond) Bauters; ***Diplacrum*** *africanum* (Benth.) C.B.Clarke; ***Eleocharis*** *acutangula* (Roxb.) Schult., *atropurpurea* (Retz.) J.Presl & C.Presl, *brainii* Svenson, *complanata* Boeckeler, *decoriglumis* Berhaut*, *dulcis* (Burm.f.) Trin. *ex* Hensch., *geniculata* (L.) Roem. & Schult., *minima* Kunth*, *minuta* Boeckeler*, *nigrescens* (Nees) Kunth*, *nupeensis* Hutch., *retroflexa* (Poir.) Urb.*;

Fimbristylis *bisumbellata* (Forssk.) Bubani, *cymosa* R.Br., *dichotoma* (L.) Vahl, *dipsacea* (Rottb.) C.B.Clarke, *ferruginea* (L.) Vahl, *littoralis* Gaudich., *nigritana* C.B.Clarke, *quinquangularis* (Vahl) Kunth, *scabrida* Schumach., *schweinfurthiana* Boeckeler*, *squarrosa* Vahl, *striolata* Napper*; ***Fuirena*** *ciliaris* (L.) Roxb., *leptostachya* Oliv., *pubescens* (Poir.) Kunth, *stricta* Steud., *umbellata* Rottb.; ***Rhynchospora*** *angolensis* Turrill*, *brevirostris* Griseb., *candida* (Nees) Boeckeler, *contracta* (Nees) J.Raynal*, *holoschoenoides* (Rich.) Herter, *perrieri* Cherm., *triflora* Vahl; ***Schoenoplectiella*** *articulata* (L.) Lye, *erecta* (Poir.) Lye, *juncea* (Willd.) Lye, *lateriflora* (J.F.Gmel.) *proxima* (Steud.) Lye*, *roylei* (Nees) Lye, *senegalensis* (Steud.) Lye; ***Schoenoplectus*** *lacustris* (L.) Palla*, *subulatus* (Vahl) Lye*; ***Scleria*** *bambariensis* Cherm.*, *catophylla* C.B.Clarke, *depressa* (C.B.Clarke) Nelmes, *foliosa* Hochst. *ex* A.Rich., *gaertneri* Raddi, *globonux* C.B.Clarke, *gracillima* Boeckeler, *guineensis* J.Raynal*, *lacustris* C.Wright*, *melanomphala* Kunth, *rehmannii* C.B.Clarke, *unguiculata* E.A.Rob.*

FOREST CLIMATE GROUP. ***Bulbostylis*** *pilosa* (Willd.) Cherm.; ***Cyperus*** **(*Cyperus*)** *buchholzii* Boeckeler, *compressus* L., *fertilis* Boeckeler, *mapanioides* C.B.Clarke, *renschii* Boeckeler; ***Cyperus*** **(*Kyllinga*)** *brevifolius* (Rottb.) Hassk., *erectus* (Schumach.) Mattf. & Kük., *hortensis* (Salzm. *ex* Steud.) Dorr, *mindorensis* (Steud.) Huygh., *obtusatus* (J.Presl & C.Presl) Mattf. & Kük., *richardii* Steud., *sesquiflorus* (Torr.) Mattf. & Kük.; ***Cyperus*** **(*Mariscus*)** *pseudopilosus* (C.B.Clarke) Govaerts*, *soyauxii* Boeckeler, *tenuis* Sw.; ***Cyperus*** **(*Pycreus*)** *cataractarum* (C.B.Clarke) K.Schum. *ex* Engl., *lanceolatus* Poir.; ***Cyperus*** **(*Torulinium*)** *odoratus* L.; ***Diplacrum*** *capitatum* (Willd.) Boeckeler; ***Eleocharis*** *confervoides* (Poir.) Steud., *naumanniana* Boeckeler, *variegata* (Poir.) C.Presl; ***Fimbristylis*** *aphylla* Steud., *microcarya* F.Muell.; ***Hypolytrum*** *africanum* Nees *ex* Steud.*, *heteromorphum* Nelmes, *pahiense* Xanthos*, *poecilolepis* Nelmes*, *purpurascens* Cherm., *schnellianum* Lorougnon*, *senegalense* Rich.*; ***Mapania*** *amplivaginata* K.Schum., *baldwinii* Nelmes*, *coriandrum* Nelmes*, *ivorensis* (J.Raynal) J.Raynal*, *jongkindii* Mesterházy*, *liberiensis* D.A.Simpson*, *linderi* Hutch. *ex* Nelmes*, *macrantha* (Boeckeler) H.Pfeiff.*, *mangenotiana* Lorougnon*, *minor* (Nelmes) J.Raynal*, *rhynchocarpa* Lourignon & Raynal; ***Rhynchospora*** *corymbosa* (L.) Britton, *gracillima* Thwaites; ***Scleria*** *achtenii* De Wild., *lithosperma* (L.) Sw., *mikawana* Makino, *naumanniana* Boeckeler, *secans* (L.) Urb., *verrucosa* Willd., *vogelii* C.B.Clarke

COASTAL GROUP. ***Abildgaardia*** *triflora* (L.) Abeyw.*; ***Bolboschoenus*** *grandispicus* (Steud.) Lewej. & Lobin*; ***Cladium*** *mariscus* (L.) Pohl; ***Cyperus*** **(*Cyperus*)** *capitatus* Vand.*, *crassipes* Vahl, *subtilis* (Kük.) Väre & Kukkonen*, *tenax* Boeckeler; ***Cyperus*** **(*Kyllinga*)** *afrorobustus* Lye, *tibialis* (Poit. *ex* Ledeb.) Govaerts*; ***Cyperus*** **(*Lipocarpha*)** *crassicuspis* (J.Raynal) Bauters*; ***Cyperus*** **(*Mariscus*)** *ligularis* L.; ***Cyperus*** **(*Remirea*)** *pedunculatus* (R.Br.) J.Kern; ***Eleocharis*** *mutata* (L.) Roem. & Schult.; ***Rhynchospora*** *rubra* (Lour.) Makino, *tenerrima* Nees *ex* Spreng.*; ***Scleria*** *chevalieri* J.Raynal*

INSELBERG GROUP. ***Afrotrilepis*** *jaegeri* J.Raynal*, *pilosa* (Boeckeler) J.Raynal; ***Bulbostylis*** *abortiva* (Steud.) C.B.Clarke, *angolensis* (C.B.Clarke) Larridon & Roalson, *briziformis* (Hutch.) Larridon & Roalson, *coleotricha* (Hochst. *ex* A.Rich.) C.B.Clarke, *densa* (Wall.) Hand.-Mazz., *pusilla* (Hochst. *ex* A.Rich.) C.B.Clarke, *scabricaulis* Cherm.; ***Cyperus* (*Ascolepis*)** *proteus* (Welw.) Bauters; ***Cyperus* (*Cyperus*)** *karlschumannii* C.B.Clarke, *niveus* Retz., *submicrolepis* Kük.; ***Cyperus* (*Kyllinga*)** *tenuifolius* (Steud.) Dandy; ***Cyperus* (*Lipocarpha*)** *lipofiliformis* Goetgh., *purpureoluteus* (Ridl.) Bauters; ***Cyperus* (*Mariscus*)** *cuspidatus* Kunth, *dubius* Rottb.; ***Cyperus* (*Pycreus*)** *capillifolius* A.Rich., *melas* Ridl., *pauper* Hochst. *ex* A.Rich.; ***Eleocharis*** *setifolia* (A.Rich.) J.Raynal; ***Fimbristylis*** *alboviridis* C.B.Clarke, *barteri* Boeckeler, *complanata* (Retz.) Link, *debilis* Steud., *ovata* (Burm.f.) J.Kern; ***Microdracoides*** *squamosus* Hua; ***Rhynchospora*** *eximia* (Nees) Boeckeler; ***Schoenoplectiella*** *oxyjulos* (S.S.Hooper) Lye; ***Scleria*** *bulbifera* Hochst. *ex* A.Rich., *distans* Poir., *flexuosa* Boeckeler*, *iostephana* Nelmes, *lagoensis* Boeckeler, *liberica* Bauters*, *melanotricha* Hochst. *ex* A.Rich., *parvula* Steud., *pergracilis* (Nees) Kunth, *pooides* Ridl., *robinsoniana* J.Raynal*, *schimperiana* Boeckeler, *spiciformis* Benth.*, *tessellata* Willd.

MONTANE GROUP. ***Bulbostylis*** *guineensis* Cherm. *ex* Bodard*, *laniceps* C.B.Clarke *ex* T.Durand & Schinz, *neocapitata* Larridon & Roalson*, *oritrephes* (Ridl.) C.B.Clarke, *schoenoides* (Kunth) C.B.Clarke; ***Carex*** *chlorosaccus* C.B.Clarke, *echinochloe* Kunze, *neochevalieri* Kük. *ex* A.Chev., *petitiana* A.Rich.; ***Coleochloa*** *abyssinica* (Hochst. *ex* A.Rich.) Gilly; ***Cyperus* (*Cyperus*)** *baronii* C.B.Clarke, *dichrostachyus* Hochst. *ex* A.Rich., *koyaliensis* Cherm., *nduru* Cherm.; ***Cyperus* (*Kyllinga*)** *breviglumis* Lye, *melanospermus* (Nees) Valck.Sur.; ***Cyperus* (*Lipocarpha*)** *leucaspis* (J.Raynal) Bauters, *persquarrosus* T.Koyama; ***Cyperus* (*Mariscus*)** *albopilosus* (C.B.Clarke) Kük., *angolensis* Boeckeler, *luteus* Boeckeler, *tomaiophyllus* K.Schum.; ***Cyperus* (*Pycreus*)** *aethiops* Welw. *ex* Ridl.*, *africanus* (S.S.Hooper) Reynders, *elegantulus* Steud., *nuerensis* Boeckeler, *rubidomontanus* (J.Browning) Larridon, *scaettae* (Cherm.) Reynders, *smithianus* Ridl,; ***Hypolytrum*** *cacuminum* Nelmes*; ***Isolepis*** *fluitans* (L.) R.Br.; ***Rhynchospora*** *rugosa* (Vahl) Gale; ***Schoenoplectiella*** *mucronata* (L.) J.Jung & H.K.Choi; ***Schoenoplectus*** *corymbosus* (Roth *ex* Roem. & Schult.) J.Raynal; ***Scleria*** *monticola* Nelmes *ex* Napper*, *woodii* C.B.Clarke.